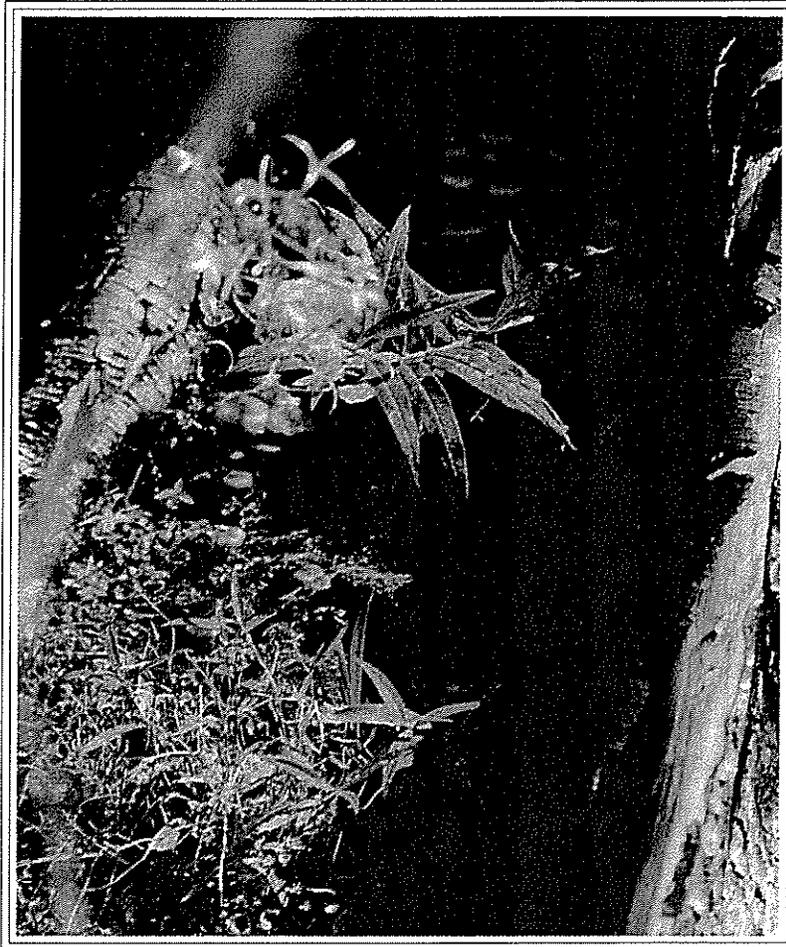


*The Ecological Implications of
Fire in
Greater
Yellowstone*



PROCEEDINGS

SECOND BIENNIAL
CONFERENCE
ON THE
GREATER
YELLOWSTONE
ECOSYSTEM

YELLOWSTONE NATIONAL
PARK[®]
SEPTEMBER 19-21, 1993

FIRE

EDITED BY JASON M. GREENLEE

·1996

PUBLISHED BY THE INTERNATIONAL ASSOCIATION OF WILDLAND FIRE
FAIRFIELD, WASHINGTON

*Proceedings of the
Second Biennial Conference on the Greater Yellowstone Ecosystem*

The Ecological Implications of Fire in Greater Yellowstone

**September 19-21, 1993
Yellowstone National Park, Wyoming**

**Edited by Jason Greenlee
1996**

**Published by the International Association of Wildland Fire
Fairfield, Washington**

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PO Box 328
Fairfield, WA 99012 USA
(509) 283-2397

ISBN 1-887311-00-9

Contents

Opening Remarks	v
<i>Superintendent Robert D. Barbee</i>	
A Model for Prehistoric Economies of the Yellowstone Plateau During the Altithermal	1
<i>Kenneth P. Cannon</i>	
Landscape-Level Fuel Manipulations in Greater Yellowstone: Opportunities and Challenges	7
<i>Philip N. Omi</i>	
Simulation of Crown Fire Effects on Canopy Seed Bank in Lodgepole Pine	15
<i>Don G. Despain, David L. Clark, and James J. Reardon</i>	
Post-fire Patterns of Whitebark Pine (<i>Pinus albicaulis</i>) Germination and Survivorship in the Greater Yellowstone Area	21
<i>Diana F. Tomback, Katherine S. Carsey, and Mary L. Powell</i>	
Tourism in Montana After the 1988 Fires in Yellowstone National Park	23
<i>David J. Snepenger, Jerry D. Johnson, and Nikki Friede</i>	
Media Coverage of Fire Ecology in Yellowstone After 1988	25
<i>Conrad Smith</i>	
The Role of Fire in the Greater Yellowstone Ecosystem: Development of Instructional Units	35
<i>John F. Burger</i>	
Impact of 1988 Yellowstone Fires on Snowmelt Water Yields	39
<i>Phillip E. Farnes</i>	
Effect of Fire on Streamflow and Sediment Transport in Shoshone National Forest, Wyoming	43
<i>C.A. Troendle and G.S. Bevenger</i>	
Consequences of Fire on Aquatic Nitrate and Phosphate Dynamics in Yellowstone National Park	53
<i>James A. Brass, Vincent G. Ambrosia, Philip J. Riggan, and Paul D. Sebesta</i>	
Changes in Transport and Retention of Course Particulate Organic Matter in Streams Subjected to Fire	59
<i>Michael J. McIntyre and G. Wayne Minshall</i>	

Diatom Assemblages in Cache Creek, Yellowstone National Park Following the 1988 Wildfires	77
<i>Christopher T. Robinson, Samuel R. Rushforth, and G. Wayne Minshall</i>	
Response of Benthic Macroinvertebrate Populations in Cache Creek, Yellowstone National Park to the 1988 Wildfires	83
<i>Timothy B. Mihuc, G. Wayne Minshall, and Christopher T. Robinson</i>	
Preburn Root Biomass/Basal Area Influences on the Response of Aspen to Fire and Herbivory	95
<i>Roy Renkin and Don Despain</i>	
Notes on Postfire Aspen Seedling Establishment.....	105
<i>Roy Renkin and Don Despain</i>	
Response of Shrub-Aspen to Yellowstone's 1988 Wildfires; Implications for "Natural Regulation" Management	107
<i>Charles E. Kay and Frederic H. Wagner</i>	
Large Mammal Mortality in the 1988 Yellowstone Fires	113
<i>Marilynn Gibbs French and Steven P. French</i>	
Effects of Wildfire on Grizzly Bear Movements and Food Habits	117
<i>Bonnie Blanchard and Richard R. Knight</i>	
Pronghorn Migration and Habitat Use Following the 1988 Yellowstone Fires	123
<i>M. Douglas Scott and Hannes Geisser</i>	
Physiological Responses of Yellowstone Elk to Winter Nutritional Restriction Before and After the 1988 Fires: A Preliminary Examination	133
<i>Glenn D. DelGiudice and Francis J. Singer</i>	
Post-fire Effects on Coarse Woody Debris and Adult Trout in Northwestern Wyoming Streams	137
<i>Michael K. Young and Michael A. Bozek</i>	
Monitoring the Impacts of the 1988 Wildfires on Yellowstone's Major Lakes	145
<i>Richard G. Lathrop</i>	
Habitat Requirements for the Reestablishment of Litter Invertebrates Following the 1988 Yellowstone National Park Fires.....	147
<i>Tim A. Christiansen and Robert J. Lavigne</i>	
Bark Beetle Activity and Delayed Tree Mortality in the Greater Yellowstone Area Following the 1988 Fires	151
<i>Kevin C. Ryan and Gene D. Amman</i>	

Responses of Elk to the 1988 Yellowstone Fires and Drought	159
<i>David J. Vales and James M. Peek</i>	
Yellowstone Elk Population Responses to Fire — A Comparison of Landscape Carrying Capacity and Spatial-Dynamic Ecosystem Modeling Approaches	169
<i>Michael B. Coughenour and Francis J. Singer</i>	
Comparative Ecosystem Properties in Summer and Winter Ungulate Ranges Following the 1988 Fires in Yellowstone National Park	181
<i>Benjamin F. Tracy and Samuel J. McNaughton</i>	
Winter Range Plant Production and Elk Use Following Prescribed Burning	193
<i>Fred Van Dyke, Michael J. Deboer, and Grant M. Van Beek</i>	
Banquet Presentation:	
The Aldo Starker Leopold Memorial Lecture	
If I Were Superintendent	201
<i>Mark S. Boyce</i>	
Poster Session:	
Interpretation of the National Fire Danger Rating System for Yellowstone National Park	
211	
<i>Patricia L. Andrews and Larry S. Bradshaw</i>	
Physical and Chemical Responses of Streams in Yellowstone National Park Following the 1988 Wildfires	217
<i>Christopher T. Robinson and G. Wayne Minshall</i>	
Effects of the Yellowstone Fires of 1988 on Elk Habitats	223
<i>J.E. Norland, F.J. Singer, and L. Mack</i>	
Summary:	
The Ecological Implications of Fire in Greater Yellowstone: A Summary	
233	
<i>Dennis Knight</i>	

Opening Remarks

by Superintendent Robert D. Barbee

Five years ago this week, many of us—I see some of those faces in this room—had just survived the most amazing experience of our lives. For three months we had alternated between frantic, exhausting exertion and stunned awe as Yellowstone gave us an unforgettable lesson in ecological power and human frailty. And then, just about this time, in September of 1988, it was suddenly over. A little rain, a little snow, and it was over.

But of course it wasn't over. It was only the beginning. Ecologically, the fires were just the opening act of a very long drama, one that has run successfully on this stage for more than 10,000 years.

Politically, the fires had even more far-reaching effects. In the dialogues that ensued, the power-position-takers jockeyed so effectively with one another that none really made much of a gain. We still have a natural fire policy, we still can't control fires like those in 1988, and we still keep trying to make the most of the opportunities provided by Yellowstone and the challenges of its management.

Scientifically, our progress is clearest. From the first postfire research consortium, at Montana State University in the fall of 1988, it was plain that the scientific

community recognized the unique opportunity the fires gave us, an opportunity to ask questions about how unmanipulated landscapes function on a scale rarely studied. And the scientific community did deliver: In Yellowstone Park alone, more than 250 research projects began on the post-1988 environment. Some final results of those studies you'll hear today. Some won't be final in our lifetimes.

What you are about to witness is a major part of all that creative enthusiasm. From many disciplines, and we're especially pleased to see the humanities represented, we will be hearing what the fires did, what the fires meant, and what the fires yet may mean.

That may be the best news of all to come out of this conference: the opportunity to learn did not go to waste. Whatever may become of the policy dialogues, it is reassuring to know that Yellowstone has not lost its ability to teach us, and inspire us. I hereby open this Second Biennial Conference on Science in the Greater Yellowstone, confident that these wondrous landscapes will continue to teach us, as long as we care to watch, and study, and learn.

A Model for Prehistoric Economies of the Yellowstone Plateau During the Altithermal

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Abstract. One of the more debated issues in western North American prehistory is the effect of postglacial maximum warmth and aridity on hunter-gatherer groups. Antevs (1955) described the *Long Drought*, or Altithermal, as a period of warmer than present conditions, with increased aridity, that occurred between 7500 and 5000 bp. The decrease in effective moisture would have had deleterious effects on vegetative cover and animal populations, as well as landscapes, due to increased erosion. Several scenarios about the impacts of climate on prehistoric groups of the region have been presented. These scenarios argue for: complete abandonment of the basins and plains; technological shifts in tool kits; and an expansion in the diversity of the economy. Palynological evidence from northwestern Wyoming indicates that this climatic shift began as early as 9500 years ago. During this time, the forest overstory diminished and the grasslands expanded. Fire frequency may also have increased, creating a landscape with a high degree of patchiness. Modern studies of fire indicate post-burn environments are much richer in species diversity. Thus an increased frequency of fire would potentially create a more economically diverse environment for hunter-gatherer subsistence. Although this time period has been insufficiently investigated in the Park, an economic model can be developed by integrating ecological studies from Yellowstone with data recovered from regional archeological work. This paper will examine these data and the implications for understanding prehistoric economies of the Yellowstone Plateau during the early portion of the Holocene (ca. 9500 to 7500 bp).

Keywords: Fire History; Archeology.

Introduction

Post-glacial warming and drought, termed the *Long Drought* or *Altithermal* by Antevs (1955) may be one of the most debated periods of time in North American

archeology. During the past five decades, archeologists have vigorously discussed the effects that climatic changes during this period might have had on prehistoric groups in western North America.

Events proposed to be associated with the Altithermal include sustained drought, increased warmth, and dwindling plant and animal resources, resulting in significant reduction in the human carrying capacity. Mulloy (1958), in an initial cultural chronological sequence for the region, described this time period as "the Gap without Evidence."

Mulloy was working at a time when relevant archeological data were limited. Also, radiometrically-dated deposits were few. Mulloy's ideas, however, have been reiterated in the archeological literature (e.g., Reeves 1973). These reviews, particularly Bender and Wright (1988), lack a clear classification of sites and the confusion over what represents the plains and the intermontane basins has obfuscated their argument (Husted 1992; Chomko 1991). Frison et al. (1976:33) sum up the implications of suggesting a cultural hiatus as being unfortunate, by strongly implying an absence of people in the region which essentially stifled alternate model presentations, such as shifts in settlement and economic systems. Fortunately a more complex view of this time period has developed. Investigators now realize that previous arguments concerning the post-glacial climatic optimum and perceived forced abandonment of the basins and plains were overly simplistic.

More recent archeological work in the upper Green River basin (Miller and Francis 1993), as well as previous work by Frison et al. (1976) and Larson (1990) elsewhere in Wyoming, indicate that Archaic peoples were more sedentary, or less mobile, and relied more on task groups than previously thought (e.g., Mulloy 1958, 1965). Pit house excavations in the sand dune areas of the interior intermontane basins provide the best evidence for this pattern. Within these structures numerous features include fire pits and cache or storage pits and grinding

stones, with a paucity of faunal remains (Frison 1991:84). The amount of labor expended on the building of these structures, and the storage facilities, suggest a pattern of increased sedentism, with task specific groups moving out occasionally to procure various resources and returning.

Current paleoecological studies in the Yellowstone region (Whitlock 1993) provide evidence that climate was warmer and drier in the early Holocene (ca. 9500 bp) and may have resulted in increased fire frequency. This increased frequency of fires may have created a landscape with a higher diversity of plants and animals that were of importance to human groups. Thus, in this paper I would like to present a review of the archeological and palynological record, in association with current knowledge, and how prehistoric groups may have oriented themselves to take advantage of post-fire environments.

Archeological Review

Speculation on the effects of the Altithermal on human populations has a long history in the archeological literature. Antevs (1955:320) initially described this period, dating between 7500 to 4000 bp, as a "maxima of grass-chenopod-composite pollens, low lake levels, wind erosion, dunes, arroyo cutting, and calichification." His work was based on evidence from radiocarbon dated archeological occupations and geologic landforms in the Great Basin and Southwest.

Mulloy (1958) pointed out the paucity of archeological evidence for human occupation of the basins during the Early Middle Prehistoric Period (7500 to 4000 bp). The most striking diagnostic artifact from this time period is the large side-notched projectile point. Ground stone implements also appear at this time and suggests wild plant seed processing. This shift in projectile point styles from lanceolate to side-notched and the appearance of ground stone implements has often been interpreted as a technological adaptation to the climatic regime and the resources available.

Large scale population shifts, perhaps on a continent-wide scale, were proposed as a common and successful adaptive response to the severe climatic change associated with the Altithermal (Husted 1969; Benedict 1978, 1979). Both Husted and Benedict, as well as others (see Bender and Wright 1988) have championed the idea that the uplands and mountains adjacent to the Plains were the haven sought by Early Archaic groups.

Reeves (1973) views the idea that the Plains were abandoned as the result of sampling vagaries, geological variables, and the non-recognition of artifact types from surface collections. He has argued, based on his review of archeological and paleoecological data from the northern Plains, that a grassland environment capable of supporting viable populations of bison existed during the

Altithermal. Since Reeve forwarded his hypothesis, at least one bison kill site (the Hawken site) dating to the Altithermal has been reported (Frison et al. 1976).

The archeological record from Yellowstone National Park for the Altithermal is currently limited to a few projectile points collected from the surface, as well as some from currently unanalyzed subsurface deposits. If we expand the data set to include the Greater Yellowstone Area (GYA), we still find few excavated and radiometrically dated deposits (Figure 1). One of the obvious factors contributing to the paucity of information from this time period is the infrequency of problem-oriented archeological projects. Contract archeology projects, while providing critical data, are often uneven in data collection strategies and reporting, and constitute the bulk of our knowledge. To put this in numerical terms, less than five percent of Yellowstone has been surveyed for archeological sites, with less than one percent of the known sites being assessed for subsurface deposits.

Environmental Record

Pollen studies from northwestern Wyoming, most notably by Baker (1976, 1983) and Whitlock (1993; Barnosky et al. 1987), provide a provocative model for the interpretation of human settlement of the region during the Early to Mid-Holocene.

A rise in *Pseudotsuga* (Douglas fir) and *Populus* (aspen) pollen between 9500 and 5000 years ago indicates a period of maximum warmth and aridity for the region, some 2000 years earlier than proposed by Antevs (1955), implying the phenomenon is time-transgressive. Upslope migration and local extinction of more mesic species, such as spruce, fir, and whitebark pine, evidenced by a reduction in their pollen, is also seen as testimony to the increase in warmth and aridity (Baker 1976; Whitlock 1993).

Lodgepole pine forests also reached a maximum in the pollen record about this time. Lodgepole pine, Douglas fir, and local increases in quaking aspen, all of which are fire adapted species, suggest not only increased warmth, but also more frequent fires than at present (Whitlock 1993:189).

With increased fire frequency, a mosaic of stand ages can be expected. More open forests and a retreat of the forest boundary is also supported by a rise in the pollen record of *Artemisia*, beginning about 7000 years ago (Baker 1983:115-116).

Fire History

Recent studies of fire behavior and its effects on ecosystems provide analogues for understanding past systems. Fire studies indicate that intensity, duration, and

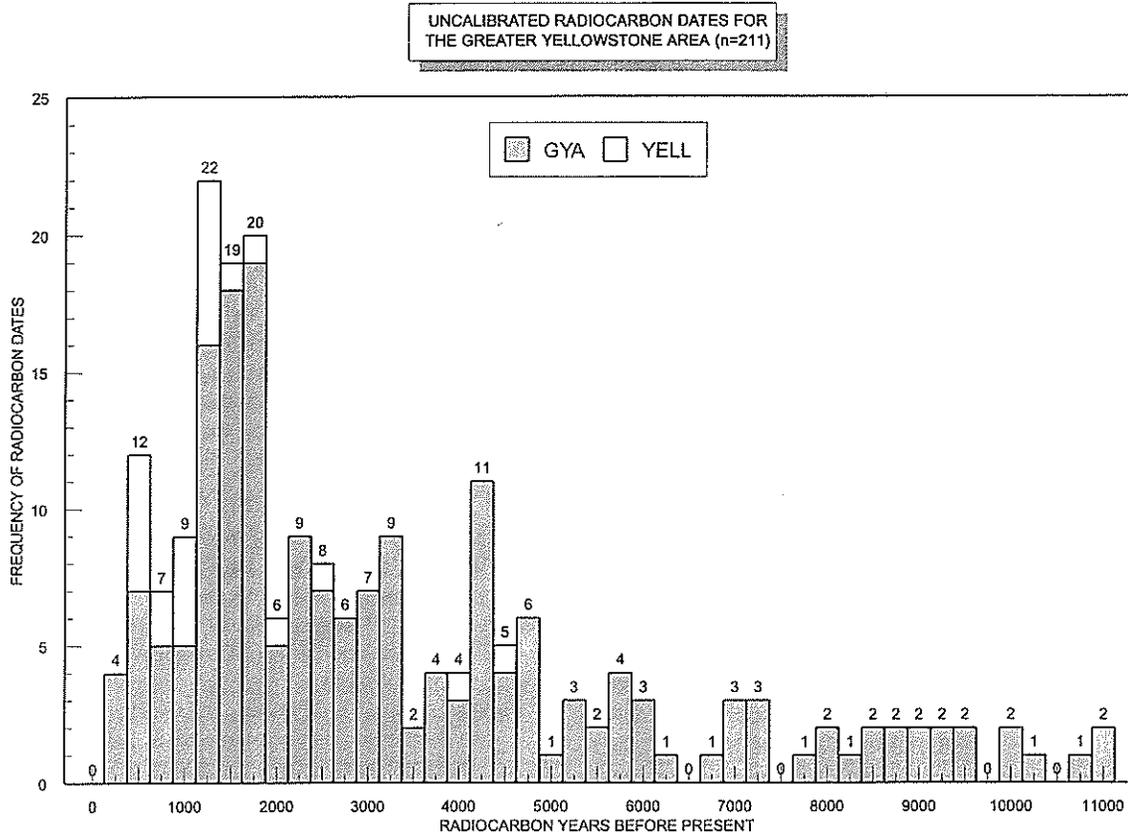


Figure 1. Frequency (n = 211) of radiocarbon dates from the Greater Yellowstone Area. Ages are presented as uncalibrated radiocarbon years before present.

the rate of spread of fires are influenced by a number of factors including fuel, wind, and topography (Pyne 1984). Most fires tend to be small, burning out in a few acres. Few fires burn more than 1000 acres under natural fire conditions, and most are under 100 acres. The limited scale of the burns creates a mosaic of various aged stands.

If we examine the average modern intervals between fires for species common during the early to mid-Holocene we would expect the entire region to be a mosaic of various-aged open forests, with expanses of grasslands. Fires range from 20-25 years in grasslands and Douglas fir to 50 to 100 years for aspen and 100 to 200 years for lodgepole pine (Houston 1973). However, the charcoal record from Cygnet Pond on the Central Plateau suggests that fire intervals have probably changed through time due to community structures and climate implying that modern fire return intervals should be applied cautiously to past systems (Whitlock and Millspaugh 1994).

The mosaic of post-fire vegetation and various-aged stands would provide numerous opportunities for prehistoric exploitation. However, the post-fire communities would be most important economically, for these early successional communities include a number of plant species economically important to prehistoric people that are not common in climax forests. Burning enhances the

growth and production of numerous economic species, such as camas, avalanche lily, spring beauty, various *Vaccinium* (huckleberry) species, wild raspberry, onion, as well as game forage plants (Turner 1991).

Taylor's (1969) study of lodgepole pine fire succession indicates that the number of species of plants, birds, and mammals increases continuously for about 25 years after fires, then decreases rapidly following canopy closure. Increased fire frequency, and the opening of forests, may have had significant effects on the local fauna, both in terms of density and diversity.

The use of fire by aboriginal people has been studied worldwide. These studies show that people have intimate knowledge, not only of the positive effects of fire for increasing yield, but also the technological aspects of burning, for example the best times of the year, moisture content of fuels, etc. (Turner 1991 and articles cited within). As Anderson (1990:11) states, "All human groups know fire, and most use it to clear the land for food production or similar purposes." If people acquired this knowledge by either direct observation or experimentation, the controlled use of fire to maintain certain habitat conditions or enhance the production of important plant and animal resources must have considerable time depth.

The Cultural Model

If we assume: (1) that Archaic hunter-and-gatherers were logistically oriented and had intimate knowledge of their environment, which allowed detailed prediction and planning for resource procurement; and (2) this knowledge included the ability to predict and exploit post-fire environments and take advantage of the increased diversity, and presumed productivity of these areas; then we must conclude that the subsistence base of these groups should have been of high nutritional value. The high level of productivity of post-fire environments would allow people to select for resources of high nutritional value such as bison, elk, deer, and bighorn sheep, as well as herbaceous plant species.

Frequent and recurrent fires created an environment of high diversity in which prehistoric groups could focus on resources of the highest economic value, such as large ungulate species. This idea for the Yellowstone area is in contrast to other economic models of the Altithermal (e.g., Lyman 1992) which have argued that reduced large mammal biomass, a direct result of a reduction in plant biomass, would have forced human groups to diversify their diet, causing exploitation of less desirable species.

Analysis of faunal remains from Mummy Cave (Harris n.d.), located east of Yellowstone along the North Fork of the Shoshone River, and the Meyers-Hindman site (Lahren 1976), just north of Livingston in the Upper Yellowstone River Valley provide enticing evidence for assessing the Yellowstone model.

From Mummy Cave, the Altithermal faunal assemblage is represented by numerous species, one-third of which are bighorn sheep and deer. Smaller fauna represent the remaining two-thirds, suggesting a more diverse subsistence pattern. A large portion, however, of the assemblage remains to be analyzed (Hughes 1993).

Similarly, large game—elk, bison, deer, and bighorn sheep—represents more than seventy-five percent of the animal remains at the Meyers-Hindman site.

Although both of these archeological cases exhibit variation in local environment, site function, preservation, and recovery techniques, they do provide invaluable information for assessing the model.

I have presented an explanatory model for prehistoric economies during the early to mid-Holocene. The model incorporates current knowledge of the paleoenvironmental sequence, as well as the possible effects of increased fire frequency. This model provides new insights about the prehistoric economy during the Archaic that can be tested during future archeological investigations.

Acknowledgments. The preceding paper benefited greatly from a number of individuals: Rob Bozell, Julie Francis, Wil Husted, Sarah Millsbaugh, and Alan Osborn, as well as two anonymous reviewers. However, I could not persuade any of them to take any responsibility for errors or misinterpretations of the information. This is my burden.

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Landscape-Level Fuel Manipulations in Greater Yellowstone: Opportunities and Challenges

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Abstract. The burn pattern of the 1988 Yellowstone Fires, especially the large unburned islands of older-age forest, raise questions about the efficacy of landscape fuel manipulations to manage future fire episodes. Whereas traditional fuel treatments have been conducted for purposes of fuel hazard reduction, concerns with landscape ecology suggest needs for a much broader analytical framework. Effects on historic fire regime and indicators of biological integrity must be considered, as well as treatment costs. Three alternatives are compared according to this framework: reliance on natural processes; area-wide fuel treatment; and selective fuel treatment in high priority areas. Area-wide landscape manipulation may be justified, especially in conjunction with a robust prescribed natural fire program.

Keywords: Fire regime; Forest fires; Fuel management; Landscape effects.

Introduction

Every year large fires recur with anticipated regularity throughout the western USA. Although the fire return intervals in Greater Yellowstone landscapes are prolonged by the high elevation, continental climatic regime, we can assert with confidence that large, high-intensity fires will recur. The rich variety of vegetation in Greater Yellowstone interacts with topography and climate to produce ideal fuel beds for episodic fire events as witnessed in 1988. However, the exact location and timing of future fire events cannot be predicted with certainty.

Notwithstanding the relatively low frequency of 1988-type episodes (Romme and Despain 1989a), the plant communities exhibit characteristic adaptations which allow certain species to persist in spite of, or even due to, repeated fires. Decades of fire suppression may have contributed to higher than expected fuel levels in certain Yellowstone areas (Houston 1973, Bonnicksen 1990 as

cited in Lee 1991), although the hypothesis that the 1988 fires burned with higher intensities due to fire suppression is largely unverifiable and doesn't need to be resolved — what really matters is what we can learn from 1988 to optimize future management options in Greater Yellowstone. Of particular interest to the current discussion are the large unburned areas, including islands of old growth forest, resulting from the spread patterns in 1988. These features are illustrated in maps of the 1988 Yellowstone burn area (Greater Yellowstone Post-fire Resource Assessment Committee 1988) and pre- and post-fire vegetation (Despain, unpublished maps). These large unburned areas contribute to the high degrees of landscape diversity following the 1988 fires (Christensen et al. 1989). Substantial expanses of older growth lodgepole pine (*Pinus contorta*) are included in some of the unburned areas, including areas in the 100-300 yr and >300 yr age classes.

The susceptibility of these older forests to episodic fire (Romme and Despain 1989b, Romme and Knight 1982) leads me to question whether large-scale fuel modification treatments might ever be justified in or adjacent to such areas. My curiosity is heightened by the prospect that once ignited, historic wind and spread patterns provide evidence of substantial threats to developed areas both within and outside park boundaries. Further, I question if (and when) landscape fuel treatments might ever be justified in areas burned in 1988, as biomass accumulates over time in response to environmental gradients and disturbance regimes.

Additional reasons for considering this topic include questions raised in the landscape ecology literature (e.g., Risser 1987, Turner et al. 1993) over the role of disturbance in creating and sustaining landscape heterogeneity. The 1988 fires altered the impact of future disturbances by changing the structure within and between patches of vegetation. Interesting questions relate to the role of heterogeneity in increasing or decreasing the severity of future disturbances, both natural and human-caused. Other

questions relate to whether large-scale fires can be accommodated within the confines of the Yellowstone landscape.

Fire scientists accept as axiomatic that little can be done to preempt large, high-intensity fires through weather or topographic modification. Further, we are schooled to believe that potential exists to actively modify the vegetation so as to manage the undesirable consequences of eventual fire outbreaks. However, in thinking about effective vegetation or fuel modification in Greater Yellowstone, care is required so that treatments are applied with ecological sensitivity—especially in considering landscape-scale treatments. My objective for this paper is to apply such thinking in developing a case for considering landscape fuel manipulations, including the advantages and disadvantages of candidate techniques. Before developing this proposition in greater detail I will review some basic terminology, practices, and previous research, then indicate how these apply to the special circumstances in Greater Yellowstone.

Traditional Fuel Treatments

From the fire management literature, we know that fuels modification in advance of episodic fire recurrence holds the most promise for managing eventual fire impacts (Countryman 1974), especially since weather or topographic attributes cannot be managed in a landscape so large as Greater Yellowstone. Techniques for modifying fuels include disposal, rearrangement, removal, conversion, or isolation of flammable materials (Table 1). The examples in Table 1 indicate that fuel treatment methods fall into the following categories: use of

Table 1. Fuel modification techniques and examples used in the western United States (after Omi and Kalabokidis 1994). Not all are appropriate for use in Greater Yellowstone.

Techniques	Examples
1. Disposal (on-site reduction)	Dozer or Hand Pile and Burn Broadcast Burning Underburning Biological (grazing) Natural Decomposition
2. Rearrangement (on-site redistribution)	Lop and Scatter Crushing Chipping
3. Removal (off-site)	Firewood Removal Tractor/Dozer Removal Yarding Unmerchantable Material
4. Conversion (changing flammability)	Vegetation Conversion Herbicides Chemical Retardants Prescribed Fire
5. Isolation (breaking up continuity)	Fuelbreaks Firebreaks Green Belts

machines or crews to cut, scatter, and pile materials; prescribed burning (broadcast, pile, or understory burning); biological agents (grazing); or chemical (herbicides or retardants) treatments. Although these techniques have been used throughout the western US, I am not suggesting that all would be appropriate for widespread use in the Greater Yellowstone area. All involve costs and risks. Some techniques are more appropriate for boundary areas or to buffer high value developments, e.g., rearrangement or removal. Reliance on natural decomposition or biological agents for fuel removal is time-consuming; chemical applications are probably not appropriate in wildland preserves. Prescribed fire and fuelbreaks offer the greatest potential for managing landscapes but implementation may involve considerable controversy and ecological risk.

Prescribed fire is the intentional application of fire to achieve pre-determined objectives, confined to a pre-determined area, under pre-specified fuel and environmental conditions. Prescribed fire is distinguished from wildfire because of the implied managerial controls over the environmental influences on fire behavior and effects. These controls are facilitated by careful selection of the appropriate timing and frequency of treatment(s). Our knowledge and controls over prescribed fire effects are enhanced through careful specification of the fire prescription for intentional or natural ignitions. Some (e.g., Romme and Despain 1989b) contend that the appropriate technology and expertise is lacking for carrying out successful application of large-scale prescribed burns in Yellowstone's older forest types. Certainly the required skills may be more challenging than required for fire applications in wildland areas characterized by shorter fire-return intervals. But within the fire management community there are a small, but growing number of trained professionals who have been applying fire with reasonable success in similar circumstances (e.g., Zimmerman et al. 1990).

A **fuelbreak** is a strategically located, pre-existing fire control line upon which a low volume fuel is maintained as an alternative to the more dense, flammable natural vegetation. A distinction should be drawn between fuelbreaks and **firebreaks**, in that the latter are typically narrower and cleared to mineral soil, with no subsequent attempt at maintaining vegetation cover in the cleared area (Omi 1979). Natural fuelbreak examples include recent burns, riparian areas, or aspen clones. Artificial fuelbreaks constructed to 30-100 m width and maintained with grass, shrub, or thinned tree density (i.e., a shaded fuelbreak) might also warrant consideration. Fuelbreaks are not designed to stop a fire's spread, but to provide options for managing fire episodes.

We need to realize that landscape fuel manipulations, such as prescribed fire and fuelbreaks, may also be considered as disturbances and will affect landscape heterogeneity. Structural and functional relations be-

tween and within affected ecosystems will result. Spatial, temporal, material, and energy relations between and within ecosystem patches also will be affected.

In spite of extensive localized application, relatively little information exists on the effectiveness of treatments listed in Table 1. Most have been applied in the name of fuel hazard reduction. In reality, traditional treatments have been applied with scant knowledge of anticipated reductions in subsequent fire activity; even fewer have been applied with sensitivity toward understanding ecological impacts or effects specific to particular ecosystems and landscapes.

The absence of concrete information on treatment effectiveness can be explained from several perspectives. Productivity measures related to hazard reduction (i.e., reductions in wildfire costs and losses) are elusive since fuel profiles may become more flammable with the passage of time, even if fuel volumes have been reduced successfully during initial treatment. After all, these profiles merely reflect biomass accretion and decomposition processes which occur naturally in all plant communities. Further, the context for assessing fuel treatments has changed dramatically in the past decade, from sole focus on hazard reduction to concern for spatial and temporal ecological impacts on a landscape scale. Thus, in the context of the current discussion, successful landscape manipulations are those which will result in enhancements to biological integrity (Angermeier and Karr 1994) or other general indicators of ecosystem sustainability/health, along with enhancing future fire and resource management options. Mere reductions in fire activity (i.e., frequency, rate of spread, and intensity of subsequent fires) are no longer sufficient; also required are quantification of benefits in terms of biological integrity and ecosystem health indicators.

Fuel treatment evaluation is further complicated since performance testing is elusive. Fuel treatments are best tested by actual fires, yet an ignition may not occur to allow tests of effectiveness. Even if an ignition occurs, the analysis of fire spread and effects are confounded by spatial and temporal variations in the fire's environment, including fuel, topography, and weather changes. In a few cases, computerized or expert simulations have served as acceptable proxies for actual fires. The natural history of flammability in an area also must be considered, especially as related to historic fires, plant species composition, successional patterns and processes, insects, and diseases (Knight 1987). Under these circumstances it becomes difficult to isolate the effects due to fuel treatment. Finally, great uncertainties exist over the scale of treatments and expenditures required to significantly reduce the likelihood of disastrous fire outbreaks. To date, area-wide hazard reduction for most wildland applications have not been economically justifiable (Deeming 1990), although several studies have indicated marginal benefits in selected, high priority areas (Davis 1965; Omi

1977; Wood 1979). No such studies have been conducted for park and wilderness areas, especially within the context of suppression costs (approximately \$120 million) associated with fire control efforts in Greater Yellowstone during 1988.

Productivity measures for landscape fuel manipulations on the order of several km² are even trickier to establish, especially in park and wilderness areas where nonmarket values may predominate. The challenge is to ascertain whether the landscape fuel manipulations make sense in terms of ecological outcomes, management objectives, and costs. Such an analysis requires information on treatment effects on fire regime (frequency, intensity, size, and seasonality of future fires), and impacts on indicators of interest (e.g., landscape and economic effects).

Conceptual Framework

Figure 1 suggests a conceptual framework that could be used for assessing the viability of landscape fuel treatments, once management objectives were specified. In the figure, a decision to treat fuels on a large scale changes the landscape by virtue of effects on fuel profiles (consequently on types of fires effects experienced). A decision against large scale treatment suggests reliance on more traditional, status quo practices (i.e., small prescribed fire projects and continued fire suppression). The vegetation mosaic resulting from landscape fuel treatments will differ considerably from the status quo, primarily due to changes such as species, age distribution, fuel availability, vertical structure, and horizontal continuity. Conceivable impacts from non-treatment may include fuel buildups in localized areas and future recurrence of 1988-type events.

The viability of landscape fuel treatments must be assessed in terms of specified management objectives, effects on fire regime, and landscape spatial/temporal indicators. The specification of objectives would require that managers identify and manipulate areas to achieve desirable future configurations for the landscape. These desired configurations could then be compared with actual changes monitored over time, recognizing that intentional and prescribed natural fires would induce effects at multiple spatial and temporal scales. Further, landscape manipulations could alter disturbance patterns of prescribed natural fires in the absence of fuel treatments. Thus policy evaluation of landscape treatments will need to incorporate spatial and temporal indicators of biological integrity along with traditional measures for assessing fire management effectiveness (e.g., cost and impacts on fire size).

The framework suggested in Figure 1 presents a convenient comparative analog to actual fires, providing suitable simulation or computerized models for fire spread

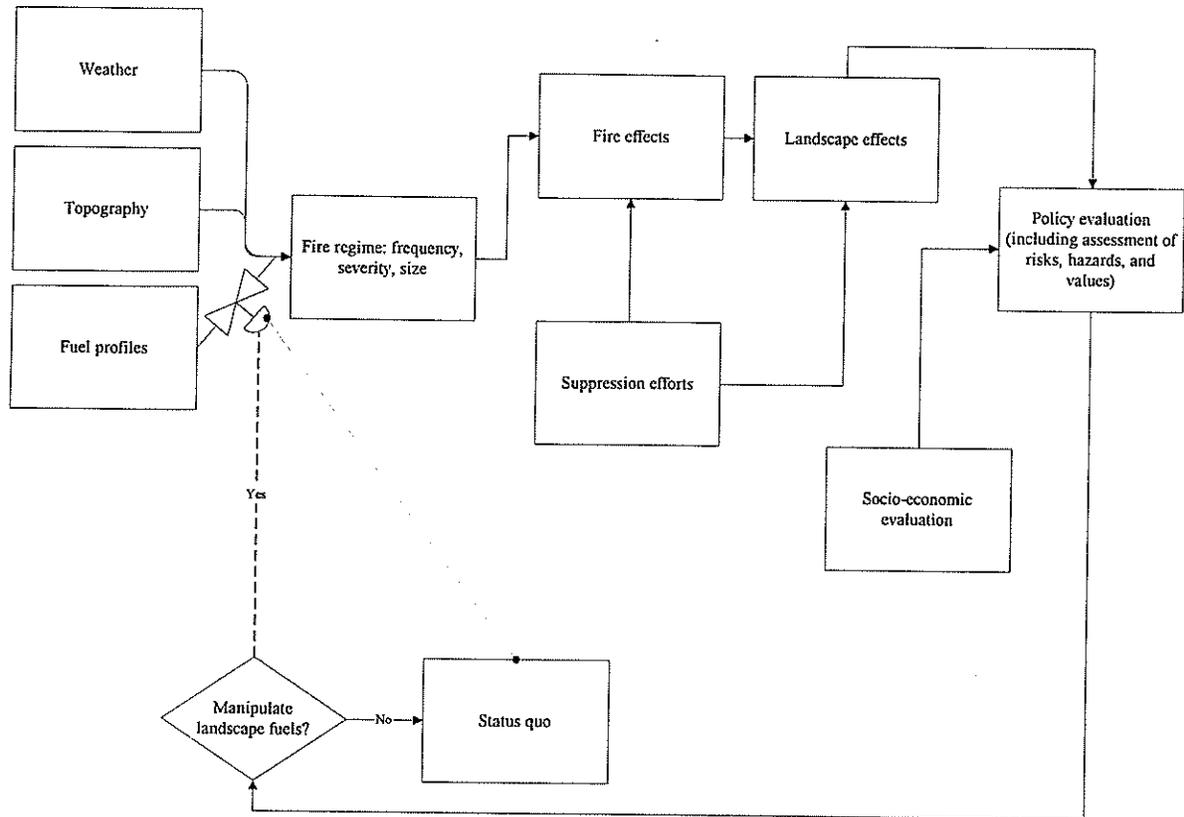


Figure 1. Framework for assessing the impact of landscape-level fuel manipulations a status quo (i.e., occasional small-scale treatments and continued fire suppression). Although fuel profiles are affected in either case, significantly different impacts can be expected in resultant fire regimes (frequency, severity, and size of future burns).

and effects can be used. Accordingly, the impact of fuel profile changes should be borne out in the modeled behavior of subsequent fires. Existing computer routines such as FARSITE (Green et al. 1995) and FIRESUM (Keane et al. 1989) could provide rough approximations for spread and ecological effects, though considerable refinement and other models would be required. Further, stochastic assessments would probably provide more meaningful interpretations, although such tools have not been developed fully to date.

Application of Framework to Assessing Landscape-level Fuel Manipulations

For the moment, let's assume suitable computer models are available so that we can apply the framework in Figure 1 to analyzing landscape fuel manipulations in Greater Yellowstone. To do so, information will be required on viable alternatives, treatment costs, effects on fire regime resulting from fuel treatment, and spatial/temporal effects on landscape indicators of interest.

To simplify the analysis, I will focus on the opportunities and challenges associated with those large expanses of older lodgepole pine, including those interspersed with Engelmann spruce (*Picea engelmannii*) and subalpine fir

(*Abies lasiocarpa*) which did not burn in 1988. The older forest areas are of interest because presumably they are susceptible to future crown fires with increasing age (Romme and Despain 1989b), even though flammability changes occurring in a human life-time might escape the notice of casual observers. However, we need to recognize that over time the adjacent burned areas will also present some interesting fuel management possibilities. Conceivably, the fuel recovery on areas burned in 1988 is insufficient to justify consideration of fuel treatment immediately, but opportunities may need to be examined as these areas increase in flammability in the future.

For analytical purposes we might be interested in comparing at least three alternatives for these older stands: 1) Reliance on natural processes; 2) Area-wide treatments such as prescribed fire, or fuelbreaks; and 3) Selective application of fuel management techniques, including prescribed fire, in high priority areas (such as boundaries or around high-value developments). As indicated above, in previous case studies of fuel treatment in non-park areas, only selective treatments have been economically justifiable. On the other hand, the unique management circumstances in park and wilderness areas might dictate another look at large-scale fuel manipulations especially if carried out in conjunction with a vigorous prescribed natural fire program. As indicated

above, uncertainties in information and computerized models are large, but do not necessarily prevent an analysis.

Effects on Fire Regime and Landscape

The mosaic resulting from disturbance history before (and subsequent to) the 1988 fires provide insight into possible outcomes from manipulating landscapes through fuel treatment such as intentional or lightning-ignited prescribed fires. Wildland managers have witnessed that lightning fires will occur in older forest stands but most will remain small (Sellers and Despain 1976). Where conditions are right (winds, fuel moisture, temperature) fires may grow and involve tree canopies, but fire size and severity are limited by encounters with younger stands, previous burn areas (Despain and Sellers 1977, Sweaney 1985), and other fuel discontinuities. Conventional wisdom suggests that fire spread and severity of future fires will be lessened in recently burned areas, due to reductions in the availability of fine and intermediate dead fuels (<2.5 cm diameter). This effect remains so long as fuel availability remains below levels supported in adjacent unburned areas, i.e., due to the abundance of green, moist, and relatively non-flammable plant tissue in burned areas (Christensen 1991).

Reduction in fuel availability also was at least partially responsible for reduced fire severity in intensively managed stands within the 1988 North Fork Fire in Greater Yellowstone (Omi and Kalabokidis 1991). Our comparative study was motivated by recognition of dramatic fire severity differences in mature forests as compared to recently-established forest plantations, where fuel disposal was included in the silvicultural prescription following timber harvest on national forest land. Our assessment of the higher spread rates and consequent fire intensities (arrived at through existing computer models) were borne out in our field measurements of measured fire severity in mature forest vs. manipulated sites.

With fire exclusion over a landscape, fuels will accumulate and flammability will increase with resultant increase in fire intensity. Christensen (1991) asserts that under such circumstances, ecosystems become increasingly unstable with stand development, especially when fire has been an essential and inevitable agent of biomass decomposition.

These studies suggest that area-wide and selective fuel treatments will alter the fire regime, depending on the scale and magnitude of treatments. In specific, it seems likely that the frequency, severity, and size of future fires will be changed through programmatic fuel reductions over a large enough area. Whether this is desirable is another issue. Unfortunately, we have incomplete information on the ecological impacts of such large-scale treatments. Still some inferences are possible with respect to the fuel manipulation scenarios considered above.

Reliance on Natural Processes

To examine this alternative, it is useful to focus on the certainty that areas unburned in 1988 will burn at some point in the future. Areas burned in 1988 will become flammable with time. The timing and intensity of future fires in current old forest patches largely will be a function of weather conditions (Romme and Despain 1989a); in areas burned in 1988, future flammability will depend as well on fuel accumulations accompanying plant succession. If future burns occur under conditions similar to 1988, we could expect high intensity crown fires in the older forests and possible breaching of fuelbreaks and jurisdictional boundaries. Further, with time the 1988 burn areas will increase in flammability to the point where sustained fire activity could develop.

Under such conditions diversity within the landscape could increase if the 1988 burn areas functioned as natural fuelbreaks and natural or intentional fires were allowed to burn up to fuelbreak boundaries, thereby creating a variable age-class mosaic. It is also possible that diversity could actually decrease from current levels if all the older, unburned forest in an area were to burn in a single event. Much depends on the size of future fires relative to the size of landscape, and the time since last disturbance relative to time required for recovery (Turner et al. 1993). Over time "boom or bust" cycles in biological diversity could develop within the Yellowstone landscape; further we would have to contend with whichever outcomes might be dealt to us by natural events (including fire, insects, disease, and successional patterns and processes). In the absence of fuel treatments, many of the outcomes could be chaotic and random.

Area-wide Fuel Treatment

In the old-growth forest patches, large-scale prescribed burns and fuelbreaks would likely require extensive pre-treatments to prepare fuelbeds for treatment. In addition, rotational prescribed burns might be scheduled in the future for strategically-located areas burned in 1988. Priorities for treatment areas could be established using the framework suggested in Figure 1 to develop indicators of relative fire risks, fuel hazards, and values as these change over time (with and without landscape treatment). Planning efforts could also incorporate assessments of natural barriers (lakes, river corridors, rock outcrops, roads, recent burns, etc.) which would augment buffer lines that might need to be constructed prior to treatment. Issues relating to desired burn area, site-selection, and execution would need to be resolved via interagency planning assessments based on ongoing research, budget constraints, and management capabilities.

Assuming that such a strategy could be implemented, future fire frequency could be increased, while intensity and size could be decreased due to lower fuel availability on treated sites. Changes in seasonality of burning are less likely, especially since prescribed burns

would probably need to be conducted in the traditional fire season (June-September) in order to be effective. Effects due to large-scale prescribed burns or extensive fuelbreaks would depend on the size of treatment area and conditions under which treatments were applied. To date, no studies have been developed to field-test hypotheses relating biological integrity to wide-scale prescribed burns and fuelbreaks, although diversity might be highest with area-wide fuel treatments conducted in conjunction with a vigorous prescribed natural fire program.

Selective Fuel Treatments in High Priority Areas

To date no studies have been developed to test hypotheses on this strategy for park and wilderness areas, but by definition such treatments would probably be of such small scale and therefore have little impact on landscape diversity. On the other hand, as with traditional fuel treatments (Table 1) the potential payoffs in terms of protection of developed areas or along jurisdictional boundaries could be high.

Costs

Costs of fuel treatment are important in comparing fuel treatment alternatives. Hazard fuel and resource management prescribed fire treatments within the National Park Service have been analyzed by Omi et al. (1994). Our study analyzed prescribed fire cost requests from park units nationwide, stratified by numerous independent variables including geographic region, fuel profile, treatment type (fire, mechanical, chemical, and biological), complexity of treatment, and natural resource ranking score. We found a (ln-ln) negative linear relationship between costs (\$/ha) and treatment size (ha) for 348 projects nationwide (including four Yellowstone projects). Thus unit costs are high for small projects and decrease as the project size increases. Not included are costs for planning, preparing, and evaluating treatments, nor escaped fire costs.

Management By Natural Processes

Treatment costs under this alternative are minimal since no active management activities will be undertaken. Future costs could be high, especially as related to suppression of large fires which breach jurisdictional boundaries or threaten developments.

Area-wide Fuel Treatment

Treatment costs in older forests could be high due to required pre-treatments. Fuel conditions in areas burned in 1988 could be monitored and prioritized for treatment, so as to balance increasing flammability with age against costs of treatment as plant succession proceeds. Treatments could conceivably be carried out at low unit cost and unit costs could be decreased further by increasing the size of treatment. Treatments involving prescribed

fire could breach jurisdictional boundaries or threaten developments.

Selective Fuel Treatments in High Priority Areas

These treatments would be most costly on a unit basis due to their small size. As with area-wide fuel treatment, maintenance costs would also be incurred to manage fuel levels over time.

Economic returns from fuel treatment are difficult to calculate under any scenario; in fact, such calculations are impossible given the management objectives in park and wilderness areas. While the resistance to estimating returns is understandable (due to difficulty of calculations), this reluctance essentially places a priceless value on the resources (Omi 1989), thereby justifying any level of land management costs. However, a judicious fuel treatment program at minimum holds out the potential for significant reduction in the level of sky-rocketing suppression costs associated with large-scale fire events.

The ecological impacts and costs of these three alternatives are summarized in Table 2. The potential exists for area-wide fuel treatment to promote high levels of biological diversity over the landscape at lower units costs, especially if implemented in conjunction with a vigorous prescribed natural fire program. In fact, area-wide fuel treatment might be the only viable method for overcoming the problem posed by Christensen et al. (1989), that is, of remaining tracts of wild areas being too small to allow natural forces to run their course.

Management Implications

Ecological impacts of large scale fuel management alternatives need further study. The manipulations themselves are admittedly controversial and implementation of the proposed framework (Figure 1) would require ambitious model specification and development by researchers and managers. Although I have focused on old-growth forests extant after 1988, we also need to be mindful of opportunities and challenges associated with recently burned areas. Eventually these areas will mature to the point of supporting high intensity canopy fires.

Before proceeding with any fuel treatments, managers would have to establish an ecological rationale for large scale fuel manipulations. This will require clear specification of ecological processes to be preserved and management objectives. In contrast to fuel treatment case studies elsewhere (in which area-wide treatments were not justified), landscape fuel manipulations might be justified in park and wilderness areas, especially where such treatments improve future options with respect to the prescribed natural fire program. This perspective might be especially useful for buffering the effects of periodic large, intense fires which threaten jurisdictional boundaries or developed areas.

Table 2. A comparison of effects on fire regime and ecological consequences of fuel treatment alternatives, assuming treatments are implemented in conjunction with a vigorous prescribed natural fire program. Unit treatment costs are based on inferences from Omi et al. (1994).

Fuel Treatment Alternative	Effects on Fire Regime	Ecological Effects (e.g., Landscape Diversity)	Unit Treatment Costs (\$/ha)
Natural Processes	None	Landscape diversity could increase; boom/bust cycles also possible	None—but future costs, e.g., wildfire suppression could be high
Area-wide	Frequency ↑, Intensity ↓ Size ↓, Season (NC)	Unstudied	Low
Selective	None	Negligible	High

Landscape manipulations involve risks, but are important to consider from the standpoint of protecting communities and developed areas. Moreover, area-wide treatments (prescribed fire and fuelbreaks) might provide the only plausible solution to overcoming the size constraint of park and wilderness areas in which large-scale disturbances are the norm. Selective fuel treatments in high priority areas are more costly (due to their small size) and may have negligible impact on landscape diversity. Regulation solely by natural processes may subject nearby communities and developed areas to undesirable outcomes.

Managers in Greater Yellowstone have been presented with a unique opportunity for studying the efficacy of landscape fuel manipulations. As an unstudied alternative, area-wide manipulation of 1988 burn sites hold potential for managing the diversity of the Yellowstone landscape. Alternatives for fuel treatment can be analyzed systematically in terms of effects on biological integrity and costs, but uncertainties about temporal and spatial effects must be considered. Foremost among these uncertain effects are the ecological consequences of allowing large-scale fires, limiting the size of future large-scale fires, or allowing fires to roam freely over substantial portions of the Yellowstone landscape.

If the adoption of large-scale fuel manipulations should prove too controversial or risky, land managers might want to direct attention to evaluating wider uses of prescribed natural fires where safer fuel mosaics can be established. At any rate, given the state of knowledge about ecological consequences, land management agencies within Greater Yellowstone should go slowly in terms of implementing and testing hypotheses about landscape fuel manipulations. Still, most of the questions about its viability will remain unanswered until some test areas are established. Logical test areas should be identifiable on the basis of mapped burn areas, current vegetation, and proximity to high value areas. Further justifications might be decided on the basis of risk, fuel hazards, ecological sensitivity, and research opportunity.

Acknowledgments. The author gratefully acknowledges financial support from McIntire-Stennis cooperative research funds at Colorado State University, USDA Forest Service contract RMFRES 28-CR9-496, and USDI National Park Service contract CA 1268-1-9002. Helpful suggestions from two anonymous reviewers are appreciated.

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Simulation of Crown Fire Effects on Canopy Seed Bank in Lodgepole Pine

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Abstract. Analysis of video footage taken of crown fires during the 1988 fire season in Yellowstone National Park indicated that the most frequent length of time required to completely burn tree crowns was 15-20 seconds. Lodgepole pine (*Pinus contorta* Laws.) seeds were tested for ability to germinate after exposing both serotinous and nonserotinous cones for 10 to 60 seconds in a flame front designed to simulate a crown fire. Heating enhanced germination of seeds from serotinous cones but not those from nonserotinous cones. Maximum germination rates for serotinous cone seeds ranged from 37 to 64 percent and occurred after 10-20 seconds exposure of cones to flames. Germination after 60 seconds exposure averaged 0.3 to 14 percent. Maximum germination of seeds from nonserotinous cones was about 80% and occurred with no exposure and after 10 seconds.

Keywords: Fire Behavior; Regeneration; *Pinus contorta*

Introduction

Lodgepole pine has long been known as a fire-adapted species partially because of its ability to produce abundant seed from serotinous cones immediately post fire (Clements 1910). These cones must be subjected to temperatures higher than is normally found in the tree crowns before they will open and release their seed (45 to 60° C, Perry and Lotan 1977). The lower range is within that achieved at the soil surface in full sunlight and the upper temperature is well below that found in the flames of burning vegetation. The heat necessary to open cones could easily come from the combustion of surface fuels as the hot gases pass up through the canopy as well as from burning crowns themselves. Serotinous cones would be of little advantage, however, if conditions common in burning tree crowns killed the seed.

Not all lodgepole pine trees produce serotinous cones. Some produce cones that release their seed when they

reach maturity (nonserotinous cones). The physical properties of each type of cone appear to be identical, however. The proportion of trees with serotinous cones is greater in stands resulting from stand replacing fires (Muir and Lotan 1985) and may be greater in lower elevation stands than in those of higher elevations (Lotan 1968). In lodgepole pine stands of the northern Rocky Mountains, the percent of trees that bear mostly serotinous cones varies from 0 to 80% (Lotan 1968).

In Yellowstone National Park, crown fire is responsible for most of the area burned in any given year. Crown fire is a spectacular phenomenon. Forest fires simultaneously burning the crowns of trees over large areas release a lot of energy in a short time. Values exceeding 50 to 60 megawatts per meter square in less than 40 seconds are not uncommon (Rothermel 1991). Spectacular smoke columns rise thousands of meters into the air. These are very intense fires and can have considerable ecological effects. One possible result often attributed to such fires is the death of seed in the tree crowns (Anderson and Romme 1991). However, this is not documented and given the number of lodgepole pine seedlings appearing after crown fires there is reason to question this assumption.

Knapp and Anderson (1980) showed that seed germination was not adversely affected by temperatures required to open the cones. They did not, however, investigate the effects of the high temperature of burning tree crowns on seeds enclosed in cones. Beaufait (1960) investigated the effect of fire in a muffle furnace on the seeds in jack pine (*Pinus banksiana* Lamb.) cones and Clements (1910) reported on lodgepole pine cones subjected to the flame of a Bunsen burner for 10 and 30 seconds. Neither of these treatments is very similar to conditions occurring in burning lodgepole pine crowns. Fire behavior models could give an estimate of the length of time the cones would be subjected to the flames but crown fire models are largely preliminary (Rothermel 1991) and we are not aware of any observations of burn

duration (fire residence time) reported for lodgepole pine crowns.

We undertook this study to determine the length of time cones in lodgepole pine trees are subject to flames during crown fire and the effect of that exposure on the ability of the seed to germinate.

Methods

The typical duration of flames maintained in tree crowns was determined by examining videotape footage taken during the 1988 fires in Yellowstone National Park. Duration was recorded for all instances of crown fire where both beginning and end of flame duration was visible on the tape segment. A video editor was used to analyze the tapes. Suitable segments were located with a rapid scan. The beginning frame where flame was just beginning in the crown was marked and then the final frame was located when no more flame was visible. The elapsed time was displayed by the editor and recorded. Species of the trees involved could not be reliably detected in all cases so all instances were recorded regardless of species.

Of the 115 tapes recorded, 20 were found to contain suitable segments. Duration was obtained for 102 segments, 18 of which were of single trees. The remaining 84 were of stands where all the crowns burned simultaneously (area ignition from spot fires). Both beginning and end of flaming could not be observed during advancing flame fronts because of camera movement or because the flames were obscured by smoke before flaming ended.

In the fall of 1991, five trees bearing mostly serotinous cones and five trees bearing mostly nonserotinous cones were felled near Madison Junction (near the center of Yellowstone National Park.) The trees were approximately 120 years old. Sufficient cones were collected from each tree to provide five cones for each of five temperature treatments. Serotinous cones representing three different age classes (current year, two yrs., and three to five yrs.) were collected. The nonserotinous cones were taken from the current year's crop and had not yet opened.

The flame front of a crown fire was simulated by burning dry lodgepole pine branch wood, 1-5 cm diameter. The fire was free burning in the open air (an oversized campfire approximately one m diameter). Wood was added periodically to keep visible flames approximately 20 to 50 cm above the wood. Our fire did not provide the preheating and postheating that a natural crown fire would have produced but we feel that the exposure to the very high temperatures of the flames was well represented. Five cones from each age class were selected from each tree and subjected to flame treatments within a few hours of collection. The five cones were

placed in a wire basket and held in the visible flames for 10, 20, 40 and 60 seconds. Each batch of cones was cooled momentarily in a metal can and then transferred to small paper bags for final cooling and storage.

Seeds remaining in the cones and those in serotinous cones not subjected to heat were extracted by mechanically removing the cone scales. The untreated nonserotinous cones opened and released their seed as they dried out in the paper bags.

All of the seeds from each treatment combination were germinated at room temperature on wet paper towels in trays covered with clear plastic. Water was added periodically to keep the towels moist. Germinated seeds (those with at least 3 mm of radicle growth) were counted and removed each week until no more germinated seeds were observed for two or more weeks.

Statistical analyses were accomplished using SYSTAT 5.01 (Wilkinson 1990). Length of time effects on proportion of seeds germinating were tested using ANOVA and linear regression. Because most values were between 20 and 70 percent the values were not arcsine-transformed. Student's t-test was used to test the difference between the percent of seeds germinating from unheated serotinous cones and those heated for 10 seconds and for differences between flame duration of single trees and stands.

An early criticism of our study was the lack of temperature measurements. Therefore the fire was rekindled on the same spot with similar wood and maintained in the same way. Flame temperatures were measured with an unshielded and nonaspirated 0.005 mm chromel-alumel thermocouple attached to an Omega Model H23 Datalogger so the actual temperature will be few degrees higher than reported (Walker and Stocks 1968). The thermocouple was held in visible flames for five minutes. Temperature was recorded at one second intervals.

Burning crowns consume mostly needles rather than dry wood and the temperature of burning needles could differ from that of burning wood. Flame temperatures from burning needles were measured by adding live lodgepole pine branches to the fire. The thermocouple was held in the flames of the burning needles until the needles were consumed and the flames stopped. This took approximately one minute.

Results

The crowns of canopy trees remained flaming for an average of 24.5 seconds with a standard deviation of 9.6 seconds. Minimum time was five seconds and maximum 48 seconds. Flame duration distribution is skewed toward the shorter times with a definite mode at 15-20 seconds (Figure 1). There was no significant difference between single trees and stands of trees in the time the crowns remained flaming ($p=0.796$).

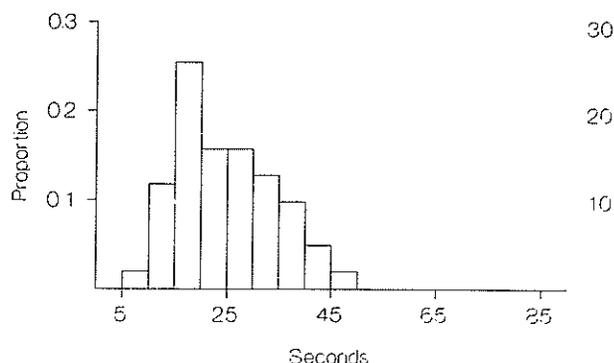


Figure 1. Distribution of flame duration in burning crowns of lodgepole pine trees and stands

The ten-second treatment was enough to open all the cones and the 60-second treatment was long enough to cause some cones (especially older ones) to ignite. Those cones, however, stopped flaming when they were removed from the fire. Time in flames caused significant differences in germination ($p < 0.001$) as did origin (serotiny) of seed ($p = 0.002$). No significant differences were detected between the 10, 20, and 40 second flame treatments and cone age had no effect (Table 1).

Table 1. Analysis of variance of percent germination. Dependant variable=percent germination, $n=100$, multiple $R=0.781$, multiple $R^2=0.610$

Source	sum-of-squares	DF	Mean-square	F-ratio	p
Serotiny	36.78.379	1	3678.379	10.084	0.002
Time In Flame	39047.094	4	9761.774	26.762	0.001
Age	0.925	1	0.925	0.003	0.960
Serotiny*TIF	8058.527	4	2014.632	5.523	0.001
Error	32464.006	89	364.764		

Seeds from nonserotinous cones germinated as well after 10 seconds in the flames as they did without being heated. Germination then declined linearly to near zero at 60 seconds. Linear regression showed a significant negative relationship ($p < 0.001$) between proportion germinated and time spent in the flames (proportion germinated = $0.882 - 0.014 * \text{time in flames}$, adjusted $R^2 = 0.802$).

Seeds from serotinous cones, however, responded quite differently. Germination of the unheated seeds was significantly lower than seeds from nonserotinous trees ($p < 0.001$). They then showed a stimulation of germination after 10 and 20 seconds in the flames (Figure 2). The curves for each of the cone ages were parallel and were not significantly different from each other.

Flame temperatures in the simulated crown fire front were as high as 1067°C . The distribution of temperatures taken at one second intervals was similar in flames from both dry roundwood and green branches (Figure 3 and

Figure 4). The average temperature for the roundwood fire was $843^\circ\text{C} \pm 9.8\text{ SE}$, $N=305$. Needle flames averaged a little cooler at $700^\circ\text{C} \pm 12.6\text{ SE}$, $N=147$. Both distributions were skewed to the higher temperatures, possibly because of moving the sensor to remain within the flames.

Discussion

The difference between seeds from serotinous and nonserotinous cones was surprising to us. There is apparently more to serotiny than cone opening. It appears that short duration heat like that generated by the burning crowns may have a stimulating effect on germination of seeds from serotinous trees.

Peak germination corresponded exactly with the most frequent flaming duration for crown fires and both the serotinous and nonserotinous seeds germinated at the same rate at that exposure. The slope of the regression line for nonserotinous seeds suggests that each second in the flames decreases survival about 1.5%. If this is the case then 70 to 80% of the canopy seed bank in lodgepole pine would be left alive by the most common crown fires. This would decrease to 25 to 30% for the maximum duration recorded.

Seed crops in lodgepole pine forests near Yellowstone have been shown to exceed four million per hectare (Lotan 1968). If only 10% of those four million seeds were viable and only 1% of those became established there could still be four thousand seedlings per hectare. This would vary, of course, according to the seed crop in the tree crowns at the time of a fire and the weather conditions during seedling establishment.

Our results agree with similar work done on jack pine (Beaufait 1960). Jack pine is physically and ecologically similar to lodgepole pine. The cones are very similar in

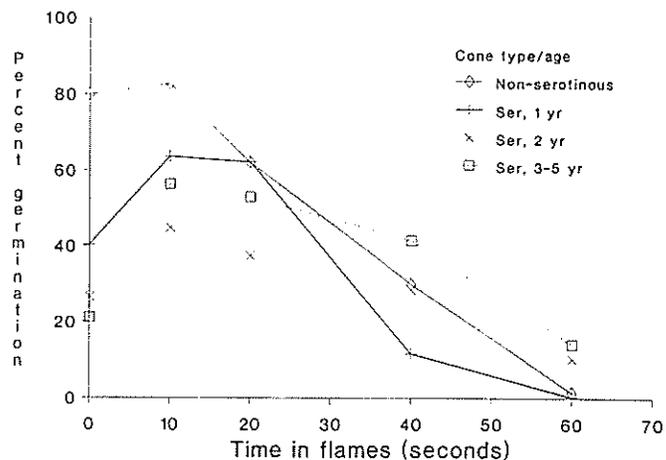


Figure 2. Effect of length of exposure to flames on lodgepole pine seed germination

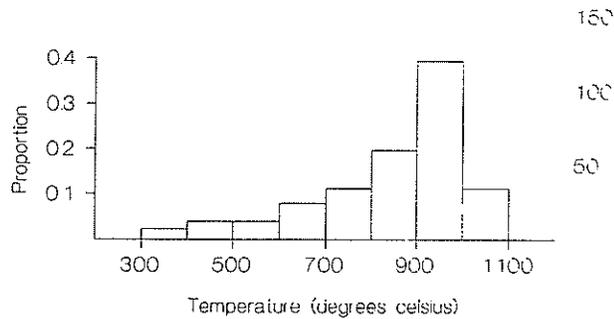


Figure 3. Distribution of temperatures at one second intervals for burning wood

habit and morphology. The two species are known to hybridize where their ranges overlap (Mirov 1967).

Beaufait found that seeds remained viable in the cones until the cones ignited. He also showed that 88% of the seeds remained viable after cones were exposed for 30 seconds at 480° C and that no viable seed remained after 60 seconds. Clements (1910) showed higher seed germination after heating cones in hot water and after 10 seconds in the Bunsen burner flame

Judging from the size of branches left in the canopy of lodgepole pine following crown fires, there would not appear to be sufficient heat generated to completely dry out and consume the cones during the typical time that flaming combustion is sustained in the crown. If a crown fired tree has no cones left in the canopy, the cause is probably not the result of the fire. It is more likely that there were simply no cones before the fire. Thus, low seedling density in a regenerating burn and few cones remaining in the burned crowns does not necessarily indicate an extremely severe fire. It more probably indicates a stand with a poor prefire cone crop.

In the crowns of the trees the cones are probably subjected more to flaming needles than dry wood. Flame temperatures from burning dry roundwood were slightly higher than flaming combustion fueled by needles. This

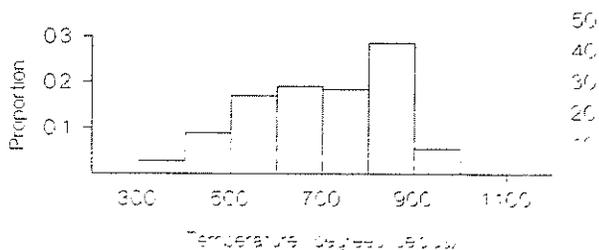


Figure 4. Distribution of temperatures at one second intervals for burning needles

is probably a consequence of the higher moisture content of the needles. Thus, the cones subjected to direct flame contact in our study may have experienced slightly higher temperatures than they would have in actual crown fires.

The temperatures recorded by the thermocouples varied from 300° to over 1000° C. This probably results from the turbulence of the hot gases rising from the wood and the mixing of cooler air. Each lot of cones in the study would have been subjected to a variety of temperatures, which may account for some of the variation encountered in the germination results. The temperatures recorded are typical of wood fueled fires measured by others (Zicherman 1978, Anderson 1969, DeBano and Conrad 1978, Muraszew, Fedele, and Kuby 1979) which is near the theoretical flame temperature of wood (Tillman 1981, p. 109).

The typical duration of flaming combustion in the canopy of lodgepole pine trees subjected to crowning is well within the ability of the cones to protect a significant portion of the seeds. Enough viable seed generally remains in the tree crowns to restock lodgepole pine stands even in the areas burned by severe crown fire.

The results of this study have some important implications for future stand dynamics. Viable seed in the crowns of very large flame defoliated lodgepole pine patches would negate the need for seed to migrate into the burned patches from unburned edges. Central areas in the larger patches may not have as many seeds available as areas near the edge where only surface burning may have occurred, but there would still be enough to replace the stand. The areas subjected to surface fires would have the full complement of seeds available in the crowns. Heat from the burning of surface fuels would probably be sufficient to open most of the serotinous cones. This could result in the high seedling density found in areas that had experienced only surface fires as described by Anderson and Romme (1991). Future stand characteristics will, of course, depend on all the other factors that determine seedling establishment and survival such as seedbed conditions and postfire climatic conditions but lack of seed source would be a minor consideration.

Acknowledgements. This paper was greatly improved by comments from Martin Alexander and an anonymous reviewer. Jennifer Whipple helped with the cone roasting.

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Post-fire Patterns of Whitebark Pine (*Pinus albicaulis*) Germination and Survivorship in the Greater Yellowstone Area

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Abstract. We are presenting a study in progress on the post-fire regeneration of whitebark pine (*Pinus albicaulis*), a subalpine and treeline conifer. Some of the results and interpretations that we report must be regarded as preliminary. Whitebark pine is the only New World species of *Cembrae* pine, a group characterized by large, wingless seeds and indehiscent cones. *Cembrae* pines are dispersed by nutcrackers, birds that bury seed caches for winter and spring food. Because 1 to 15 or more seeds are buried per cache, whitebark pine regeneration is often in the form of seedling clusters. The Clark's nutcracker (*Nucifraga columbiana*) is the primary seed disperser of whitebark pine. Successional whitebark pine (*Pinus albicaulis*) communities are critical habitat for grizzly bears and support a variety of other wildlife in the Greater Yellowstone Area. Periodic fire is essential for the renewal of these communities. Thus, the 1988 fires provided an important opportunity to study early post-fire whitebark pine germination and survivorship.

We are investigating whitebark pine regeneration with respect to moist and dry sites, unburned controls, and char depths. These studies are funded by the USDA Forest Service Intermountain Research Station. In 1990 we established a total of 275 circular, permanent plots, each 20 m² in area, in two study areas. The following treatments are represented in the Cooke City study area: dry, severely burned; moist, severely burned; dry, unburned; and moist, unburned. In the Mt. Washburn study area, plot treatments include dry, severely burned; moist, severely burned; and moist, moderately burned. For each plot we took five char depth measurements and calculated a mean and standard deviation. Individual whitebark pine seedlings were mapped and followed from year to year. Seedling density calculations are as of our field survey dates (late July and early August) each year; new regeneration in late summer is recorded the next year. Based on our previous work in 25 year-old burns in western Montana, we predicted greater densities of regeneration on moister slopes and in burned rather than unburned forest.

The mean char depths were lowest and least variable for the Cooke City dry, severely burned plots ($x = 1.2 \pm 0.5$ cm) and greatest and most variable for the Mt. Washburn moist, moderately burned plots ($x = 3.6 \pm 1.2$ cm). In 1990 there was no whitebark pine regeneration on any burned treatment in either study area. This was curious, because the cone crop in 1989 had been exceptionally heavy. Seedlings appeared on all burned treatments in both study areas in 1991; in 1992, only the moist, severely burned Cooke City treatment and moist, moderately burned Mt. Washburn treatment had new regeneration. Delayed germination of seeds cached in 1989 may account for the 1991 seedlings; this is supported by other lab and field studies.

Whitebark pine plot densities in 1992 ranged from a low of 0.002 regeneration sites per m² on the Cooke City dry, unburned treatment to a high of 0.038 sites per m² on the Mt. Washburn moist, moderately burned treatment. The Cooke City severely burned treatments had higher regeneration site mortality rates (losses of entire seedling clusters) 31% and 57% for dry and moist treatments, respectively) than did the Mt. Washburn study area (highest = 46% for moist, moderately burned treatment). For those seedling clusters recorded in 1991 that survived to 1992, we examined within-cluster mortality. For all burned treatments, the mean number of seedlings per regeneration site decreased. The regeneration sites that disappeared for the most part had the smallest numbers of seedlings per cluster.

In summary, the moist, burned treatments had the highest densities of regeneration in 1991 and the only new regeneration in 1992 but also higher mortality rates than the dry, severely burned treatments. Burned treatments had greater whitebark pine regeneration than did unburned treatments, as predicted. Finally, there appears to be a greater chance that a tree may be established at regeneration sites with larger seedling clusters.

Tourism in Montana After the 1988 Fires in Yellowstone National Park

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Introduction

During the summer of 1988 Yellowstone National Park experienced historic levels of fire activity. Many members of the tourism industry in Montana and adjacent states believed that the fires would negatively impact the tourism industry. This paper utilizes secondary data to monitor tourism in Montana after the 1988 fires in an effort to understand the relationship between a natural resource catastrophe and the overall tourism economy. Specifically, the study examines the following three research questions:

1. What happened to YNP visitation from 1985 through 1992?
2. What has happened to tourism in Montana as measured by accommodation tax receipts from 1988 through 1992?
3. Is annual visitation to YNP correlated with Montana accommodation tax receipts?
4. Where do tourists spend the most nights in Montana?
5. Has tourism activity in Montana become more concentrated or dispersed after the fires of 1988?

To address these questions two data streams were employed. The first utilized annual visitation to YNP from 1985 through 1992. The source of these data was YNP Visitor Services. The indicator for tourism in Montana was accommodation tax data from 1988 through 1992. These data were provided by the Montana Department of Commerce. The tax is four percent of all lodging receipts. Revenues from the tax are earmarked for state tourism promotion and research. Although the accommodation tax was implemented July 1, 1987, annual data are not available until 1988.

Findings

What Happened to YNP Visitation From 1985 Through 1992?

Visitation to YNP over the last eight years has systematically increased. The sole exception was the year of the fires when visitation declined 15% from the previous year. By 1989 the rate of growth had surpassed 1987 levels and has continued to grow. In 1982 the Park experienced slightly over 3,186,000 visits.

What Has happened to Tourism in Montana as measured by Accommodation Tax Receipts from 1988 Through 1992?

The accommodation tax data reveal that tourism in Montana increased every year from 1988 through 1992. During this time period, tax receipts grew by 54%. Few of the 56 counties in Montana shared in the tourism growth during this time period.

Is Annual Visitation to YNP Correlated with Montana Accommodation Tax Receipts?

Visitation to YNP and tourism activity in Montana is highly correlated ($r = .94$). Not surprisingly YNP is a major if not the primary attractor of tourists to Montana and the region. The growth rate of tourism in Montana and YNP is not linear. From 1988 through 1991 accommodation tax receipts for Montana have grown at a faster rate than has visitation to YNP. In 1992 YNP's visitation grew faster than did Montana's accommodation tax receipts.

Where do tourists spend the most nights in Montana?

The data showed that over 80% of all tourism activity occurs in nine of the 56 counties in Montana. Much of the tourism activity is focused in four counties (Flathead, Gallatin, Missoula and Yellowstone). Besides each of these counties having a major airport and interstate highway access, they also contain significant tourism

attractions. In particular, Gallatin and Flathead are adjacent to YNP and Glacier NP and have destination year around resorts. The other counties form a travel corridor between YNP and Glacier National Park.

Has tourism activity in Montana become more concentrated or dispersed after the fires of 1988?

Over the five year period the primary and secondary counties have continued to contribute over 80% of all accommodation tax receipts to the state of Montana. As tourism activity has increased throughout the state in terms of absolute dollars, the relative contribution of specific counties has varied. Gallatin and Flathead counties have increased their market share of statewide tourism. At the same time, Yellowstone and Missoula counties have seen their absolute dollar amounts increased but their relative proportion of statewide accommodation receipts decline. Gallatin and Flathead counties continue to grow due to the interest in the adjacent national parks, national forests, and destination ski areas. The data

indicate that tourism activity in the state has become more unequal as the tourism counties increase in activity while the rest of the state maintains a more status quo level of tourism activity.

Conclusions

Important implications can be drawn from the longitudinal analysis. The fires in 1988 enhanced YNP as a attraction for tourism. The increased tourism was not centered solely on the park. The fires contributed to the tourism economies adjacent to the National Parks and National Forests in Montana. Nine counties experienced tourism growth as visitation to YNP increased. However, the economic activity of tourism is not shared by the other 47 counties in Montana. Findings from this study suggest that natural resource management practices in YNP which allow for natural processes, such as fires, are likely to have positive monetary impacts on the regional tourism economy.

Media Coverage of Fire Ecology in Yellowstone After 1988

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Abstract. The 1988 fires provided an opportunity for journalists to produce stories about wildfire ecology in the Greater Yellowstone Ecosystem (GYE). This paper looks at the kinds of stories that resulted, examines the degree to which coverage of fire ecology changed after the 1988 fires, and offers a theoretical rationale for why coverage followed certain patterns.

Boolean logic was used to search an electronic database containing full texts of major American newspapers and magazines for stories about wildfire ecology in the GYE published between January 1, 1989 and August 31, 1993. The effort identified 29 newspaper and four magazine stories that focused on fire ecology in Yellowstone, 25 from 1989 and four from the subsequent years.

The research indicates that wildfire ecology received more media attention after 1988 than before, even after eliminating stories specifically about Yellowstone. About 14 percent of 442 post-1988 newspaper wildfire stories discussed ecological issues, compared to less than six percent of 375 wildfire stories published before 1988.

Five factors appear to influence how the media report wildfire: 1) the degree to which possible news angles resonate with cultural values, 2) the degree to which stories can be personalized and anthropomorphized, 3) the degree to which potential news sources actively seek media attention, 4) the degree to which fires occur in rural rather than urban areas, and 5) the newness of related developments. These factors suggest journalists are more likely to report wildfire as a disaster than as a science story.

Introduction

In the summer of 1988, wildfires in Yellowstone National Park were front-page news and led national television newscasts. Before that, the public appears to have been generally unaware of the prescribed natural fire

policy that had been adopted primarily for ecological reasons in American national parks and Forest Service wilderness areas, including Yellowstone and designated wildernesses in some of the adjacent national forests. Before 1988, the primary source of information about wildfire for most Americans was the Smokey Bear public education campaign. This effort, designed to reduce human ignitions, implied that wildfire is harmful because it destroys forests.

Because of intense public interest in the fires, the events of 1988 provided an opportunity for journalists to explain in lay terms the ecological context in which the fires burned. This paper briefly reviews how the fires were reported in 1988, describes some of the relevant media research, examines coverage of ecological issues related to wildfire in stories published after 1988, and offers a theoretical rationale to explain why news coverage followed the patterns it did.

Background

For an earlier research project (Smith, 1992), I examined 936 news accounts about the Yellowstone-area fires that appeared during 1988 in three Yellowstone-area newspapers (the *Billings* [MT] *Gazette*, *Bozeman* [MT] *Daily Chronicle* and *Casper* [WY] *Star Tribune*), in three nationally known newspapers (*The Los Angeles Times*, *New York Times* and *Washington Post*) and in the evening newscasts of the three television networks. I found that the majority of stories focused on the fires themselves rather than on the scientific context in which they burned.

After several of the 1988 fires made major runs on August 20, many reporters followed the lead of local residents and their political representatives who used prescribed natural burn policy as an explanation for why the fires were still burning a month after they became national news. Only one of the 936 stories, published in December after the fires were out, provided a detailed description of the ecological foundation of that policy

(Matthiessen 1988). Six paragraphs of this *New York Times Magazine* article trace the evolution of Yellowstone's fire policy through its roots in the cessation of predator control in the 1930's and the natural regulation philosophy described in the 1963 Leopold Report.

Surveys of reporters who covered the fires in 1988 and of the sources named in their stories indicated that many in each group believed the Yellowstone fires were poorly reported. The most common complaints were that reporting was exaggerated or sensationalized, and that stories did not provide enough information about the political or geographical context in which the fires burned. Reporters tended to blame poor coverage on ignorance, preconceived notions about fire, logistical problems with access and communications, deadline pressure, and on sometimes-inept Park Service fire information officials.

Several panels of fire experts judged network television stories during the height of the 1988 coverage less accurate than those before and after the peak coverage period. The network correspondents who did the largest number of stories about the fires for ABC, CBS and NBC television news each acknowledged afterwards that their 1988 stories exaggerated the impact of the fires.

In 1989, reporters from the television networks and from nationally-known newspapers and magazines returned to Yellowstone to assess how the park looked after the 1988 fires. In 1993, reporters again returned for five-year-retrospective stories about the fires. Some of the post-1988 news accounts addressed ecological aspects of wildfire. Because these stories were features rather than hard news, there was more opportunity than in 1988 to explore the scientific aspects of wildfire.

News, Context, Accuracy and the Sociology of Journalism

Journalists have been criticized for making factual errors, for exaggerating and sensationalizing events, and for not providing enough context in their stories. Understanding some of the workplace constraints inherent in news work will help explain why these problems occur.

Media scholar James Carey has suggested that it is uncharitable to criticize daily news reports for their lack of context (Carey 1986). That is perhaps the most common complaint about how journalists report events. The scholarly literature indicates that other structural constraints also interfere with good and thorough reporting.

Most journalists place a high value on factual accuracy, but accuracy alone does not necessarily characterize good reporting. Describing the number of acres charred does not explain why wildfires are burning, the social, economic or ecological impact of the flames on the burned areas, or the political ramifications of the fires. Reporters and their sources who covered the 1988 fires

and responded to my surveys were more critical of omitted information and missing data than of factual errors in stories about the Yellowstone fires.

Several scientific studies suggest that omitted facts and lack of context are more serious journalistic shortcomings than overt factual errors (Borman 1978; Ryan and Owen 1977; Lundburg 1984). In this context, the scholarly literature on reporting suggests that news accounts are socially-constructed realities designed to meet the needs of the journalistic workplace rather than objective accounts of issues and events (Altheide 1976; Bantz 1980; Fishman 1980; Tuchman 1978).

In an ideal world, reporters' news sources would be chosen entirely on the basis of the relative expertise of those sources. More often in the daily grind of journalism, however, sources are chosen for their accessibility rather than knowledge (Gans 1980). Sources eager to influence how journalists report events often succeed in doing so (Entman 1989; Molotch and Lester 1974, 1975, Sigal 1973).

Media research also indicates that science and technology are more poorly reported than other topics (Nelkin 1987; McCall 1988; Dunwoody and Scott 1982; Dunwoody and Ryan 1985). In part, this is because newspapers tend to give science a low priority (Nunn 1979) and because scientific ignorance is widespread (Ahearn 1988).

The cited research suggests that only a small proportion of post-fire stories about the Yellowstone wildfires are likely to discuss the fires in biological terms, that these reports will often lack some of the relevant scientific context, and that news sources named in the stories will be selected more for their availability than expertise. This, in turn, suggests that the most available news sources will have an opportunity to exert considerable influence on how the relevant stories are framed.

Because the Yellowstone fires brought so much media attention to the park's ecologically-based prescribed natural fire policy, I expected that a larger, if still small, proportion of post-1988 than pre-1988 stories about wildfire would contain ecological information.

Method

The NEXIS electronic database contains the full text of several hundred newspapers and other periodicals published during the last sixteen or fewer years, depending in the specific publication. I used Boolean logic to search through the texts of seven major newspapers (the *Boston Globe*, *Chicago Tribune*, *Christian Science Monitor*, *Los Angeles Times*, *New York Times*, *USA Today* and *Washington Post*), three American news magazines (*Newsweek*, *Time* and *U.S. News*), and two general-interest monthly magazines (*Life* and *Smithsonian*). The NEXIS database contains the full text of all of these

publications at least as far back as January, 1989.

The initial search, for stories that contained the word "Yellowstone" and the terms "fire" or "wildfire," identified 589 newspaper stories published between January 1, 1989 and August 31, 1993. Articles that did not mention Yellowstone or fire ecology in the first three paragraphs were discarded, leaving the 25 stories described in Appendix 1. None of the stories in USA Today met the second stage search criteria. A similar search of the five magazines identified 40 stories, four of which addressed fire ecology in the first three paragraphs.

I obtained the 29 newspaper and magazine stories in computer form and made printed copies. I then examined these copies for mentions of biologically-related wildfire effects. I assigned each story the two ecological evaluation scores described in Table 1: one assessing the number of ecological fire effects described, the other assigning each story to one of four levels of ecological awareness.

The score for the number of biological fire effects counted the references to direct effects such as the mosaic nature of most burns (one or two points depending on the extent of the description). I treated the fact that fires create a mosaic by burning some areas while leaving others untouched as an indication of greater ecological

awareness than the more simplistic notion that everything inside the fire perimeter has burned). Other biological effects included the effects on wildlife (one point each for explaining that most moved out of the way or for citing statistics on the few known to have perished), of fire on lodgepole pinecones (one point if the story simply said heat "popped" the serotinous Lodgepole pine cones that open only in intense heat, two points if the story explained that Lodgepole pines reproduce both through serotinous cones that open during wildfires and through non-serotinous conventional pine cones), etc.

The scores that divided stories into four levels of ecological awareness were based on face-validity evaluation of the degree to which reporters explained the way in which fire effects were interrelated (for example, level one if the story described only wildlife killed by the fires; level two if it explained that some died but most others simply moved out of the way). Stories were put into the level three category only if they explained forest succession following wildfire (the process by which different species dominate different stages of forest regrowth), and into the highest level (4) only if they made it clear that the involved natural processes change continuously over long periods of time.

The story printouts were then examined to identify the 98 named news sources to whom information was attributed, as described in Table 2. Each source was assigned to a relevant category such as "scientist" or "tourist."

The computer story files were then reformatted for examination with software (ISYS) capable of performing low-order analysis of how language was used in each story. Preparation consisted of making a separate file for each story and then stripping the headlines and other identifying material contained in the original NEXIS files. Table 3 describes results of the computer language analysis.

A separate Boolean search of the database was used to determine the proportion of stories about wildfire published during the three-year periods before and after 1988 contained ecological information. In this case, the somewhat simplistic criterion for identifying stories about wildfire ecology was any that contained the terms "fire" or "wildfire" and "national park" or "national forest" or "wilderness" and any word formed from the root "ecolog..." In the more detailed study in which 589 Yellowstone fire stories were examined to determine whether they covered fire ecology, about two-thirds (18 of 29) of the final stories included words formed with the root "ecolog..."

This search was limited to five newspapers (The Chicago Tribune, Christian Science Monitor, Los Angeles Times, New York Times and Washington Post) for which the NEXIS database contained complete files back to the beginning of 1985 as well as for the three-year period following 1988.

Table 1. Ecological Evaluations of the 29 Stories (see Appendix 1 for Story Citations)

Story Number	Ecological Score ^a	Scientific Level ^b
7	1	1
10	1	1
24	1	1
5	2	1
9	2	1
14	2	1
20	2	1
28	2	1
13	3	1
19	3	1
23	3	1
6	4	1
8	6	1
1	6	1
29	1	2
16	2	2
21	4	2
2	5	2
26	6	2
12	7	2
4	8	2
17	8	2
18	8	2
11	10	2
15	5	3
25	3	3
3	2	4
22	16	4
27	9	4

a Based on the number of biological fire effects described.

b Level 1: Isolated facts about recent fire effects.

Level 2: Interrelated facts about recent fire effects

Level 3: Description of forest succession.

Level 4: Broader evolutionary perspective: biology as an evolutionary process.

Table 2. News Sources named in 29 Stories about Fire Ecology in Yellowstone.

1. Experts: 46 of 98 Source Citations	
A. National Park Service Scientists: 18 of 98 Source Citations	
Stuart Coleman	Cited In 1 Story
Don Despain	Cited In 4 Stories
Terry McEneaney	Cited In 1 Story
Roy Renkin	Cited In 2 Stories
Henry Shovic	Cited In 1 Stories
John Varley	Cited In 9 Stories
B. USFS, State and Independent Researchers:	
7 of 98 Source Citations	
Frank Craighead	Cited In 1 Story
John Craighead	Cited In 1 Story
Steve French	Cited In 1 Story
Richard C. Rothemel	Cited In 1 Story
Dan Tyers	Cited In 2 Stories
Gary Wolf	Cited In 1 Story
C. College and University Researchers:	
13 of 98 Source Citations	
James Agee	Cited In 1 Story
Tom Bonnicksen	Cited In 1 Story
Norman L. Christensen	Cited In 2 Stories
Mary Ann Davis	Cited In 1 Story
Dan Janzen	Cited In 1 Story
Charles Kay	Cited In 1 Story
William Romme	Cited In 3 Stories
James G. Schmitt	Cited In 1 Story
Conrad Smith	Cited In 1 Story
Wayne Sousa	Cited In 1 Story
2. Representatives of Yellowstone National Park:	
29 Of 98 Source Citations	
Joan Anzelmo	Cited In 3 Stories
Robert Barbee	Cited In 13 Stories
David Cowen	Cited In 1 Story
Marsha Karle	Cited In 4 Stories
Greg Kroll	Cited In 1 Story
Fred Paulsen	Cited In 1 Story
Phil Perkins	Cited In 2 Stories
George Robinson	Cited In 1 Story
Dan Sholly	Cited In 1 Story
Sandy Snell	Cited In 1 Story
Amy Vanderbilt	Cited In 1 Story
3. Representatives of Federal, State and Local Agencies	
Outside Yellowstone: 8 of 98 Source Citations	
Don Bianci	Cited In 1 Story
Gene Bryan	Cited In 1 Story
John Cada	Cited In 1 Story
Syvev Shimek	Cited In 2 Stories
Mark Petroni	Cited In 1 Story
Manuel Lujan Jr.	Cited In 2 Stories
4. Tourists: 8 of 98 Sources	
Mike Allen	Cited In 1 Story
Verna Baker	Cited In 1 Story
Jennifer Gode	Cited In 1 Story
Eldon Marti	Cited In 1 Story
Myrna Marti	Cited In 1 Story
Scott Rogers	Cited In 1 Story
Edgar Smith	Cited In 1 Story
Miriam Smith	Cited In 1 Story
5. Yellowstone-Area Residents: 5 of 98 Source Citations	
Jim Cole	Cited In 1 Story
Ed Francis	Cited In 1 Story
Betty Morton	Cited In 1 Story
Evva Sandve	Cited In 1 Story
Eleanor Williams	Cited In 1 Story
6. Representatives of Advocacy Groups: 3 of 98 Source Citations	
Ed Lewis	Cited In 1 Story
Bill Schilling	Cited In 1 Story
Michael Scott	Cited In 1 Story
7. Miscellaneous: 7 of 98 Source Citations	
Alston Chase	Cited In 4 Stories
Alan Simpson	Cited In 3 Stories

Results

Of the 589 newspaper stories examined for this study, 10 percent (59) mentioned Old Faithful, five percent included references to Yellowstone superintendent Robert Barbee and four percent (22) used the word "rebirth" to describe the park the year after the 1988 fires.

All but four of the ecological stories published during the 55-month study period appeared in 1989, the year after the fires. Of the 25 in 1989, all but three appeared during the first six months. Thus, more than three-quarters of the stories appeared during the first 11 percent of the study period: most of them soon after it became possible for reporters to return to the park after a harsh winter.

There were some surprising factual errors and inconsistencies in the stories. An otherwise thorough article in the *Boston Globe* (Black 1989) said that Yellowstone Park is "roughly 100 miles by 80 miles," more than twice its actual size. On February 22, the *New York Times* said the fires "burned about 9 percent" of bison and elk winter feeding range (Egan 1989). Two days later, the *Chicago Tribune* said the same fires had "wiped out about 34 percent of the normal winter range of elk, bison and other animals" (Coates 1989). A generally well-done story in *Time* illustrated the human rather than geological time perspective of most reporters when it said "Old Faithful geyser ... sends its geyser spumes as much as 180 feet into the sky, just as it always has" (Witteman 1989, emphasis added).

Examination of Table 1 indicates that only five of the 29 stories were judged complete enough to merit inclusion in the two highest ecological information categories, levels 3 and 4. This indicates that most reporters were content to describe fire ecology in terms of the fire's immediate effects and those visible during the following year, without considering how the park has changed and will change over a period of decades or centuries, much less how it has changed and will change over geological time.

Table 3 indicates the degree to which these ecological news accounts anthropomorphized the fires in terms of their effects on large charismatic mammals. Although insects are as much a part of the ecological process as bison or elk, all of the stories collectively contain only one mention to any specific category of insects (ants), but 332 references to large mammals such as elk and bears. There are 44 mentions of various kinds of birds, 12 of small mammals, and 4 of reptiles. Despite fears that fire-caused erosion would degrade the quality of park waters, there are only two references to fish, both to cutthroat trout. The park flora, which were more directly affected by fire, merited 155 mentions.

The word "canopy" occurs 28 times in the 29 stories, suggesting it has come into the journalistic mainstream. The words "serotinous" and "serotiny," however, de-

Table 3. Word Frequencies in 29 Stories about Fire Ecology in Yellowstone.

A. Words Describing Life Forms: 153 Occurrences	
Animals	67
Beasts	1
Birds	13
Critters	1
Fauna	2
Fish	2
Flora	4
Insects	7
Mammals	6
Megafauna	2
Raptors	1
Wildlife	47
B. Words Describing Fauna: 395 Occurrences	
1. Large Mammals 332 Occurrences	
Antelope	10
Bambi	2
Bears	64
Bighorn Sheep	13
Bison	62
Buffaloes	23
Coyotes	7
Deer	11
Elk	121
Moose	11
Smokey Bear	3
Wolves	5
2. Small Mammals 12 Occurrences	
Beavers	2
Chipmunks	1
Marmots	2
Mice	3
Pocket Gophers	2
Porcupines	1
Voles	1
3. Birds 44 Occurrences	
Bluebirds	6
Chickadees	1
Crossbills	1
Eagles	7
Falcons	2
Flickers	4
Grouse	1
Hawks	3
Hérons	1
Magpies	2
Nutcrackers	1
Nuthatches	1
Owls	1
Osprey	1
Ravens	3
Sandhill Cranes	2
Thrushes	1
Woodpeckers	6
4. Reptiles 4 Occurrences	
Lizards	1
Snakes	2
Rattlesnakes	1
5. Insects 1 Occurrence	
Ants	1
6. Fish 2 Occurrences	
Cutthroat	2
C. Words Describing Flora: 155 Occurrences	
1. Plant Categories 38 Occurrences	
Flowers	10
Shrubs	5
Wildflowers	23

Table 3. con't.

2. Specific Plants 117 Occurrences	
Aspens	10
Balsamroot	2
Biscuitroot	1
Bistort	1
Buttercups	3
Dandelions	1
Fescue	1
Forbs	2
Geraniums	3
Lillies	2
Lodgepoles	63
Sagebrush	14
Strawberries	2
Subalpine Fir	2
Wheatgrass	2
Whortleberry	1
Whitebark Pine	7

scribing the role of wildfire in propagating lodgepole pine, occur only a total of four times, suggesting that lodgepole pine serotiny is not yet in the lay vocabulary, even in stories that focus on the ecological aspects of wildfire. Although several of the 29 stories described forest succession, the word itself appears in only one story (Stevens 1989).

Table 2 describes the news sources named in the 29 stories. Nearly half of them — 46 of 98 — were experts of one kind or another. Scientists named in post-1988 stories outnumbered tourists and area residents combined by more than three to one, almost the inverse of the ratio of scientists to tourists in stories published during the height of the fires in the summer of 1988.

The search of 817 pre-1988 and post-1988 wildfire stories supports the idea that journalists are more aware of fire ecology following the Yellowstone fires than they were before 1988. Among 375 wildfire stories published during 1985, 1986 and 1987, eight, eight and three percent respectively contained words generated from the root "ecolog...." Among 442 similar stories published in 1989, 1990 and 1991, 15, 14 and 11 percent, respectively, contained words generated from the same root. The figure for 1992 (N=113) was 10 percent; and for the first nine months of 1993 (N=39), 18 percent.

Discussion

The research described here indicates that less than five percent of 589 American newspaper and magazine stories containing the words "Yellowstone" and "fire" or "wildfire" contain ecological information in the first three paragraphs. Of these 29 stories, only 17 percent (N=5) go beyond the description of immediate fire effects to explain the long-term role of fire in forest ecosystems. Readers hungry for scientific information clearly did not get very much of it from these publications. This raises two questions: 1) why do the media pay so little attention to the scientific aspects of a story with so much scientific

potential, and 2) is it reasonable to expect more?

The theoretical rationale described below is based on an extensive study of media coverage of the 1988 Yellowstone fires (Smith 1992) and on research about how the media reported three other major stories: the Exxon Valdez oil spill (Smith 1992), the Loma Prieta earthquake (Smith 1992), and on climatologist Iben Browning's unscientific projection that an earthquake would strike New Madrid, Missouri on or about about December 3, 1990 (Smith 1993).

In each major news event, the amount and kind of reporting appears largely to have been a function of five factors: 1) the amount of enterprise exhibited by potential news sources, 2) the degree to which elements of the story resonated with cultural norms, 3) the salience of relevant issues, 4) the newness of the event and 5) the degree to which the setting for the story was rural or urban. I will attempt to explain by discussing each factor in more detail.

Source enterprise

One of the traditions of journalism is that reporters attribute information to named sources. As Gans (1980) noted, news is weighted towards sources eager to be heard. Molotch and Lester (1974, 1975) described news coverage as a battle among sources with vested interests to define events in self-serving ways. Entman (1989) suggested that journalistic practices make it so easy to manipulate news that public officials who talk honestly with reporters do so at their peril. Because of deadlines, there is often not enough time for even the most conscientious reporter to find the best sources. This journalistic fact of life makes reporters vulnerable to the most easily accessible sources, especially during crises such as earthquakes and wildfires.

The "source enterprise" factor describes the degree to which news sources successfully court media attention. Success is measured by the degree to which resulting stories legitimize the source-generated viewpoints and news angles. A representative of an environmental advocacy group who sought media attention would rate high on source enterprise if the resulting story focused on environmental aspects of the event. A politician who sought media attention to portray wildfire as an economic disaster would display high source enterprise if the resulting news account took that perspective. Consider these examples:

After the Exxon Valdez oil spill, the State of Alaska, which received much of its revenue from oil and which had approved the ineffective oil spill contingency plan, launched a propaganda effort in 1989 to portray itself as the innocent victim of Exxon. President George Bush, who caused substantially reduced safety precautions in

Prince William Sound because of Coast Guard funds diverted to support his program of drug interdiction, dispatched cabinet officials and high-ranking Coast Guard officers to Alaska to assure the public that the government was responding in appropriate ways.

Alaska Commissioner of Environmental Conservation Dennis Kelso and Coast Guard Commandant Paul Yost delivered sound bites that made good copy and obscured the culpability of each government body in the lax enforcement of safety standards and oversight of preparedness for large spills. The most-quoted Exxon official, Frank Larossi, was less skilled in dealing with reporters, exacerbating Exxon's public relations problems.

After the Loma Prieta earthquake, United States Geological Survey (USGS) geologists, who had been courting reporters for 25 years (Wallace 1990), rated news of that event coverage much more accurate and complete than seismic engineers, who had not sought media attention in any organized way.

Although Iben Browning had no standing as a seismologist and only one supporter among academic seismologists, his unscientific earthquake prediction was often reported as scientifically credible until the USGS intervened by releasing a report by a committee of 11 respected scientists that discredited Browning's prediction. Regression analysis indicated that this source enterprise by the USGS was the single largest factor explaining the variance in the accuracy of news accounts about Browning's prediction (Smith 1993).

In 1988 coverage of the Yellowstone fires, federal agencies were relatively unsuccessful in their attempts to influence reporters in ways that focused attention the natural role of fire in forest ecosystems. Examination of the expert sources named in post-1988 stories shows that about half are associated with Yellowstone National Park, suggesting renewed opportunity for source enterprise. Although many of the stories were ecologically superficial, most expressed a more positive attitude towards the park than stories published in August and September of 1988.

The Intermountain Fire Sciences Laboratory in Missoula, described twice in stories about the Yellowstone fires (Malcolm 1988 and Maugh 1988), was mentioned only once among the 29 post-1988 stories (Chandler 1989). If the fire sciences lab had been cultivating media contacts for a quarter century as the USGS in Menlo Park had been doing, coverage of the 1988 fires and their aftermath might have turned out differently. My research indicates that active cultivation of reporters by the USGS was a major factor in the high quality of reporting about scientific aspects of the 1989 California earthquake.

Cultural resonance

If the message offered by news sources resonates with widely accepted cultural values (e.g., Bambi terrorized by fire; Smokey Bear's admonitions that fire is bad), it will take less enterprise to influence reporters than if the perspective offered by sources contradicts popular wisdom.

Because journalists hold oil companies in low esteem (Meyer 1987: 234, 235), and because the drunken sailor is a part of maritime myth, the perspectives that alcohol caused the wreck of the Exxon Valdez and that the company was responsible for failed efforts to contain the spilled oil resonated with cultural values. Other causes identified by the National Traffic Safety Board, such as poor Coast Guard oversight, resonated less with popular conceptions and received less media attention, independent of efforts by news sources to influence coverage. Because Alaska symbolized uncorrupted wilderness for many Americans (Nash 1982: 308, 309), the idea that the state bore no responsibility for the spill or unsuccessful cleanup efforts resonated with popular wisdom. For that reason, the state could get favorable coverage with considerably less enterprise than Exxon.

Most of the damage from the Loma Prieta earthquake occurred outside San Francisco in places such as Oakland, Santa Cruz and Watsonville. But San Francisco is better known than the other cities, and the 1906 earthquake there is part of our cultural lore. Because San Francisco is a familiar reference and resonates with our knowledge of earthquakes, media accounts of the 1989 earthquake focused on San Francisco far more often than the distribution of seismological effects would have suggested.

Iben Browning's earthquake prediction resonated with the cultural myth that earthquakes can be predicted by observing animal behavior and through other simple means. Perhaps for that reason, inaccurate reports that Browning had earlier predicted the Loma Prieta earthquake and the eruption of Mt. St. Helens were initially described by journalists as fact without being investigated.

Because we are culturally conditioned to think of fire as destructive, it will take no source enterprise to persuade journalists to portray wildfire pejoratively. In face of this widespread conception, source enterprise is particularly important in communicating the biological context of wildfire to reporters. If agency managers and fire information officers are content to answer reporters' questions without actively providing scientific information about wildfire, they will unwittingly reinforce the Smokey Bear message that fire is always bad.

Issue salience

The salience of an issue or event — the degree to which it captures our attention — is another factor that appears to influence how events are reported. Thus wildfires in Yellowstone National Park, which is widely known, received considerably more media attention than equally intense fires in lesser-known areas such as the Scapegoat Wilderness between Missoula and Great Falls Montana.

Of the stories described here, the two earthquake stories probably had the highest cultural resonance. Because most of us drive over bridges and on freeways, we could relate personally to stories about how those structures collapsed and killed people. Iben Browning's dubious prediction — a 50-50 chance of a major earthquake near New Madrid, MO within two days of December 3, 1990 — had greater specificity than USGS predictions that estimated the probability of a Bay-area earthquake over a period three decades. The Browning prediction was therefore more journalistically salient and received greater coverage.

The Alaska oil spill and Yellowstone wildfires were salient in symbolic ways. Each symbolized the corruption of innocence by outside forces. Alaska, the pristine last frontier, and Yellowstone, the Crown Jewel of the national park system, were portrayed as innocent victims of bad management by inept administrators. In Alaska, journalists increased issue salience by portraying environmental damage in terms of doomed sea otters instead of explaining that the real threat was that mortality among less charismatic species in some parts of a complex aquatic ecosystem might eventually affect other parts of that system. In Yellowstone, issue salience was greater because journalists focused on national icons presumably threatened (e.g., Old Faithful Geyser) and on presumably terrorized megafauna rather than on less charismatic stands of lodgepole pine.

Wildfire ecology probably has considerably less salience than threatened national icons and allegedly inept land managers, and is therefore much less likely to be the focus of stories about wildfire.

Newness

Where a wildfire has burned since yesterday, who or what is now most at threat, and the most recent administrative actions will always be newer than ecological issues, and therefore more newsworthy. In Alaska, stories about today's events (sea otters rescued, beaches cleaned) and symbols (oiled shorelines and wildlife) were always more newsworthy than information that would help prevent future spills. In California after the 1989 earthquake, stories about damage and victims were always more newsworthy than information about past

zoning decisions and funding cutbacks that assured widespread damage to buildings and roads. Stories about Iben Browning's earthquake prediction focused on public reactions to it rather than its scientific merit.

The urban rube

Most of journalism is practiced in urban areas. In 1988, I would have said wildfires burn in rural places, though later events in the Berkeley Hills, Santa Barbara and Spokane temper that observation. Urban reporters are generally better qualified to report urban than rural phenomena, and generally more interested in urban events. Urban crime, politics and scandal are appropriate staples of news, because cities are where most of us live.

We've all heard stories about the country rube who goes to the big city and gets taken because he doesn't know the ways of the city. You can take the boy out of the country, etc. But the same concept works in reverse when urban journalists report rural events. A reporter who is quite sophisticated about the subtleties of Washington politics may be completely out of his or her element in a story about federal lands in rural areas. Thus Bill Greenwood, Washington correspondent for ABC, reported in 1988 "there's no doubt the flames [in Yellowstone] will cost the timber industry tens of millions of dollars" (World News Sunday, September 18).

In Valdez, Alaska, reporters from prestigious national news organizations generally knew much less about the background and issues relevant to the Exxon Valdez oil spill than their counterparts from Alaska-based news organizations. In California, Bay Area reporters generally had lived through other earthquakes, and many had working relationships with USGS scientists in Menlo Park. Reporters who flew to San Francisco from other urban areas had fewer bearings and were more likely to buy into the myth that earthquakes are somehow more dangerous than other natural disasters, such as the hurricanes that sweep through the southeast every few years.

The New Madrid fault, which traverses a predominantly rural area, was the focus in 1990 of stereotypical stories about simple folks in small-town America and their fears about the great earthquake. In Alaska, stories about the Exxon Valdez oil spill perpetuated myths about the primitive lifestyles of native peoples, portraying them as less assimilated into the cultural mainstream than they really were. In Yellowstone, many reporters used urban concepts to explain rural fires. If the fires were still burning, the thinking appears to have been, somebody must have screwed up. By the same logic that fires can destroy buildings, they can destroy rural landscapes.

Having offered my theoretical explanation of why the media reported so little and, in some cases, so superficially about wildfire ecology in Yellowstone after the 1988 fires, I now come to the second question: is it reasonable to expect more? My conclusion is that the

practical constraints on journalists are such that reporting on wildfire ecology and other scientific subjects will not change very much until scientists and other expert sources take a considerably more active role in cultivating reporters and actively educating them about both the methods and results of their research.

A Washington, DC-based reporter who covered the 1988 Yellowstone fires observed that "Forest fires aren't a [news] beat most of the time, even in the Western states." Because there are fewer reporters with expertise in wildfire than, say, in politics or crime, journalists covering wildfire must depend more on their sources for the kind of information that takes reporting beyond routine descriptions of threatened towns, suppression efforts, and acres burned.

In the rush to meet deadlines, overworked reporters are not likely to ask questions about the characteristics of forest fires that distinguish them from urban structure fires. Until fire scientists and land management administrators take a more active role in educating journalists and the public about wildfire, poor reporting is likely to be the norm. Fire information officers can help by providing perspective and by directing journalists to knowledgeable sources, but little change is likely until scientists themselves in the fire community begin to actively cultivate contacts with reporters as the USGS has done for 25 years.

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Appendix 1. Chronological List of 29 Stories about Fire Ecology in Yellowstone, 1/01/89-9/31/93

1. Reid, T. R. 1989. Spring Promises Rebirth Of Fire-Scarred Yellowstone; Officials Say Damage Was Exaggerated. *The Washington Post*. January 2, Final Edition: A1. NEXIS.
2. Chandler, D. 1989. Forest Service Plays Down Effects Of Fires. *The Boston Globe*. January 20, City Edition: 10. NEXIS.
3. Rensberger, B. 1989. Letting Yellowstone Burn. *The Washington Post*. January 23, Final Edition: A10. NEXIS.
4. Borcover, A. 1989. Forest Fires Changed Yellowstone, But Didn't Devastate It. *Chicago Tribune*. February 5, Final Edition: Travel, 3. NEXIS.
5. Coates, J. 1989. Yellowstone's fires continue to exact toll. *Chicago Tribune*. February 22, North Sports Final Edition, News, 1. NEXIS.
6. Egan, T. 1989. Limited Winter Range Starves Yellowstone Elk. *New York Times*. February 20, Late City Final Edition: A8. NEXIS.
7. Gerth, J. and Shabecoff, P. Elks, Parks and Bambi. *The New York Times*. March 6, Late City Final Edition: B6. NEXIS.
8. Reid, T. R. 1989. Yellowstone, Up From The Ashes; Observing the Park's Rebirth After The Wildfires Of '88. *The Washington Post*. March 26, Final Edition: E1. NEXIS.
9. Repanshek, K. J. 1989. PR Campaign Aims To Restore Luster To Crown Jewel; Despite Fires, Yellowstone Park Is Alive . . . And Well. *Los Angeles Times*. April 9, Bulldog Edition: 16. NEXIS.
10. Coates, J. 1989. Yellowstone Is Fearful As Bears Wake To A Feast. *Chicago Tribune*. April 22, North Sports Final Edition: 1. NEXIS.
11. Black, C. 1989. Ecology; Fires Clear Way For New Life; Nature Begins A Cycle Of Regrowth At Yellowstone Park. *The Boston Globe*. May 8, City Edition: 25. NEXIS.
12. Satchell, M. 1989. Last Summer's Spectacular Blaze Has Changed The Landscape But Not Destroyed This American Eden. *Yellowstone lives! U.S. News & World Report*. May 15: 24. NEXIS.
13. Schmidt, W. E. 1989. From Yellowstone Ashes, New Life And Approach. *The New York Times*. May 21, Late City Final Edition, 26. NEXIS.
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The Role of Fire in the Greater Yellowstone Ecosystem: Development of Instructional Units

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Abstract. A dominant theme that emerged following the fires that swept through the Greater Yellowstone Ecosystem (GYE) in 1988 was how little most people, including biologists, knew about the processes of large, stand-replacing fires in natural ecosystems. Although the fires generated much negative publicity initially, they offer an unprecedented opportunity to study the effects of fire in a large, reasonably undisturbed system. We have a unique opportunity to educate future generations about the role of fire in systems like the GYE and to "feed" the results of the many research projects now in progress into a variety of teaching units adapted to different audiences.

Development of teaching units for students in introductory biology and other biological science disciplines is presented. The units are organized into sections that include vegetation zones, natural succession of plant communities, fire history, the Natural Fire Policy of Yellowstone National Park (YNP), state of the vegetation prior to 1988, the 1988 fires: causes and effects, regeneration 1989-present, and the future of a natural fire policy.

Visual aids used include commercial videos, written materials and photographs, and a special set of paired slides taken in identical locations throughout YNP 23-35 years apart demonstrating how the 1988 fires have changed the "face" of Yellowstone. Specific sites are established to document the year-to-year changes in different vegetation zones and in aspen stands. We have a rare opportunity to document in detail for future generations the role of fire in a large natural area, and to incorporate the results of post-fire research projects into instructional materials.

Keywords: Education; Ecology

Introduction

The fires that visited the Greater Yellowstone Area in 1988 illustrated dramatically how little most people knew

about the role of fire in western montane ecosystems. The extreme reaction by politicians, members of the news media and the general public was symptomatic of the lack of knowledge about the importance of fire in natural succession, and suggested that education about the role of fire in natural succession was sorely needed at all levels. The 1988 fires presented a unique opportunity to study the short- and long-term effects of large-scale fires in a relatively undisturbed environment and to develop educational materials based on research stimulated by the fires.

Introductory biology courses and courses in ecology and natural resources often have a component dealing with succession in natural ecosystems. A dramatic event can be very useful for introducing concepts of ecological succession, particularly for students in introductory science courses. For some, it may be their only exposure to ecology. The Yellowstone fires provided an opportunity to introduce concepts of natural succession into instructional materials for the following reasons:

1. The fires were a dramatic, highly publicized event.
2. Public reaction was strongly negative, with predictions of Yellowstone's "destruction".
3. A large area cherished by millions of people and managed for wilderness values was involved.
4. An unprecedented volume of research that can be used in educational programs is currently in progress.
5. Long-term change in Yellowstone provides a biological laboratory for explaining ecological succession to future generations.

Since 1959, I have accumulated an extensive photographic record of many areas in Yellowstone National Park. Following the fires, I realized that this record could be used effectively in demonstrating what Yellowstone was like before 1988 and how the fires have changed the face of the land.

Beginning in 1990, I developed a photographic record of the effects of the fires and early plant succession in selected areas of the Park. It was possible to photograph the same sites in 1990-1993 as had been photographed in 1959-1967. Approximately 50 comparative slide pairs have been developed to date, with others being added each year. The comparative slide pairs show vegetation before and after the fires in specific sites. The slide pairs are from all vegetative zones of the Park from sagebrush-grassland near Gardiner, Montana to alpine tundra on the eastern boundary. Many of the slide pairs are in the Lamar River drainage that was affected by the Clover-Mist fire.

I have used these photographic materials, as well as videotapes and written materials generated since the 1988 fires to develop instructional units for introductory biology classes, advanced classes in plant community ecology and natural resource management. Initially developed for a lecture format supplemented with slides and videotapes, the units have now been adapted for a discussion format in which students examine possible options in the use of fire in ecosystem management. Also, in the planning stage is a 3 week field course (outdoor laboratory) to be held in Yellowstone National Park that will include extensive field observations on the process of succession in areas of different burn intensity and in areas unaffected by fire in 1988, and the adaptations of vegetation to periodic fires. These instructional units have been very popular and are consistently the highest rated unit by students in introductory biology courses (written and verbal evaluations are conducted at the end of the courses). The dramatic and tangible example of natural change over time is very effective for stimulating the interest of students. Some students have inquired about the possibility of studying fire ecology in Yellowstone, suggesting that a field-oriented course, as mentioned above, might be a more effective way to introduce the role of fire in ecosystem function than the straight lecture or discussion format. Subject matter has been adapted for four different audiences to date: (1) introductory biology courses; (2) a plant community ecology course; (3) natural resources and wildlife management courses; (4) general audiences (Elderhostel groups, garden clubs, service organizations, forest fire wardens, retirement associations). Introductory Biology Courses

The general outline of presentation for an introductory biology course is presented.

Fire: A Force for Change and Regeneration in Natural Ecosystems

- I. The Greater Yellowstone Ecosystem
- II. Yellowstone National Park — Vegetation Zones
- III. The Yellowstone Fires — 1988

- A. State of Vegetation in 1988
- B. Weather
- C. The Fires
- D. The Aftermath. Political Firestorms. "Yellowstone in Ashes"
- IV. The Role of Fire in the Yellowstone System
 - A. Vegetation Types
 - B. Natural Succession
 - C. Fire History
 - D. Fire Management Policy: Trees Good, Fires Bad ???
- V. Regeneration
 - A. Beyond the Fires and "Blackened Forests"
 - B. Yellowstone Today and Tomorrow
- VI. Are Large-scale Fires in Yellowstone Inevitable?

The Greater Yellowstone Ecosystem is introduced first. The biotic and administrative complexity of this area is emphasized. The second section introduces the national park "idea" (management for wilderness values with a minimum of human intervention), followed by an introduction to the major vegetation zones within Yellowstone National Park. Management philosophy in national parks is briefly contrasted with those of surrounding areas (national forests, private land etc.). The third section deals with the 1988 fire season, beginning with the state of the vegetation (succession) in 1988, and emphasizing the increasing age of lodgepole pine forest. This is followed by a brief discussion of a "normal" summer weather pattern, which is then contrasted with the 1988 summer season of unusual drought. The 1988 fire season is then summarized, with emphasis on the origins of the fires, fire behavior and the progression of the fires during the summer. Finally, the initial reaction to the fires is presented, with contrasting accounts from the news media, politicians and NPS personnel.

The fourth section deals with the role of fire in Yellowstone. First, selected vegetation types are summarized, with emphasis on how specific vegetation assemblages are adapted to periodic fire (particularly sagebrush-grassland, Douglas fir, aspen and lodgepole pine) followed by historical patterns of plant succession. Next the history of fire in Yellowstone is summarized to emphasize the past and present role of fire in shaping the vegetation of Yellowstone. Finally, fire management policy is briefly summarized with a short discussion of Yellowstone's natural fire management policy and the controversy about and its effect on the extent and severity of the 1988 fires.

The fifth section deals with plant succession since 1988. Initial stages of "recovery" in burned areas are shown, and the differences in regeneration rates are related to burn intensity and soil conditions in specific areas. Slide pairs taken 23-35 years apart are shown for specific sites to demonstrate the nature of the vegetation

before and since the fires. Areas affected by fire and those untouched by fire are shown to demonstrate how dramatically fire can alter the composition of vegetation, compared with the slow pace of change in unburned areas. The role of fire in nutrient cycling in arid and semi-arid regions of western North America is contrasted with nutrient cycling in more mesic areas of eastern North America. Beginning in Fall, 1993, slide pairs taken at 3 year intervals will be used to demonstrate the rapidity of change in areas affected by the fires in 1988. The first set of 3 year interval slides from 23 sites (1990-1993) are now available for use. Finally, the probable course of succession in specific vegetation zones of the park are discussed briefly.

Section six deals with the question of whether fire is an inevitable force that will continue to shape the vegetation in Yellowstone, despite human intervention. This leads to a discussion of fire management policy. Yellowstone's new fire management plan will be a focus for discussion. The specific adaptations of major vegetation types to periodic fire suggests that fire has been and will continue to be a force for change in Yellowstone.

A Plant Community Ecology Class

For advanced courses such as plant community ecology, there is greater emphasis on plant succession dynamics, and more time is used to discuss specific plant communities in Yellowstone, as well as their response to periodic fire. Emphasis is on successional changes in lodgepole pine and spruce-fir forests and in aspen stands and how different fire behavior affects different vegetative complexes.

Natural Resources Management and Wildlife Management Courses

For courses in natural resource management and wildlife management, additional emphasis is given to policy issues in management of large wilderness areas and in differences in management policy in national parks, national forests and national wildlife refuges. Effect of the 1988 fires on management policy and on wildlife populations is discussed. For wildlife management students, there is additional opportunity to discuss changes in wildlife management policy in Yellowstone since 1972 and how wildlife populations have changed over time. Emphasis is on elk and bison populations.

General Audiences

For presentations to general audiences, the basic outline for introductory biology classes can be used, but emphasis is placed on the more dramatic aspects of the 1988 fires to focus attention on the role of fire in natural

environments. Comparative slide pairs can be very effective in demonstrating how dramatic the changes in Yellowstone have been since 1988. Greatest emphasis is given to the adaptations of plants to periodic fire and the necessity of fire for maintenance of particular plant communities. Information is presented in as non-technical a manner as possible, but this depends on the composition of the group being addressed.

Conclusion

As the many research projects initiated since the 1988 fires continue to add to our knowledge of the role of fire in Yellowstone, it is important to distill research results into general summaries and to integrate results from disparate disciplines into a coherent picture of how fire affects ecosystems in Yellowstone. Yellowstone personnel and researchers have a unique opportunity to study a natural phenomenon on a scale rarely witnessed in a large natural environment managed for wilderness values, and to translate results into a coherent picture of the role of fire in natural ecosystems for the general public and for generations of students who will be the future managers and stewards of our national parks and other public lands. I believe we have an obligation to provide the best possible information for future generations of Americans so that they will view natural fire in a more enlightened manner than in 1988.

Impact of 1988 Yellowstone Fires on Snowmelt Water Yields

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Abstract. An analytical method utilizing the percent of the drainage with canopy burn for each precipitation zone and habitat cover type is used to estimate runoff increases for drainages in and near Yellowstone National Park. This method suggests that most Yellowstone area streams will have a one percent increase in the April through July runoff for every three to four percent of the drainage area that has a canopy burn. Streamflow forecast equations developed for the pre-fire period on two watersheds having U.S. Geological Survey stream gage stations and significant canopy burn in the drainage were used to evaluate increases in water yield by comparing forecasted runoff with actual measured runoff. The two methods show the average increase in April through July runoff for the five years, 1989-1993 as result of 1988 fires to be 2.7 to 4.3 percent for the Yellowstone River at Corwin Springs and 5.9 to 7.6 percent for the Madison River near Grayling gaging stations. Results can be transferred to ungaged watersheds where predominantly lodgepole pine areas are burned, killed by insects, or logged providing the habitat cover types and average annual precipitation are known.

Keywords: Streamflow; Fires; Snowmelt; Watersheds; Precipitation.

Introduction

Historically the USGS (US Geological Survey) has maintained stream gaging stations, the SCS (Soil Conservation Service) has coordinated the snow survey program and forecasted potential streamflow for agricultural and other uses and NWS (National Weather Service) has collected climatological data and forecasted flood levels. Many other agencies and companies have assisted with the collection of basic data.

The extensive wild fires of 1988 added an unknown dimension of potential changes in streamflow volumes, and the timing and amount of peak flows. Downstream

water users and agencies responsible for disaster actions were concerned with these potential changes in runoff beginning in the 1989 runoff year.

To address the potential increase in yields, studies of forest canopy and snowpack (Codd 1959; Farnes 1971), relationships between annual precipitation and annual runoff (Farnes 1978), preliminary burned area survey (Despain et al. 1988), unpublished studies by the author on streamflow response to removal of forest canopy by logging, and numerous other reports and studies were used. The results of these projected changes in runoff were presented by Farnes and Hartman (1989). This paper suggests that these projections be compared to actual runoff after a few years of records are available to determine if this is a sufficiently accurate analytical method to determine water yield changes resulting from alteration of the forest canopy whether by fire, insects or logging.

Study Area

The largest impact of the 1988 fires in and near Yellowstone National Park (YNP) was in the Yellowstone River Drainage, Madison River, and Snake River drainages. Evaluations suggest the water yield changes in these drainages would be more extensive than other drainages in and near YNP. Burned areas north of YNP but in the Yellowstone River drainage that flow into the Park were included in these studies. In the Madison River drainage, approximately 1460 ha of burn west of YNP but in the drainage above Grayling was included.

Methods and Results

Two methods were used to evaluate the extent of runoff modification due to the 1988 fires: an analytical procedure and a forecast procedure. The analytical

procedure related the extent and kind of forest modification to changes in effective snow and precipitation interception which in turn is related to spring and summer runoff.

The forecast procedure involves developing a snowmelt runoff forecast equation for the pre-fire period using antecedent fall soil moisture, winter snowpack and spring precipitation regressed against snowmelt runoff.

The forecast equation was used to estimate the post fire snowmelt runoff, assuming no fire. The measured runoff includes fire. The difference is attributed to changes in runoff resulting from the 1988 fires. As more years of post fire records become available, a more accurate assessment of long-term runoff change.

In some situations, it is possible to use a double-mass analysis between adjacent drainages to assess runoff changes but this method has limited usefulness in evaluating the effects of 1988 Yellowstone fires as nearly all adjacent drainages were affected to some extent by the fires.

Analytical Procedure

The analytical procedure developed by Farnes and Hartman (1989) requires accurate assessment of precipitation patterns, and location, size and type of forest canopy alteration. This method implies that reduced interception of snow and rain in predominantly lodgepole pine forests resulting from timber removal allows more snow and rain to reach the soil surface which is then transformed into increased runoff. Preliminary figures of burn areas available in the winter of 1988 and spring of 1989 were generally for perimeter of burn areas. This resulted in larger canopy burn areas used in the 1989 Farnes and Hartman paper than was obtained after more detailed studies (Despain et al. 1989). Current areas of canopy and mixed canopy burn, by drainage, by average annual precipitation zones was obtained from Yellowstone National Park Geographic Information System (GIS). To obtain an estimate of canopy burn, we assumed that one-half of the mixed canopy burn area was canopy burn and that the majority of canopy burn was in mature lodgepole pine. From Farnes and Romme (1993), the Snow Water Equivalent (SWE) under mature lodgepole pine cover type varies from about 68% for LP1.5 to 78% for LP3 (Despain, 1990) of SWE in open areas. For this study, an average value of 73% of open area SWE was used to represent the average in canopy burn areas for Yellowstone watersheds. This would represent an increase of 37% (100 divided by 73 minus 1) in SWE after a canopy burn compared to SWE in that area prior to the burn. The increase in runoff for this SWE increase was then calculated using Farnes (1971 or 1978). SWE for open locations in the study area was estimated from Figure 1 which was derived from 1961-90 data from snow courses, SNOTEL sites (Snow Survey Telemetry), NWS climato-

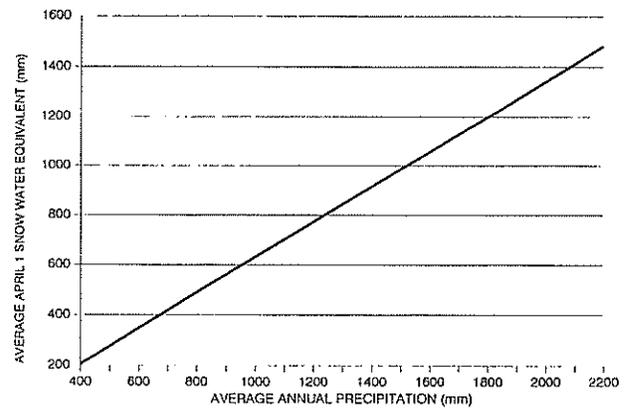


Figure 1. Relationship between April 1 snow water equivalent and average annual precipitation.

logical stations and the average annual precipitation map developed by the author.

The average April through June precipitation for 21 stations in and near the study area averaged 25% of the average annual precipitation. Previous studies reported in Farnes and Hartman (1989) indicate approximately 80% of the rain falls through the canopy. The additional runoff generated from the additional rainfall reaching the ground in a burned area was then calculated using the same procedures as for SWE increases as reported in Farnes and Hartman (1989).

Using all of the above relationships, the increased yield for each precipitation zone in the Yellowstone area was developed (Figure 2). Utilizing values from Figure 2 and GIS information, the increase in April through July runoff can be estimated for the area burned in each precipitation zone and the runoff accumulated for the various drainages. Results for nine drainages are shown in Table 1.

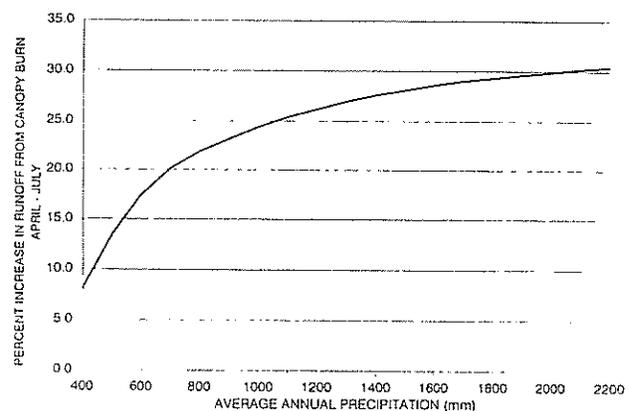


Figure 2. Increase in April-July runoff from canopy burn for various levels of annual precipitation.

Table 1. Estimated Increase in April Through July Runoff.

Drainage	Drainage Area ha 10 ³	Canopy Burn ha 10 ³	Canopy Burn %	Runoff Incr. m ³ 10 ⁶	61-90 Avg Runoff. m ³ 10 ⁶	Est. Runoff Incr %
Yellowstone River at Lake Outlet	259	36	13.9	42	1230	3.4
Yellowstone River excluding Lake Outlet	419	86	20.5	80	1637	4.9
Yellowstone River at Corwin Springs	678	122	18.0	122	2867	4.3
Gallatin River in YNP	36	4	11.1	6	174	3.4
Gallatin River near Gallatin Gateway	214	4	1.9	6	809	0.7
Madison River in YNP	175	68	38.9	71	482	14.7
Madison River near Grayling	234	69	29.5	74	977	7.6
Henry's Snake in YNP	80	6	7.5	17	665	2.6
Snake River at Flagg Ranch	126	24	19.0	46	806	5.7

Forecast Procedure

The Soil Conservation Service Snow Survey office in Bozeman, Montana has used a spring runoff (April-July) forecast equation composed of three variables: a soil moisture surrogate (November-January runoff), a spring precipitation (April-June) variable, and a winter snowpack (April 1 SWE) variable. The weight given to each variable and each station is determined by multiple regression analysis (Schermerhorn and Barton, 1968). Forecasts have been developed for the Yellowstone River at Corwin Springs and Madison River near Grayling stream gaging stations.

An April through July runoff forecast equation was generated for the Yellowstone River at Corwin Springs for 1961-88 with the assistance of Roy Ewing of Research Division, YNP. The procedure uses the November through January runoff at Corwin Springs as surrogate index of the soil moisture under the snowpack, April 1 SWE weighted for seven snow pillow locations, and April through June precipitation weighted for six locations in or near the drainage. None of the snow pillows or climatological stations were significantly altered by the fires. This equation has an R² of 0.952 and standard error that is 5.58% of the average 1961-90 April - July runoff.

Using this equation to forecast the runoff since the 1988 fires shows that the April - July actual runoff has averaged 2.7% greater than forecast for the five years 1989-93. There have been some events in the past five years such as the carryover effects of the extreme dryness

from 1988 into the 1989 water year and El Nino effects that would suggest a longer period of evaluation might be necessary to arrive at a more accurate representation of the long term increase in runoff resulting from the 1988 fires. All of the years after the fires have been within the extremes for the 1961-88 period as shown in Table 2.

Comparison of forecasts and runoff for post fire years for Yellowstone River at Corwin Springs is shown in Table 2.

An April through July runoff forecast equation was generated for the Madison River near Grayling for 1968-88 with the assistance of the Soil Conservation Service. The procedure uses the November through January runoff near Grayling as the surrogate soil moisture variable,

Table 2. Yellowstone River at Corwin Springs, April through July Streamflow, m³ x 10⁶.

Water Year	Forecast Runoff	Actual Runoff	Diff.	Percent Diff.*
89	2097	1907	- 190	- 9.5
90	1826	1876	+ 50	+ 2.5
91	1937	2091	+ 154	+ 7.7
92	1961	1727	- 234	- 11.8
93	1801	2286	+ 485	+ 24.4
Average 89-93	1924	1977	+ 53	+ 2.7

Lowest actual April-July runoff in 1961-93 period was 1121 m³x10⁶ in 1977 and highest was 2836 m³x10⁶ in 1974. Average April-July runoff is 81 percent of the average annual flow.

* Difference divided by 1961-90 Average Annual Runoff (1991) as used by SCS for calculating forecast error.

April 1 SWE weighted for five snow courses and snow pillow locations and April through June precipitation weighted for six locations. This equation has an R^2 of 0.948 and standard error that is 6.05% of the 1961-90 average April - July runoff.

Using this equation to forecast the runoff since the 1988 fires shows that the average actual runoff since the 1988 fires has been 5.9% greater than the forecast for the five years 1989-93. With the exception of 1989, each year's actual runoff has been greater than the forecast. As explained in the Yellowstone River discussion, a longer evaluation period might be desirable. The lowest and highest years in the 1961-88 period are shown in Table 3.

Comparison of forecast and measured runoff for post fire years for Madison River near Grayling is shown in Table 3.

The analytical and forecast procedures suggest the increase in spring runoff resulting from the 1988 fires is between 2.7 and 4.3 percent for the Yellowstone River at Corwin Springs and 5.9 to 7.6 percent for the Madison River near Grayling. As additional years data become available, the actual long-term increase in runoff should become more defined.

Management Implications

Until regenerated trees become high enough to effect snow and rain interception, additional runoff will be generated as a result of the 1988 fires. The magnitude of this increase is a function of the percent of the drainage where the canopy burned, and the precipitation and snowfall patterns over the entire drainage. These impacts will have some affect on downstream water users and reservoir operators. It appears the increase resulting from the fires may need to be addressed by the annual reservoir

operations on the Madison River. However, the magnitude of these changes suggests that impacts will be less than the normal variation in streamflow that occurs from annual variations related to the winter snowpack and spring precipitation and may not be noticed on streams not having reservoirs.

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Table 3. Madison River near Grayling April Through July Streamflow, $m^3 \times 10^5$.

Water Year	Forecast Runoff	Actual Runoff	Diff.	Percent Diff.*
89	4601	4367	- 234	- 5.0
90	3577	3861	+ 284	+ 6.1
91	4108	4305	+ 197	+ 4.2
92	3392	3577	+ 185	+ 3.9
93	4934	5884	+ 950	+ 20.3
Average 89-93	4122	4399	+ 277	+ 5.9

Lowest actual April-July runoff in 1961-93 period was $2788 m^3 \times 10^5$ in 1977 and the highest was $6390 m^3 \times 10^5$ in 1971. Average April-July runoff is 63 percent of average annual flow.

Difference divided by 1961-90 Average Annual Runoff (4688) as used by SCS for calculating forecast error.

Effect of Fire on Streamflow and Sediment Transport Shoshone National Forest, Wyoming

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Abstract. During late summer 1988, the Clover-Mist Wild-fire burned the majority of the 66.8-km² Jones Creek watershed. The adjacent 49.5-km² Crow Creek watershed, which is similar in many respects, was left with all but two percent unburned. Both watersheds are in the North Absaroka Wilderness on the upper North Fork Shoshone River drainage on lands administered by the USDA Forest Service. Following the fire, an interagency study was established to monitor the two watersheds. Cooperating agencies are the Shoshone National Forest, Rocky Mountain Forest and Range Experiment Station, U.S. Geological Survey, and the Wyoming Department of Environmental Quality.

Preliminary data analysis provides circumstantial evidence the fire has increased both streamflow quantity and sediment export with little effect on peak discharge or summer storm response.

Keywords: Hydrology; Sediment

Introduction

During summer 1988, the Clover-Mist fire burned 48,000 ha (118,800 ac) of the Shoshone National Forest (SNF), Wyoming (Mills 1989). Within the burn area is Jones Creek, a 6680-ha (16,510-ac) watershed in the upper North Fork of the Shoshone River drainage, one of the most severely burned areas. Adjacent to Jones Creek is Crow Creek, a 4950-ha (12,220-ac) watershed, where only two percent of the ridgetop area of the watershed was burned. Both watersheds are in the North Absaroka Wilderness, located approximately 80 km (50 mi.) west of Cody, Wyoming.

An interagency watershed monitoring study was implemented to compare the response of burned Jones Creek with unburned Crow Creek. Cooperating agencies include the SNF, U.S. Geological Survey (USGS), Wyoming Department of Environmental Quality (WDEQ),

and the Rocky Mountain Forest and Range Experiment Station (RMS). After the fire in 1988, a site was selected on each watershed to monitor streamflow, suspended sediment, and precipitation. Instruments were installed and the USGS began monitoring streamflow and sediment in March 1989. Precipitation gages were not installed until Spring 1990.

The fire essentially denuded the entire Jones Creek drainage. Assessments made by the SNF rehabilitation team indicated Jones Creek was the most severely burned watershed in the 48,000-ha burn area (Shoshone National Forest 1988). Hydrophobic soil, 2.5-10 cm deep, developed. There was also a heavy fish kill in Jones Creek, possibly due to intense heating of the water and a drastic, instantaneous change in water quality. No pre-fire water quality or streamflow data from either watershed existed; however, the apparent physical similarities of the watersheds (Figure 1), in every respect except current cover (Falconer et al. 1993), made them an excellent choice for comparing response from a burned and unburned ecosystem. Both watersheds are mostly underlined by tertiary material, primarily the Langford formation (Figure 1a). Slope steepness is quite similar (Figure 1b) with 70 percent of all slopes on each watershed ranging from 16 to 60 percent grade. The distribution of aspect facets (Figure 1c) are also quite similar. The watersheds drain to the east and are dominated by north and south facing slopes. Elevation zones are also comparable (Figure 1d). Except for size, the burned and unburned watersheds are physically quite similar.

Pre-fire vegetation surveys were minimal on the two watersheds but conditions were re-constructed using satellite imagery (Falconer et al. 1993). The dominant habitat type on both watersheds was *Abies lasiocarpa* (Figure 2) and it occupied 80 percent of Jones Creek and 86 percent of Crow Creek. The distribution of other habitat types was equally similar.

The largest difference between the watersheds is exhibited in the current vegetative cover (Figure 2a).

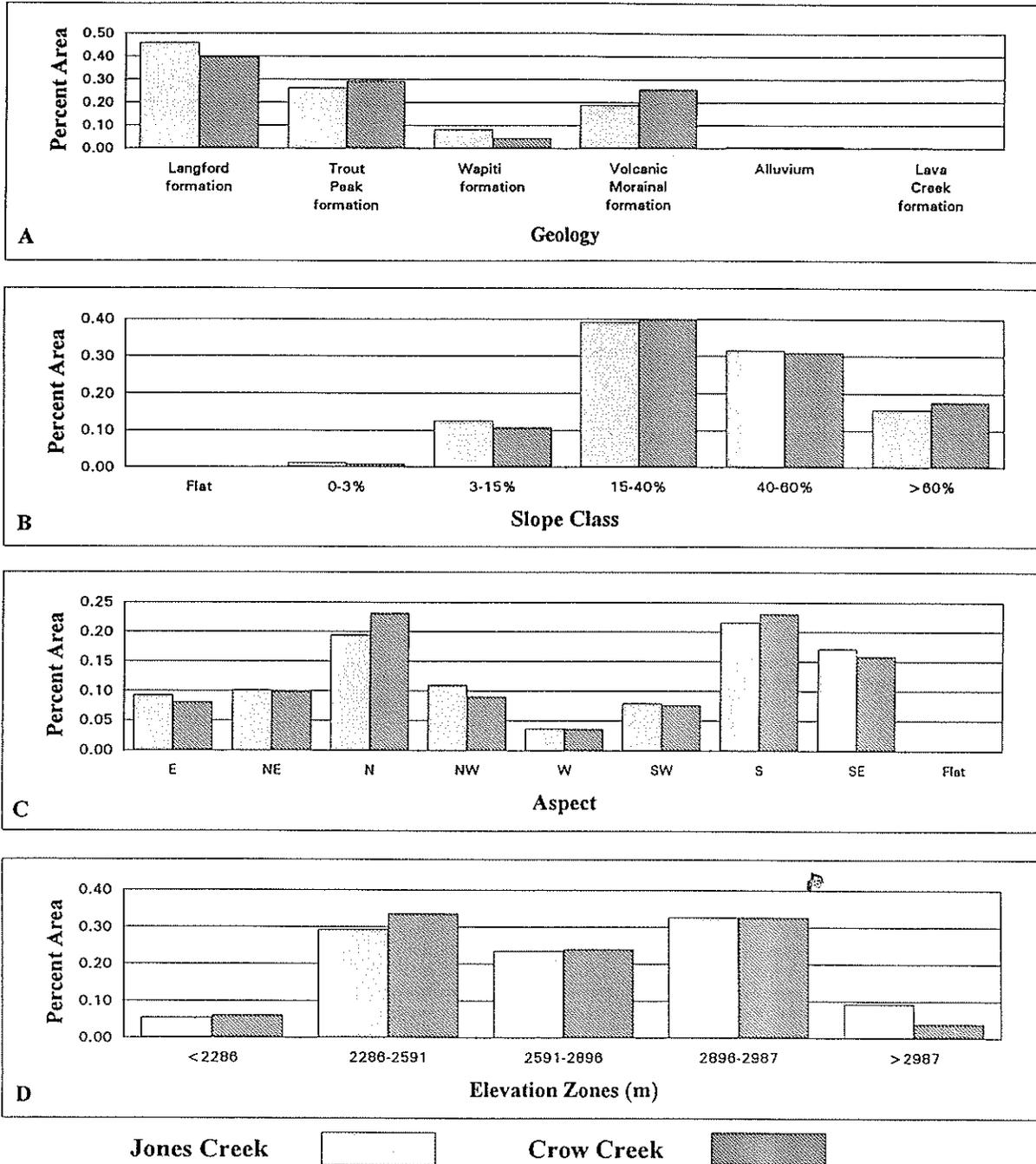


Figure 1. Physical characteristics of Jones Creek and Crow Creek (from Falconer et al. 1993).

Fifty percent of Jones Creek is in a burned state compared to less than 2 percent of Crow Creek. Over 61 percent of Crow Creek is currently forested as compared to only 15 percent of Jones Creek. In comparative terms, the net change in vegetative cover on Jones Creek, relative to Crow Creek, is almost 50 percent of Jones Creek is in a completely denuded state, as a result of the fire.

Because the two watersheds apparently were so similar (forest cover, geology, relief, aspect, slope, etc.), streamflow and sediment transport may also have been

similar and differences between the watersheds after the fire might be an index to the effect of the fire. In the absence of a pre-fire calibration, cause and effect cannot be attributed to any observed differences. However, the vast body of knowledge available on watershed response to vegetative disturbance provides a basis for hypothesizing what might be the "expected" response and then speculating if it was realized based on observed differences (Troendle and Leaf 1980; Bosch and Hewlett 1982; Helvey 1980; Potts 1983; Troendle and King 1985;

Bevenger and Troendle 1987; King 1989; Troendle and Olsen 1994).

Methods

Objectives

The objectives of this study are to 1.) compare the two drainages in terms of what might be expected to be the normal, undisturbed, hydrologic response (as indexed by Crow Creek); 2.) anticipate or hypothesize what change in the norm might occur following the fire based on previous disturbance effects elsewhere; and 3.) evaluate whether the hydrologic differences (if they exist) between Crow and Jones Creeks are a reasonable expression of the expected fire effect. This report focuses primarily on streamflow but one water quality parameter, sediment, is also considered.

The USGS collected streamflow and sediment data at both watersheds from mid-March 1989 through late September 1992. Continuous streamflow discharge measurements are compiled using a graphic recorder driven by pressure-sensing manometer.

Suspended sediment is collected daily with a Manning automatic sampler, and depending on the time of year, each sample represents a composite of either four or six sub-samples collected every 6 or 12 hours. Instantaneous suspended sediment samples are also collected during each of the twelve or thirteen site visits per year using a fixed cross-section and collecting a depth integrated

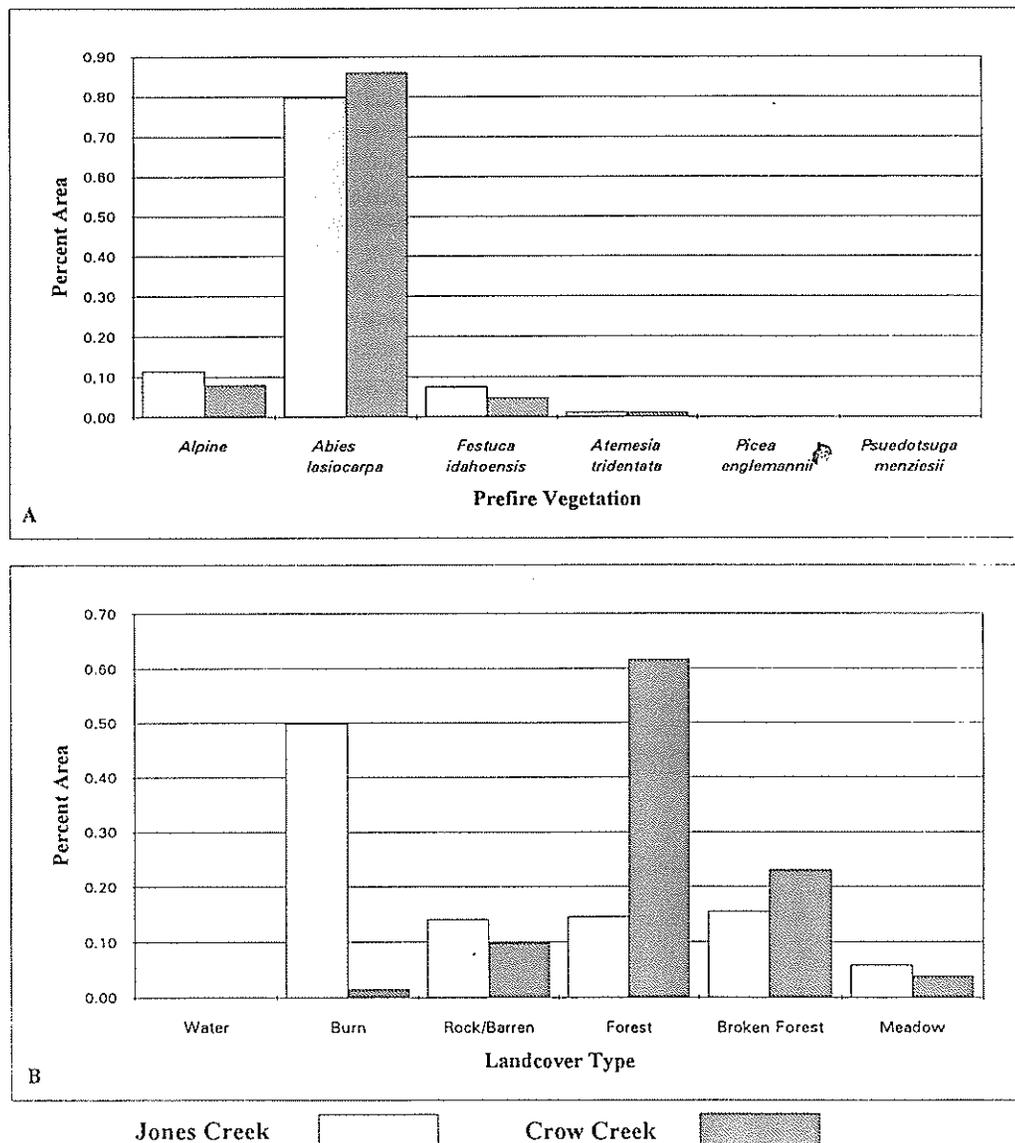


Figure 2. Relative portion of each watershed in various habitat types (a) prior to the fire and current cover types (b) following the fire on Jones Creek (from Falconer et al. 1993).

sample. Annual data and methods of collection are published in the USGS Water-Data Reports (See stations 06279790 {Jones} and 06279795 {Crow} in Druse et al. 1990, 1991, 1992, 1993).

Precipitation is being monitored using a single weighing-bucket recording gage located at the mouth of each watershed.

Streamflow

Numerous experiments world-wide have demonstrated that forest disturbance (timber harvest, insect damage, fire, etc.) can result in increases in streamflow (Bosch and Hewlett 1982; Troendle 1983; King 1989). Studies in the snow zone of central Colorado, an area climatically and vegetationally representative of the Absarokas (see hydrologic regions, Troendle and Leaf 1980), have demonstrated streamflow may increase after timber harvest by as much as 30-40 percent (40-60 mm depth of water on a unit area basis) when 30-40 percent of the vegetation has been harvested (Troendle and King 1985, 1987; and Troendle and Olsen 1994). Generally the increase in flow occurs early in the runoff season, prior to the peak, with little effect on late season flows or summer storm response. Average annual peak flows increase 20-50 percent following harvest. The largest increases in streamflow discharge occur in the wettest years. In contrast the largest increases in peak flows occur in the

driest years (Troendle and King 1987; Troendle and Olsen 1994). Annually, peak flows are snow melt driven; rainfall peaks are quite small, and storm response represents only 3 percent of summer storm precipitation. This minimal rainfall response does not appear to be influenced by forest disturbance (Bevenger and Troendle 1987).

Annual hydrographs for the four years of flow from Jones and Crow Creeks are presented in Figure 3. Daily flow is expressed in liters per second per square kilometer in order to compensate for area differences. Jones Creek has greater unit-area flow than Crow Creek with the difference occurring early in the runoff period. As with those following timber harvest, peaks appear to occur at the same time or slightly earlier at Jones Creek, and the largest relative difference appears to be in the low flow year (1992). Assuming the unit area response of the two watersheds was similar prior to the fire, the differences in response that now exist, are distributed as might be expected based on documented responses to other forms of disturbance.

Seasonal water yield (April - October) is estimated by integrating the daily flow values over time and is expressed as a depth of water over the entire watershed. Jones Creek yielded an average of 138 mm more water per year than Crow Creek (table 1). Again, 1989-1992 were not particularly wet years, yet flow from Jones Creek has averaged 540 mm while it was 402 mm from Crow Creek.

Mean Daily Discharge at Jones (burned) and Crow (unburned) Creeks for the Runoff Periods (1989 - 92)

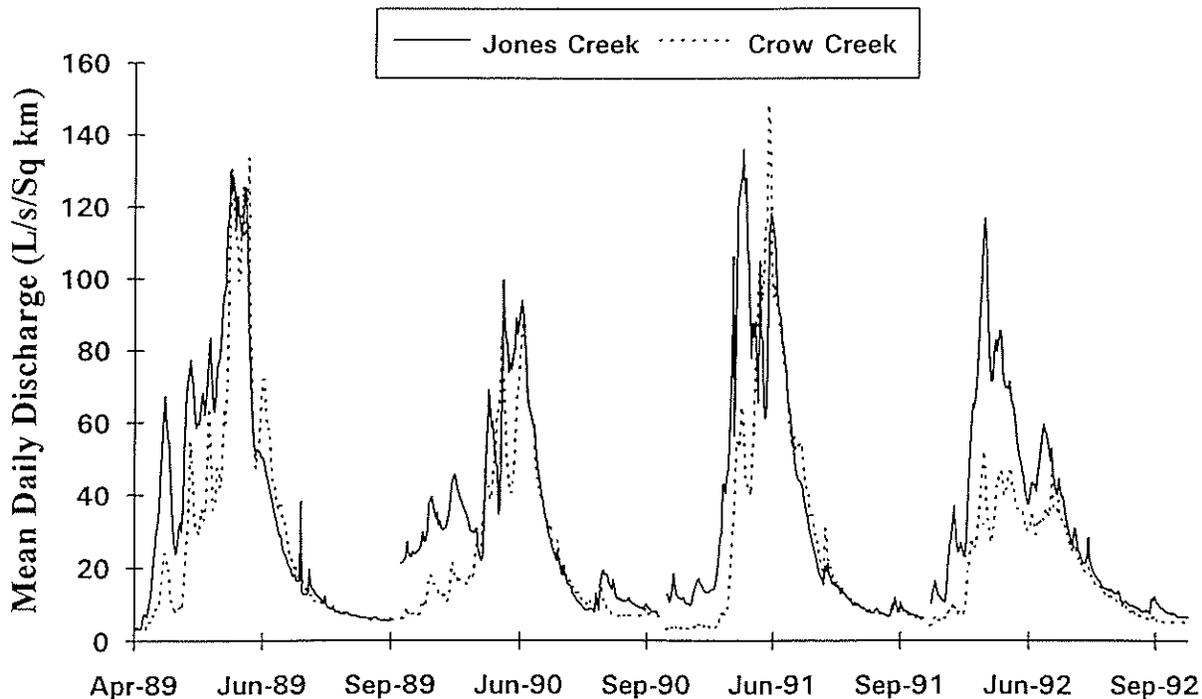


Figure 3. Annual hydrographs representing Jones (burned) and Crow (unburned) watersheds, 1989-92.

Table 1. Seasonal Water Yield from Jones and Crow Creeks. (Expressed as depth of water over entire watershed: Jones Creek 66.8 km², Crow Creek 49.5 km²)

Year	Seasonal Yield		Difference
	Jones Creek mm	Crow Creek mm	(Jones - Crow) mm
1989	596	475	121
1990	497	370	12
1991	549	445	104
1992	517	316	201
Average	540	402	138

As a comparison, the increase in seasonal water yield that occurred following partial clearcutting on Fool Creek and Deadhorse Creeks, Fraser Experimental Forest, Fraser, Colorado, varied from an average of 70 to 99 mm after 35-40 percent of the forest cover was removed (Troendle and King 1987). The 138 mm difference between Crow and Jones Creeks is consistent with, but proportionally greater than, those increases. The effective change in biomass on Jones Creek relative to Crow Creek was a 50-60 percent reduction (Figure 2a and 2b).

Perhaps of more concern than the change in seasonal water yield is the effect on peak flows, especially stormflows. Typical of high elevation and high latitude watersheds, the peak annual discharge on Jones and Crow Creeks is snowmelt driven (Jarrett 1993). However, a number of summer storms did occur (e.g. Figure 2); response to rainfall events was evaluated to determine differences between the burned and unburned watersheds.

Storm precipitation was indexed using data from the precipitation gages located at each streamgage. In total, from 1990-92, there were eight simple storms that occurred on both watersheds and that produced a separable stormflow response for which all data were available. The hydrograph for the storm event was separated, using the quickflow method of Hewlett and Hibbert (1967) with a 0.01 rather than 0.05 csm separation line, into quickflow and baseflow in order to index basin response. The percentage of precipitation returned as quickflow (stormflow) was calculated by dividing the volume of quickflow by the estimated precipitation. Similar analyses on watersheds in Wyoming and Colorado indicated three percent of individual summer rainfall events was typically returned as stormflow or quickflow (Bevenger and Troendle 1987, Troendle and King 1987). Analysis indicates that although summer storm response on Jones Creek is slightly higher than Crow Creek, the maximum observed storm response on Jones Creek was less than 3.5 percent of the precipitation (Figure 4) and this falls within the range of response observed on Crow Creek as well as on other undisturbed watersheds in this hydrologic region (Troendle and Leaf 1980). Individual rainfall events used in the analyses varied from a few millimeters to over 25 mm of water.

Peak annual discharge currently does not appear to differ between the two watersheds (Figure 5). The data indicated on Figure 5 includes the four annual snow-driven peaks as well as the summer storms used in the earlier analysis. The 1:1 line indicates equality between the watersheds and, with exception of the 1992 annual peak, all events fall very close to it. The 1992 peak flow

Percent Response at Jones Creek (burned) vs Percent Response at Crow Creek (unburned)

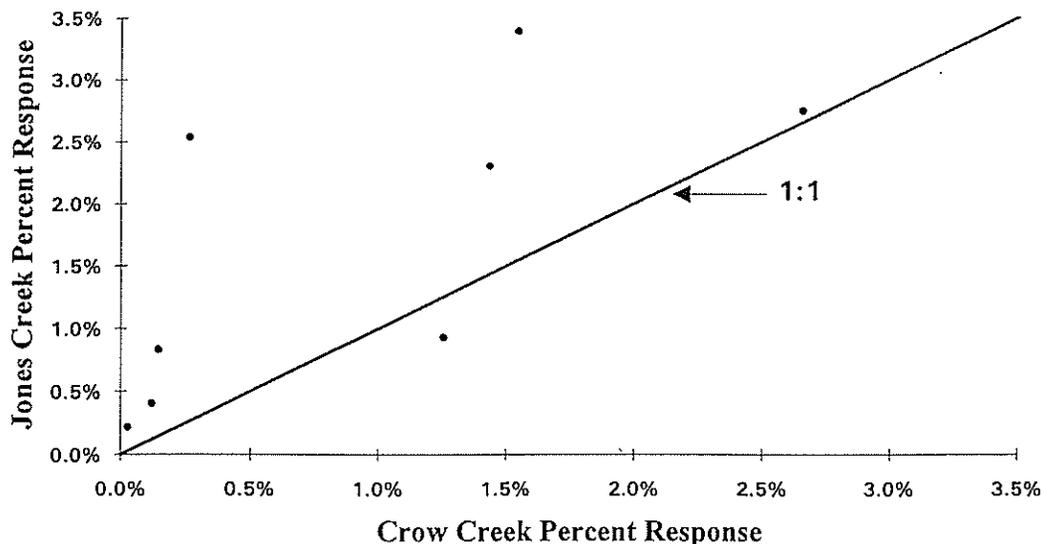


Figure 4. Summer storm response (percent of storm precipitation returned as stormflow) for Jones Creek plotted over Crow Creek. The solid 1:1 line implies equality.

Storm and Seasonal Peak Flows for Jones (burned) and Crow (unburned) Creeks (1989 - 92)

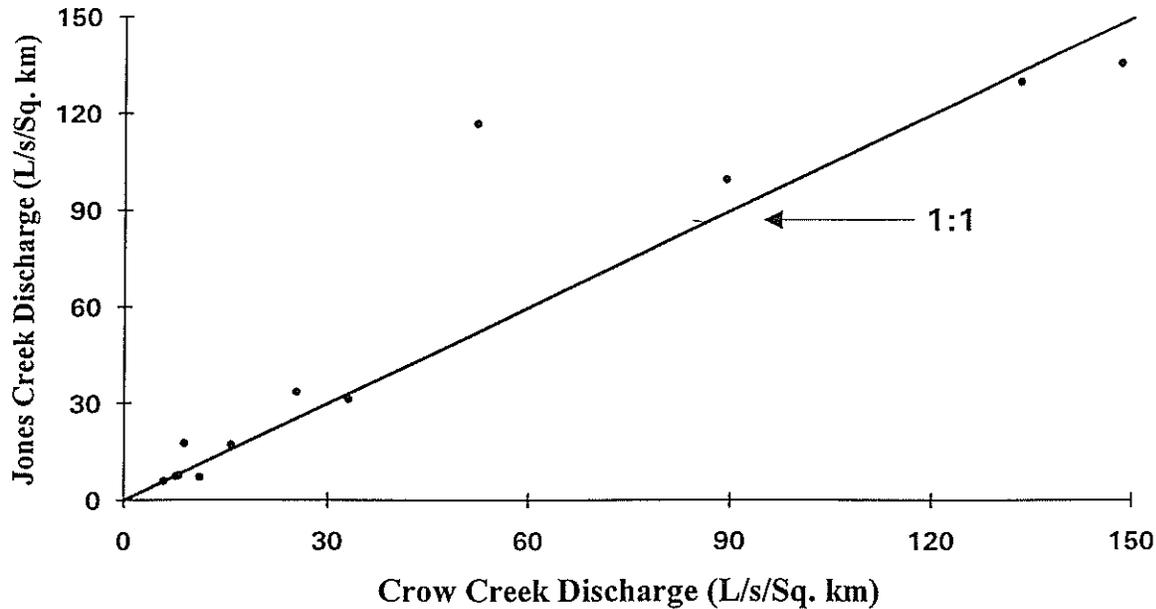


Figure 5. Storm and peak flow response from Jones Creek over Crow Creek. The four largest values represent the annual peak flows from both watersheds; the eight smaller values represent the summer storm responses (depicted in Figure 4).

from Jones Creek appears elevated (unless Crow Creek is low for some reason) but it should be noted that a significant portion of the seasonal flow record (including the actual peak measurement) for Crow Creek was lost and had to be estimated using data from gages elsewhere (Druse et al 1993). It can also be noted that the peaks resulting from summer rainfall events are quite small relative to the snow melt peak.

The effect of disturbance on the flow regime can also be evaluated by comparing flow-frequency or flow-duration curves. Again, to provide a base for comparison, 40 percent of the Fool Creek watershed was clearcut, and flow-frequency curves for the expected flow (based on pretreatment calibration) were compared with the post-harvest observed flow (Troendle and Olsen 1994). The largest (or least frequent) flows from Fool Creek (Figure 6) were not affected by timber harvest, but the frequency of lesser, mid- to high-level flows, or those in the "bankfull" range nearly doubled. In comparing the flow-duration curves from Jones and Crow Creeks (Figure 7), there is also a greater frequency of occurrence mid- to high-level flows on Jones Creek with little effect on the highest flows. Again, the difference in flow-duration curves for Jones and Crow Creeks (Figure 7) is consistent with observed differences after other forms of forest disturbance.

Suspended Sediment

Suspended sediment production from Jones Creek has also been substantially greater than Crow Creek in terms of both concentration (Figure 8) and total suspended load (Figure 9). Most of the total annual suspended load (flow weighted aggregate) is exported by high flows during snowmelt; however, the highest concentrations, which are perhaps the greatest potential threat to biota, are associated with the individual summer storm events. In the four years since the fire, the highest suspended-sediment concentration occurred during a storm in late July 1989 when an average $3630 \text{ Mg.l}^{-1} \text{ day}^{-1}$ (Figure 8) occurred for one day. Young (in press) noted significant relocation of large woody debris during 1990-91, which may have made available large amounts of sediment for later movement. Bozek and Young (in press) noted a significant fish kill and habitat change associated with the 16 August 1990 storm and the attendant sediment export.

Sediment transport is a function of flow and availability. Although the native soils are quite erodible and background sediment concentrations and load are quite high (i.e., Crow Creek, Figure 8 and 9), the sediment export from Jones Creek increased considerably due to both greater availability and greater flow. The average sediment concentration from all samples (four years of record) is 59 mg/L for Jones and 20.8 mg/L for Crow

Flow Frequency Curve for Fool Creek (1957-91) Comparing the Mean Duration Predicted from E. St. Louis Creek vs the Actual Mean

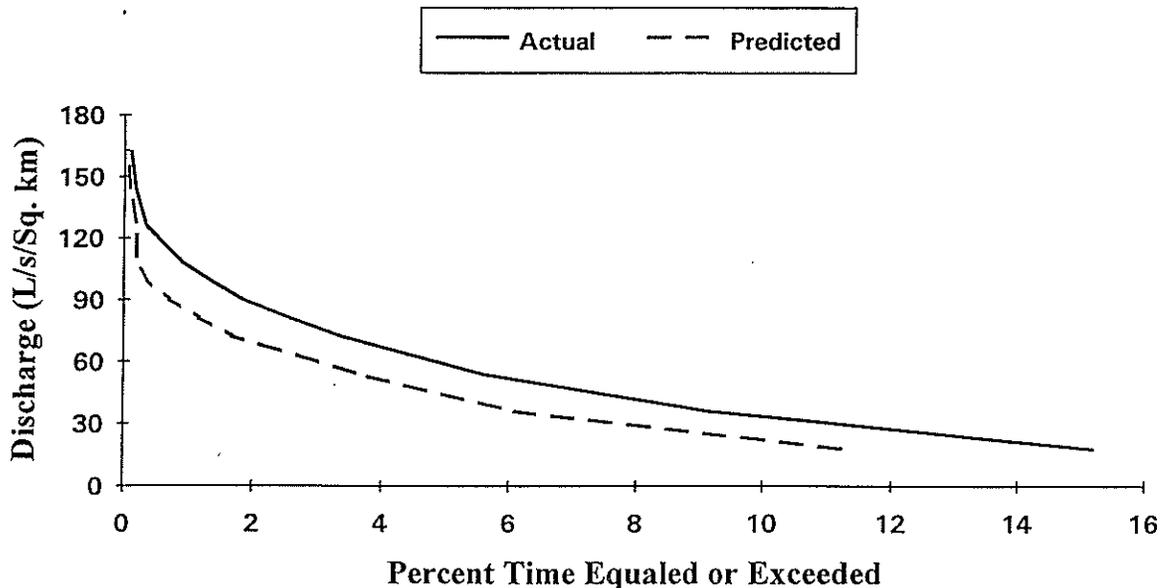


Figure 6. Flow-frequency curve for the higher levels of flow from Fool Creek Watershed following timber harvest (actual) compared with expected frequency (predicted) estimated from pre-harvest calibration with a control watershed (from Troendle and Olsen 1994).

Flow Frequency Curves for Jones (burned) and Crow (unburned) Creeks Based on Daily Flow Values (1989 - 92)

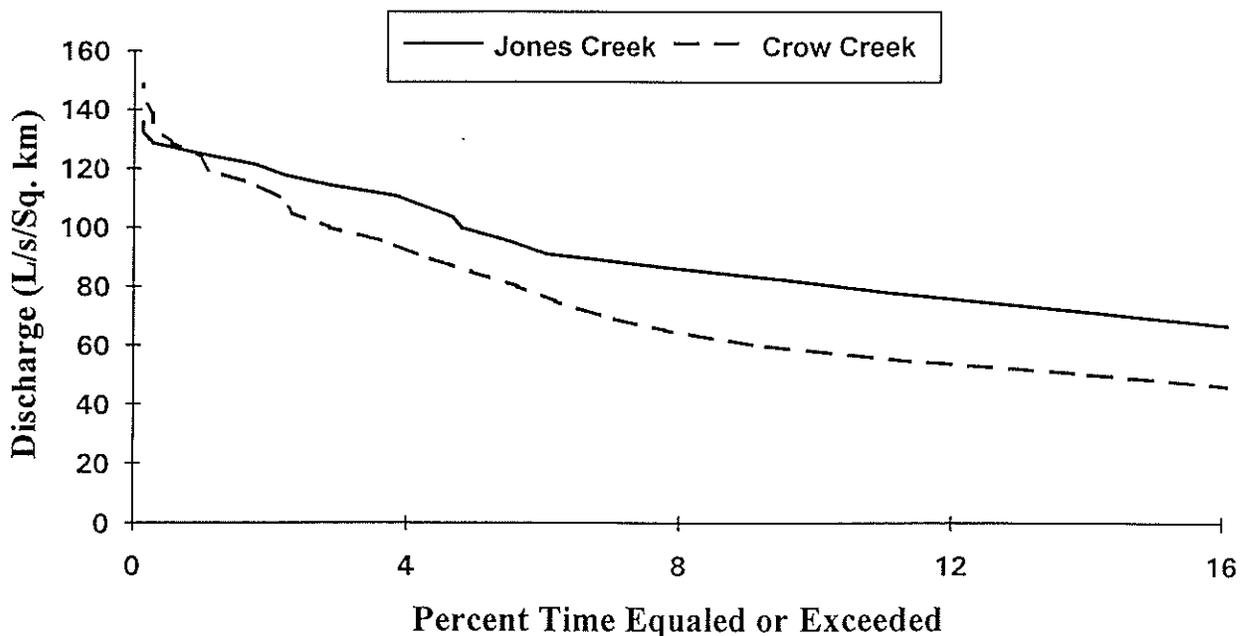


Figure 7. Flow-frequency curve for higher levels of flow from Jones (burned) and Crow (unburned) Creeks. Data used represent highest flows during 1989-92 seasonal runoff record.

Suspended Sediment Concentrations at Jones (burned) and Crow (unburned) Creeks (1989)

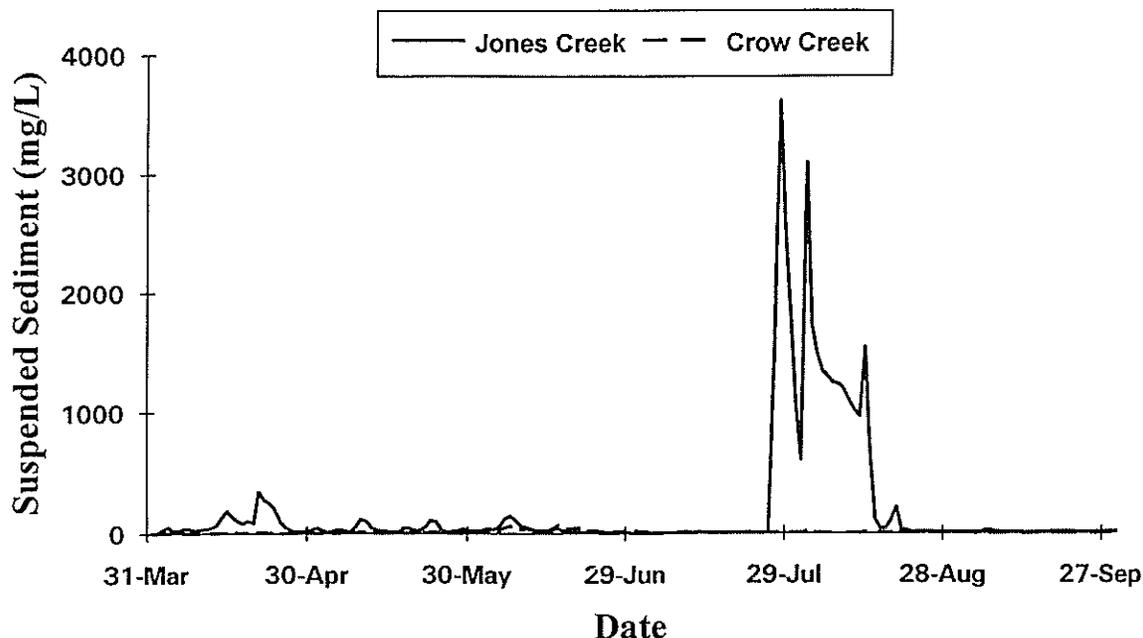


Figure 8. Suspended-sediment concentrations, for the 1989 runoff season, from Jones and Crow Creeks.

Suspended Sediment Load at Jones (burned) and Crow (unburned) Creeks (1989)

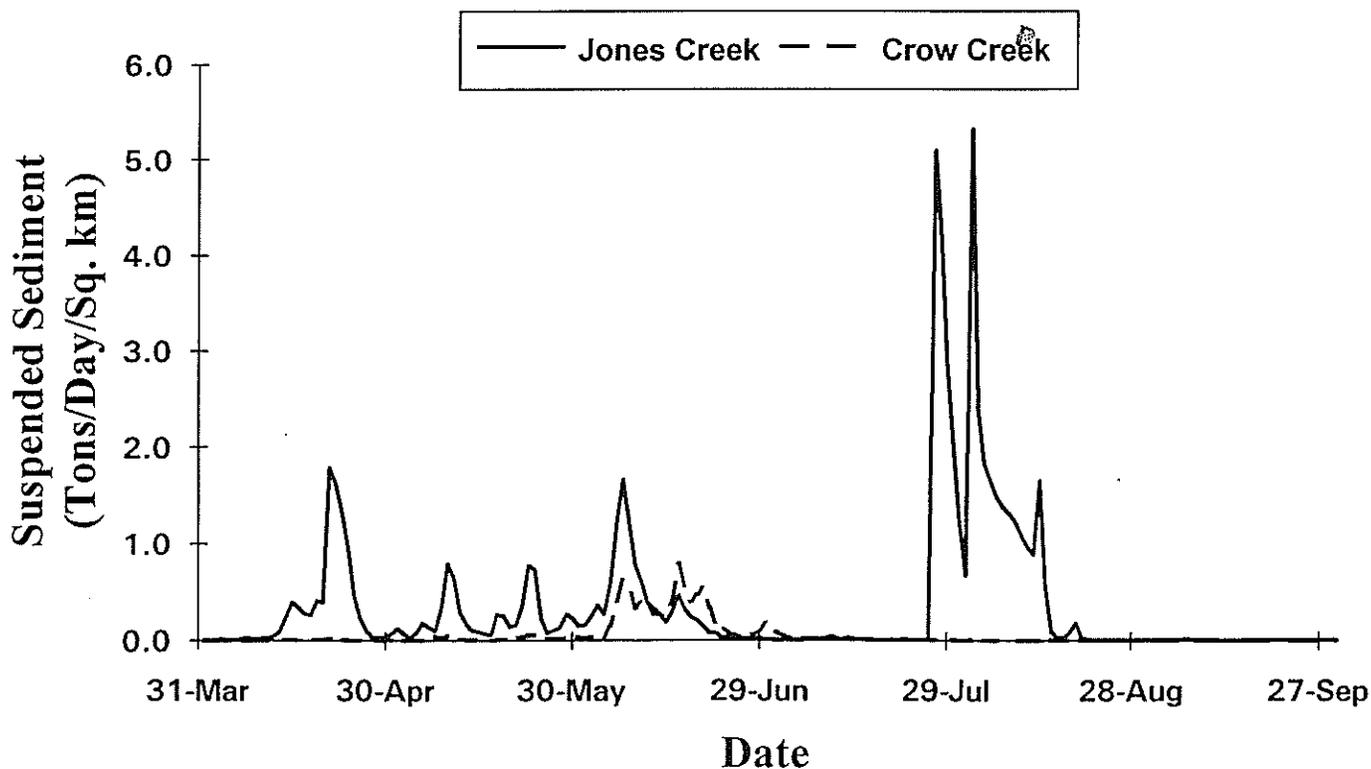


Figure 9. Suspended-sediment load (concentration x daily flow) from Jones and Crow Creeks, for 1989.

Creeks. These means are significantly different ($P=0.001$). The stormflow analysis did not indicate drastic differences in storm response between the watersheds, thus implying minimal pathway change. The data do not indicate the hillslopes have unraveled and delivered greater amounts of material to the riparian/channel environment. Some increased delivery is inevitable, but to date the storm response appears to be from near or within channel sources minimizing the opportunity for off-site delivery. The fire devastated the riparian vegetation, including both woody debris and root systems (Young 1994). As a result, alluvial material, already in place, may be more readily available because it is no longer stable. The material already in the bed and banks of the primary and secondary channel system might be a source of what is being moved.

For the four year period, an average load of 59 metric tons/km² was yielded from Jones Creek compared to only 13 tons/km² from Crow Creek (table 2).

Summary and Conclusions

The similarity between Jones and Crow Creeks facilitated a case study monitoring the effect of fire on watershed response. Although differences have been identified the lack of pre-fire information precludes any direct statistical assessment of cause and effect.

The effect of the fire on hydrologic response is easiest to address, at least qualitatively because the percent area burned, or vegetation destroyed, can be equated to other forest disturbance practices and differences compared. Water yield from Jones Creek averages 138 area mm more than Crow Creek and is a reasonable extrapolation of what would be expected to occur based on observations of hydrologic response to forest disturbance, given the climatic regime that occurred during the four years after the fire. The difference in flow volume between the watersheds occurs early in the run-off period, as would also be expected. In the absence of extreme rainfall events, or severely wet antecedent moisture conditions, observed storm response appears to have been minimally increased and this also is the expected response based on

past experience with timber harvest. Peak flows were not significantly greater on the burned watershed either.

Suspended sediment export from Jones Creek was significantly greater than Crow Creek with at least one event (16 August 1990) having been observed to be fatal to some portion of the fish population. Again, because storm response to rainfall input does not appear to have changed, the opportunity for increased erosion and introduction of new sediment to the channel system appears to have been minimal. Assuming revegetation is stabilizing the side slopes and extreme events causing surface rilling and mass failures do not occur; one can speculate that in the long run (10 - 20 - 30 years) the sediment export will balance out between Jones and Crow Creeks with little net difference between the two.

In total, the fire devastated the Jones Creek watershed, but the moderate climatic regime and storm events that followed the fire caused minimal and expected responses.

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Table 2. Seasonal Sediment Yield from Jones and Crow Creeks.

Year	Seasonal Yield		Difference (Jones - Crow)
	Jones Creek	Crow Creek	
Tonnes/sq km			
1989	65.62	9.66	55.96
1990	40.93	4.65	36.28
1991	67.73	23.56	44.17
1992	61.55	14.57	46.98
Average	58.95	13.11	45.84

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Consequences of Fire on Aquatic Nitrate and Phosphate Dynamics in Yellowstone National Park

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Abstract. Airborne remotely sensed data were collected and analyzed during and following the 1988 Greater Yellowstone Ecosystem (GYE) fires in order to characterize the fire front movements, burn intensities and various vegetative components of selected watersheds. Remotely sensed data were used to categorize the burn intensities as: severely burned, moderately burned, mixed burn, lightly burned, and unburned. Water samples were then collected in six streams, under various burn conditions, for the next five years. Those samples, collected twice a day, for the summer months following snow melt, were analyzed with a Dionex ion chromatograph in order to determine the chemical concentrations of nitrates (NO_3) and phosphates (PO_4) in the streams. Those nitrate and phosphate levels were compared to a reference stream (unburned) in order to determine the change in chemical concentrations under various burning conditions. Our results indicate that stream nitrate remains high, even after five years of ecosystem recovery. Nitrate levels, found in various burn conditions, ranged from 2.6 to 33 times greater than our reference, unburned stream concentrations. Phosphate concentrations exhibited similar conditions with levels 2.0 to 29 times greater than background levels. These results indicate that burn intensities regulate stream water nitrate and phosphate concentrations; that aquatic ecosystem alterations are of much longer duration than previously thought; and that remotely sensed data can be used effectively to predict burn intensities which relate to watershed chemical changes that will affect aquatic conditions.

Keywords: Remote sensing; Nitrate; Phosphate; Burn intensities; Water chemistry; Yellowstone National Park; Greater Yellowstone Ecosystem (GYE).

Introduction

The Greater Yellowstone Ecosystem (GYE) fires of 1988 provided a dramatic natural experiment of fire

impacts on both terrestrial and aquatic environments. Fires affect the biotic community by altering soil chemistry, mobilizing nutrients, removing the soil cover, and changing the stand composition of vegetative components. Streams and water bodies are also severely altered by the sudden influx (through runoff) of nutrients and debris during and following a fire. The application of ammonium phosphate fire retardants can also significantly alter the nutrient levels following fires. This issue was investigated and no retardant was in use in the Park near our sampled streams during the fire suppression activities (Despain 1995). Spencer and Hauer (1991), provided experimental evidence to support their hypothesis that increased phosphate concentrations in streams (monitored during a wildland fire in Montana) were the cumulative result of entrapment of smoke in watersheds. They theorized that the concentrations would decrease as the fire decreased and that phosphate levels would return to normal background levels in a short period of time (weeks to months). Their field analysis during and following the burn provided supporting evidence of their hypothesis. Riggan et al. (1985), has shown that the stream nitrate and phosphate concentrations measured after controlled burns in a Mediterranean ecosystem (chaparral) in Southern California exhibited increases for extended periods of time. Those authors theorized that concentrations may remain elevated for periods up to five years. Experiments conducted in Canadian pine forests (Cofer et al. 1988), and Brazilian grass/woodlands (Riggan et al. 1993) also support the conclusion that burn intensities and emission factors control nitrate loss and are a major long-term input to stream chemical composition changes. Those results have led us to hypothesize that nitrate and phosphate concentrations are tied more directly to the intensity of the burn and less directly to the vegetation being consumed during the fire.

In Yellowstone, remote sensing and water chemistry analysis were used to document pre- and post-fire aquatic system conditions. The objectives were to determine the

severity of burning condition on montaine forest watersheds utilizing remote sensing instrumentation and to determine the rate of nitrate and phosphate concentrations in downstream flows from watersheds experiencing various burn intensities. We hypothesize that nitrate and phosphate inputs from watersheds experiencing various burn intensities will exhibit short-term peaks (2-5 years) after fires. We expected that as regrowth occurs, nutrient-rich runoffs will diminish and subsequent inputs to streams will diminish. Therefore, following the wildfires of 1988, water sampling and chemistry analysis of six streams within Yellowstone National Park were performed in order to determine the effects of fire in Lodgepole pine (*Pinus contorta*) dominated, montaine forest ecosystems. Various burn intensities for the stream watershed areas were determined from the airborne Daedalus multispectral Thematic Mapper Simulator (TMS) scanner data and used to quantify nitrate and phosphate changes. We provide evidence that nutrient pulse trajectories vary with burn intensity.

Methodology

Remote Sensing Collection and Analysis

Various burn intensities for Yellowstone National Park were determined from digital and photographic data collected from the NASA high altitude ER-2 aircraft. Digital data was collected by the Daedalus AADS1268 multispectral Thematic Mapper Simulator (TMS) scanner. The Daedalus instrument collects information in 12 distinct bandpass regions of the electro-magnetic spectrum, (Table 1). Given the system IFOV of 1.25 milliradians (mrad), at nominal ER-2 altitude, spatial resolution is approximately 24.5 meters at sea level.

The TMS data was analyzed using a standard image processing software package (IDIMS). The TMS data, collected 15 September 1988, during the waning days of the fires were used to determine burn severity of various watershed complexes (Table 2). Similar data collection

Table 1. Spectral wavelength regions of the Daedalus AADS1268 multispectral Thematic Mapper Simulator (TMS) scanner and corresponding bands of Landsat Thematic Mapper (TM).

Daedalus Channel	Wavelength (μm)	Spectral Region	TM Equivalent
1	.42 - .45	Blue	TM-1
2	.45 - .60	Blue/Green	
3	.52 - .60	Green	TM-2
4	.60 - .62	Green/Red	
5	.63 - .69	Red	TM-3
6	.68 - .75	Red	
7	.76 - .90	Near Infrared	TM-4
8	.91 - 1.05	Infrared	
9	1.55 - 1.75	Short Wave IR	TM-5
10	2.08 - 2.35	Short Wave IR	TM-7
11	10.4 - 12.5	Thermal (Low Gain)	TM-6
12	10.4 - 12.5	Thermal (High Gain)	TM-6

systems available on the NASA-Ames C-130B Earth Resources Aircraft were also utilized for discrimination of burn intensities. The C-130B airframe supports the NS-001 scanner, a Thematic Mapper Simulator developed at NASA-Ames Research Center. Data from that scanning system was also used in post-fire analysis to assist in determining the vegetation recovery rate in the park for a period of a few years following the fires of 1988. The method for determining fire intensity closely follows that described by Riggan et al (1993), and involves determining the ash composition at longer wavelengths. The temperature of the ash layer can remain as high as 345° Kelvin (K) under solar heating. This allows for subtle discrimination in burn efficiencies using mid-infrared, or longer wavelengths to determine ash temperatures. The color of the ash in infrared wavelengths also assist in discriminating burn efficiencies. An intense wildfire, burning at very high temperatures will effectively remove living vegetative matter completely, leaving a white/gray ash color. Lower efficiency fires will leave more carbon on the soil surface, contributing a darker color to the ash layer (Ambrosia and Brass 1988). These two factors, combined with the analysis of similar phenomenon on aerial, infrared photography collected after the fires allowed the discrimination of discrete burn intensities.

Burn intensities were divided into five categories based upon analysis of the imagery: (Severely burned, Moderately burned, Mixed burning, Lightly burned, and Unburned). The analysis focused on selecting burned watersheds dominated by dense stands of Lodgepole pine on moderate/steep slopes (Cache Creek), mixed stands of Lodgepole pine and graminoid communities on relatively flat, gentle terrain (Blacktail Deer Creek and Soda Butte Creek), and mixed burning and mixed vegetation watersheds dominated by major stream/river systems (Snake River and Lamar River). An unburned watershed, with similar topographic and vegetative characteristics was also selected as a reference stream in order to allow comparative analysis of stream chemistry compositions. That watershed, Amphitheater Creek, is dominated by dense stands of Lodgepole pine on moderate to steep slopes. The Amphitheatre Creek watershed is adjacent to the Cache Creek drainage.

Stream Data Collection and Analysis

Six stream watersheds were chosen for nitrate and phosphate analysis in the park following the 1988 wildfires. The six streams were selected in the late spring of 1989 based on numerous factors. Those factors included: the existing burn intensities for the area, vegetation composition, and previous long-term stream monitoring by both the National Park Service (NPS) and the U.S. Geological Survey (USGS), Water Resources Division. Three of the streams chosen for sampling were coincident

Table 2. NASA ER-2 and C-130B flights and data collection over the Greater Yellowstone Ecosystem (GYE). Flight numbers are reference for Flight Summary Reports (FSR) available from NASA-Ames Research Center.

Aircraft Type	Flight Number	Mission Date	Data Collection	
			Photography	Scanner
ER-2	88-123	2 Sep. 1988	—	yes
ER-2	88-125	6 Sep. 1988	yes	yes
ER-2	88-126	9 Sep 1988	—	yes
ER-2	88-129	15 Sep. 1988	yes	yes
ER-2	88-149	29 Sep. 1988	yes	—
ER-2	89-005	6 Oct. 1988	yes	—
ER-2	89-158	30 Aug 1989	yes	—
ER-2	89-159	1 Sep. 1989	yes	—
C-130B	91-009-04	9 Aug. 1991	yes	yes
C-130B	91-010-15	20 Sep. 1991	yes	yes

tally monitored by the USGS: Blacktail Deer Creek, Soda Butte Creek, and the Lamar River near the junction with the Yellowstone River (M. K. White 1993). Five of the watersheds were located in the north/northeastern section of the park, with the sixth, the Snake River, being monitored at the southern boundary of the Park. The Snake River was included in the area covered by the Snake River Complex and the Huck Complex fires of 1988. Cache Creek, Soda Butte Creek, and the Lamar River were included in the Clover-Mist Complex, and Blacktail Deer Creek was part of the Wolf Lake Complex. Elevation ranges for all the stream sampling stations were similar, with point sampling elevations ranging from 6000 feet ASL (Lamar River) to 6905 feet ASL (Amphitheatre Creek).

Stream water sampling in Yellowstone National Park was undertaken using ISCO waste water samplers. The ISCO samplers were programmed to collect one litre of water twice in a 24-hour period. Each sampler contains 28 bottles, enough for two samples a day for fourteen days of sampling. During collection and servicing, at the end of the two-week period, the samples are removed, transferred to sterile 100ml bottles, labeled for time/date of collection, packaged and sent to the U.S.F.S. Riverside Fire Lab, California for analysis.

Nitrate and phosphate analyses were performed using a Dionex Series 4000i ion chromatograph. The absorption column separates chemical ions in a carrier solution into distinct bands based on their affinity for the absorbant. Concentrations of individual ions are determined using an electrical conductivity detector and comparing the areas under their curves on the chromatogram with those of a calibration curve. Results are expressed as PPM (mg/L) of NO₃ and PO₄. QA/QC data were analyzed and a report generated. The QA/QC procedures consisted of generating a calibration curve using six calibration standards at the beginning of the run and drift correcting against the single highest standard at the end of the run. A normal run contains approximately 50 samples, two pair of duplicated samples and two in-house standard reference material samples, one at the beginning of the run and one

at the end. Lab protocol dictates that duplicates and SRM's be in tolerance of less than 10% for means greater than .50 mg/L; 5% for means less than .50 mg/L or the run is not valid. In actuality, the error rates for the Yellowstone samples were far less. The 1989 data was not available at the time of this paper preparation because the data had not been sufficiently transferred to the computer for analysis.

Results

Nitrate and phosphate levels on the reference stream, Amphitheatre Creek remained constant throughout the recording periods (June - September). Due to the stable nature of the concentrations on Amphitheatre Creek, sampling was discontinued after the 1991 season, although the data provided a baseline to relate the other stream concentrations to our reference. Nitrate concentrations on Amphitheatre Creek averaged 0.3 mg/L during June/July 1990 and 1.0 mg/L during August/September 1990. Phosphate concentrations peaked at 0.3 mg/L during precipitation events in late August and late September of 1990, and again in late July of 1991. Phosphate concentrations remained relatively stable at, or under, 0.15 mg/L during the remainder of the recording period.

Blacktail Deer Creek, an intensely burned watershed, exhibited nitrate concentration averages 4 to 10 times greater than Amphitheatre Creek with short-term concentrations 20 to 30 times the average for Amphitheatre. The short-term, elevated concentrations, generally coincided with precipitation events. The phosphate concentrations for Blacktail Deer Creek exhibited average levels of approximately 0.3 mg/L, with peaks over 2.0 mg/L. These phosphate levels are 2 to 10 higher than Amphitheatre concentrations. Both nitrate and phosphate concentrations for Blacktail Deer Creek were highest during 1992, although individual peak concentrations were highest during the 1991 period.

Cache Creek, a severely burned watershed, exhibited high nitrate concentrations during the whole monitoring period. Average concentrations from 1990-1993 were 3.5 mg/L with short-term peak concentrations well above 10.0 mg/L. These levels are 10-33 times greater than on Amphitheatre Creek. The highest average nitrate concentration occurred during 1992. Phosphate concentrations averaged 0.4 mg/L during recording periods, with one peak occurring 13 August 1990 (3.2 mg/L) and another occurring 18 June 1993 (8.74 mg/L). These levels are 2.7-29 times greater than our reference watershed.

The Lamar River, a mixed burned composition watershed above our sampling station, exhibited nitrate concentrations of 1.5 mg/L with numerous peak levels at or near 8.0 mg/L. For the 1990-1993 period, concentrations were consistently higher during early June, decreasing at a constant level through late September. Nitrate levels

were 5 times higher on average while peak concentrations were 8 times higher on average than peak concentrations occurring on Amphitheatre Creek. The Lamar River phosphate concentrations averaged 0.2 mg/L, with the highest average occurring in 1990. The highest peak concentration occurred 12 June 1992 (12.66 mg/L). These concentrations are 1.3 times higher than our reference average, although peak concentrations are 42 times higher than peak concentrations in Amphitheatre Creek.

The Snake River, a moderately burned watershed above our sampler, exhibited pronounced nitrate pulses related to snow melt and precipitation events. Concentrations averaged 1.5 mg/L with peaks of 5.0-5.2 mg/L. These levels are 5 times greater than the Amphitheatre average, while peak concentrations were 5.2 times greater than peak Amphitheatre concentrations. The Snake River phosphate concentrations were very low during our recording periods, although peak concentrations occurred during precipitation cycles and were from 0.1-0.8 mg/L. The average phosphate concentration was below that of Amphitheatre Creek, although peak concentrations following precipitation events were 2.6 times greater. Due to the size of the Snake watershed and the degree of mixed burning above our sampling station, the values for the Snake may be no different than occurred in normal years before fires.

Soda Butte Creek, a lightly burned watershed, exhibited uncommon nitrate concentration patterns. Concentrations remained low, averaging approximately 0.8 mg/L, although frequent peaks occurred between 4-8 mg/L. The highest peak concentration occurred on 15 September 1992, when nitrate concentrations were measured at 27.09 mg/L. These average levels are 2.6 times greater than Amphitheatre, while peaks were 4-27 times greater. Phosphate concentrations exhibited similar characteristics. Averages were similar to Amphitheatre Creek, although periodic peak concentrations were 8.4-11.8 times greater. All stream nitrate and phosphate concentrations are summarized in Table 3.

Conclusions

The Greater Yellowstone Ecosystem fires of 1988 allowed us the unique opportunity of analyzing the effects of various burn intensities on stream NO_3 and PO_4 dynamics. We analyzed infrared and thermal digital scanner data collected both during and following the fires to determine the intensity of burning in watersheds dominated by old-growth Lodgepole pine communities. Subsequent data collection missions were undertaken in order to monitor the ecosystem recovery effort. We chose six watersheds with varying burn intensities for further stream analysis. Burn intensities were in those watersheds were grouped as severe, moderate, mixed, lightly burned and unburned. In those streams, both nitrate and phosphate concentrations were measured to determine the influence of burn intensities on NO_3 and PO_4 concentrations. Previous studies by Riggan et al. (1985) in southern California (chaparral community), have indicated stream nitrate changes in severely burned watersheds are 10 to 60 times greater than from unburned watersheds, and 7 to 8 times greater than from moderately burned watersheds. We found similar results in our studies in Yellowstone. Unburned watersheds exhibit little or no change in their stream chemical makeup.

In Yellowstone, we recorded nitrate concentrations that were 4 to 33 times greater on average than reference levels, while peak levels were 10 to 33 times greater. As expected, concentrations in moderately burned watersheds were lower, averaging 5 to 8 times higher than our control stream. Soda Butte Creek, a lightly burned watershed, exhibited nitrate concentrations 2 to 6 times greater than levels recorded on Amphitheatre Creek, while peak concentrations were 4 to 27 times greater. For all streams, higher concentrations (than Amphitheatre) were recorded for all five years of the study. The short-term peak levels suggested by Spencer and Hauer (days to weeks), following major watershed fires, may be consistent with our findings, although our sampling of burned watersheds did not occur until the following spring season, eight months after the fires. Our research suggests that the concentrations may persist for longer periods of time than Spencer and Hauer suggest.

Table 3. Nitrate and phosphate concentration levels in Yellowstone National Park watersheds under various burn intensities as compared to the control stream, Amphitheatre Creek. The ranges relate to the peak concentration conditions encountered.

Stream Watershed	Burn Condition	Nitrate Levels	Phosphate Levels
Amphitheatre Creek	Unburned Reference	0.3 - 1.0 mg/L	0.1 - 0.3mg/L
Soda Butte Creek	Lightly Burned	2.6 times Greater	0 - 11.8 times greater
Lamar River	Mixed Burn	5.0 times greater	1.3 times greater
Snake River	Mixed Burn	5.2 times greater	2.6 times greater
Blacktail Deer Creek	Moderately Burned	4 to 10 times greater	2 to 10 times greater
Cache Creek	Severe Burn	10 to 33 times greater	2.7 - 29 times greater

Phosphate concentrations in severely burned watersheds exhibited a 2 to 29 time increase over Amphitheatre Creek concentrations. Phosphate concentrations were 1 to 2 times greater in moderately burned watersheds than our unburned watershed. Peak concentrations were up to 42 times greater, although most peaks, following precipitation events were 2 to 3 times greater. We documented significantly lower phosphate concentrations in our lightly burned watershed, Soda Butte Creek. Concentrations were on par with Amphitheatre Creek, although peak discharges were measured at 8 to 12 times greater than peak discharges on Amphitheatre Creek.

Results of our field and lab investigations strongly suggests that fire intensity, temperature and fire duration play a dominant role in determining downstream NO_3 and PO_4 composition. Our results also indicate that the duration of stream nitrate and phosphate concentrations are long-term, possibly affecting watersheds in excess of five years. The nitrate and phosphate levels in our monitored watersheds were consistently elevated above the levels recorded for the unburned watershed. Peak concentrations, coinciding with periodic precipitation events, were highly elevated above both Amphitheatre Creek as well as above the levels on the individual burned watersheds. This suggests that the burn severity controls the runoff potential (leaching) of the nitrates and phosphates by regulating the entrapment power of remaining or new biomass material. We suggest that peak concentrations on severely burned watersheds were much more elevated because of the increased runoff from those sites, where little or no biomass material on or above the soil structure impeded increased erosion flows. Conversely, the less severe burn areas retained more biomass, thereby restricting runoff, erosion, and nutrient transport into the stream ecosystem.

The authors conclude that burn severity can be modeled from remotely sensed data, that the severity of burning contributes to increased erosion and runoff, and that increased erosion and runoff help regulate the nitrate and phosphate nutrient influxes in streams and water bodies. NO_3 and PO_4 concentrations remain at an enhanced level for extended periods of time, and receive periodic pulses immediately following precipitation events. Our continual monitoring of the recovering Yellowstone National Park watersheds should enhance our knowledge of long-term environmental and aquatic alterations following major conflagrations.

Acknowledgments. The authors would like to thank numerous individuals for their support, assistance, field sampling, and review of the research. Those people include: Robert Barbee, Roy Ewing, Don Despain, John Varley, Carol Kenefick, Robert Lockwood, Richard Lathrop, Kathy Hibbard, Laurie Richardson, Daniel Wolf, Dave Griswold, Dan Carty, Dave LeConte, George McKay, Scott Dungan, and Jeff Myers.

Postscript

The material presented at the 1993 Second Biennial Conference on the Greater Yellowstone Ecosystem: The Ecological Implications of Fire in Greater Yellowstone, September 19-21, 1993 and in this proceedings paper are a summation of the researchers ongoing efforts in Yellowstone National Park. Similar material, data and results were presented at another venue, The Second Thematic Conference on Remote Sensing for Marine and Coastal Environments. Portions of this paper are derived, with consent, from an article prepared by V.G. Ambrosia, et al. entitled, "Long-Term Dynamic Stream Nitrate And Phosphate Changes Following Watershed Wildfires." The sole intent of this article is to consolidate materials presented at the Yellowstone Conference and to provide a summation of the research to a different readership.

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Changes in Transport and Retention of Coarse Particulate Organic Matter in Streams Subjected to Fire

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Abstract. Between June and September 1988, fires burned over 400,218 hectares or 44.5 percent of Yellowstone National Park, U.S.A. The effects of fire on transport and retention of coarse particulate organic matter (CPOM) in streams was the focus of this study. CPOM dynamics were investigated in five first order streams (two reference, two 100% burned and one 70% burned) for two years following the fires. Retention of CPOM was examined in four ways: as transported (TOM) and benthic (BOM) organic matter, number of debris dams along 300 m of stream, and short- and long-term retention of CPOM analogs. Reference streams had more coarse BOM (>1 mm) than burn streams, while burned streams transported significantly more organic matter than did reference streams. Reference streams retained more CPOM analogs, had shorter travel distances, and higher rates of removal in the short- and long-term retention tests, than burn streams. Debris dams in reference streams caught 98% of released analogs in the short-term retention test in reference streams, but only 45% in burn streams. In long-term retention tests, debris dams caught 80% of CPOM analogs in reference streams, while 43% was caught in burn streams. Burn streams had 1 and 3 debris dams per 50 m of stream, whereas reference streams had 6 and 9 dams per 50 m of stream. Results for the 70% burned stream were intermediate to those of the reference and 100% burned streams. These data suggest that fire reduces the capacity of burned streams to store CPOM by altering the types and magnitudes of retention barriers, and by altering CPOM inputs from the watershed.

Introduction

Detritus in streams consists of dead decaying leaves, twigs, fecal matter from consumer organisms, and dead algae and vascular plants or their remains. Detritus is transformed into various particulate forms and sizes through physical and biological processing. Detritus is a major source of carbon, and a primary source of energy

in lotic food webs (Webster et al. 1990). Allochthonous (from outside the stream) and or autochthonous (from within the stream) detritus can comprise up to 45% of the dry mass of organic matter in streams (Bilby and Likens 1980). Detritus also contains a pool of vital elements such as nitrogen, phosphorus, and sulfur (Meyer 1989). The concentration of nutrients and carbon in allochthonous detritus affect overall production, metabolism, and decomposition in streams, and determines whether they are autotrophic or heterotrophic systems.

Retention can be viewed as the "in situ" storage or holding of organic and inorganic particles (Swanson et al. 1982). Boulders, rocks, pools, debris dams, and riparian vegetation contribute to trapping organic matter or hindering its transport in streams. Retention allows time for organic matter in streams to be taken up biologically and "processed" before being passed downstream. Researchers have pointed out the importance retention or storage of organic matter has in stream ecology (Naiman and Sedell 1979, Bilby and Likens 1980, Wallace et al. 1982, Minshall et al. 1983, Rounick and Winterbourn 1983, Speaker et al. 1988). Triska et al. (1990) state, "the retentive properties of channels are those most critical to biota, because it is retention that sustains the lotic community." Meyer (1989) noted that the retentiveness of a reach is pivotal in assessing ecosystem function. Wallace et al. (1982) suggested that retention and associated biological processing provide continuous inputs of nutrients to streams, precluding serious washouts of organic matter with high flows. Since detritus plays an important role in lotic ecosystems as a primary energy source, its retention and storage in the streams should be equally important.

If retention is reduced, organic matter is more vulnerable to periodic washouts with high flows, representing a significant loss of energy to the entire system. A stream with a high loss, or export, of particulate and dissolved organic carbon is less efficient in carbon use compared to another stream with less loss and higher on-site

utilization (Webster and Golladay 1984). Such streams may experience decreased abundance of secondary producers or loss of entire functional groups (Rounick and Winterbourn 1983, Culp and Davies 1983).

Disturbance in lotic ecosystems can be defined as "any relatively discrete event in time that is characterized by frequency, intensity, and severity outside a predictable range" (Resh et al. 1988). Minshall et al. (1985) and Resh et al. (1988) have recognized the important role disturbance has on stream structure and function, by disrupting or changing resources (i.e., nutrients, solar inputs, allochthonous inputs) and/or the physical environment. Temperate headwater streams have the maximum stream riparian interface (contact) of all flowing waters and thus are tied closely to their terrestrial settings (Vannote et al. 1980). Forested headwater streams receive most of their energy from allochthonous detritus (Hynes 1975, Vannote et al. 1980, Speaker et al. 1988). Because headwater streams are tied so closely to their watersheds, it follows that any disturbance of the watershed can potentially disturb and change stream structure and function as well (Hynes 1975, Webster et al. 1990).

Fire can be a major disturbance mechanism both to terrestrial and stream ecosystems by altering the amount and type of riparian vegetation, which in turn changes the quality, quantity, form, and timing of organic inputs to streams (Minshall et al. 1989, Britton 1990). Few studies have documented effects of fire on organic matter retention in streams. What has been reported suggests that retention is reduced and less organic matter is retained by streams following a fire. Albin (1979) conducted a study of streams in Yellowstone National Park that burned 45 and 36 years previously. He found streams, in burned watersheds, were still exporting more organic matter than unburned streams. This would indicate that even after 45 years stream retention had not recovered to pre-burn conditions. Minshall et al. (1981), in a study of streams in the Middle Fork of the Salmon River, found burned streams to be exporting "substantially" more organic and inorganic material than unburned streams one year after the fire. This pattern of increased organic and inorganic matter export continued for several years following the fire (Minshall et al. 1989). Tiedmann (1979) in his review of fires on streams, noted that burned streams experienced increased flow and run-off as well as sediment transport. Minshall et al. (1989) noted some of the same changes in their study. These included increased water yield and channel movement along with erosion and transport of stored in-channel sediments.

Other types of disturbance to stream ecosystems are various land management activities occurring within a watershed. Several researchers have looked at logging and its effects on streams. Webster and Golladay (1984) found elevated transport of organic matter 10-20 years following clearcut logging in a stream in North Carolina. Bilby and Likens (1980) simulated disturbance by remov-

ing all debris jams in their study stream and found organic matter export increased 500% from pre-disturbance levels. Webster et al. (1990) found disturbance from logging increased export and accelerated turnover of benthic particulate organic matter. They also determined that disturbed (logged) watersheds were experiencing a net loss of benthic material, through a decline in woody debris dams.

These studies suggest that fire can reduce the organic matter retention capacity of streams by increasing runoff, which in turn increases erosion and may furnish the energy necessary to remove or break down retention barriers. However, these conditions have never been carefully documented with respect to fire. We tested this idea using streams in Yellowstone National Park. Streams are viewed as a continuum of gradients from headwaters to downstream reaches, wherein ecosystem dynamics in the downstream sections are influenced by organic matter inputs from upstream sections (Vannote et al. 1980). Forested headwater streams are major processors of coarse particulate organic matter and downstream linkages are dependent on inputs of fine particulate organic matter from upstream reaches. In Yellowstone National Park, many headwater watersheds and streams burned in 1988, drastically changing riparian and terrestrial conditions, and hence, the nature of allochthonous organic matter inputs and possibly retention capacity. This could have dramatic consequences on both headwater and downstream levels of organic matter availability and conditioning. Fire is recognized by scientists and resource managers as an integral part of terrestrial ecosystems, having positive benefits for both plants and animals (Smith 1990, Christensen et al. 1989). A comparable understanding for stream ecosystems remains to be demonstrated.

From early June 1988 to late September 1988 fires burned over much of Yellowstone National Park. Thirteen major fires created a mosaic of habitats both in terms of space and intensity of burn. A total of 400,218 hectares (988,925 acres) were burned, 44.5 percent of the total 890,340 hectares (2.2 million acres) that comprise Yellowstone National Park. Half of this nearly 400,218 hectares (1 million acres) was classified as canopy burn (intense combustion of all ground debris along with small branches and needles), the other half being ground or surface fire (moderate to light intensity) (Wuerthner 1989).

Minshall et al. (1989) hypothesized that the impact to streams from fires in Yellowstone should be proportional to the intensity and extent of fire in the watershed. They further stated that the greatest impact to streams should be from canopy-type burns in "headwater" streams. Intensely burned watersheds and streams should experience changes in woody debris, suspended sediments, nutrient cycling, and leaf litter inputs. Because of changes to the riparian vegetation along these burned

streams, food resources and organic matter retention capacity also should change (Minshall et al. 1989).

The primary objective of this study was to determine if fire had any effect on coarse and fine particulate detritus retention in first order streams, one and two years after the 1988 Yellowstone fires. The second objective was to ascertain whether fire changes the nature of retention barriers in streams.

Study Area

This research was conducted in first order streams located in the northeast corner of Yellowstone National Park, U.S.A. (Figure 1) The Absaroka mountain range borders this portion of the Park. The Lamar River is the main tributary draining this corner of the Park. It flows into the Yellowstone River, 24 km west of the study area. All of the study streams drain to the Lamar River, except for Blacktail Deer, which drains into the Yellowstone

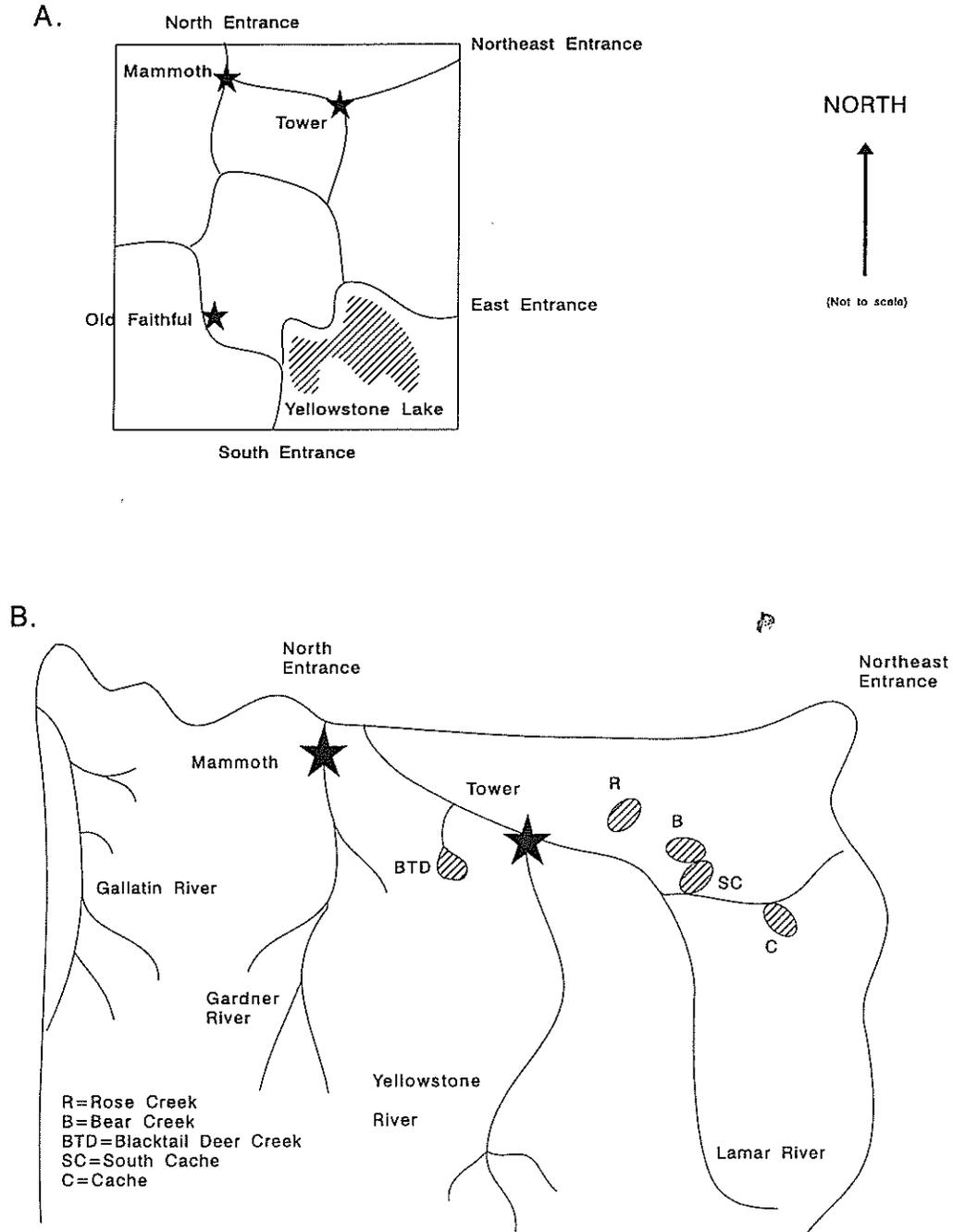


Figure 1. A. Yellowstone National Park, showing major landmarks. B. Study portion of Yellowstone National Park, showing major rivers and study watersheds.

River. The topography of the study area consists of steep-sided slopes with deep u-shaped valleys cut by streams and glaciers. The uplands are covered generally with extensive stands of mature lodgepole pine (*Pinus contorta*), with some Douglas fir (*Pseudotsuga menziesii*) on the drier south, and southwest facing slopes. Stream bottoms and riparian zones in particular are dominated by large diameter old-growth Englemann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*). Where openings occur in the stream riparian areas, alder (*Alnus* sp.) is found, along with mountain maple (*Acer glabrum*).

The northeastern portion of the Park was selected for study because it has fairly uniform geology, climate, and streamflow regimes. These three characteristics have been identified as the most important factors in site consideration for investigations of stream disturbance (Resh et al. 1988). A second factor in selecting this study area was that this section of the Park was identified as having higher potential for experiencing maximum post-fire impacts due to unstable geology and steep topography (Minshall et al. 1989).

Precipitation in this area is mostly in the form of snow, between the months of October and March. However, intense localized summer thunderstorms are common. Precipitation data by month during the study period are listed in Table 1. Precipitation was near normal for the two years of this study. Flow regimes follow a sequence typical for this area of the Rocky Mountains, with snowmelt and peak run-off in late May and base flow in September (Table 2). For purposes of recognition, the five streams chosen for this study are referred to by names given by the author. These streams are referenced and numbered according to a standardized system for Yellowstone Park (Table 3).

Study Streams

Our reference streams (unburned) were Rose Creek and Bear Creek. Blacktail Deer Creek and South Cache Creek were located in burned watersheds. For purposes of this study "burned" refers to percentage of the watershed burned by canopy fire, including the stream riparian zone. Cache Creek was only 70% burned, not 100% as first thought (Table 3).

Rose Creek (latitude 44° 53' north, longitude 110° 14' west) is a 1.1 km stream that lies in a 2 km², southwest-facing watershed. It has an average channel slope of 9%, with a watershed elevation high point of 2895 meters and a low of 2292 meters (Table 3). The first order tributary used for study is approximately 2.6 kilometers up Rose Creek from the Lamar Cooke City road. Flow data for Rose Creek during sampling and for subsequent study streams are listed in Table 2. These flow measurements were taken at the study sites. Flows ranged from 0.1147 to 1.53x10⁻⁴ m³/s in 1989 and from 0.0533 to 2.9x10⁻⁴ m³/s in 1990.

Bear Creek (latitude 44° 52' north, longitude 110° 09' west) lies in a 4.5 km² west-facing watershed, and has 1.8 km of stream channel. Stream gradient is 11%, with a watershed high point of 3017 meters and low of 2048 meters. Bear Creek lies 1.2 kilometers east of Soda Butte cone, on the south side of Soda Butte Creek (Figure 1). Flows in Bear Creek ranged from 0.067 to 1.534x10⁻⁴ m³/s in 1989 and from 0.08 to 5.3x10⁻⁴ m³/s in 1990.

Blacktail Deer Creek (latitude 45° 54' north, longitude 110° 35' west) drains a 10.9 km² basin, having a north-northwest facing aspect. Channel slope is 7% and stream length is 2.2 kilometers, with a watershed elevation high and low point of 2743 and 2133 meters, respectively. The first order tributary of Blacktail that we studied was in the East Fork of Blacktail Deer Creek approximately 1

Table 1. A. USGS Precipitation data for Yellowstone National Park at Tower Junction: Water Years 1989 and 1990. B. USGS Flow data for the Lamar River at Tower junction, Yellowstone national Park: Water Years 1989 and 1990. Departure is +/- from mean.

A.														
	1988			1989										
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total	Total
Precipitation (cm)	0.38	3.73	1.93	2.69	2.34	4.85	2.72	8.08	4.42	4.50	3.00	0.66	Total	39.30
Departure (cm)	-2.5	1.9	-1.6	0.41	-0.1	0.00	-0.5	3.18	-1.3	0.53	-0.9	-3.0	Total	-3.88
	1989			1990										
Precipitation (cm)	5.46	1.93	4.62	4.11	0.94	2.03	3.61	5.64	4.42	2.84	5.97	2.72	Total	44.29
Departure	2.54	-0.9	1.07	0.46	-1.5	-0.8	0.43	0.74	-0.9	-1.1	1.98	-0.9	Total	1.12
B.														
	1988			1989										
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Total	Total
Flow (m ³ /s)	3.09	2.79	2.84	2.03	2.23	3.11	27.7	112	113	31.0	9.92	5.58	Total	315.30
Departure (m ³ /s)	-3.0	-1.6	-0.5	-0.9	-0.6	0.15	15.8	38.6	-4.3	-7.16	0.04	-0.8	Total	35.73
	1989			1990										
Flow (m ³ /s)	7.12	5.60	4.46	3.34	2.93	3.92	47.6	67.4	124	34.0	12.6	7.33	Total	320.30
Departure (m ³ /s)	1.03	1.19	1.11	0.37	0.10	0.95	35.7	-6.5	5.97	-3.42	12.8	0.87	Total	40.17

Table 2. Flow data by sampling period (m³/s) for study streams. Reference stream flows are significantly different (Mann-Whitney test on log transformed data) from burn stream flows by sample period (p<.001), but only for summer and fall when adjusted for area (*). All are first order streams. Two flow calculations are listed for those streams where discharge changed during sampling. () indicated extent of watershed burned.

Reference	Year	Spring	Summer (*)	Fall (*)
Rose	1989	.1147	.0072	.000153
	1990	.0533	.0066	.00029
Bear	1989	.0670 .0800	.0097	.000153
	1990	.0624	.0097	.00053
Burn				
Blacktail Deer (100%)	1989	.2200 .4480	.1344	.0300
	1990	.2443 .2776	.1042	.0540
South Cache (100%)	1989	.1830 .4780	.0660	.0056
	1990	.1279 .1529	.0510	.0065
Cache (70%)	1989	.3430 .4360	.0366	.0071
	1990	.1830	.0282	.0063

kilometer upstream from the confluence of the East Fork and West Fork Blacktail Deer Creek. Flows in Blacktail Deer Creek varied from 0.4488 to 0.03 m³/s in 1989 and from 0.2776 to 0.054 m³/s in 1990.

South Cache Creek (latitude 44° 49' north, longitude 110° 07' west) drains a 4.7 km² basin with a south-southwest facing aspect and a channel slope of 8%. It's high and low watershed elevation points are 3017 and 2195 meters, with 1.6 kilometers of channel length (Table 3). This creek lies 1.6 km east of the Cache Creek, Lamar River trail junction, on the north side of Cache Creek (Figure 1). Sampling occurred approximately 200 m

above where the Cache Creek trail crosses this tributary. Flows ranged from 0.478 to 0.0056 m³/s in 1989 and from 0.1529 to 0.0065 m³/s in 1990.

Cache Creek (latitude 44° 49' north, longitude 110° 05' west) has 1.2 kilometers of stream in a 4.1 km² watershed basin. Slope is 9%, and aspect is north-northwest. High and low elevations are 2715 and 2195 meters, respectively (Table 3.) This unnamed tributary is on the south side of fourth order Cache Creek, 1.5 kilometers downstream from the junction of third order Cache Creek and third order South Fork Cache Creek (Figure 1). Flows ranged from 0.436 to 0.0071 m³/s in 1989 and from 0.1803 to 0.0063 m³/s in 1990. The lower 2/3 of this drainage burned, while the upper 1/3 did not. Our monitoring station was located approximately 200 m below the unburned portion.

Methods

Benthic organic matter sampling:

Ten BOM samples were collected randomly in pool and riffle habitats during May, July, and September 1989 and 1990 for all streams, using a modified Hess sampler (605 cm²), as described in Waters and Knapp (1961), with a 53 µm nitex mesh bag. Samples were not collected in spring 1990 for Cache Creek due to logistic limitations with high water. Fall samples were collected in mid-October rather than September in 1990. Samples were proportioned by percent of pool/riffle habitat occurring in the study reach. A railroad spike was used to disturb and dislodge sediments and organic matter to a depth of 10 cm. The collector bag was removed and the contents placed in labeled Whirl-pack bags, which were then placed in a cooler containing ice until they could be frozen and stored for later analysis.

Velocity was measured at all sites during all visits with a small C-1 Ott, according to the method described

Table 3. Stream and watershed information. Number in parenthesis is the stream number according to Yellowstone Park Service identification system.

Reference	Watershed Elevation	Area (km ²)	Aspect	Slope (%)	Channel Length (km)	% Burn
Rose (10331202)	2292 Low 2895 High	2	SW	9	1.1	0
Bear (10331701)	2048 3017	4	W	11	1.8	0
Burn						
Blacktail Deer (101705)	2133 Low 2743 High	10.9	NNW	1.5	2.2	100
South Cache (10332202)	2195 3017	4.7	SSW	8	1.2	100

in Platts et al. (1983). Discharge was then calculated using velocity, width and depth measurements according to Platts et al. (1983). If discharge changed during sampling, according to a stage measurement taken with a meter stick, a second flow measurement was made (Table 2). This occurred during some of the spring visits.

Transported organic matter sampling

TOM was sampled on the same dates as BOM. Transport nets of 53 μm mesh nitex netting attached to plastic collars (207 cm^2 area) were used to collect organic matter within the water column. Four samples were collected during each visit for each stream, except Cache in spring 1990 (see BOM methods). Water depth and velocity measurements were taken in front of each net, using a meter stick and small C-1 Ott meter, to calculate the volume of water passing through each. Between 5 and 20 minutes was allotted for collection of seston, dependent on amount of flow and visual observation. The difference in time was to prevent clogging of the nets, which could produce back-pressure and loss of sample. Samples were placed in Whirl-top bags in a cooler containing ice, until they could be frozen and stored for later analysis.

Short-term coarse particulate organic matter (CPOM) analog retention test

This test was done once per stream in September, 1989 using 300 (4 cm x 10 cm) plastic flags as analogs of coarse particulate organic matter after Speaker et al. (1984). The flags were dropped in the middle of each stream, by shaking a handful at a time over the water, to avoid clumping. The flags were left undisturbed for 3 hours. A weir of galvanized metal fencing (1 cm^2 mesh) was placed 50 m below the release point to catch any flags that might be transported the entire 50 m. Flags retained within the 50 m after 3 hours were collected. Distance traveled from point of entry, number retained, and retention barrier type were recorded. Retention barrier types were boulders, debris dams, sticks, algae, and backwater. Stream discharge and stage height were measured before and after each test.

Long-term coarse particulate organic matter (CPOM) analog retention test

A long-term CPOM retention test was conducted from May through July 1990 (initiated prior to spring runoff) for each stream. 500 plastic flags (4 cm x 10 cm) were released in a 5 minute time span on May 5-7, 1990. On July 21-24, 1990 a search of each stream was conducted from the point of entry downstream for 300 m. Distance traveled from the release point and type of retention barrier were recorded for each of the recovered flags.

Laboratory processing of samples

Both BOM and TOM samples were split into five different size fractions using ASTM brass sieves. The five sieves used were 1 mm, 500 μm , 250 μm , 125 μm and 53 μm mesh. All organic matter remaining in the 1 mm sieve was considered coarse particulate organic matter (CPOM). The material in the four remaining sieves is collectively termed fine particulate organic matter (FPOM).

The material retained in each of the five sieves was placed in porcelain crucibles and dried at 60° C for 24 hours or until a constant dry weight was obtained. The samples were then ashed at 550° C for 4 hours in a muffle furnace, rehydrated with distilled water, and dried at 60° C for another 24 hours. Organic matter was calculated in g/m^2 using ash-free dry mass. In the case of TOM this was done by multiplying by mean depth to convert g/m^3 to g/m^2 . TOM is assumed to be uniformly distributed throughout the water column due to turbulent mixing.

Information from the short-term CPOM retention test was fitted to a negative exponential model as described by Young et al. (1978), and Speaker et al. (1984, 1988). The formula is $Ld = L_0 e^{-kd}$, where:

- Ld = number of flags caught at maximum distance from drop point
- L_0 = number of flags released (300 for short-term and 500 for long-term)
- d = maximum distance moved from release point in meters
- k = instantaneous rate of flagging removal.

Number of Debris Dams

In October 1990 the number of debris dams in 300 m of each stream were counted as another indicator of retention. The criteria used for dam consideration were: 1) any wood >10 cm in diameter, 2) in contact with the stream bed, and 3) spanning at least 1/4 of the wetted channel.

Statistical analyses

All statistical analyses were performed on either an IBM or Macintosh PC computer using Complete Statistical System (CSS) and/or Statgraphics SE+. A Mann-Whitney test was performed on log-transformed flow data and area adjusted flow (flow/km^2) data to see if any differences occurred during sampling periods. A Mann-Whitney test was also used to test for differences in instantaneous rates of flagging removal (k values), and for differences in total numbers of flags retained in the long term CPOM retention test. A repeated measures ANOVA was run on BOM and TOM to test for differences between treatments. A second ANOVA was run

with only the 100% burned streams, less Cache Creek, the intermediate burned stream. This analysis was done to block comparable treatments (100% burned). A Kolmogorov-Smirnov test was used to determine if there was a difference in the way the flags were retained, and their distribution, in the long-term CPOM retention test.

Results

Benthic organic matter

When Cache Creek (70% burned) was included in the ANOVA, no significant differences between BOM and TOM were evident. However, when Cache Creek was removed from the second ANOVA, treatment effects were significant. With the exception of Cache Creek, burn streams had up to twice the total benthic organic matter than reference streams in spring of 1989, however no apparent difference existed in summer (Figure 2). In

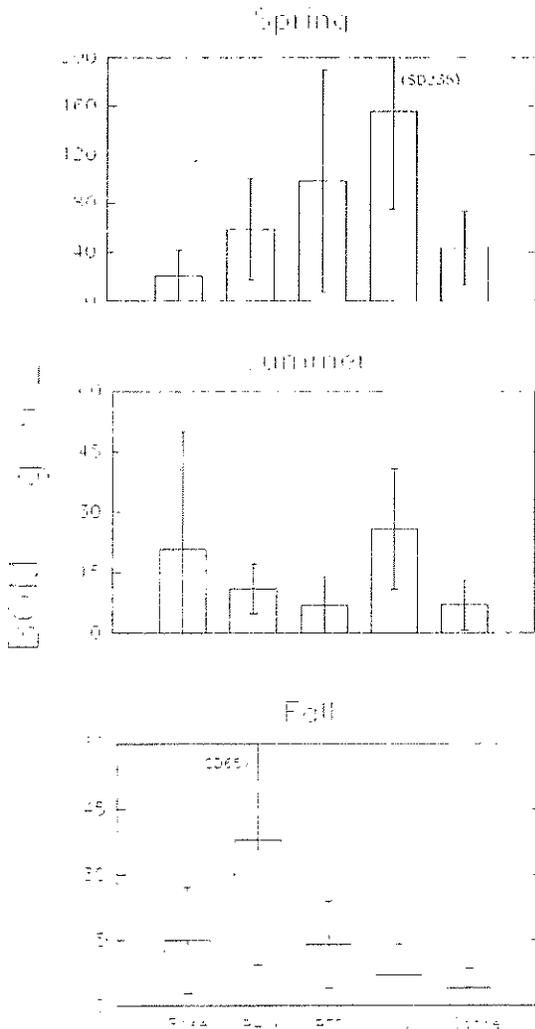


Figure 2. Total BOM for 1989 by stream. Error bars are + or - one standard deviation. BT = Blacktail Deer, SC = South Cache. N = 4 for all samples.

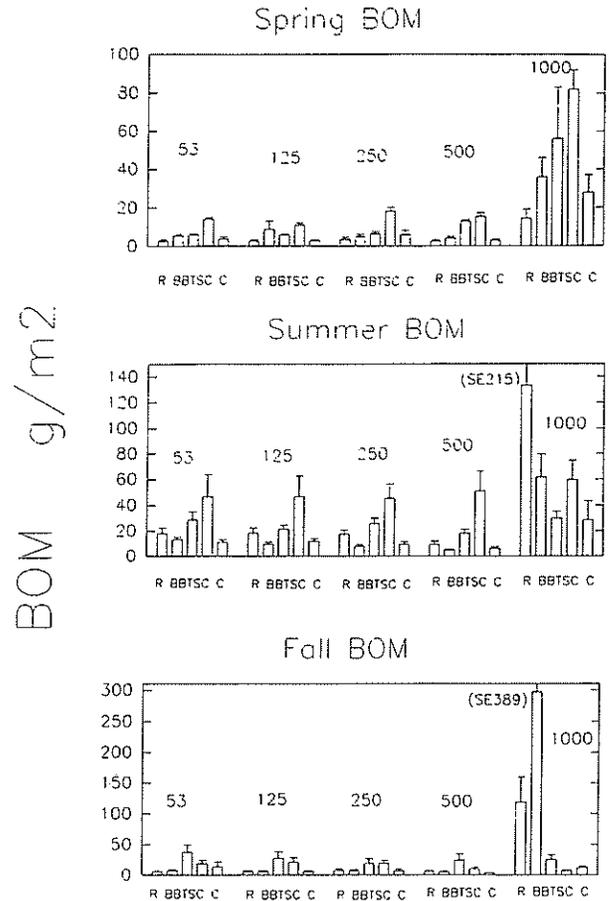


Figure 3. 1989 BOM (g/m²) by size and site. R = Rose, B = Bear, BT = Blacktail Deer, SC = South Cache, C = Cache. Error bars are + or - one standard error. n = 10 for all sizes.

contrast, reference streams had more total benthic organic matter (15-40 mg/m²) in the fall of 1989 than burn streams (7-15 mg/m²). This pattern changed somewhat in the spring of 1990 (1990 data not shown), with burn streams having near equal amounts of BOM as reference streams. The fall pattern of reference streams having more total organic matter than burn streams continued in 1990.

Reference streams had less benthic organic matter in the 53 µm, 125 µm, 250 µm, and 500 µm categories than burn streams in summer (Figure 3). They had nearly equal amounts in the 1000 µm category at this time. In the fall of 1989, reference streams had significantly (p<0.041) more organic matter in the 1000 µm size than the burn streams. This pattern was even more pronounced in the fall of 1990. The composition of CPOM in fall was different between reference and burn streams. In reference streams CPOM was largely composed of needles, dead leaves, and pine cones, while CPOM in the burn streams consisted mostly of charcoal.

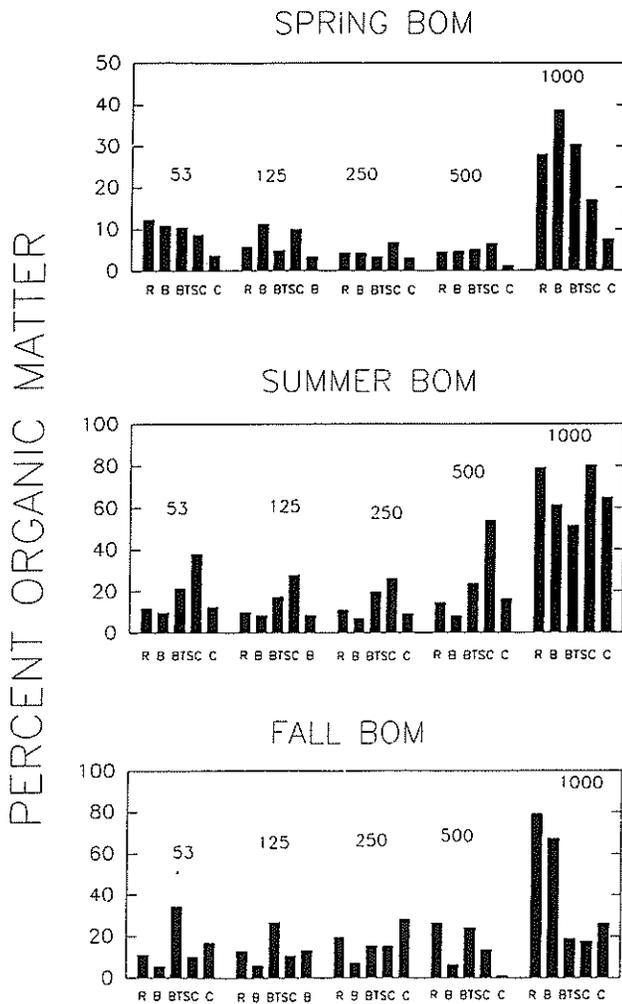


Figure 4. Percent organic matter in BOM by size, season and stream. R = Rose, B = Bear, BT = Blacktail Deer, SC = South Cache, C = Cache. $n = 10$ for each size and site.

CPOM (1000 μm and larger) had the highest percent organic matter of all size fractions in both reference and burn streams (Figure 4). In the fall, reference streams had significantly ($p < 0.007$) higher percentages of organic matter in the coarse particulate organic matter fraction.

Transported organic matter

TOM was converted to mg/m^2 from conventional units of mg/m^3 , by multiplying by depth, to facilitate comparison with BOM. 100% burned streams transported significantly ($p < 0.020$) more material (g/m^2) than reference streams in summer and fall (Figure 5). During this same time period, they also had significantly more TOM in the fine particulate size categories (53 μm , 125 μm , 250 μm , 500 μm) than reference streams (Figure 6).

Reference streams had a greater (though not significant) percent organic matter in the fine particulate size transport categories (53 μm , 125 μm , 250 μm , 500 μm) in spring (Figure 7). In summer and fall, there was no

significant difference in percent organic matter of TOM between burn and reference streams. TOM for both burn and unburned streams was found to be strongly correlated with flow, for all sampling periods ($r = 0.98$).

We analyzed the ratio of BOM/TOM in spring, summer, and fall (as described in Minshall et al. 1983) to see if there were any differences between detritus storage and transport in reference and burn streams. This method of analysis was termed "reach retention, or RR" by Minshall et al. (1983). In spring, reference stream RR was 1.94 and 7.1, while the burn streams RR ratio was 3.87 and 4.15 (1.0 for Cache Creek). In summer RR ratios in the reference streams were 12 and 59, whereas the burn streams ratios were 1.5 and 6.5 (22 for Cache Creek). TOM was a much larger component in the burn streams, causing the RR ratio to be less than the reference streams RR. This was even more pronounced in fall where RR ratios in the reference streams were 210 and

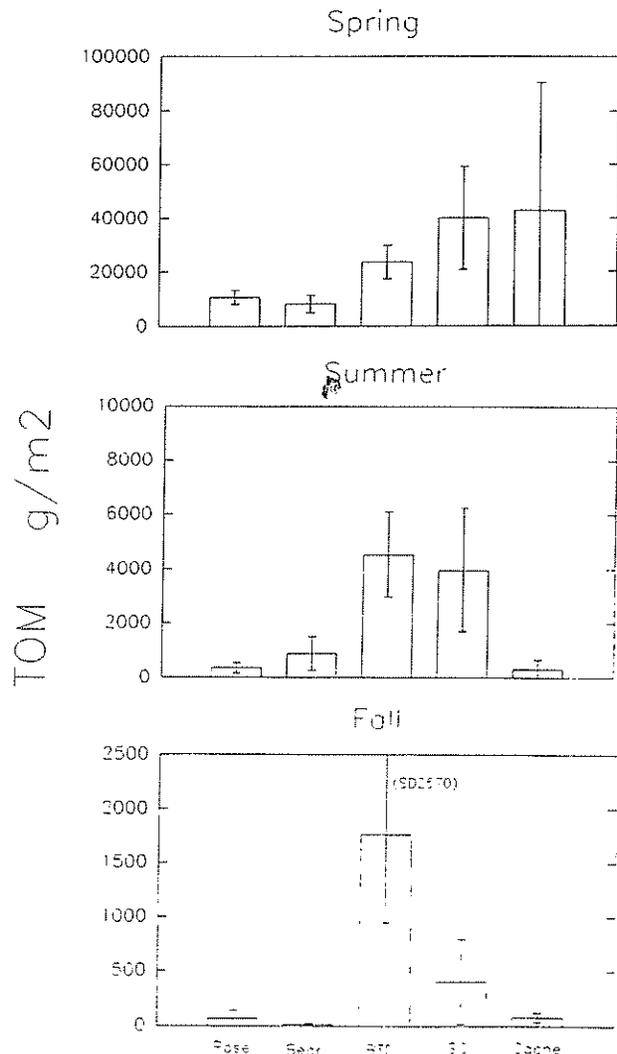


Figure 5. Total TOM (g/m^2) for 1989 by stream. Error bars are + or - one standard deviation. BT = Blacktail Deer, SC = South Cache. $n = 4$ for all samples.

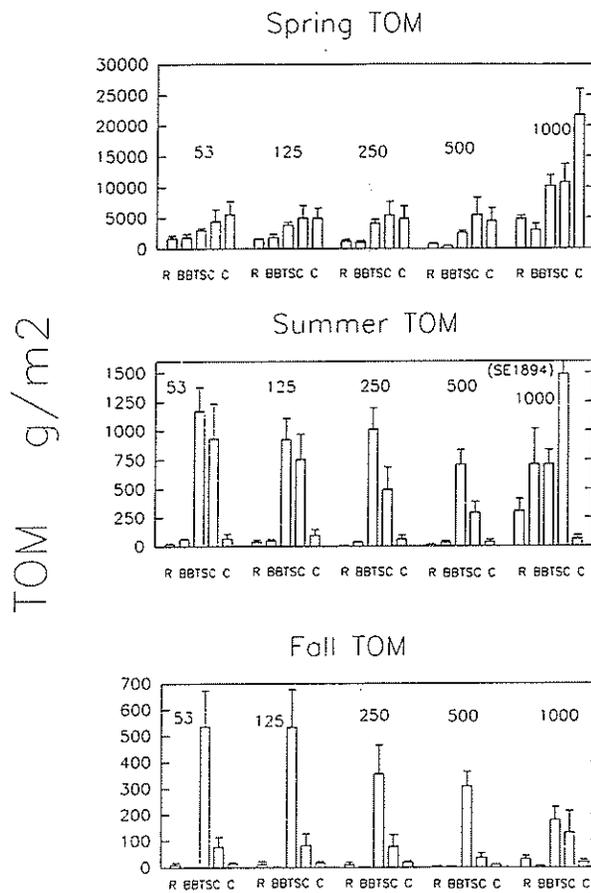


Figure 6. 1989 TOM (g/m²) by size and site. R = Rose, B = Bear, BT = Blacktail Deer, SC = South Cache, C = Cache. Error bars are + or - one standard error. n = 4 for all sizes.

2923 and 8 and 17 in the burn streams (50 in Cache Creek).

Short-term coarse particulate organic matter retention

The two reference streams had higher instantaneous rates of analog removal (k) and shorter analog travel distances, indicating higher retention capacity (Table 4). A regression of "k" values to flow, indicated there was a significant positive relationship between them (r=0.99).

Debris dams were the only significant retention barrier in the reference streams, catching fully 98% and 99% of the released leaf analogs in Rose and Bear Creeks, respectively (Figure 8). Burn streams had more types of retention barriers and a more even distribution in terms of percent flags caught among barriers than reference streams. Some of these other retention devices were sticks, gravel, boulders, and algae. Debris dams accounted for 48% of recovered flags in Blacktail Deer and 40% in Cache (Figure 8). South Cache Creek had no debris dams in its 50 m test section.

Table 4. Number of flags found (out of 300) and maximum travel distance in short-term CPOM retention test. Test performed 9/89 over a 50 m section of each stream. "k" = instantaneous rate of flagging removal. "k" values for reference streams are significantly different from burned streams (p<0.03). () indicate extent of watershed burned.

Stream #	Flags Found	maximum Distance (m)	k
Reference			
Rose	2	3.0	1.4
Bear	2	3.2	1.4
Burn			
Blacktail Deer (100%)	8	50.0	0.06
South Cache (100%)	1	17.7	0.30
Cache (70%)	14	6.3	0.42

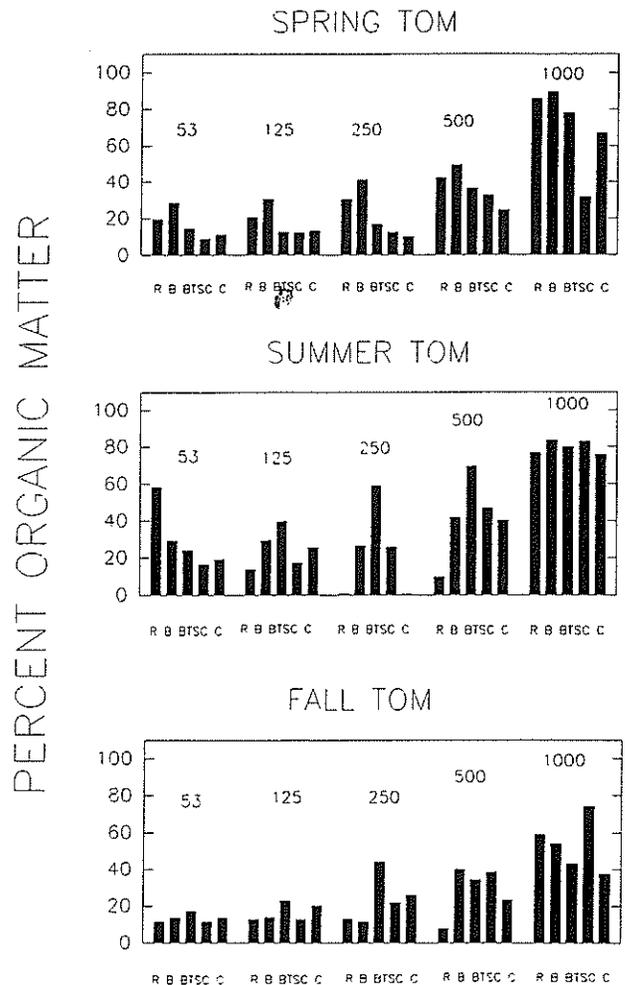


Figure 7. Percent organic matter in TOM by size, season and stream. R.= Rose, B = Bear, BT = Blacktail Deer, SC = South Cache, C = Cache. n = 10 for each size and site.

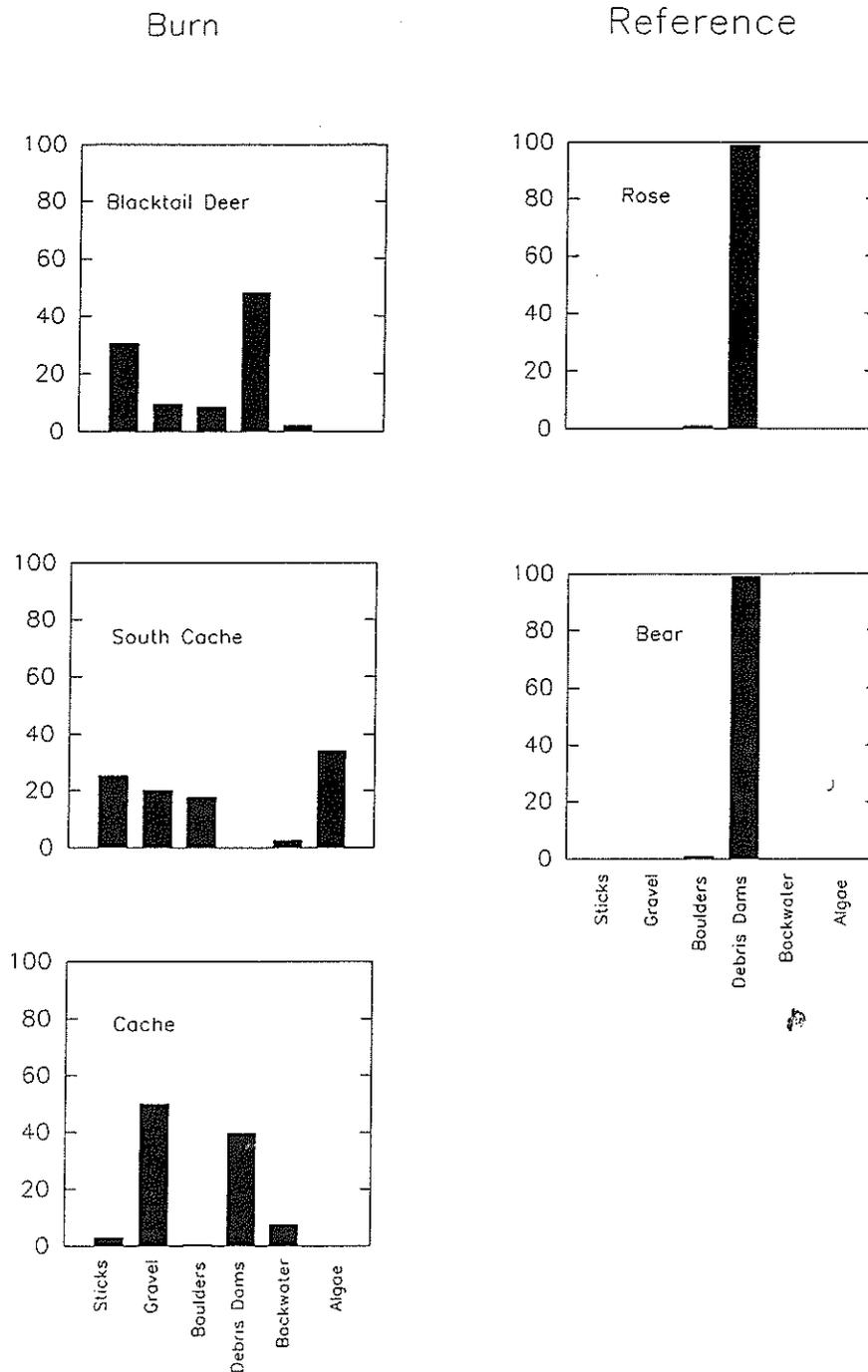


Figure 8. Results of short-term CPOM retention test. percent retention by device and site. N = 300 initially for all sites.

Algae played an important role in retention of CPOM analogs in South Cache Creek, retaining 50% of those released. This was the only stream where this was noted. Sticks accounted for 30%, 25%, and 3.1% of the retained flags, in Blacktail Deer, South Cache and Cache Creeks, gravel retained 10%, 20%, and 50%, respectively.

Long-term coarse particulate organic matter retention

Reference streams retained significantly ($p < 0.003$) more plastic flag analogs after 2.5 months in 300 m, than

burn streams (Figure 9). Rose Creek retained 68% of the 500 released flags, while Bear Creek retained 65%. The burn streams exhibited lower long-term CPOM retention of CPOM analogs, with Blacktail Deer Creek retaining only 13%, South Cache 25%, and Cache Creek 43% in 300 m (Figure 9).

The manner in which the reference streams retained CPOM analogs was somewhat different than that in the burned streams (Figure 9). Within the first 150 m of stream, reference streams retained greater than 50% of the released flags, while the burned streams retained less

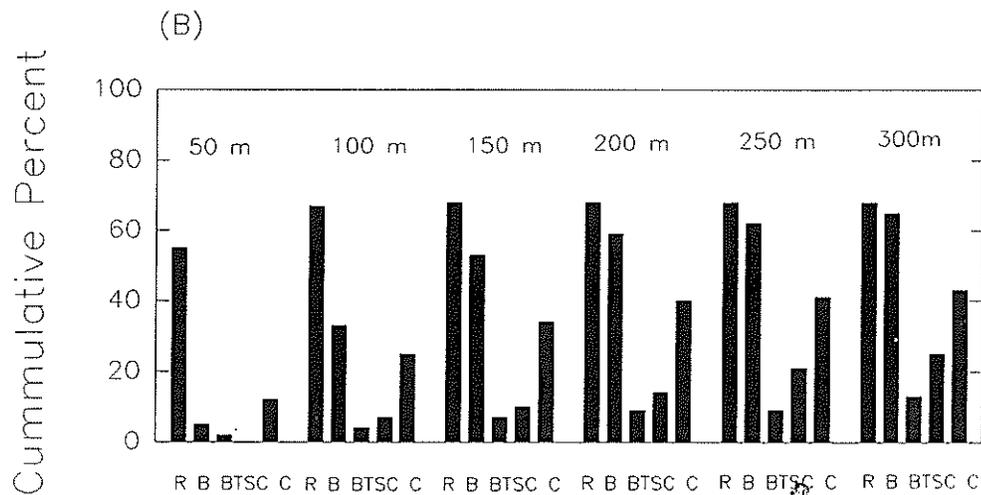
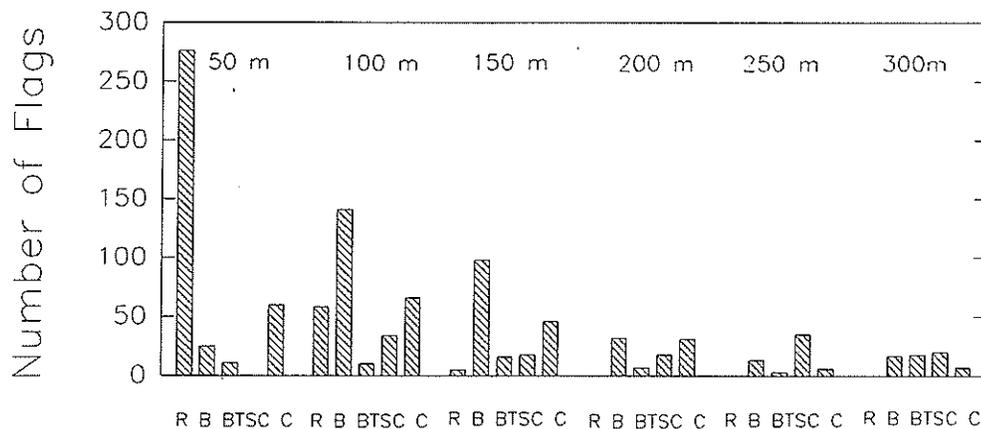


Figure 9. Results of long-term retention CPOM test.

A. Shows absolute number of flags found/50 m.

B. Shows cumulative percent by interval. R = Rose, B = Bear, BT = Blacktail Deer, SC = South Cache, C = Cache.

than 25%. However, a Kolomogrov-Smirnov test performed on reference vs. burned analog numbers, indicated there was no significant difference in retention distributions between reference and burned streams for the entire 300 m ($p < .193$).

Debris dams caught 80% of the released flags after 2.5 months in reference streams, while in burn streams they caught from 40% to 60% (Figure 10). Sticks, gravel, and banks retained 10%, 5% and 10% respectively, in reference streams. In burn streams sticks, gravel and banks retained 20-40%, 3-8%, and 10% respectively.

Number of debris dams

Reference streams had a greater number of debris dams than burn streams. The reference streams had 6.8 and 8.6 debris dams per 50 m of stream, compared to 1.5 and 2.5 per 50 m for the burn streams (6 for Cache Creek).

Flow differences between reference and burn streams

A Mann-Whitney test was performed on log transformed flow data to see if any differences existed between reference and burn streams. Significant ($p < 0.001$) differences existed on all sampling dates in both 1989 and 1990 between reference and burn streams (Table 2). A second Mann-Whitney performed on flows adjusted for area, showed no difference in spring, but a significant difference in summer and fall ($p < 0.017$).

Discussion

Burn streams transported more organic matter in all seasons, particularly in the FPOM category, than reference streams (Table 5). The only difference in BOM appears in the fall where reference streams have 14x more in the 1000- μ m size category. Burn streams exhibit larger flows throughout the year than reference streams.

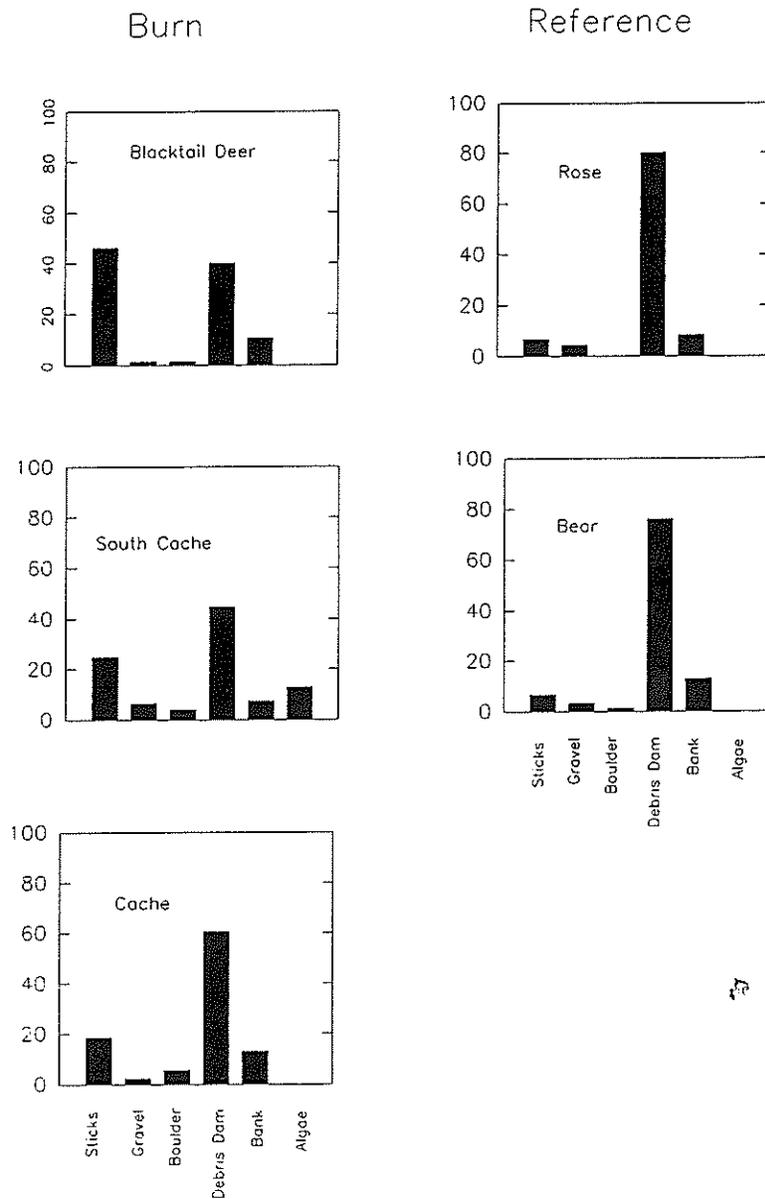


Figure 10. Results of long-term CPOM retention test. Percent retention by retention device and site. N = 500 initially for all sites.

When flows are adjusted for area, burn streams still show larger flows in summer and fall than reference streams. Reference streams had lower travel distances and instantaneous rates of CPOM removal than burn streams in the short-term retention test, with reference streams retaining 98% of the CPOM analogs in debris dams and burn streams retaining only 40-48% in debris dams. In the long-term retention test, reference streams retained more CPOM-analogs and had higher retention efficiencies than burn streams. Reference streams retained 80% of the analogs in debris dams after 2.5 months, while burn streams retained 20-40%. This was apparently because burn streams had fewer debris dams than reference

streams. These results suggest that fire has changed the type and timing of CPOM inputs to streams from the watershed along with changing the nature of retention barriers. This suggests the capacity to retain or store CPOM has been reduced in the burn streams.

Almost without exception Cache Creek falls closer to the two reference streams for any measured retention parameter. Reference streams had 6.8 and 8.6 debris dams per 50 m, while Cache Creek had 6. The reference streams had retention efficiencies of 65 and 68%, Cache had 48%, and the other two burned streams had only 13 and 25%. In the long-term CPOM retention test, reference streams had 80% of the flags caught by debris dams,

Table 5. Summary of findings and test results regarding effects of fire on retention of CPOM and retention barrier dynamics.

Test	Reference Streams	Burned Streams (100%)	Intermediate Burned Stream (70%)
BOM	In fall, reference streams had significantly more organic matter in the CPOM (1000 µm) category than burn streams. BOM is highly variable in all streams at all times.		
TOM	Burn streams had significantly more organic matter in transport (total) and in the fine (53 µm to < 1000 µm ² size category than reference streams in summer and fall.		
Reach retention (BOM/TOM)	535	29	44
Flows (Spring/Fall Q)	393	29	44
Short-term retention test (SIRT) (3hrs.) max. d (m)	3, 3.2	17.7, 50	6.3
k = Inst. rate of flagging removal in SIRT	1.4, 1.45	.064, .3	.422
Retention barriers in SIRT	98-99%	debris dam 0, 48% sticks 25, 30% gravel 10, 20%	3% 50%
Long-term retention test (LTRT) (2.5 mo.) total no. flags retained	326, 339	65, 125	216
Retention efficiency (LTRT)	65, 68%	13, 25%	43%
Retention barriers in LTRT	80% 10% 5% 10%	debris dam 40, 45% sticks 22, 40% gravel 2, 6% bank 7, 9%	60% 18% 3% 13%
Number of debris dams (in 50 m)	6.8, 8.6	1.5, 2.5	6

versus 60% in Cache Creek. With the exception of the first sampling after the fire (April 1988), Cache Creek had total and size of transported organic matter values closer to the reference streams than the burn streams (Figures 5,6).

Initially, this stream was identified as 100% burned. However, it was found that only 70% of the canopy burned, according to GIS mapping done in late 1989. Further, the 30% of the watershed that did not burn was located approximately 200 m above the study location. This may account for the apparent inconsistency in detritus retention between this site and the other two 100% burned watersheds. As Minshall et al. (1989) suggested, the intensity and extent of fire in a watershed affects the response of the stream.

Comparison with results of other researchers

The pattern of more debris dams in reference streams and fewer in the burn streams fits the pattern found in other studies of disturbed and undisturbed watersheds (Trotter 1990, Bilby and Likens 1980, Molles 1982, Webster et al. 1990). In these studies of either fire or logging in forested watersheds, debris dams were more

numerous in undisturbed streams. This is the same pattern we observed in our streams, with reference streams having more debris dams than burned streams (Table 5.)

Britton (1990) found benthic organic matter to be highly variable in burned and unburned streams in South Africa. Webster et al. (1990) found estimation of detrital storage to be difficult due to its patchy distribution. We also found benthic organic matter standing crop to be highly variable in both reference and burn streams (Figures 2,3). Golladay et al. (1987) found benthic organic matter to be very clumped and hence quite variable. However, they did note that the logged streams had significantly less benthic organic matter. We did not find significant differences in BOM between burned and unburned watersheds in our study, except during the fall in the 1000 µm fraction. As noted earlier, the composition of CPOM between the reference and burn streams was quite different. CPOM in reference streams consisted of dead leaves, needles, and twigs, while CPOM in burn streams was mostly charcoal. We suspect the modified Hess sampler does not adequately sample benthic organic matter, especially at low flow periods. In the modified Hess, the collector bag is 10 cm above the bottom of the sampler. So in late summer or fall when

streams are at their low flow period, the collector bag may be right at the water line or even above it. Additionally, in summer and late fall benthic material dislodged from within the Hess is not "pushed" into the collector bag because of low water velocities present in many streams at this time of year. This situation was observed during our study. Other researchers may have avoided this by using Surber samplers or other samplers that sit directly on the bottom of the channel with no mesh in front of them to reduce already low water velocities.

BOM standing crop was not correlated with watershed area or flow. Petersen et al. (1989) also found no correlation between detritus standing crop and either flow on the date of sampling or maximum flow. They suggested there was no significant monthly or seasonal pattern in total detritus standing crop in their study stream.

In terms of TOM, burn streams clearly transported more FPOM than reference streams (Figure 5). Burned streams transported more material in all sizes for all sample periods. The greatest proportion by weight was in the fine particulate fraction (53 μm to <1 mm). The predominance of FPOM over CPOM was especially true for the burned streams. Domination of transported seston by FPOM also was noted in studies of unburned streams by Naiman and Sedell (1979) and Minshall et al. (1983).

TOM usually is strongly correlated with discharge (Gurtz et al. 1979, Cuffney and Wallace 1989, Webster et al. 1990). Cuffney and Wallace (1989) noted that maximum discharge was the only parameter which adequately predicted FPOM export. They also noted that the relationship between discharge and export of CPOM was not as strong or consistent as those for FPOM. TOM in our study was strongly correlated with discharge ($r=0.98$) in both reference and burn streams.

Webster et al. (1990) and Speaker et al. (1988) using the same methodology as in this study, reported maximum travel distances to be close to ours for undisturbed watersheds. They showed greater travel distances in disturbed (logged) watersheds as did we in burned watersheds. They had maximum travel distances in undisturbed streams of 1.3 m, where we had maximum distances of 3.2 m. In their disturbed streams the maximum travel distances were 2.2 m, while ours were 6.3 to 50 m in burned streams. It should be noted that Webster et al. (1990) were sampling 13 years after disturbance, while we were sampling 1 and 2 years after disturbance.

Minshall et al. (1983) reported BOM/TOM ratios as reach retention of 923 and 441 for headwater streams in Idaho and Michigan. We had reach retention values of 535 for reference streams and 12.9 for burn streams. This shows the dominant influence transport, as TOM, has in burn streams. While in the reference streams benthic storage played a much more important role than TOM.

Source of transported organic matter in burn streams

It is widely accepted that fires increase water yields in streams. Increased overland flow (run-off) and reduced evapotranspiration and interception, accompanied by elevated snow accumulation, add more water to the stream throughout the year (Christensen et al. 1989). Fetter (1988) stated that reduced evapotranspiration implies increased runoff and groundwater infiltration. He noted also that conversion of one plant cover to another can increase streamflow by several hundred percent. Knight and Fahey (1985) noted actual evapotranspiration accounted for 33-95% of total annual precipitation in their study of water outflow from lodgepole pine forests. They found transpiration accounted for 50-60% of evapotranspiration, with significant transpiration occurring during the spring drainage period.

Burn streams had significantly higher flows than reference streams in summer and fall, but not spring, when adjusted for watershed area (Table 2). Bear Creek, a reference stream has a watershed area of 4 km², while South Cache and Cache Creek have watersheds of 4.7 and 4.1 km² respectively. So, even though these three watersheds are fairly close in size and water generating potential, the flows in Bear Creek are an order of magnitude lower in all three seasons than Cache and South Cache Creek. We proposed examining the ratio of spring to fall flows as a way of looking at relative affects. In reference streams it ranged from 749 to 522, while for burn streams the ratio ranged from 74 to 15 for 1989. In 1990 the ratio in the reference streams was 118 to 183, and in burn streams it was 5 to 28. The pattern was similar when area adjusted flows were used in this convention. These ratios indicate noticeable increases or inputs of water in the burn streams outside the snow melt runoff period. This may be due, in part, to reduced evapotranspiration from dead trees in the watershed, especially in the riparian zone. Live trees remove water from the riparian water table in the reference streams and lose much of it through transpiration. To test this idea we conducted our fall sampling during October of 1990. We expected there to be less difference in flow between the reference and burn streams after prime transpiration had ceased in the reference streams. No observable increases in flow in the reference streams occurred. As Knight and Fahey (1985) observed though, a significant transpiration period occurs in early spring, which may deplete groundwater outflow later in the fall. This may account for the lack of flow difference in reference streams after cessation of transpiration.

Increased detritus in transport in the burn streams is most likely coming from overland transport and from deep in-channel storage sites as erosional and transport capacity is increased after a fire, due to increased water yield. Webster et al. (1990) found a pattern of increased TOM in logged watersheds. They determined that in-

creased TOM was coming from deep in-channel organic matter storage. In addition to scouring of in-channel organic matter, increased TOM may also result from reduced channel heterogeneity, hence reduced retention. Webster et al. (1987) noted organic matter retention increased with increasing channel roughness and substrate complexity. The more heterogenous a stream channel the higher its retention capacity. Fire may, through increased flow, restructure channel morphology, and thereby reduce channel heterogeneity.

Given the fire intensity in these drainages, CPOM was significantly altered. This may be another explanation of why burn streams had greater amounts of FPOM in transport than reference streams. Secondly, we would expect FPOM to move at a faster rate than CPOM, given its low mass and size. Webster et al. (1987) noted seston retention was directly related to particle size. Their data showed smaller particles were more easily entrained and traveled further. This coupled with altered particulate material, could increase the rate and amount of FPOM delivery to streams in burned watersheds. However, Harmon et al. (1986), found large severe fires added massive amounts of coarse woody debris to the stream, because large branches and stems were not consumed by fire.

Quality and consequences of detritus changes in burned streams

Our data indicate the amount and percentage of organic matter (detritus) in transport has increased significantly, especially coarse particulate (>1 mm) organic matter in the burned streams. Reduced amounts and percent organic matter in disturbed streams can impact the aquatic organisms present and adapted to a particular quantity, quality, and input regime of organic matter (Rounick and Winterbourn 1983). Minshall et al. (1989) speculate that given changes in the quantity and quality of organic matter input, the presence and importance of certain aquatic insects should change after a fire.

As a consequence of fire, the amount and percent of TOM in the fine particulate category (53 μm to 1 mm) increased. As particle size of detritus decreases, microbial activity increases, apparently from the greater density of microbes on materials of greater total surface area (Petersen et al. 1989). Our data indicate burn streams have more FPOM in transport than unburned streams. If microbes are selecting for material of greater surface area, irrespective of whether it is burned or not, then increased microbial activity may be conceivable. This may mean that given increased microbial activity, coupled with elevated water temperatures and increased light, stream productivity could be enhanced after fire.

Input and fate of large woody debris in burned streams

With the exception of Cache Creek, 100% burned streams have fewer debris dams. Increased discharge resulting from fire may have washed out debris dams and this may be a partial explanation of why 100% burned streams have fewer debris dams than reference streams. However, it has been our observation that, although debris dams are made up of large diameter woody debris (tree boles), an equally important role is played by smaller sized limbs, twigs, and needles. These smaller sized particles act as the grout in debris-dam complexes by filling in the interstitial spaces, increasing the dam's retention capacity. Speaker et al. (1988) referred to this phenomena of small woody debris, such as branches, sticks and twigs, increasing retention, as a sieve. Indeed, our data (Table 5) suggest that the number of debris dams in burned streams is reduced relative to the number in reference streams and the amount and percent of CPOM is greatly reduced. In combination these could lead to reduced organic matter retention and storage capacity.

Minshall et al. (1989) hypothesized that in the first two years after fires, one would find a decline in the amount of woody debris. They suggested that after a 2-3 year decline in woody debris input, a net increase would start to take place as the standing fire-killed snags fall into the streams and forest revegetation begins to take place. Hedin et al. (1988) suggested that this large woody debris decline continues for up to 25 years before a net increase takes place. Our data for the first two years following the Yellowstone fire shows a net decline in debris dams and CPOM as suggested by Minshall et al. (1989).

Some studies have shown or suggested that large woody debris (LWD) increases significantly immediately after a fire (Harmon et al. 1986, Lawrance 1991). We feel LWD is added during and immediately after the fire, but this material, due to its size relative to the size of the stream, generally ends up bridging the stream. Minshall et al. (1989) in their study of post-fire effects on streams in Idaho, observed incorporation of LWD as functioning debris dams, at about 10 years. Apparently at least 10 years are necessary (in the Intermountain region) for wind, decay, and channel re-positioning to occur, before LWD becomes incorporated into the stream debris system.

Fire intensity and its effect of streams

In a report of fire effects on BOM and TOM, Britton (1990), found no significant difference between unburned and burned streams. Britton (1990) stated that the burn he studied was a "cool ground" fire and not an intense canopy fire. In the Yellowstone fires, intense canopy fires were common. This suggests that the intensity of a fire, whether it burns everything or only the material on the ground, greatly determines the impact of fire to

streams. When a cool or less intense fire does not remove or significantly alter the riparian vegetation, a short-term, low impact can be predicted for the stream. If, on the other hand, an intensive and extensive fire occurs and the riparian vegetation is significantly altered, a more pronounced change and longer lasting impact on streams is likely to occur.

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Diatom Assemblages in Cache Creek, Yellowstone National Park Following the 1988 Wildfires

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Abstract. The Cache Creek catchment was one of the more extensively burned areas of the 1988 wildfires, with over 80% of the catchment being burned. We examined temporal changes in diatom assemblages at five sites located on 1st through 4th order streams. Samples also were collected at Rose Creek, a 2nd order stream, which was unburned. Composite diatom samples were collected in October 1988, and August 1989, 1990, 1991 and 1992. Results were expressed in terms of species richness (S), Shannon's diversity (H'), Simpson's Index (C), changes in individual taxa, Kendall's Coefficient of Concordance (W), and Principal Components Analysis (PCA). Species richness and diversity were reduced in Cache Creek in the years following 1988, being especially evident in the 1st and 2nd order Cache streams. Substantial increases were observed in the relative abundances of *Navicula permitus*, *Cymbella sinuata*, and *Nitzschia inconspicua* at Cache Creek sites relative to Rose Creek. Kendall's W indicated among year similarities ranging from 0.41 in South Fork Cache Creek to 0.69 in 1st order Cache Creek. Rose Creek had a Kendall's W of 0.47. PCA results showed diatom assemblages in 1988 were separate from the following years, and Rose Creek was distinct from the Cache Creek sites. The PCA results suggest that Cache Creek diatom assemblages are still changing, probably reflecting temporal changes in local environmental conditions. We suggest that assemblages will continue to change as terrestrial/riparian vegetation increases and instream environmental conditions stabilize.

Keywords: Community structure; Diatoms; Disturbance; Streams; Wildfire; Yellowstone National Park.

Introduction

The Greater Yellowstone Area ecosystem experienced numerous and extensive wildfires during 1988. Indeed, over 32% of Yellowstone National Park stream systems, involving 20 separate river basins, were affected

by these wildfires (Minshall and Brock 1992). Affected streams ranged in size from 1st to 5th order (Minshall and Robinson 1993). The Cache Creek catchment was one of the more extensively burned areas in the park. Cache Creek has experienced dramatic changes in stream morphology and other physical properties since the 1988 fires (Minshall and Robinson 1993), thus providing the opportunity to document temporal changes in diatom assemblages along the longitudinal length of the same stream system.

Diatoms (Bacillariophyta) are often the predominant algae in oligotrophic stream systems draining montane areas. Freshwater diatoms are influenced by, and highly sensitive to, a variety of physical and chemical factors (Molloy 1992) and thus are excellent indicators of environmental change in streams. We hypothesized that diatom assemblages would reflect the degree of physical disturbance, resulting from the wildfires, experienced by streams of different size in the Cache Creek catchment.

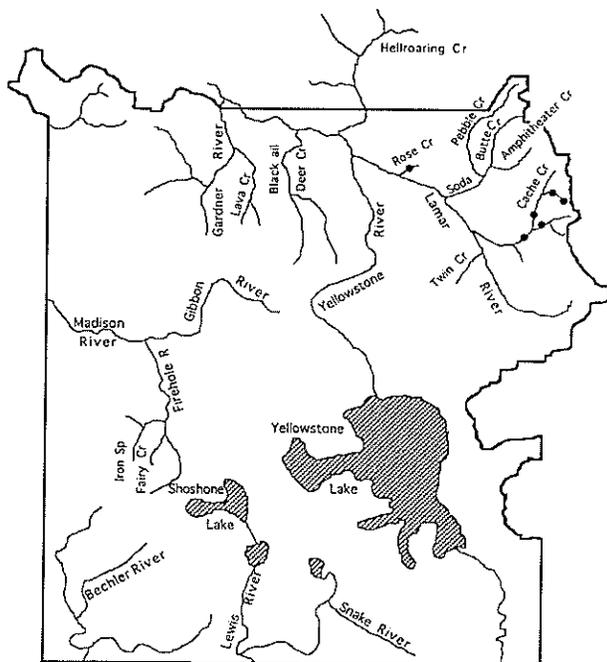
The present study examined diatom assemblages from five sites along Cache Creek and one from Rose Creek, an unburned catchment, within the Lamar River drainage in the northeast corner of Yellowstone National Park from 1988 through 1992. Four stream sizes (1st-4th order) were surveyed on Cache Creek. The primary objective of the present study was to document the temporal changes in diatom assemblages following the 1988 wildfires in Cache Creek relative to temporal changes in physical environments among study sites. We compared these observed changes in diatom assemblage structure and stream morphology in Cache Creek streams to those measured in unburned Rose Creek.

Methods

Five sites, comprising 1st through 4th order sized stream reaches, were located along Cache Creek (Figure 1). An additional site was located on 2nd order Rose Creek, an unburned catchment (Table 1). Cache Creek study

sites ranged from having 39% (South Fork Cache Creek) of the catchment burned to 71% burned at the 2nd order site. Stream gradients ranged from 8-13% in the 1st and 2nd order sites to 2-3% in the 3rd and 4th order sites (Table 1). Minshall and Robinson (1992) have published complete physical and chemical descriptions for the study sites.

Physical characteristics used to determine habitat changes among years included the range in annual stream temperature, bankfull width, mean embeddedness, mean bottom water velocity, mean water depth, mean substrate size, median substrate size, width:depth ratios, channel area change, and channel area ratios (present year divided by previous year) between years. The average amount of channel area change, channel area ratios, bankfull widths, and width:depth ratios were determined from five permanent cross-sectional transects located at each site. Transects were placed about 50 m apart along the stream at each site and profiles recorded once each year. Mean embeddedness, water depth, bottom velocity, and substrate size were recorded each year at 100 random locations situated along a 200-m reach of each stream. Temporal change for each measure was estimated using Coefficients of Variation (CV) based on the yearly means (i.e., $N = 5$ years for CV). These ten CV's were summed for an overall indication of habitat change among years for each site and regressed against the percent (%) catchment burned.



Yellowstone National Park

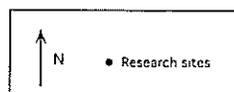


Figure 1. Map of study site locations.

Table 1. General physical characteristics of study sites.

Stream	Order	Catchment Area (ha)	Percent Burned	Slope (%)	Discharge (m ³ /s)
Cache	1	138	64	13	0.001
Cache	2	377	71	10	0.004
Cache	3	12052	68	2	0.184
SF Cache	3	5780	39	3	0.280
Cache	4	17994	59	2	0.386
Rose	2	2390	0	8	0.009

Diatom samples were collected from each stream site in early October 1988, and August 1989, 1990, 1991, and 1992. The October 1988 samples were collected within two weeks to a month following the fires. Composite diatom samples were collected from stone substrates comprising riffle, run, and pool habitats at each site, preserved with 5% formalin, and returned to the laboratory. The composite sample was boiled in concentrated nitric acid, rinsed, mounted in Naphrax mountant, and examined under 1000X oil immersion using a Zeis RA microscope with Nomarski optics (St. Clair and Rushforth 1976). Counts of 600-1000 diatom valves were made from each slide to determine relative density.

Diatom assemblages were analyzed in terms of species richness, Simpson's Index, and Shannon's Diversity (H') using relative abundance data for each site and year. In addition, year to year changes in diatom assemblages were examined for each site using Principal Components Analysis (PCA) based on the 20 most abundant taxa (Statsoft 1991). These taxa generally comprised at least 5% of the assemblage at most sites. Similarity in diatom assemblages among years for each site was determined using Kendall's Coefficient of Concordance (Zar 1984).

Results and Discussion

Summed Coefficients of Variation (CV's) of the physical measures ranged from a low of 1.41 at Rose Creek to a high of 3.66 at 1st order Cache Creek (Table 2). Summed CV's decreased from 3.66 in 1st order Cache Creek to 2.05 in the 4th order Cache site, suggesting that smaller streams experienced greater temporal influence from the wildfires than larger streams. The smaller streams of Cache Creek showed substantially higher CV's for channel characteristics than the larger stream sites and Rose Creek. There was a significant positive correlation of summed CV scores against the % catchment burned ($r^2 = 0.71$) (Figure 2), suggesting a differential physical response of these streams to different degrees of fire. The absence of sideslope and riparian vegetation enhances the occurrence of overland flow, surface erosion and input of sediments into streams (Tiedemann et al. 1979). Essentially, the increase in overland flow and input of fine sediments following wildfire results in increased physical disturbance to streams

Table 2. Mean values and among year CV's for important habitat characteristics for each study site.

Stream	Order		Annual Temp. (°C)	Channel Area Change (m ²)	Ratio Channel Area	Width/Depth Ratio	Bankfull Channel Width (cm)	Embedded-ness (%)	Near-bed Velocity (cm/s)	Water Depth (cm)	Substrate Size (mean) (cm)	Substrate Size (median) (cm)	Summed CV's
Cache	1	mean	16.3	1.14	1.01	141.9	704.8	37.0	0.1	5.7	7.2	3.6	3.66
		CV	0.08	0.62	0.03	0.64	0.49	0.32	0.38	0.34	0.27	0.49	
Cache	2	mean	20.3	2.54	1.04	83.9	764.8	37.0	0.2	9.4	8.4	5.7	3.27
		CV	0.20	0.69	0.03	0.59	0.56	0.19	0.29	0.07	0.15	0.50	
Cache	3	mean	20.5	8.5	1.04	242.6	4607	32.0	0.3	19.4	14.0	10.1	3.21
		CV	0.09	0.77	0.10	0.23	0.12	0.21	0.94	0.11	0.28	0.37	
South Cache	3	mean	20.5	1.57	1.04	106.7	1707	31.0	0.3	16.2	16.2	10.2	2.24
		CV	0.22	0.54	0.07	0.21	0.17	0.11	0.31	0.09	0.25	0.27	
Cache	4	mean	19.3	1.03	1.00	120.3	2052	43.0	0.3	18.2	16.7	11.5	2.05
		CV	0.13	0.48	0.03	0.30	0.03	0.26	0.22	0.21	0.10	0.28	
Rose	2	mean	12.0	0.36	1.01	40.7	416.2	31.0	0.2	10.3	12.7	8.2	1.41
		CV	0.10	0.38	0.02	0.09	0.04	0.15	0.24	0.10	0.13	0.15	

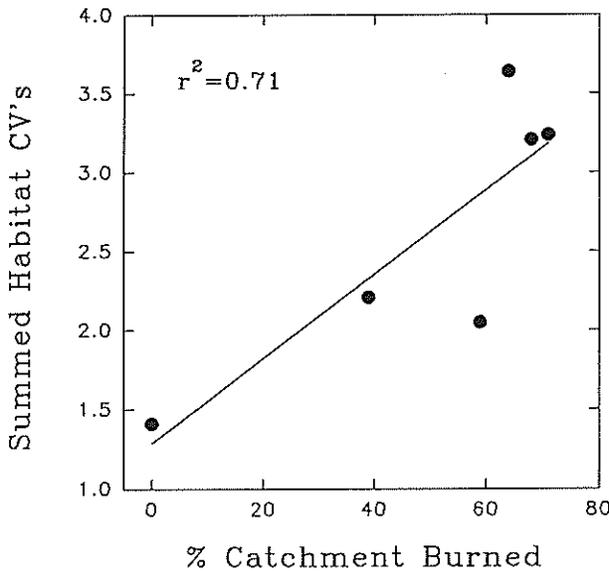


Figure 2. Regression scattergram of summed coefficients of variation for physical measures against the percent catchment burned. See Table 2 for list of physical measures used in analysis.

through channel scouring, increased instream flow, and the redistribution of substrata (Tiedemann et al. 1979, Minshall et al. 1989, Minshall and Robinson 1993, Minshall and Brock 1992).

Sites located in more extensively burned areas displayed greater amounts of temporal physical change than those in less extensively burned catchments, although being influenced by stream size. To illustrate, Figure 3 shows the respective amount of channel change for the six study sites, with a channel change ratio of one indicating no channel change from the previous year. Channel morphology for Rose Creek remained essentially unchanged over the five years of study (Figure 3), whereas most of the Cache Creek sites showed major

changes in channel morphology. Indeed, the 1st and 2nd order sites displayed major channel changes in 1989, whereas the 3rd order sites changed dramatically in 1991 and 1992. However, 4th order Cache Creek showed little channel change during the five years of study. The less channel change for 1st order Cache Creek relative to other Cache Creek sites was simply a result of its small size. In general, future temporal changes in channel stability should reflect vegetation recovery on catchment side-slopes (Minshall and Brock 1992).

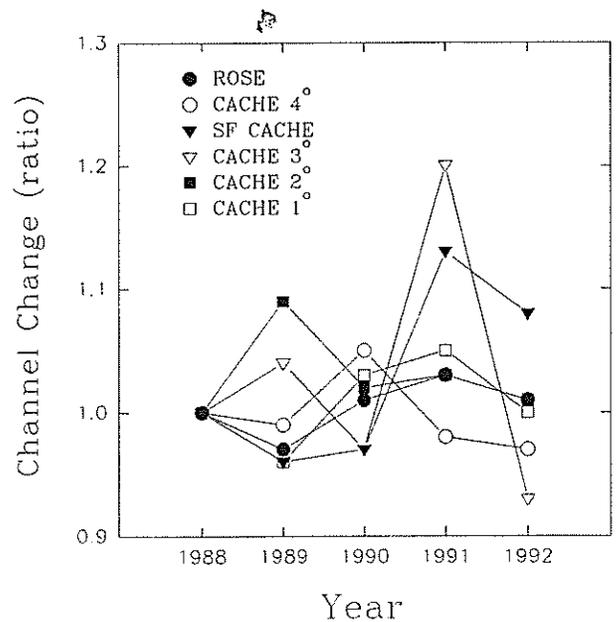


Figure 3. Relative amount of channel change over the study period for the study sites. Ratio determined from cross-sectional channel profiles (see Methods) and based on current year divided by previous year. A ratio of one would indicate no change from current year to previous year.

In general, species richness and Shannon's diversity (H') decreased, and Simpson's dominance index increased in all Cache Creek sites except the 4th order site and Rose Creek the 1st year following the fire (Figure 4) suggesting a few diatom taxa predominate in the burned sites. H' increased in 1990 then decreased for most Cache sites and Rose Creek in 1991 and 1992, however no clear patterns emerged for species richness or Simpson's index. Greater insight into assemblage changes were derived at the taxon level, perhaps because of the relatively high richness of diatom assemblages in general.

Principal Components Analysis (PCA), based on the relative abundance of the 20 most abundant taxa, provided a quantitative expression of the degree of temporal change in assemblage structure. The first two PCA-axes explained 62% of the variation among sites and years. PCA-1 was loaded highly with the diatoms *Nitzschia hantzschiana*, *Synedra ulna*, *Fragilaria vaucheriae*, *Nitzschia dissipata*, and *Gomphonema parvulum*. PCA-2 was loaded highly with the diatoms *Navicula cryptocephala* var. *veneta*, *Navicula permitis*, *Nitzschia inconspicua*, *Rhoicosphenia curvata*, and *Cocconeis placentula* var. *lineata*. The PCA results clearly show that diatom assemblage structure changed dramatically in the Cache Creek sites following the fires, as indicated by the 1988 samples being grouped distinctly from post-fire

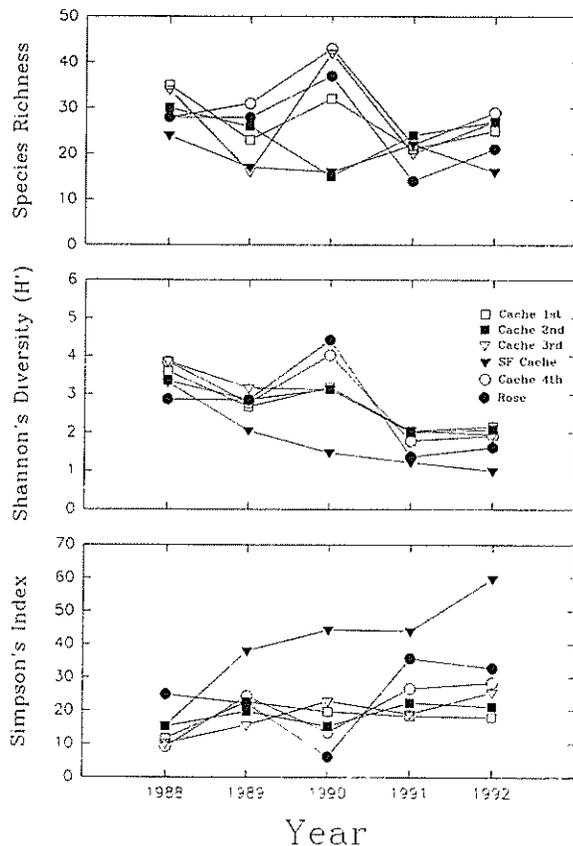


Figure 4. Species richness, Shannon's diversity (H'), and Simpson's dominance index for the study streams during the five years of study.

samples (Figure 5). In contrast, little change was observed for the unburned Rose Creek site based on the PCA results. These data suggest that the effects of fire on diatom structure may be reflected better via taxonomic differences among years than in community indices.

Analysis of specific taxon changes over time revealed increases in the relative abundances of *Cymbella sinuata*, *Navicula permitis*, *Nitzschia inconspicua*, and *Rhoicosphenia curvata* in Cache Creek relative to Rose

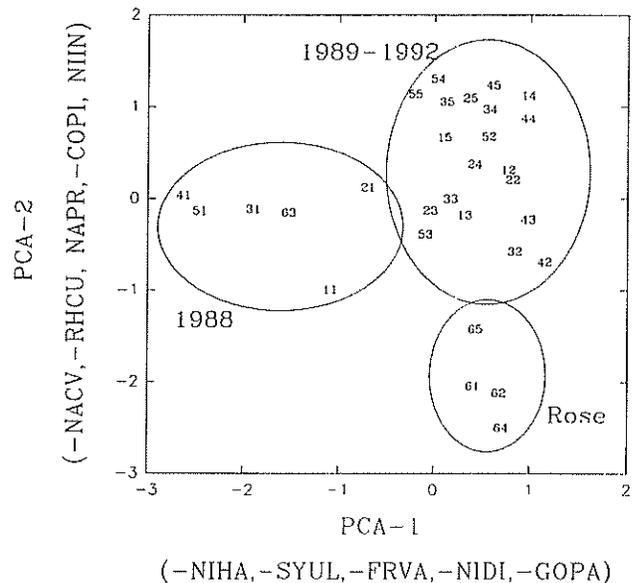


Figure 5. Scattergram of site scores from Principal Components Analysis (PCA) based on the 20 most abundant (as percent) diatom taxa found in the samples. Diatom species are notated; where NIHA = *Nitzschia hantzschiana*, SYUL = *Synedra ulna*, FRVA = *Fragilaria vaucheriae*, NIDI = *Nitzschia dissipata*, GOPA = *Gomphonema parvulum*, NIIN = *Nitzschia inconspicua*, NAPR = *Navicula permitis*, COPI = *Cocconeis placentula* var. *lineata*, RHCU = *Rhoicosphenia curvata*, NACV = *Navicula cryptocephala* var. *veneta*. Sites abbreviated on figure where the first number represents site as in Table 1 and the second number is the year of study as 1 = 1988, 2 = 1989, 3 = 1990, 4 = 1991, and 5 = 1992. First two axes explained 62% of the variation among sites and years.

Creek following the wildfires (Figure 6). *Rhoicosphenia curvata* then decreased in relative abundance in 1991 and 1992 in Cache Creek. *Navicula permitis* and *Cymbella sinuata* continued to increase in relative abundance in 1992, four years after the fires. Both *N. permitis* and *N. inconspicua* are extremely small adnate diatoms and are probably highly resistant to physical disturbance. The apparent increase in disturbance frequency and magnitude in the burned sites maintain the predominance of disturbance favored taxa at these sites, even after four years. We expect diatom assemblage structure to change as riparian and terrestrial landscapes recover, reflecting changes in physical habitats such as solar input/regime and decreases in the frequency and magnitude of within stream disturbances, e.g. stabilization of riparian areas and stream channels.

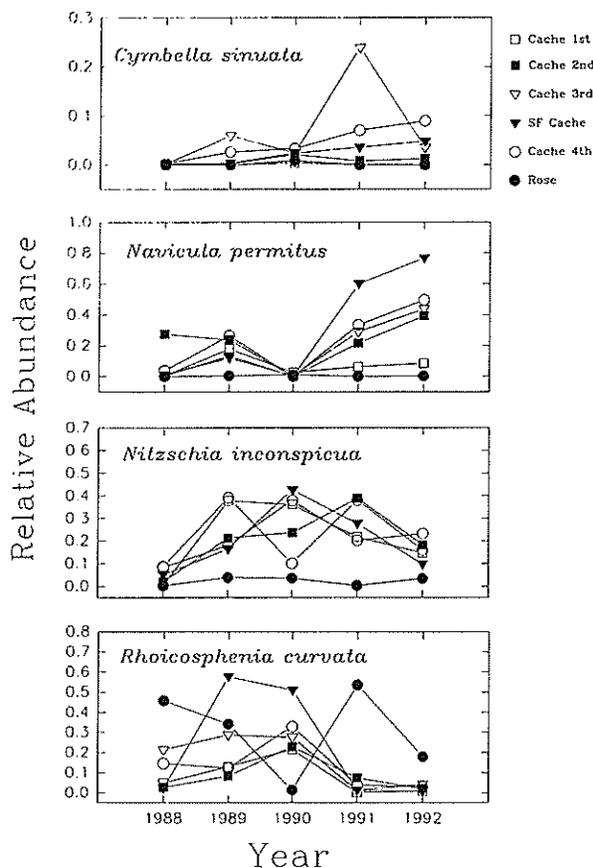


Figure 6. Relative changes in the diatoms *Cymbella sinuata*, *Navicula permitus*, *Nitzschia inconspicua*, and *Rhoicosphenia curvata* across the five years of study.

Kendall's Coefficient of Concordance (W), based on the 20 most abundant taxa, was calculated for each site over the five years of study. Kendall's W ranged from a low of 0.41 for South Fork Cache Creek to a high of 0.69 for Cache Creek 1st order. Elimination of 1988 from the Cache Creek data dramatically increased Kendall's W values, further suggesting most changes occurred following 1988. A significant positive correlation existed between Kendall's W and respective summed CV's of habitat measures ($r^2 = 0.53$) (Figure 7). These data suggest that the more disturbed (extensively burned) sites displayed greater similarity in diatom assemblages among years following the fires. These data, in conjunction with the low diversity (H') in the more disturbed streams, imply that streams draining extensively burned areas in the Cache Creek catchment have yet to stabilize physically. We hypothesize that recovery in these disturbed streams will reflect the recovery of the adjacent terrestrial landscape.

Acknowledgments. Numerous individuals have assisted in the collections, processing, and analysis of the diatom samples and physical data over the study period, especially G. T. Boltz, D. G. Carty, P. D. Dey, D. L. Mahony, M. J. McIntyre, J. M. Minshall, G. C. Mladenka, D. C. Moser, C.

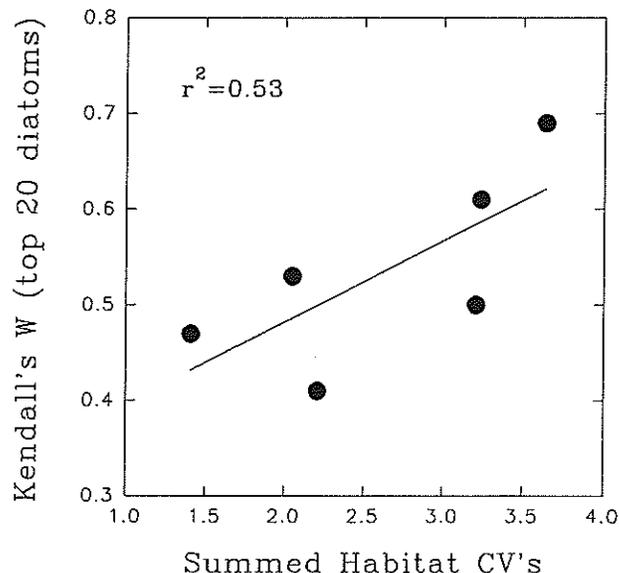


Figure 7. Scattergram of Kendall's (W) Coefficient of Concordance based on the 20 most abundant diatom taxa over the five years of study against the summed coefficients of variation for the physical measures as described in Table 2.

A. Nelson, B. E. Olenick, S. E. Relyea, and R. L. Vannote. T. V. Royer and two anonymous reviewers commented on an earlier draft of the manuscript. We thank R. E. Gresswell and R. D. Jones of the U.S. Fish and Wildlife Service and J. D. Varley of the National Park Service for their efforts to facilitate our work in Yellowstone National Park. Funding for the project was provided by the National Park Service, National Science Foundation, Idaho State University, and Brigham Young University.

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Response of Benthic Macroinvertebrate Populations in Cache Creek, Yellowstone National Park to the 1988 Wildfires

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Abstract. Benthic macroinvertebrate populations were monitored yearly from 1988-1992 at six burned sites in Cache Creek, Yellowstone National Park (YNP) and 4 unburned (reference) sites to examine response to wildfire. Benthic macroinvertebrate responses were correlated with environmental variables using canonical correspondence analysis. Examined taxa responded to post-fire conditions in an individualistic manner. Individual responses also differed according to stream size. Most taxa exhibited either an initial decrease in abundance and biomass during the first post-fire year, followed by a recovery (increase in abundance and biomass) in years 2-4 or a decrease followed by no recovery. The primary factors controlling the response of taxa were physical changes in stream habitat and alteration of resource availability. Taxa that display a wide range of physical habitat preferences such as *Baetis bicaudatus* and *Zapada columbiana* appear to be best adapted to the conditions found in post-fire streams. Taxa that exhibit habitat requirements for stable riffles or slower current velocities responded with a decline in abundance and biomass following the wildfires.

Keywords. Wildfire; Disturbance; Stream; Benthic macroinvertebrate; Population; Environmental variables; Yellowstone National Park.

Introduction

The 1988 Yellowstone wildfires provided an opportunity to assess the impact of whole catchment disturbance on stream macroinvertebrate populations and communities. In this study we examined the response of stream macroinvertebrate populations in 1st through 4th order streams (spatial scale) for four years (temporal scale) following the 1988 Yellowstone wildfires. Macroinvertebrates are of importance to the overall ecosystem because they are the trophic base of aquatic systems, representing the primary and secondary consumer trophic levels that support the salmonid fishery.

Most studies of stream responses to fire have focused on community level parameters such as diversity, richness, and functional feeding groups (Minshall et al. 1989, Minshall and Brock 1991, Richards and Minshall 1992). Little is known about how individual populations in streams respond to catchment level fire. The population level of ecological organization may prove to be the proper scale at which to address the effects of fire on stream macroinvertebrates, particularly if species respond in an individualistic manner. It is well known that stream macroinvertebrates exhibit species-specific habitat preferences and that some taxa are better "adapted" to certain conditions than others, e.g. *Baetis* sp. is known to thrive in streams with highly variable flow regimes (Robinson et al. 1992).

Fire in the catchment areas of a stream can alter benthic macroinvertebrate populations by removal of riparian vegetation, resulting in the decline of detritivorous primary consumers. Increased runoff and sedimentation resulting in harsh physical conditions for in-stream inhabitants is also a consequence of wildfire on stream systems (Minshall et al. 1989). Community level descriptions of stream responses to wildfire disturbance may not be adequate if they don't parallel trends of key individual species. Considering the post-fire response of individual taxa will allow differentiation of those which respond in an individualistic manner and grouping of those which respond in a similar fashion to wildfire disturbance.

Analysis of disturbance at the proper spatial and temporal scale is imperative in order to understand its importance at all hierarchical levels (Pickett et al. 1989), and is crucial when considering disturbance dynamics in streams (Minshall 1988). For example, catchment-level disturbance such as wildfire can affect stream macroinvertebrates at spatial scales ranging from microhabitats to whole catchments and temporal scales ranging from days to decades (Minshall 1988). Response is scale dependent, both spatially and temporally, therefore sampling must include both spatial and temporal scales. In this study the temporal scale was four years following the

1988 wildfire disturbance and the spatial scale was 1st through 4th order stream systems in YNP.

Individual responses of the 26 most abundant taxa in six Cache Creek, YNP sites and four reference sites were correlated with environmental variables using canonical correspondence analysis. Canonical correspondence analysis allows the investigator to interpret a data set of multiple species responses along a non-linear gradient of multiple environmental variables (Ter Braak 1986). This type of analysis can provide useful interpretation of a multivariate data set in which environmental variables are correlated with trends in species abundance. Indirect gradient analysis techniques have been utilized in stream ecology to assess patterns in functional feeding group composition (Bruns et al. 1982) and species composition (Rabeni and Gibbs 1980) and then attempt to relate them to environmental variables *post hoc*. The development of a multivariate direct gradient analysis technique such as canonical correspondence analysis allows a set of species and a set of environmental variables to be related directly (Ter Braak 1986). Further, this method is non-linear, avoiding the assumption of linearity in other multivariate methods (Ter Braak 1987).

Methods

The ten study sites were located in the Lamar river catchment, YNP (Figure 1). Six burned sites were sampled in the Cache Creek catchment, a fourth order tributary to the Lamar river. The Cache Creek drainage was extensively burned in the 1988 wildfires (Table 1). Three unburned (reference) sites were located in the Soda Butte

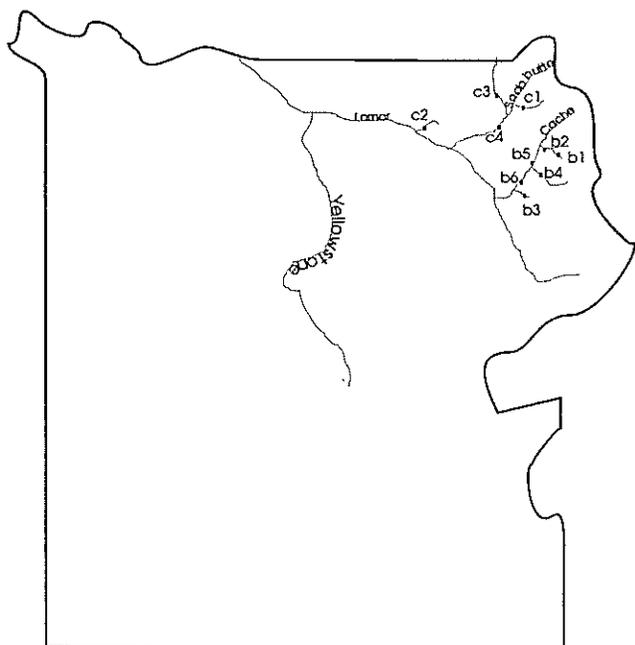


Figure 1. Location map of the 10 study sites in Yellowstone National Park. Site descriptions are found in Table 1.

Creek catchment, a fourth order tributary to the Lamar river (Figure 1). The Soda Butte Creek catchment was not extensively burned in the fires (Table 1). One unburned site (Rose Creek) was a second order tributary of the Lamar River (Figure 1). Samples were taken during August of 1988-1992 at all sites, except the Soda Butte fourth order site (C4) which was sampled only in 1991 and 1992.

Physical environmental variables measured at each site included stream width, base flow, channel area, annual stream temperature, mean depth ($n=100$ measurements), water velocity ($n=100$ measurements), mean embeddedness ($n=100$ measurements) and mean substrate size ($n=100$ measurements). Channel area was measured at 5 transects located 50 m apart at each site. Base flow was measured at one of the 5 transects at each site. Channel area change between years and several hydraulic parameters (Froude number, boundary Reynolds number, substrate roughness (K_v), shear velocity (U) and shear stress (TAU)) were calculated from these variables. Biotic environmental variables measured were chlorophyll *a* ($n=5$ per site), ash free dry mass (*AFDM*) of periphyton ($n=5$ per site), biomass/chlorophyll ratio of periphyton (*B/C*), benthic organic matter content (*BOM*) ($n=5$ per site), and % charcoal in the *BOM* ($n=5$ per site).

Benthic macroinvertebrates were sampled at each transect during August of each year using a Surber sampler. One sample was taken at each transect ($n=5$ per site). Samples were taken to a depth of at least 15cm. Two environmental variables, benthic organic matter content (*BOM*) and % charcoal in the *BOM*, were determined from these samples. Results of the benthic samples are presented as the mean relative abundance (#/m²) and biomass (mg/m²) for each year sampled. Mean abundance data for each site in each sample year was used in the statistical analyses to relate species abundance to the environmental variables.

Spatial and temporal comparison between benthic macroinvertebrate abundance and the environmental variables was made using canonical correspondence analysis. The mean relative abundance of the 26 most abundant macroinvertebrate taxa and 12 of the environmental variables (channel change, % burn, % charcoal, *BOM* content, periphyton *AFDM*, periphyton *B/C*, water depth, K_v , flow, boundary Reynolds number, U , TAU) were used in the analysis as in Ter Braak (1986). Input for this analysis consisted of a species-by-sample matrix and environmental variable-by-sample matrix of all sites through all years. A summary of the total relative abundance throughout the four year study for the 26 taxa studied and the environmental variables used in the analysis appears in Table 2.

Spatial comparison of the macroinvertebrate assemblage among sites was determined by cluster analysis (Ward's linkage method) using all sites in each sample year. Separate analyses were performed for each year.

Table 1. Description of the 10 study sites. Small streams are defined as 1st, 2nd order. Large streams are 3rd, 4th order.

	Site	Stream order	Catchment area (ha)	% Burned	Discharge (m ³ /s)	Slope
C1	Amphitheater Creek	2	2534	2	.150	5
C2	Rose Creek	2	2390	0	.027	8
C3	Pebble Creek	3	5888	17	.590	3
C4	Soda Butte Creek	4	26791	10	2.69	1.2
B1	Upper 1 Cache	1	137	64	.004	10
B2	Upper 2 Cache	2	376	71	.012	10
B3	Lower Cache	2	780	47	.012	9
B4	South Fork Cache	3	5780	39	.200	3
B5	Cache mainstem	3	12052	68	.474	2
B6	Cache mainstem	4	17994	59	.667	1.3

Temporal comparison of macroinvertebrate assemblages at each site was determined by using Kendall's w coefficient of concordance. Rankings of the ten most abundant taxa at each site were used to evaluate year-to-year stability of the assemblage.

Results and Discussion

Temporal trends

Environmental variables that were measures of disturbance intensity (channel change, % charcoal, % burn) were important in explaining temporal variation in the species data (Figure 2). In the ordination plot (Figure 2) environmental variables are described by arrows. Each arrow indicates an axis for an environmental variable, or group of similar variables, with the length indicating stronger correlation with the two ordination axes (x and

y). Taxa which fall close to the arrow-head of an environmental variable indicate that variable is important in explaining temporal variation in the mean abundance of that taxon. Taxa which fall on the opposite end of the diagram and along the same axis as the arrow indicate a negative relationship with that variable.

The first ordination axis (x axis) explained 42 % of the species-environment relationship and the second (y axis) explained an additional 20.4 %. Environmental variables important in determining ordination axis 1 (x-axis) were % burn, BOM, and % charcoal with positive correlation coefficients of 0.50, 0.54, 0.58, respectively with axis 1, and water depth and K_v with correlation coefficients of -0.49 and -0.49, respectively with axis 1. Variables important in determining ordination axis 2 (y-axis) were % burn, channel change and periphyton B/C with correlation coefficients of 0.49, 0.54, and 0.42, respectively, with axis 2.

The three most abundant taxa in Cache Creek, Chironomidae, *Baetis bicaudatus* and *Zapada columbiana*, exhibited differential responses following the disturbance event, each relating to different environmental variables (Figure 2). Post-fire trends of Chironomidae, the most abundant taxon in Cache Creek, were related to % charcoal and BOM content (Figure 2). Chironomidae accounted for 35.9 % of the total abundance throughout the four year study in all sites. The post-fire response of *Baetis bicaudatus*, the second most abundant taxon (15.1 % of total abundance) was primarily related to degree of channel change between years (Figure 2). The third most abundant taxon, *Zapada columbiana* (6.0 % of total abundance), did not show a clear relationship with the environmental variables in the ordination (Figure 2). Most other taxa appeared to relate positively to flow variables (water depth, flow, K_v , U , TAU , boundary Reynold's number) and negatively to measures of disturbance intensity (% burn, channel change) (Figure 2).

Trends in other taxa in post-fire streams fell into two major categories: 1) those taxa which decreased initially and did not recover by year 4; and 2) those which decreased initially and showed recovery in post-fire years 3 and 4. Taxa in category 1 included *Calineuria* sp., *Cinygmula* sp., *Ephemerella infrequens*, *E. Tibialis*,

Table 2. List of species and environmental variables used in the canonical correspondence analysis. Percentage of total abundance, through all four study years, of each taxon is given.

TAXON:	% of Total abundance	Environmental variables:
Chironomidae	.359	Channel change
<i>Baetis bicaudatus</i>	.151	% catchment burn
<i>Zapada columbiana</i>	.060	% charcoal in BOM
<i>Rhithrogena</i> sp.	.052	BOM content
<i>Oligochaeta</i>	.039	Periphyton AFDM
<i>Heterlimnius</i> sp.	.038	Periphyton B/C
<i>Ephemerella infrequens</i>	.033	Water depth
<i>Drunella doddsi</i>	.031	substrate roughness- K_v
Hydracarina	.026	Base flow
<i>Suwallia</i> sp.	.024	Boundary Reynolds number
<i>Capnia</i> sp.	.024	shear velocity- U
<i>Cinygmula</i> sp.	.023	shear stress- TAU
<i>Epeorus albertae</i>	.015	
<i>Oligophlebodes</i> sp.	.011	
<i>Isoperla</i> sp.	.010	
<i>Ephemerella tibialis</i>	.008	
<i>Arctopsyche grandis</i>	.008	
Nematoda	.007	
<i>Megarcys</i> sp.	.006	
<i>Calineuria</i> sp.	.005	
<i>Ameletus cooki</i>	.005	
<i>Drunella spinifera</i>	.004	
<i>Drunella coloradensis</i>	.004	
<i>Parapsyche elis</i>	.003	
<i>Rhyacophila acropodes</i>	.003	
<i>Glossosoma</i> sp.	.003	

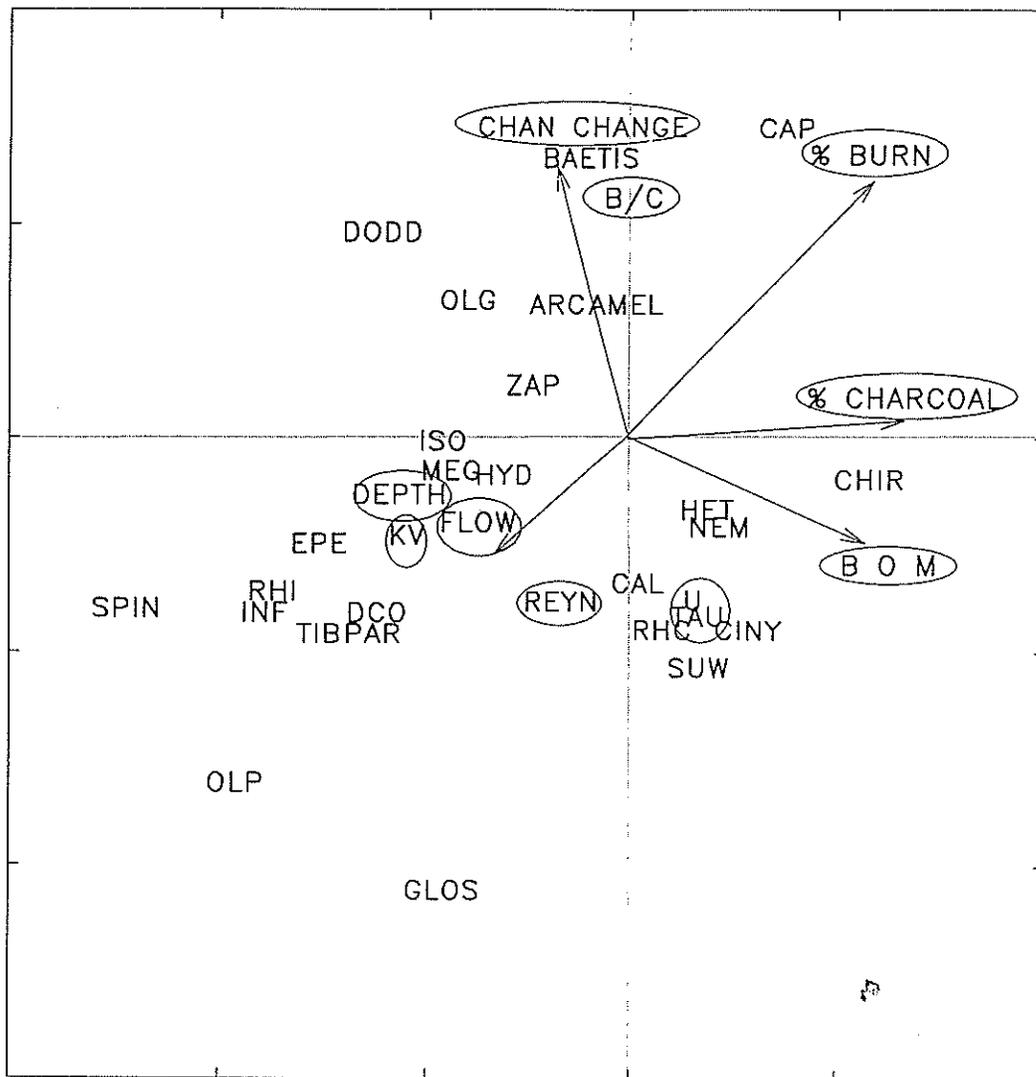


Figure 2. Ordination diagram of the 26 taxa in Cache Creek and 12 environmental variables (circled) as determined by canonical correspondence analysis. The taxa are: AMEL = *Ameletus cooki*, ARC = *Arctopsyche grandis*, BAETIS = *Baetis bicaudatus*, CAL = *Calineuria* sp., CAP = *Capnia* sp., CHIR = Chironomidae, CINY = *Cinygmula* sp., DCO = *Drunella coloradensis*, DODD = *Drunella doddsi*, EPE = *Epeorus albertae*, GLOS = *Glossosoma* sp., HET = *Heterlimnius* sp., HYD = Hydracarina, INF = *Ephemerella infrequens*, ISO = *Isoperla* sp., MEG = *Megarcys* sp., NEM = Nematoda, OLIG = *Oligochaeta*, OLP = *Oligophlebodes* sp., PAR = *Parapsyche elis*, RHC = *Rhyacophila acropodes*, RHI = *Rhithrogenia* sp., SPIN = *Drunella spinifera*, SUW = *Suwallia* sp., TIB = *Ephemerella tibialis*, ZAP = *Zapada columbiana*. Environmental variables are AFDM = periphyton biomass, B/C = periphyton biomass/chlorophyll ratio, BOM = Benthic organic matter content, % BURN = % catchment area burned, CHAN CHANGE = channel change index, % CHARCOAL = % charcoal in the BOM, DEPTH = water depth, FLOW = baseflow, KV = substratum roughness, REYN = boundary Reynold's number, TAU = shear stress, U = shear velocity.

Epeorus albertae, *Glossosoma* sp., *Heterlimnius* sp., *Hydracarina*, *Isoperla* sp., *Megarcys* sp. *Oligophlebodes* sp., *Paraleptophlebia* sp., *Parapsyche elis*, *Rhithrogenia* sp., *Rhyacophila acropodes* and *Suwallia* sp. These taxa are grouped in the ordination diagram on the opposite end of the % burn axis (indicating a negative response to this variable) and with the group of flow variables (Figure 2). Taxa in category 2 included *Ameletus cooki*, *Arctopsyche grandis*, *Capnia* sp., *Drunella doddsi*, *D. spinifera*, *D. coloradensis*, and *Oligochaetes*. These taxa apparently related to the channel change and/or % burn environmental variables (Figure 2).

Chironomids were the only taxon that responded positively during the first post-fire season (Figure 3). Chironomid abundance and biomass were higher in burned sites than in reference sites within months after the fires, with abundance values exceeding 20,000/m² in one of the large streams (B4) in 1988. This is an expected trend since most chironomid taxa in these streams are probably multivoltine sediment burrowers (Oliver 1971, Kawecka et al. 1978, Pinder 1986). Multivoltine taxa are capable of responding much faster than univoltine taxa because of a short generation time. Sediment burrowers should be favored in a post-fire stream which receives high

Chironomidae

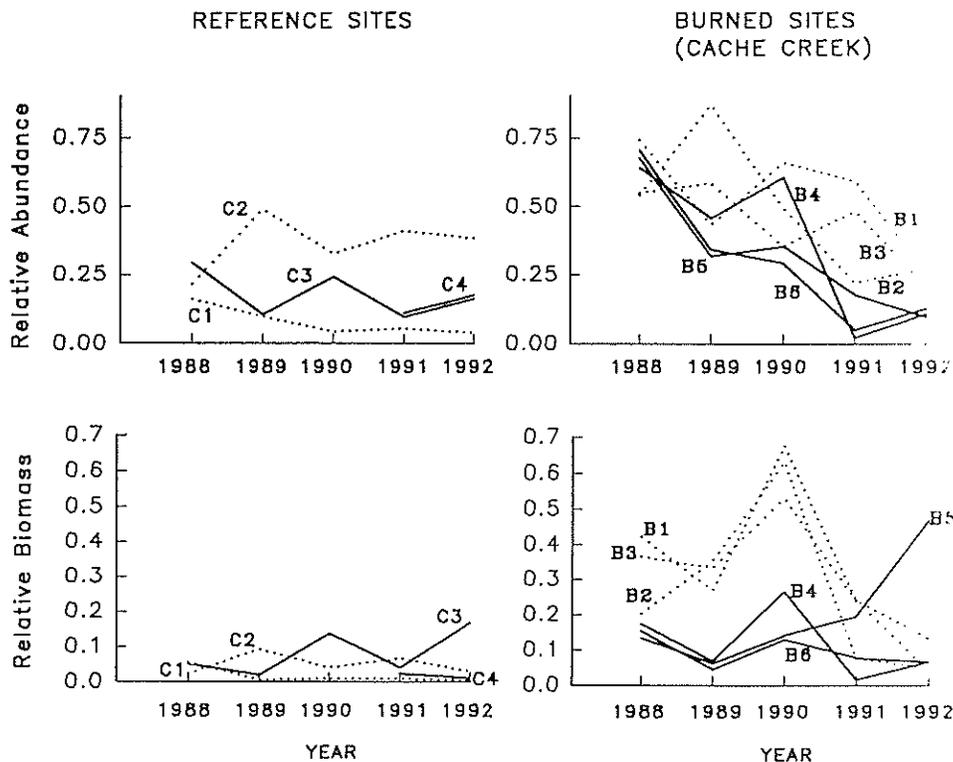


Figure 3. Mean relative abundance and biomass of Chironomidae in the reference sites and Cache Creek burned sites. Solid lines are large streams (3rd, 4th order). Dashed lines are small streams (1st, 2nd order). Site names are found in Table 1.

sediment loads following fire, resulting in an increase in habitat favored by these taxa. Chironomids accounted for 55-74 % of the relative abundance immediately after the fires (1988) in burned sites but only 16-29 % in reference sites. The benthic assemblage at burned sites was dominated by chironomids for the first two post-fire seasons (1989,1990) with relative abundance values declining to 2-18% in large streams and 22-60% in small streams by post-fire year 3 (1991). Large (3rd, 4th order) streams exhibited a faster decline in relative abundance than small (1st, 2nd order) streams. The differential response of Chironomidae between streams of differing size suggests that the level of disturbance was probably higher in small streams than larger streams.

The post-fire response of *Baetis bicaudatus* was opposite that of chironomids in Cache Creek (Figure 4). *B. bicaudatus* abundance and biomass were low during the first two post-fire years in most sites. Recovery of *B. bicaudatus* began in post-fire year 2 (1990) in small streams and post-fire year 3 (1991) in large streams, with relative abundance values increasing to 50% by 1992 in some sites (Figure 4). *B. bicaudatus* is also a multivoltine species (Clifford 1982), but did not respond in a similar manner as chironomids. *B. bicaudatus* trends

were most closely related to the channel change environmental variable (Figure 2). *B. bicaudatus* appears to be best adapted for highly variable physical conditions which result in a channel out of equilibrium with its valley (high degree of channel change between years). Many species of *Baetis* are known to exhibit high colonization rates of disturbed substrata and occur in a wide range of physical habitats ranging from pools to fast flowing riffles (Percival and Whitehead 1929, Uresk 1967, Ulfstrand 1967, Allan 1975, Minshall and Minshall 1977, Doeg et al. 1989, Robinson 1992). *Baetis* also prefers open canopy regions in streams (Hughes 1966, Behmer and Hawkins 1986) and responds positively to increases in periphyton biomass (Richards and Minshall 1988), a condition which is common in post-fire catchments. This taxon is a generalist herbivore-detritivore with the ability to utilize either periphyton or coarse particulate organic matter (CPOM) as a resource (Mihuc and Minshall 1995). *B. bicaudatus* is the only taxon that responded with an increase in abundance and biomass above reference conditions within two seasons of the disturbance event (by 1990) suggesting it is a disturbance "adapted" taxon.

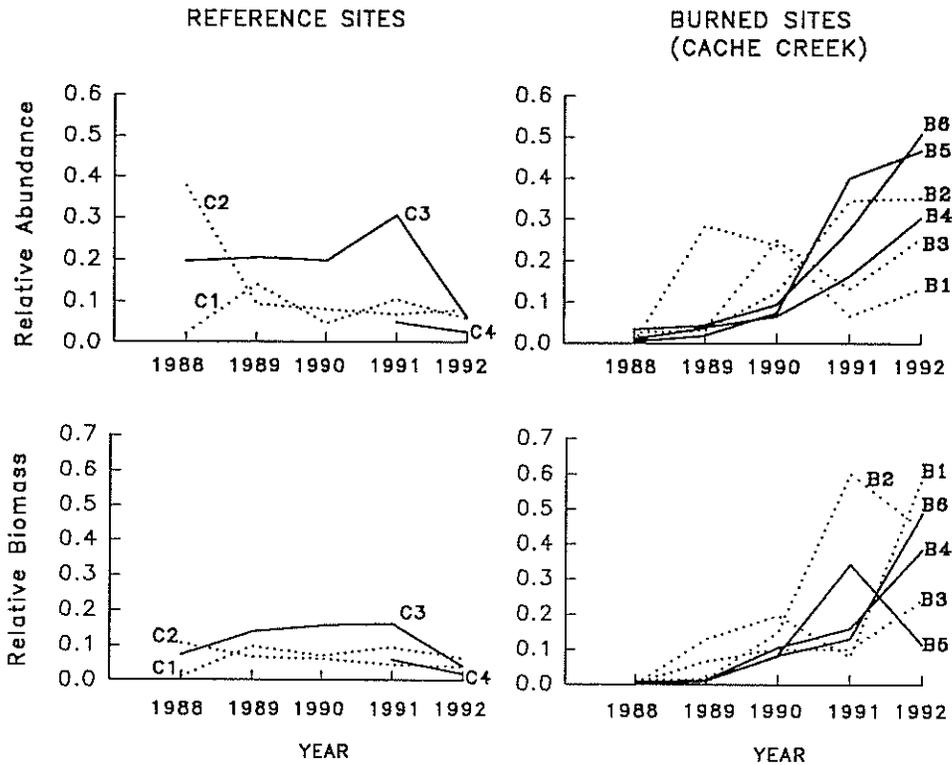
Baetis bicaudatus

Figure 4. Mean relative abundance and biomass of *Baetis bicaudatus* in the reference sites and Cache Creek burned sites. Solid lines are large streams (3rd, 4th order). Dashed lines are small streams (1st, 2nd order). Site names are found in Table 1.

Only one common taxa in these streams exhibited little or no response to wildfire. *Zapada columbiana* exhibited a slight decline in abundance, but not biomass, immediately following the fires and recovered to reference levels after only one season in large streams and two seasons in small streams (Figure 5). This taxon did not relate to any environmental variables in the ordination (Figure 2) and appeared to be tolerant of post-fire conditions to which other taxa responded. One would expect that a shredder, such as most species of *Zapada* are considered, would decline following a disturbance event that results in reduction of natural allochthonous inputs (leaf litter) to the stream. *Z. columbiana*, however, is a generalist herbivore-detritivore capable of utilizing either periphyton or natural leaf litter (CPOM) as a resource (Mihuc and Minshall 1995). *Z. columbiana* is also capable of utilizing moss as a resource (Mutch and Pritchard 1984). *Z. columbiana* prefers fast flowing riffle habitat and is often found associated with leaf packs (Mutch and Pritchard 1984, Mutch and Davies 1984). This taxon appears capable of withstanding the physical conditions following the disturbance, such as increased water velocity as stream gradient increases and has the ability to utilize both periphyton and detrital resources, suggesting that it is disturbance adapted for post-fire conditions.

The temporal response of taxa which recovered in the third post-fire year indicate individualistic responses within this group. *D. doddsi* increased in abundance and biomass in post-fire year 3 (1991) but did not continue this trend in year 4 (1992) (Figure 6) while Oligochaetes did not increase until post-fire year 4 (1992) (Figure 7). *D. doddsi* recovered only in large streams while the Oligochaete responses occurred in both small and large streams. *D. doddsi* has a narrow niche width in Rocky Mountain streams with preferences for coarse substrates, dense riparian vegetation and high gradients (Mangum and Winget 1991) and is a generalist herbivore-detritivore (Mihuc and Minshall 1995). Based on the niche width in Mangum and Winget (1991) *D. doddsi* should inhabit both large and small Cache Creek streams. Therefore, the differential responses observed in *D. doddsi* according to stream size appear to relate to a differential impact of the disturbance event on small and large streams and not to natural distribution patterns of *D. doddsi* in Cache Creek streams.

In summary, generalist herbivore-detritivore taxa with broad physical habitat preferences such as *Baetis bicaudatus* and *Zapada columbiana* appear to be best adapted for the conditions found in post-fire streams. Also, taxa which require stable riffles or slower current velocities appear to respond with a decline in abundance

Zapada columbiana

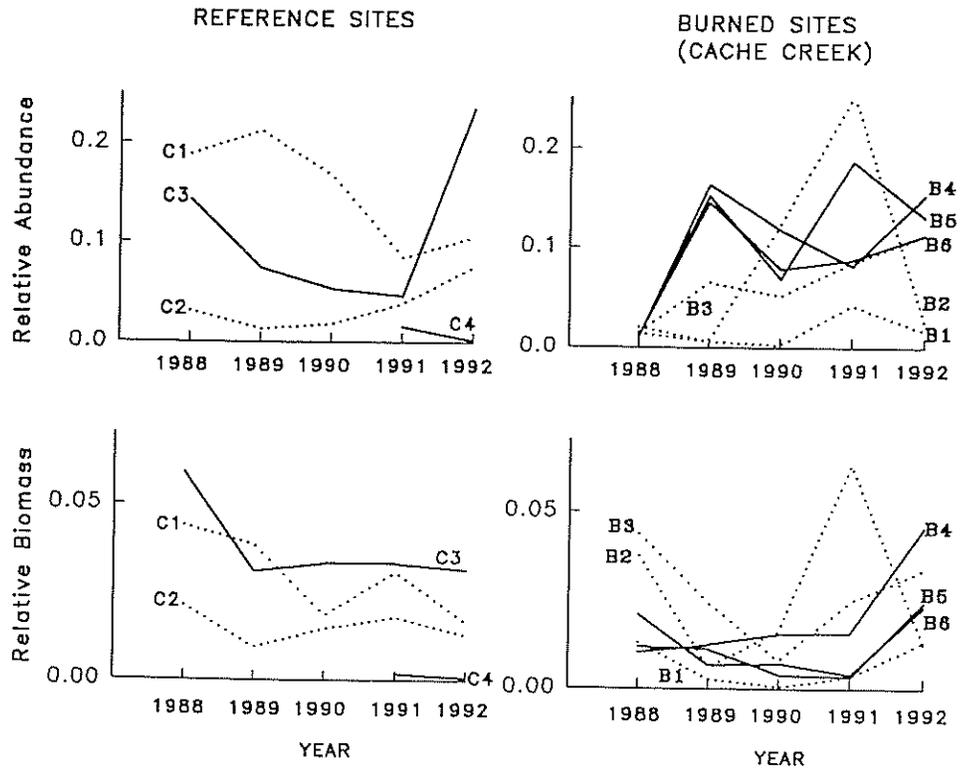


Figure 5. Mean relative abundance and biomass of *Zapada columbiana* in the reference sites and Cache Creek burned sites. Solid lines are large streams (3rd, 4th order). Dashed lines are small streams (1st, 2nd order). Site names are found in Table 1.

Drunella doddsi

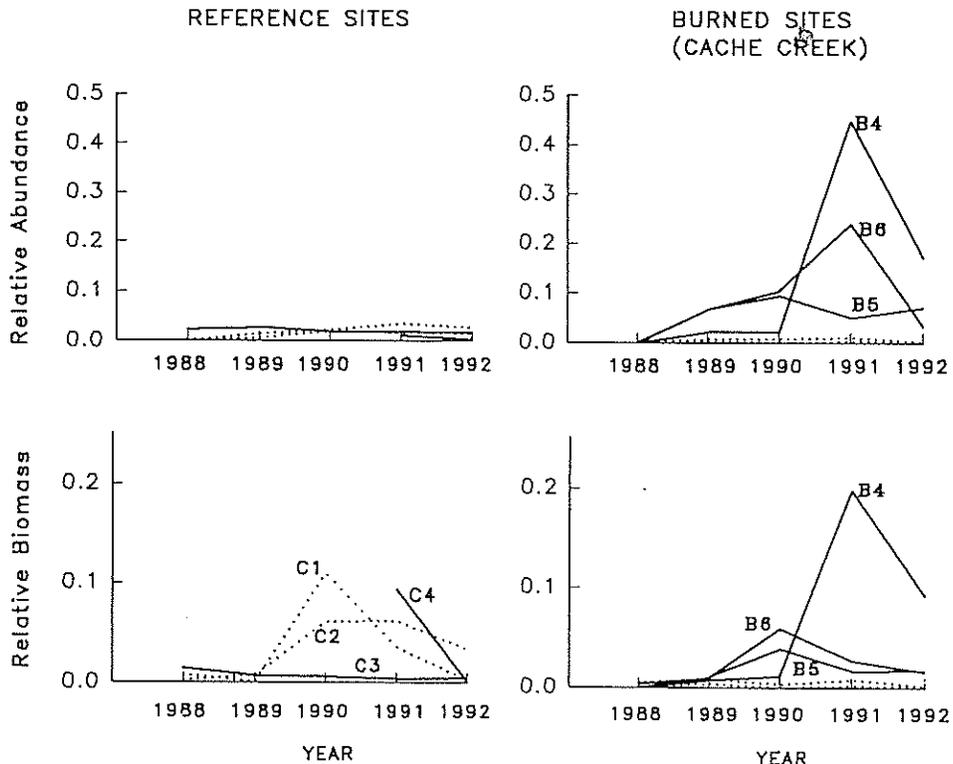


Figure 6. Mean relative abundance and biomass of *Drunella doddsi* in the reference sites and Cache Creek burned sites. Solid lines are large streams (3rd, 4th order). Dashed lines are small streams (1st, 2nd order). Site names are found in Table 1.

Oligochaeta

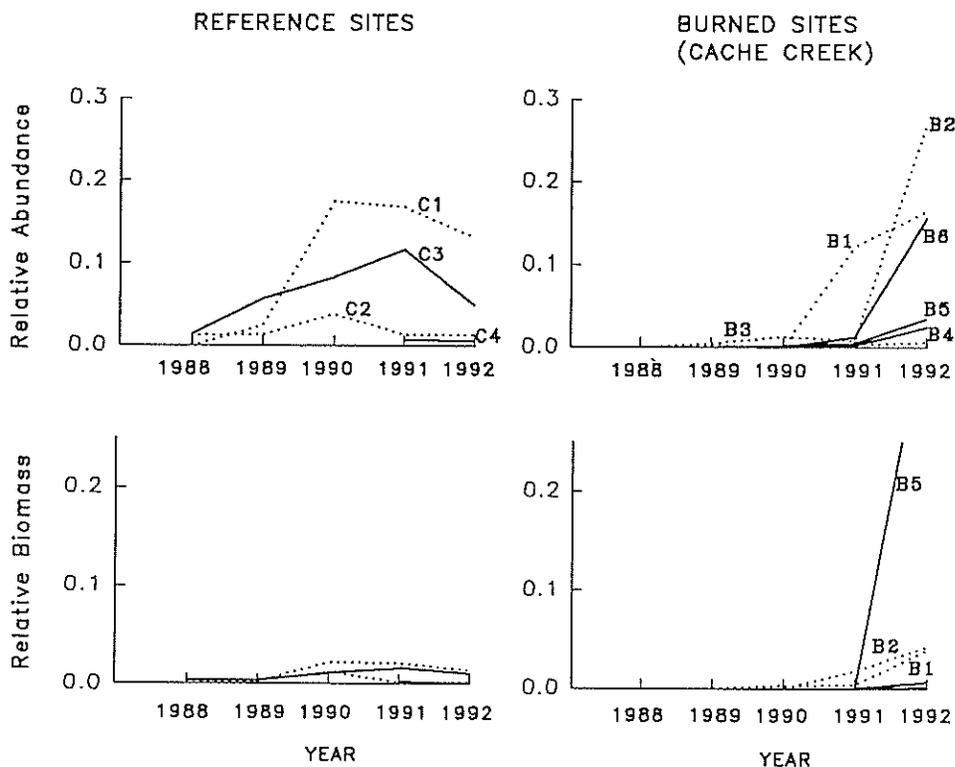


Figure 7. Mean relative abundance and biomass of Oligochaeta in the reference sites and Cache Creek burned sites. Solid lines are large streams (3rd, 4th order). Dashed lines are small streams (1st, 2nd order). Site names are found in Table 1.

and biomass, regardless of trophic niche, indicating that physical habitat requirements are more crucial for these taxa in post-fire streams than trophic requirements (e.g. *Cinygmula* sp., *Drunella coloradensis*, *D. spinifera*, *Ephemera infrequens*, *Oligophlebodes* sp., *Paraleptophlebia* sp.).

The patterns between streams of different size indicate that the disturbance had a more severe effect on habitat conditions for benthic macroinvertebrates in first and second order streams (small) than in third and fourth order streams (large) in Cache Creek. Small streams exhibited slower recovery patterns for several taxa (*Drunella spinifera*, *D. doddsi*, *Z. columbiana* and Chironomidae) than large streams. Faster recovery occurred in small streams for *B. bicaudatus*, a taxon that appears to be adapted for highly variable physical conditions.

Kendalls coefficient of concordance results indicate that composition of the benthic macroinvertebrate assemblage in the burned sites changed through time while the composition in the reference sites was similar between years (Table 3). All reference sites had high coefficients and 3 of the 4 sites had stable species assemblages through time ($p < 0.05$). The burned sites had lower

coefficients and 3 of the 5 sites exhibited unstable assemblages through time ($p < 0.05$). Interestingly, two of the small burned streams (B2, B3) exhibited stable macroinvertebrate assemblages. Many of the taxa in these streams declined in abundance and remained low throughout the study period. This reflected a "stable" assemblage because of lack of post-fire recovery among the taxa in these streams.

The population trends presented in figures 3-7 represent mean values for each sample year at each site, thus they indicate temporal trends in each population sampled across a 250 m reach. Trends in mean abundance were used because high spatial variation in the samples taken within a given year at a site (CV usually $> 100\%$) would have precluded use of individual samples in the ordination. Also, the environmental variables reflected reach scale patterns since they were not measured concomitantly at each of the 5 surber sample points during each sample event. Results presented here indicate population trends at the 250 m reach scale of the stream, not at smaller spatial scales, although high variation in abundance and biomass among the taxa at each sample event suggest that variation at smaller scales warrants further attention.

Table 3. Stability of the benthic assemblage at each site as indicated by Kendall's coefficient of Concordance.

SITE	Coefficient of concordance	p
C1	.289	.022
C2	.216	.055
C3	.400	.047
C4	.640	.011
B1	.214	.093
B2	.449	.002
B3	.510	.000
B4	.075	.591
B5	.264	.023
B6	.117	.326

Spatial patterns

Spatial patterns among sites in each year were reflected by the ordination plot and cluster analysis of sites (Figure 8). The ordination plot showed the reference sites grouped separately from the burned sites, indicating that disturbed sites exhibited a distinctly different community composition from the reference sites. The burn sites

were located along an axis described by the channel change and *BOM* variables. Spatial patterns among sites were evident from cluster analysis groupings (Table 4). In general, the reference streams were grouped together during each sample year, while the burn sites were in the other two clusters. The large burned streams (B4,B5,B6) tended to cluster together. Both spatial analyses (ordination plot and cluster analysis) indicate that the reference streams were more closely associated with each other than with burned streams.

Conclusions

Stream communities responded to catchment scale fire in an individualistic manner. Some benthic taxa can be grouped according to response trends, particularly taxa that declined in abundance and biomass initially and did not recover during initial post-fire years. Taxa that responded within the first four years related in an individualistic manner to environmental variables (Figure 2) indicating that autecology is responsible for trends in species populations following wildfire.

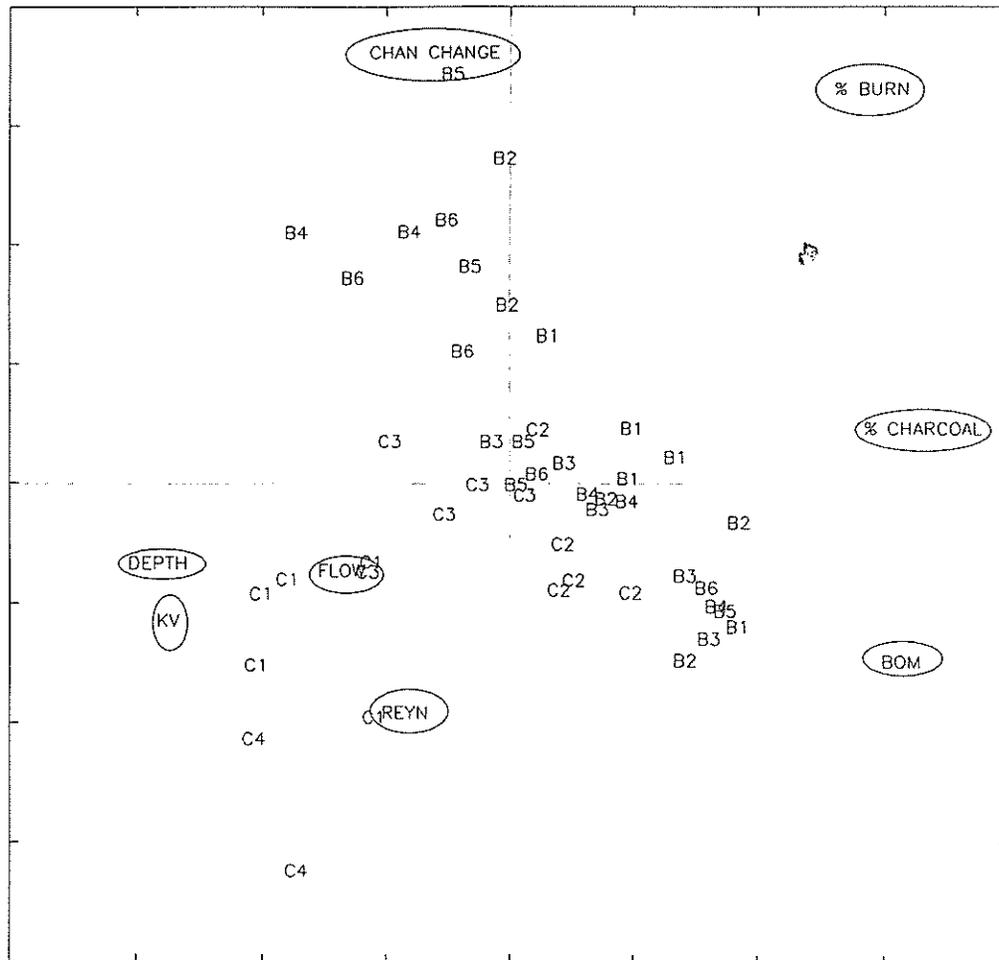


Figure 8. Ordination diagram of the reference sites (C1-C4) and burned sites (B1-B6) from canonical correspondence analysis. Environmental variables are the same as in Figure 1.

Table 4. Results of Cluster analyses. Cluster membership of the 10 sites for the first three clusters as determined by hierarchical clustering (Ward's) of species abundance.

Year	Cluster 1	Cluster 2	Cluster 3
1988	C1, C3, C2	B3, B2	B1, B4, B5, B6
1989	C1, C3	C2, B3, B1	B2, B4, B5, B6
1990	C1, C3, C2, B3	B5, B6	B1, B2, B4
1991	C1, C4	C3, B4, B5, B6	C2, B3, B1
1992	C1, C2, C3, C4	B1, B3, B4	B2, B5, B6

Hypothetical post-fire responses of five common taxa from Cache Creek appears in Figure 9. This succession is based on the empirical data through post-fire year 4 and the trends predicted in Minshall et al. (1989) for years 5-10. In general physical and biotic stress on macroinvertebrates should decrease between post-fire years 5-10 as riparian and forest vegetation recovers in both small and large catchments. Taxa that increase

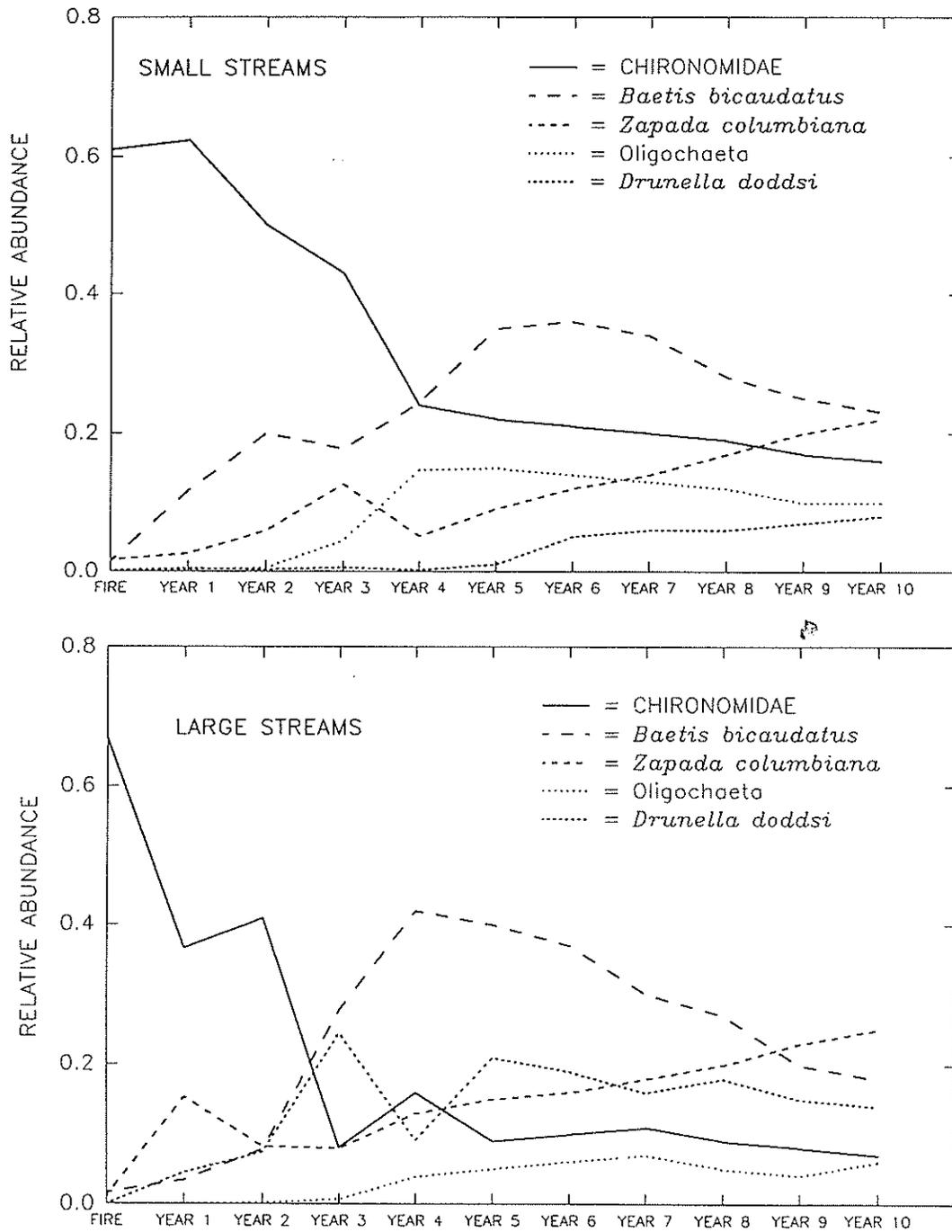


Figure 9. Hypothetical 10 year trends in abundance of the top 5 taxa from Cache Creek, YNP. Data through year 4 are based on trends in the 6 Cache Creek sites. Years 5-10 are based on predicted patterns in Minshall et al. (1989).

between years 5-10 should be herbivorous or generalist in food habits (e.g. *Zapada columbiana*, *Drunella doddsi*) and should not be restricted to those taxa that are adapted to highly variable stream environments such as *Baetis bicaudatus*. Chironomids should remain close to reference levels in years 5-10 but may increase if high spring runoff events occur. High Spring runoff in a relatively unstable watershed may serve to "reset" conditions, favoring disturbance adapted taxa such as chironomids and *Baetis bicaudatus* once again.

Taxa in small streams exhibited slower recovery patterns than those in large streams during the first four post-fire years (Figure 9). Higher slope and more burned catchment area in small streams (Figure 10) suggests the potential for more severe impacts of fire disturbance on these systems. Slower recovery in small streams should continue in years 5-10 and is probably related to the spatial scale of the disturbance. On the basis of catchment area burned (% burned) the 1988 Yellowstone fires more severely affected small (1st, 2nd order) catchments in Cache Creek than large (3rd, 4th order) catchments (Table 1, Figure 10). Two of the small catchments were > 60 % burned (Table 1). Large catchments were not as severely affected with only one >60% burned (Table 1). Large streams, therefore, contain more unburned "buffer" area in the catchment than small streams. This is probably a result of the mosaic pattern of fire behavior (Christensen et al. 1988) and the fact that smaller catchments in a

burned watershed will have a higher probability of encompassing a fire "patch" in the mosaic. The unburned area in a catchment serves to mediate the impacts of wildfire on the catchment and stream macroinvertebrates. This translated into more severe impacts on some benthic taxa in small streams during the first four years of recovery than in large streams. This trend should continue until post-fire year 10 in small Cache Creek streams. After year 10 the trend may reverse as riparian vegetation recovery facilitates stream channel/bank stabilization in small streams while large stream channels may remain relatively unstable.

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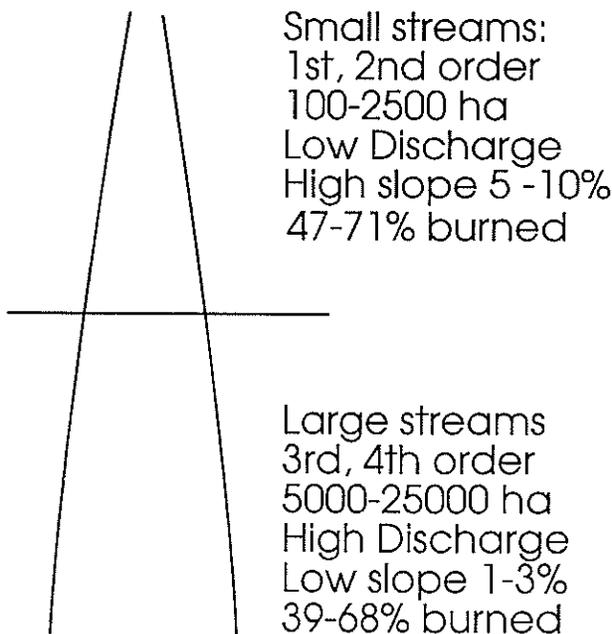


Figure 10. Characteristics of small (1st, 2nd order) and large (3rd, 4th order) Cache Creek streams.

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Preburn Root Biomass/Basal Area Influences on the Response of Aspen to Fire and Herbivory

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Abstract. Factors associated with the decline of aspen (*Populus tremuloides* Michx.) in the Yellowstone landscape are reviewed, and preliminary experimental results are presented that correlate preburn root biomass/basal area with aspen regeneration following fire both with and without herbivory. The curvilinear relationship between point estimates of preburn stem basal area and total root biomass is described, and both variables showed a significant positive correlation with the density, biomass, and average height of suckers produced the first year following fire as well as 5-7 years postburn. Fenced exclosures and subplot isolation showed that elk browsing influenced both sucker heights and age-class distribution, but had no effect on sucker density or mortality 5-7 years postburn. The data suggest that all aspen are not necessarily predisposed to prolific growth following fire, but optimal response is observed in clones that occupy more suitable sites as described by preburn stand root biomass/basal area. Consistent with these observations is a re-interpretation of historical photographic evidence advancing the "shrub aspen" growth form as a persistent yet inconspicuous component of the landscape.

Keywords: *Populus tremuloides*; Root biomass; Regeneration; Herbivory.

Introduction

Historical comparative photographs have been used to demonstrate the reduction of aspen on Yellowstone's northern winter range (Houston 1982, Despain et al. 1986, Kay 1990). About 6,000 ha of the northern winter range was estimated to be occupied by aspen during the late 1800's, declining to about 2,000 ha today. Causes for the decline have been attributed to ungulate browsing (primarily elk), climatic change, and fire suppression.

Causes for Decline: A Brief Review and Synopsis

The Browse Influence

Ungulate browsing is believed to be the primary causative agent because utilization is visually obvious. Yet the browse influence on aspen has yet to be quantified. Repeated reference to "light vs. heavy" or "severe and repeated" levels of utilization are common (Bartos and Mueggler 1981, DeByle 1985, Bartos et al. 1991, Bartos et al. 1994), and the result is perceived as a "severe and lasting impact" upon the stand (DeByle 1985). Likewise, comparison of protected (fenced) vs. unprotected stands over time have been used to imply a cause-and-effect relationship because unprotected aspen lack the height growth and canopy coverage of protected stands (Kay 1990). Such observations fail to demonstrate ecologically that the vegetative condition within the artificial environment provided by exclosure should be expected to occur where utilization is prevalent. No relationships have been demonstrated such that a level x of browsing will result in y response of aspen, and that $2x$ will result in z response. Similarly, no threshold level of browsing has been identified below which some optimal suckering response would be realized.

Interpretations and predictions based on the browse influence assume that aspen, as an immobile prey, is defenseless against herbivory. Such projections fail to recognize the chemically mediated interactions between woody plants and herbivores (Bryant et al. 1992) or other strategies that can be employed to allow for long-term coexistence. Implicit is the assumption that aspen trees establish, grow to sexual maturity, senesce, and die — a life history strategy employed by many plant species. Few authors emphasize the fundamentally persistent nature of aspen made possible by clonal behavior (e.g., Barnes 1966, Barring 1988, Shepperd 1993) or durable parent root material (e.g., Parker and Parker 1983).

To elaborate more on the quantifiable effects of browsing on aspen growth, we first revisited previous utilization data collected in the park and then sampled felled aspen trees to determine if historic levels of ungulate browsing and aspen growth response approximated current levels. Barmore (unpublished data in the Yellowstone research files) collected data on aspen leader utilization and elk-use density (from pellet mounds) in 14 aspen stands during the 1960's, a time when elk numbers were culled to artificially low levels of 5,000-7,000 (Figure 1). His data show that >25 elk-use days/acre result in 100% utilization of aspen leader stems. Given these levels of utilization, aspen suckers were not able to grow beyond the browse influence of elk and would presumably fare no better at higher elk densities following the cessation of herd reduction.

For comparison to historic browse levels, we sampled the pith trace in 10 aspen trees from each of five clones across the elevational gradient of the northern winter range. All trees had died and fallen recently and were >80 years in age. In 49 of 50 aspen sampled, previous browsing was evident on the terminal stem about 33 cm above ground level. It appears that aspen utilization levels being experienced today are not only similar to those during herd reductions, but are similar to those experienced a century ago. The determining mechanism (physiological, hormonal, phytochemical, environmental, etc.) that allowed for aspen to grow beyond the browse influence is not exerting the same influence today.

The Climatic Influence

The wide distribution of aspen across North America suggests it is tolerant of extreme climatic variation (Jones and DeByle 1985a). Climatic influences on aspen growth, however, are poorly quantified primarily because it is extremely difficult (if not impossible) to control for climatic variables in field studies. An inherent and unstated assumption in most aspen field studies is that ambient climate is optimal for the treatment/response under consideration.

Most attempts to define the influence of climate on aspen are philosophical (Houston 1982, Despain et al. 1986, Despain 1990), rather than empirical. Berrang et al. (1991), however, demonstrated that climatic variables (mean annual precipitation and minimum monthly temperature) contributed to the susceptibility of aspen to injury from varying levels of ambient ozone resulting in reduced growth rates and possible elimination of clones from local populations. Contrasting climates were attributed to differences in aspen stand structure in 3 geographic regions of Canada (Pielou et al. 1986). Field observations by Jones et al. (1985) noted that maximal sucker growth occurred at 22 degrees C (77 degrees F) in the mountains above Logan, Utah. Second year aspen seedlings grew best near a constant 15 degrees C (59 degrees F) daytime/nighttime temperature under laboratory conditions. The local effects of subtle changes in the temperature (e.g., ± 1.7 degrees C or 3 degrees F) or precipitation regime (e.g., ± 5 cm or 2 in) on aspen growth habits or mortality are virtually unknown.

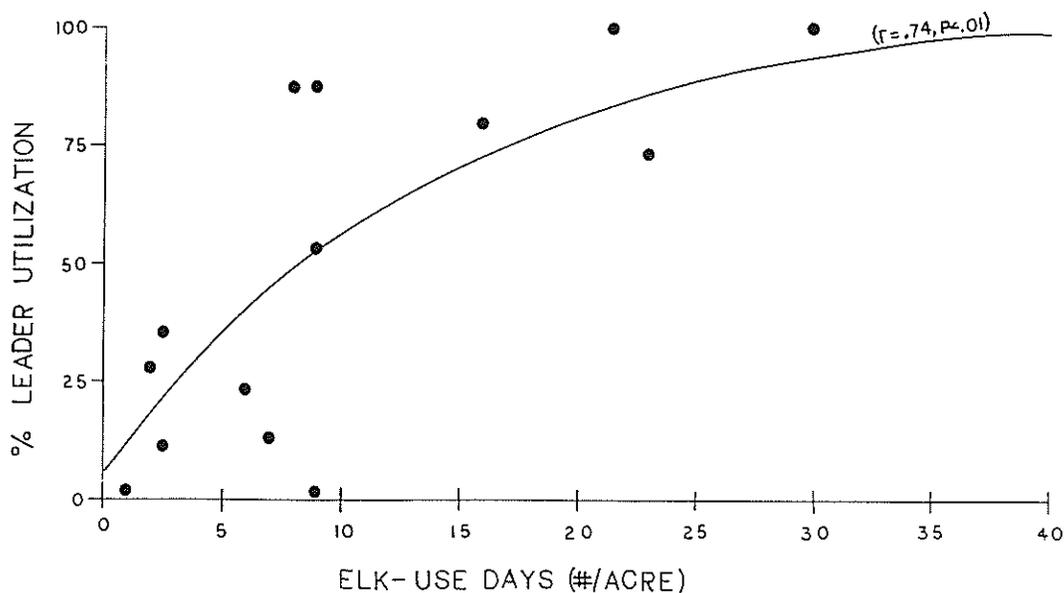


Figure 1. Percent aspen leader utilization in relation to elk-use days (#/acre) as derived from pellet mound counts for 14 aspen clones. Data were collected by W. Barmore in 1965, and are archived in the Research files, Yellowstone National Park. The relationship is described as: proportion of utilization = $0.091 + 0.054$ (days) - 0.001 (days²), $r = 0.74$, $p < 0.01$.

Nevertheless, climatic patterns over broad temporal scales were demonstrated to play a profound role in the distribution of plant species in Yellowstone based on pollen records (Whitlock 1993). Changes in the pollen profile of lakes in the northern range since the establishment of the Park were partially attributed to drying climatic conditions (Engstrom et al. 1991), reflecting an increase in summer temperatures and precipitation concurrent with decreasing winter precipitation (Balling et al. 1992). Future projections of global climatic change similarly predict major shifts in the vegetational zones of the Park (Romme and Turner 1991).

The Fire Influence

Fire has long been recognized as an agent causing structural, hormonal, physiological, and other changes resulting in prolific regeneration from established root stocks (Jones and DeByle 1985b). A lack of stimulated regeneration and subsequent aspen mortality was hypothesized to be the consequence of reduced fire frequency achieved through effective fire suppression (Houston 1973). Returning fire to historic intervals of approximately 25 years, or burning a broad expanse of aspen simultaneously to allow some suckers to grow beyond the browse influence, has been hypothesized to be required for successful aspen regeneration (Despain et al. 1986).

Fire as a treatment has met with varied results. From 3,000 to 150,000 suckers per ha (1,200 to 62,000 per acre) have been reported following fire (Brown and DeByle 1987, Bartos et al. 1991, Patton and Avant 1970). Such variance has primarily been attributed to fire severity (e.g., Bartos and Mueggler 1981), but clonal vigor, root carbohydrate reserves, site, and other environmental factors undoubtedly play some role (Schier et al. 1985).

The general thought is that some optimal fire intensity is required to maximize the suckering response (Jones and DeByle 1985b). A fire of insufficient intensity will not effectively girdle aspen to disrupt the transport of auxins from the crown to the roots, thereby lowering the potential suckering response. On the other hand, extreme fire intensities result in killing many of the surficial roots from which suckers arise, again contributing to a decrease in the potential suckering response.

In view of the extreme variance in aspen response attributed to extrinsic factors including the timing, intensity, and type of treatment, we questioned whether some intrinsic aspen characteristic could be more accurately correlated with the aspen response to fire. Subjective measures such as clone vigor, relative fire intensity, or non-absolute influence of apical dominance do not allow for quantified or predictable results. Furthermore the literature is replete with inference about, but relatively little data for, aspen root properties. We wondered if perhaps some aspen root properties could be quantified and correlated with standing crop variables, and if fire

response may be determined by some preburn condition. If so, other experimental controls (fencing) could be utilized for a more quantitative evaluation of the effects of fire and ungulate browsing on aspen regeneration.

The Experimental Design

Eighteen sites (clones) were selected across the elevational gradient of the northern range based on visual differences in ramet size and spacing. In each clone, an estimate of basal area was obtained with a basal area gauge (factor 10, units are expressed as ft²/ac) and corresponding root biomass was estimated using a modified planar intercept technique (Brown 1974) developed to measure fuel loadings. Mean diameter and specific gravity by size class, needed for the algorithm, were derived from measurement of aspen roots. All root intersections were tallied by diameter size class along a 4 m trench dug to soil parent material.

Three of these sites across the range of the basal area/root biomass curve were selected for burning. The first site (Junction Butte) was associated with an emergent spring and had been exclosed within a 2 ha fence initially constructed in 1962. The site was burned in October, 1986. A second site (Crystal Bench) was located on an alluvial fan adjacent to Crystal Creek. Given the high levels of root biomass and basal area (see Table 1, Results) observed, this site was selected to represent optimal site quality. A third site (Bunsen Peak) was representative of aspen occupying a dry site at the extreme elevational limit (2231 m) of aspen associated with the northern winter range. The Bunsen Peak and Crystal Bench sites were burned in October, 1987.

The following spring, a portion of each clone was subdivided into three 8x25 m subplots and enclosed within a 25x25 m fenced exclosure (Figure 2). In one subplot, the burned canopy was left intact and no further treatments were applied. The burned canopy was subsequently felled in the remaining two subplots, and each was isolated by trenching down to soil parent material to prevent underground communication and sharing of resources from taking place. An additional 4-6 basal area/root biomass plots were established while trenching for subplot isolation and averaged for comparison between sites. One of the two isolated subplots was allowed to grow without further manipulation, while the other was clipped at either 50% or 100% overwinter to determine sucker height, density, and amount of sucker biomass produced the first year postburn. A 1x20 m belt transect was established in each subplot, as well as outside the exclosure, to follow the age class structure and survival of aspen under the given treatments. Only the tallest three suckers were measured for yearly height growth.

Two additional sites that burned in 1988 were also selected for replication of the study design, for a total of

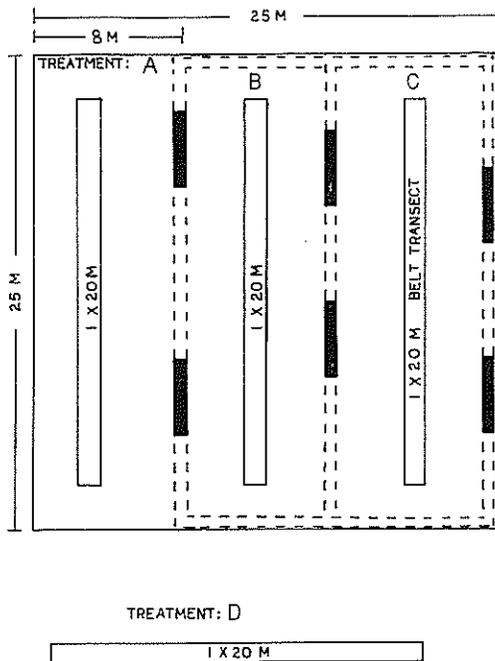


Figure 2. Experimental enclosure design for determining aspen biomass, density, and average height following fire. A 25x25 m fenced enclosure (—) was divided into three 8x25 m subplots, two of which were isolated by root trenching (---). One of 3 different treatments were applied to each subplot within the enclosure: burned canopy intact, no clipping (treatment A); burned canopy felled, clip either 50% or 100% of suckers produced (B); burned canopy felled, no clipping (C). In each subplot, as well as outside the enclosure (D, not shown), a 1X20 m belt transect was established and all aspen were sampled on a yearly basis to determine age class, height, and growth characteristics. Additional root biomass/basal area plots (—) were measured in trenches opened for subplot isolation. Root biomass/basal area was averaged and reported for 5-7 plots per enclosure site.

five experimental sites. Both the Lava Creek and Black-tail sites were dry and generally open where the majority of canopy trees had died and fallen. These sites were selected to represent poor site quality or otherwise reflect general stand decadence.

The clipped subplots at each experimental site were used for between site comparisons of sucker height, biomass, and density the first year following fire, whereas the undisturbed subplots were used to delineate sucker height and density trends 5-7 years postburn. Only limited, preliminary statistics were available for two sites to compare the undisturbed/fenced treatment with the corresponding unfenced/browsed treatment within site.

All statistical analysis was performed according to Zar (1974) using the SYSTAT (Ver. 5.03) statistical software package. Statistical significance was set at the $p < .05$ level, and sample variation is reported as the standard deviation.

Results

Pre-treatment Basal Area and Root Biomass Relationships

Basal area estimates ranged from 4.6 to 50.5 m²/ha ($\bar{x} = 23.85 \pm 15.67$) and total root biomass ranged from 1.9 to 44.4 ($\bar{x} = 17.05 \pm 12.18$) metric tons/ha at the initial 18 sample locations (Figure 3). Total root biomass showed a curvilinear relationship with basal area at a given location beneath the aspen canopy. Plots with 4-10 m²/ha of basal area supported 2-7 tons/ha of root biomass. Basal areas ranging from 10-25 m²/ha generally produced around 12 tons/ha of root material. Plots with 30-50 m²/ha showed a corresponding positive relationship with root biomass ranging from 16 to 44 tons/ha.

First-year Response of Aspen to Fire

We observed that sucker growth was initiated during late May of the first year postburn. Leader growth was rapid during June, often increasing 200-300% during each two week interval. Growth was concentrated in a single central stem, and lateral branching was very infrequent. Leaves were very large, usually longer than wide, rather than the familiar orbicular shape of mature aspen. By early July, change in stem length was reduced to less than 50% per week. Little or no increase in stem length was observed after mid-July.

Average sucker heights ranged from 23.3 to 75.3 cm ($\bar{x} = 41.8 \pm 21.2$) on the five clipped subplots at the end of the first growing season (Table 1). Sucker densities ranged from 8500 to 110,700/ha ($\bar{x} = 50,500 \pm 43,600$). The oven-dried biomass of suckers produced ranged between 0.02 and 0.49 tons/ha ($\bar{x} = 0.17 \pm 0.19$).

Aspen sucker density, height, and biomass per unit area were positively correlated with root biomass (Figure 4) as well as basal area the first year following fire. Each incremental increase of 1 metric ton/ha of root biomass accounted for 1.2 cm of sucker height, 2123 suckers per ha, and .011 metric tons/ha of sucker biomass produced. Likewise, each incremental increase of 1 m²/ha in basal area produced 1.3 cm of sucker height, 2306 suckers/ha, and .011 metric tons/ha of sucker biomass.

Although sucker heights were the same inside and outside the enclosure at each site, sucker density and biomass per unit area were not identical for subplots within a site. Two sites had a higher density of suckers inside than outside the enclosure, two sites supported a higher density of suckers outside than inside, and the last site had roughly equal densities inside and outside. Discrepancies were probably attributed to differences in root density within the area of the subplots.

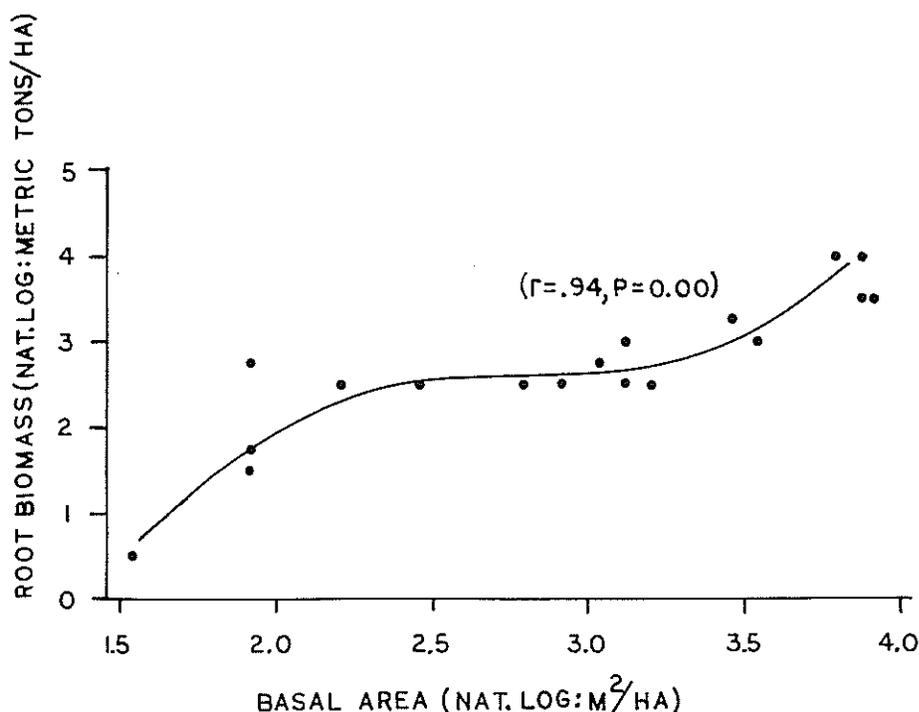


Figure 3. Aspen total root biomass (natural log: metric tons/ha) as a function of basal area (natural log: square meters/ha) for a point (plot) beneath the aspen canopy. Data were collected from 18 different clones in Yellowstone National Park. The relationship is described as: $\text{root biomass} = -18.597 + 22.22(\text{basal area}) - 7.791(\text{basal area}^2) + 0.91(\text{basal area}^3)$, $r = 0.94$, $p = 0.00$. All raw data were converted to metric units, then log transformed, prior to analysis.

Trends 5 to 7 Years After Burning

In the second growing season and beyond lateral branching was prevalent, leaf size decreased and became more orbicular in shape, and the distance between nodes was greatly reduced compared to the first year stems. Sucker densities generally declined for the first few years following the initial fire response. By the fourth year postburn, sucker densities appear to have stabilized.

Similar trends as initially reported for sucker height and density were evident in the protected, undisturbed subplots in 1993 although the relationship was exponential rather than linear (Table 1). The (log-transformed) mean of the tallest three suckers was positively correlated with (log-transformed) preburn root biomass ($y = 2.916 + \exp(.299x)$, $r = .72$, $p < .01$) and basal area ($y = 6.437 + \exp(.409x)$, $r = .61$, $p < .01$). Similarly (log-transformed) sucker density was positively corre-

Table 1. Preburn aspen clone characteristics and postburn suckering response for five experimental 25x25 m fenced enclosure sites. Sites were burned from 1986-88. Data for the first year postburn were derived from clipped subplots within each enclosure, whereas data for 1993 were derived from undisturbed subplots within each enclosure representing trends five to seven years postburn. Mean heights for 1993 were derived from measurement of the tallest 3 suckers within each subplot.

Site	Preburn Clone Characteristics		First-Year Postburn Sucker Response			1993 Sucker Response	
	Root Biomass metric tons/ha	Basal Area m ² /ha	Density #/ha	Mean Height cm	Biomass metric tons/ha	Density #/ha	Mean Height cm
Lava	4.56	6.89	26,800	23.3	.06	31,000	174.3
Blacktail	1.95	4.59	8,500	25.8	.02	500	29.0
Crystal	44.48	43.62	110,700	75.3	.49	40,000	354.3
Junction	12.15	18.37	82,000	48.4	.18	62,500	280.3
Bunsen	16.80	22.96	31,800	36.3	.11	15,500	134.0
mean	15.99	19.29	50,500	44.8	.17	29,900	194.4
st. dev.	16.99	15.62	43,600	21.2	.19	23,700	126.8

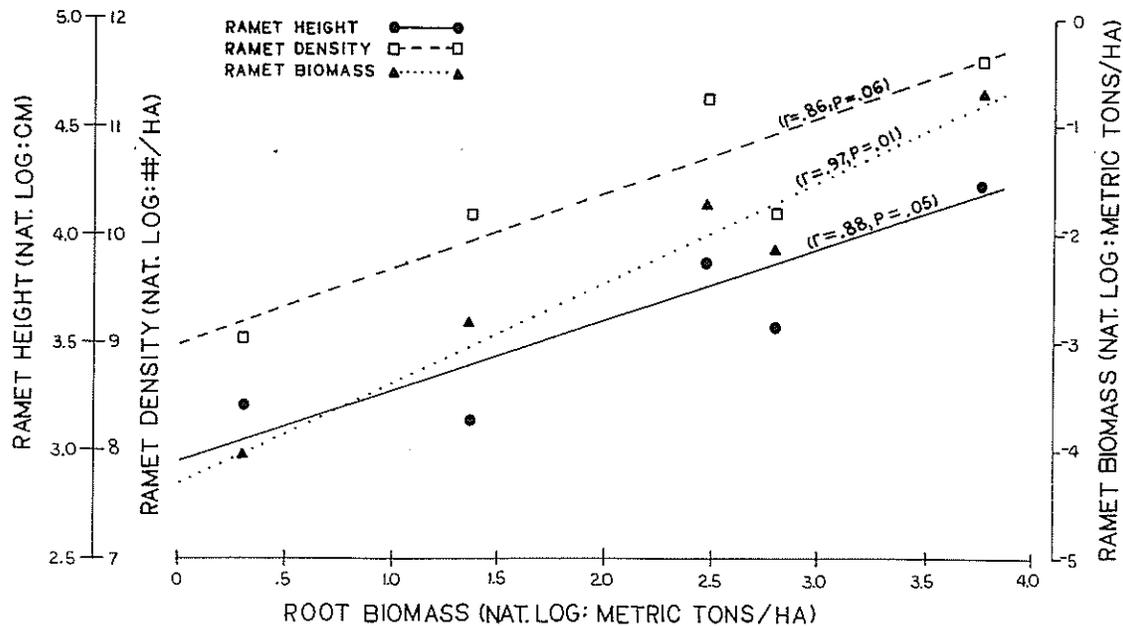


Figure 4. Aspen ramet density (natural log: #/ha), biomass (natural log: metric tons/ha), and average height (natural log: cm) the first year following fire as related to preburn total root biomass (natural log: metric tons/ha) for excluded subplots on 5 experimental sites. The relationships are described as: ramet density = $9.036 + 0.658(\text{root biomass})$, $r = 0.86$, $p = 0.06$; ramet biomass = $-4.211 + 0.89(\text{root biomass})$, $r = 0.97$, $p = 0.01$; and ramet height = $2.963 + 0.313(\text{root biomass})$, $r = 0.88$, $p = 0.05$; Similar results were obtained using preburn stand basal area (natural log: square meters/ha) as the independent variable, where: ramet density = $7.932 + 0.97(\text{basal area})$, $r = 0.86$, $p = 0.05$; ramet biomass = $-5.671 + 1.272(\text{basal area})$, $r = 0.95$, $p = 0.01$; and ramet height = $2.373 + 0.477(\text{basal area})$, $r = 0.91$, $p = 0.03$. All data were converted to metric units, then log transformed, prior to analysis.

lated with both (log-transformed) preburn root biomass ($y = 7.046 + \exp(.374x)$, $r = .62$, $p < .01$) and basal area ($y = 2.511 + \exp(.328x)$, $r = .75$, $p < .01$). Those clones with the greatest preburn root biomass/basal area still supported both more and taller aspen suckers than those with lower preburn root biomass/basal area. Sucker density averaged 29,900/ha ($\pm 23,600$) in the 5 excluded subplots in 1993. The site with the greatest root biomass/basal area supported 40,000 suckers/ha, and the tallest suckers were about 4 m. On the other hand, the site with the lowest root biomass/basal area supported 500 suckers/ha with the tallest suckers about 30 cm. Preburn root biomass/basal area thus appears to be a good indicator of the fire response for at least five to seven years postburn. The change from a linear to an exponential relationship perhaps suggests a change in root biomass from the time since burning.

A within site comparison of fenced and unfenced subplots was used to assess the ungulate influence on postburn suckering (Figure 5). Browsing by elk resulted in a mix of postburn age classes compared to an age class structure that was skewed to the older age classes on protected subplots. Heights were 2-4 times taller inside the enclosure. Browsing did not result in accelerated sucker mortality outside the enclosure. To the contrary, sucker mortality and density trends were comparable both inside and outside the enclosure.

These same general trends were evident on four of the five experimental sites. The fifth site, at Bunsen Peak, showed a 55% reduction in stem density inside the

enclosure and a 100% reduction in the unfenced subplot after 4 years. Sucker density was 15,500/ha and the tallest heights averaged 134 cm inside the enclosure. Other burned clones in the area also lack visible sucker regeneration in the understory. One hypothesis to explain this observation relates to ungulate herbivory. A resident herd of elk remains in the area year-round, and the lack of regeneration may reflect continual utilization. While utilization may partially explain this trend at Bunsen Peak, other factors are undoubtedly involved. Similar trends in sucker regeneration were not observed at one of the experimental sites located four miles to the east in a similar landscape position with a similar elk utilization pattern. Regeneration at the Bunsen Peak site may also be influenced by site conditions. At 7200 feet in elevation, the Bunsen Peak site is on the extreme limit of aspen distribution in the northern range. As evidenced during root trench excavation and subplot isolation, soils in the area are shallow, coarsely textured, and very dry with a high rock fragment content. Such soils are relatively low in nutrient and water holding capacity. There is no surface water in the area, and soil moisture is derived from snowmelt and intermittent spring rains. The site appears to be less hospitable for aspen than any of the experimental sites, and is probably much different today than when the aspen established in the past. It has been recently suggested that soil properties contribute substantially to aspen regeneration with optimal suckering observed on sites with a deep mollic horizon (Cryer and Murray 1992). If soil properties change over time, sites

may eventually lose the ability to support aspen clones. It may be that site conditions in the Bunsen Peak area, lacking a mollic horizon, are now suboptimal for aspen growth, and that fire and browsing accelerated the inevitable demise of aspen stands in the area.

A Synthesis and Summary

Analysis of burned vegetation types revealed that 526 ha, or about 1/3 of the aspen evident from aerial photographs of the park, burned during 1988. Based on observations over the past five years, it appears that most of the burned aspen will not regenerate into a forest overstory component. As evidenced here not all aspen are predisposed to prolific growth following fire, and the response is predictable based on preburn stand root biomass or basal area. Aspen capable of profuse growth are those that occupy the most optimal sites as reflected by the preburn stand characteristics of total root biomass and basal area. The data presented here suggests a preburn basal area of about 25 m²/ha or root biomass of 20 tons/ha are required for optimal aspen stocking and growth following fire.

Protected subplots demonstrate the growth potential of each aspen clone without the browse influence, and a range of growth rates were observed. While aspen at some sites were able to grow approximately 1 m during

the first year postburn, other sites barely achieved that height after 5-7 years postburn. Simply burning aspen does not ensure adequate densities and growth rates to overcome herbivory. At the lower growth rates, it would take >25 years of artificial protection for the majority of terminal aspen buds to achieve such levels. Even then the bark on the trunk of the trees would be vulnerable to browsing following exclosure removal. Based on growth rates of aspen at three of five protected subplots, it is questionable whether the majority of aspen in the landscape would proliferate even if elk densities were drastically reduced from current levels.

As evidenced by the age class structure of unprotected subplots, herbivory alone does not universally result in accelerated sucker mortality or the elimination of aspen from a given site. When suckers are browsed, resources are directed into the production of new suckers rather than the continual height growth of protected suckers produced the first year postburn. Regardless of treatment height growth is terminated during mid-summer, probably because of allocation of photosynthate to the roots for initial shoot production the following spring (Schier and Zasada 1973). This process ensures the continual production of new suckers the following season, even though sucker biomass is reduced overwinter by browsing. Such a cycle allows for the long-term persistence of aspen despite continual utilization, and represents a viable strategy to remain a component of the landscape.

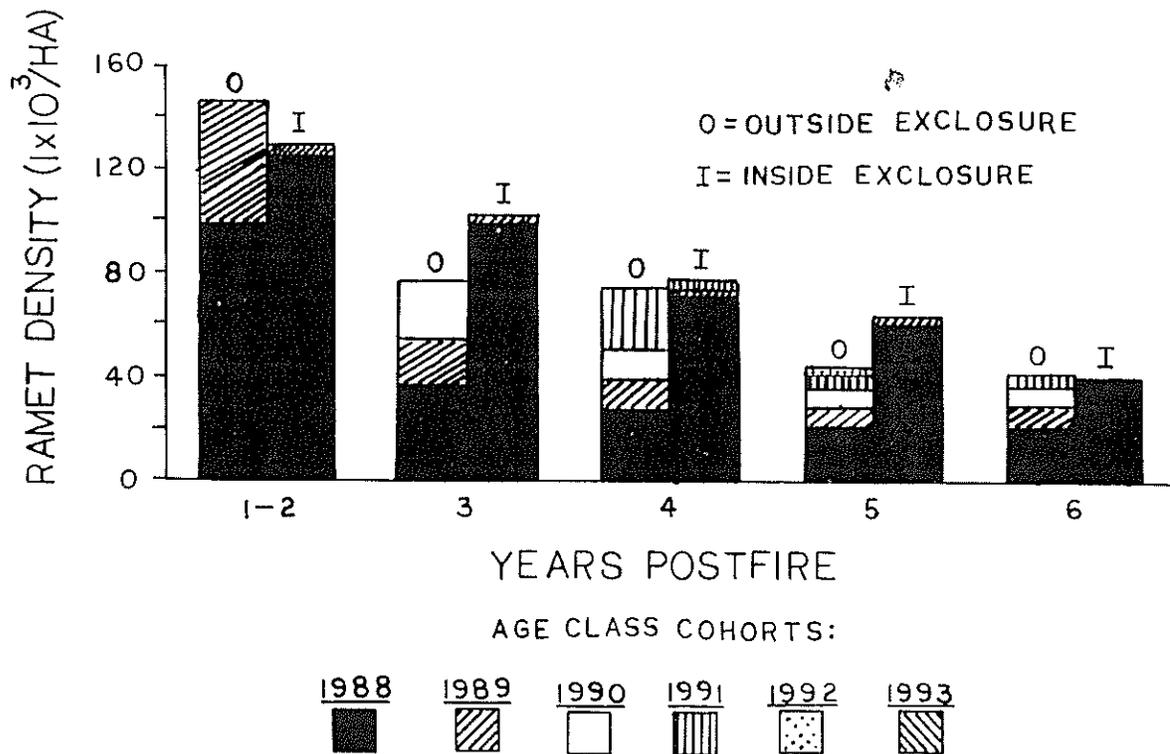


Figure 5. Aspen ramet density and age class trends for paired (inside vs. outside the exclosure) permanent 1x20 m belt transects 6 years following fire at the Crystal Bench site burned in October, 1987. Paired bars are differentiated as O = outside transect (left of the pair) and I = inside transect (right of the pair).

This strategy is consistent with observations and a reinterpretation of historical comparative photographs. Previous interpretations state that aspen has "been replaced" on site by conifers or other vegetation because aspen are no longer evident in the photos. Site inspection of a subset of these photos, however, reveals that aspen still persist on site as scattered suckers 20-60 cm in height all less than five years in age. Even though comparative photographs suggest that aspen have been "non-existent" for up to 40 years, the aspen has been exhibiting growth characteristics of a perennial forb. This inconspicuous phenomena, termed "shrub aspen", has been ignored in previous interpretations.

Shrub aspen has subsequently been found to be prevalent across the northern winter range without the aid of historical photographs or other evidence to suggest that aspen recently dominated the site as an overstory component. Such sites retain a root biomass of about 1 ton/ha, and add about 4 cm of height growth each summer. Many such shrub aspen sites burned during 1988, and did not respond with prolific growth. After 5-7 years, these shrub aspen clones are identical to their preburn condition. It should also be noted we have observed this shrub aspen condition in other ecosystems with differing elk population levels, and probably occurs frequently throughout the range of aspen in North America.

It is probable that shrub aspen is a consequence of the physical environment and reflects the inability of a particular site to support aspen as a canopy component. Combined with the many physiological and hormonal changes associated with aging, shrub aspen may represent senile yet persistent remnants that germinated and proliferated under more optimal climatic and environmental conditions. If aspen longevity and response to disturbance are directly related to site potential, many aspen could eventually be eliminated unless the rate or direction of site evolution is geomorphologically or climatically altered.

The exact physical and chemical parameters that define the optimal aspen site, and the percentage of aspen in the Yellowstone landscape occupying such sites are unknown. Quantifying such factors and influences, in addition to changes in postburn root biomass, would aid substantially to understanding aspen ecology on the northern winter range and represents the future direction of the research reported here. It appears that the underground environment is a significant factor in the long-term behavior of aspen across the landscape. If such is the case, wildfire and herbivory may be rather superficial to the continued persistence of aspen.

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Notes on Postfire Aspen Seedling Establishment

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We earlier reported the widespread germination of aspen seedlings in postfire environments and the establishment of 14 belt transects to monitor long term trends in survival and growth (Renkin, Despain, and Clark 1991). All sites still supported aspen seedlings in 1993. Many factors are playing a role in seedling survival and growth, including ungulate browsing and trampling, disease, intraspecific competition, and competition from lodgepole pine (*Pinus contorta*) seedlings.

While seedling density has generally decreased over time and average seedling height has generally increased, it remains to be seen whether postburn seedlings will continue to grow to achieve sexual maturity. In the low elevation areas of the northern range it appears elk browsing and trampling will keep seedlings at reduced heights, comparable to trends observed with aspen suckering. On the other hand, aspen will probably succumb to competition from lodgepole pine in burned areas of the high elevation rhyolite plateau.

Of particular interest, however, is the elevational zone between 1800 and 2300 m particularly within cold-air drainage microsites. Two transects located within this zone have demonstrated noteworthy trends. One site located in the Elk Creek drainage can be used to demonstrate the influence of elk browsing and competition with lodgepole pine seedlings on aspen seedling growth and survival. Here, a temporary exclosure was constructed in the fall of 1989 and paired inside and outside belt transects were established.

The density of aspen and lodgepole pine seedlings that germinated at the Elk Creek site in 1989 have remained relatively unchanged over a five year period (Table 1). Changes in density were not significant between species ($F = .024, p = .88$) or treatment ($F = .216, p = .65$). Elk have not contributed to mortality of either species, and competition between the species (at least for above-ground resources) has not yet been maximized. Different growth curves are evident between the 2 species, and slight deviation in average height is most evident between protected and unprotected aspen (Figure 1). The difference is not significant ($F = 1.45,$

Table 1. Postfire density (#/square meter) trends for aspen and lodgepole pine seedlings derived from 1x9 m belt transects inside and outside the Elk Creek exclosure site. Differences in yearly density change are not significant for either species ($F = .024, p = .88$) or treatment ($F = .216, p = .65$).

	Year				
	1989	1990	1991	1992	1993
Aspen Seedlings					
inside	2.4	1.9	1.9	1.9	1.8
outside	5.1	5.0	5.0	4.8	4.8
Lodgepole Seedlings					
inside	8.3	8.1	7.8	7.8	7.8
outside	4.1	4.1	3.8	3.7	3.6

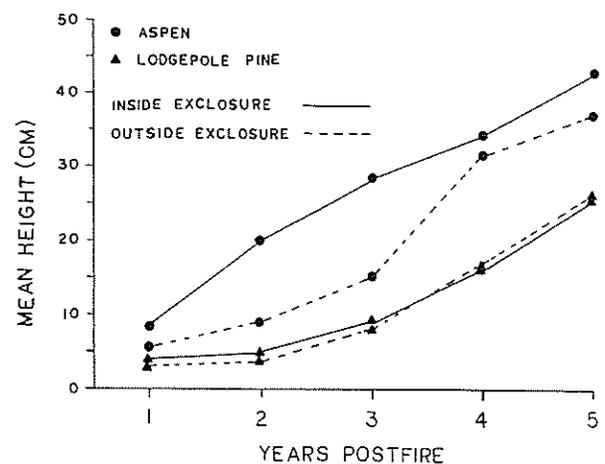


Figure 1. Postfire trends in aspen and lodgepole pine seedling height growth for paired 1x9 m belt transects inside and outside the Elk Creek exclosure site. For aspen, seedling heights were not significantly different by treatment after the fifth growing season ($p = 0.23$).

$p = 0.23$), even though 20% to 75% of the aspen seedlings have experienced overwinter browsing each year. Elk have not had a negative influence on aspen seedling height growth in this area during the initial five years since germination.

Aspen seedlings in this area have demonstrated the greatest potential to achieve sexual maturity. All seedling sites will continue to be sampled over time to monitor density and growth trends in postburn aspen seedling germinants.

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Response of Shrub-Aspen to Yellowstone's 1988 Wildfires: Implications for "Natural Regulation" Management

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Abstract. Aspen has long been a species of special concern in the Yellowstone Ecosystem. Repeat photographs show that the area visibly occupied by aspen on the northern range has declined approximately 95% since Yellowstone National Park was established and that the number of aspen trees has declined 85% since 1947 due to repeated ungulate browsing, not other factors. Although aspen trees are now absent from many areas they formally occupied, some of those sites still support a low growth of aspen suckers — termed “shrub-aspen.” Photographs indicated that aspen can maintain its presence at some locations for up to 60 years without stems ever growing taller than 1 m, again due to repeated browsing by elk and other ungulates.

Park Service biologists have postulated that shrub-aspen is the normal growth form of aspen on Yellowstone's northern range and that it does not represent retrogressive plant succession. This implies that shrub-aspen is a persistent community, and that all tree-type aspen will revert to shrub-aspen. According to this view, aspen will only grow into tree form under ideal climatic conditions or when stimulated by fire.

To test this hypothesis, we used historical photographs to locate early aspen clones on Yellowstone's northern range and then visited those sites to determine what proportion were still represented by shrub-aspen. This also allowed us to compare the area occupied by early aspen stands with the area covered by shrub-aspen today. During the course of this research, the 1988 fires burned several of the shrub-aspen sites we had previously identified. This permitted us to measure the response of those communities to fire.

We found that (1) only two-thirds of aspen clones depicted in early photos, and which today lack aspen trees, are now represented by shrub-aspen; i.e. a third of these aspen clones have completely died out. (2) Where shrub-aspen was found it occupied, on average, only 20% of the area covered by the early aspen clones. (3) Many stands that once contained thousands of aspen trees are now represented by only relatively small numbers of

aspen suckers. (4) Burning did not significantly stimulate shrub-aspen height growth, stem density, or clonal spread. Burned shrub-aspen did not revert to a juvenile growth form, as is common when burned tree aspen stands produce new suckers. (5) Shrub-aspen at sites with additional soil moisture were not able to grow into trees even after they were burned, suggesting that climatic effects are unimportant.

These data and recent studies in Colorado on aspen regeneration ecology indicate that Yellowstone's shrub-aspen is not a stable vegetation type. Instead, shrub-aspen is indicative of retrogressive plant succession. Based on vegetation changes in long-term ungulate-proof exclosures, the only known way for shrub-aspen to grow back into the types of aspen communities that existed on Yellowstone's northern range ca. 1870-1890 is if all ungulate browsing were excluded for 100 years or longer. These data do not support current “natural regulation” management.

Keywords: Elk; Aspen; Fire; Yellowstone; Natural regulation.

Introduction

The relationship between vegetation and ungulates in Yellowstone National Park has long been a subject of conflicting opinions and intense debate (Houston 1982, Chase 1986, Despain et al. 1986, Kay 1990). Until 1968, Park Service officials contended that an “unnaturally” large elk (*Cervus elaphus*) population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely “damaged” the park's northern winter

¹Terms such as “over grazing,” “range damage,” and “unnatural” elk populations are common in nearly all early, government reports on the elk herds in the Greater Yellowstone Ecosystem. Since these terms are value-laden, they are used throughout this paper only in their historical context.

range, including aspen (*Populus tremuloides*) communities (Tyers 1981). However, agency biologists now hypothesize that elk and other animals in Yellowstone are "naturally regulated," being resource (food) limited (Houston 1982, Despain et al. 1986), and that the condition of the ecosystem today is much like it was at park formation. Elk influences on Yellowstone's vegetation are now thought to be "natural" and to represent the "pristine" condition of the park.

Under "natural regulation" (Kay 1990:1-31): (1) Predation is an assisting but non-essential adjunct to the regulation of ungulate populations. If wolves (*Canis lupus*) were reintroduced into the ecosystem, they would only take the ungulates slated to die from other causes, such as starvation, and hence predation would not lower ungulate numbers. (2) If ungulates and vegetation have co-evolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or "range damage." The ungulates and vegetation will reach an equilibrium, called ecological carrying capacity, where continued grazing will not change plant species composition or the physical appearance of the plant communities. (3) At equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means that competition by elk has not reduced the numbers of other ungulates or beaver (*Castor canadensis*) since park formation.

The Park Service's "natural regulation experiment" (cf. Despain et al. 1986) is predicated on the assumption that large numbers of elk (12,000 - 15,000) wintered on Yellowstone's northern range for the last several thousand years. Park Service biologists hypothesize that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for that period of time (Despain et al. 1986). The agency now believes that any changes in plant communities since the park was established in 1872 are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. Park service biologists contend that (1) aspen is a seral species in Yellowstone which in the course of plant succession is replaced by conifers or other vegetation, (2) burned aspen stands will regenerate despite heavy utilization by elk and other ungulates, and (3) elk have not been primarily responsible for the changes that have occurred in the park's aspen communities (Houston 1982, Despain et al. 1986).

To test these predictions of the "natural regulation" paradigm, we conducted an extensive study of aspen ecology in the Yellowstone Ecosystem, including inside-outside park comparisons, inside-outside enclosure measurements, aspen burns, and repeat photographs (Kay 1990, Kay and Wagner 1994). During our research, we found that the area visibly occupied by aspen on the northern range has declined approximately 95% since Yellowstone National Park was established and that the

number of aspen trees has declined 85% since 1947 due to repeated ungulate browsing, not other factors (Kay 1990). We also discovered that although aspen trees are now absent from many areas they formerly occupied, some of those sites still support a low growth of aspen suckers — a condition we term "shrub-aspen." Repeat photographs indicate that aspen can maintain its presence at some locations for up to 60 years without stems ever growing taller than 1 m, again due to repeated browsing by elk and other ungulates. We also discovered shrub-aspen on other ranges in the Yellowstone Ecosystem where large herds of elk concentrate; e.g., Jackson Hole and the Gallatin (Kay unpub. data).

Park Service biologists, who independently observed this phenomenon (Despain 1991), have postulated that shrub-aspen is the normal growth form of aspen on Yellowstone's northern range and that shrub-aspen does not represent retrogressive plant succession. According to this view, aspen will only grow into tree form under ideal climatic conditions, such as occurred just before Yellowstone Park was established or when stimulated by fire (Despain 1990, 1991). This implies that shrub-aspen is a persistent community and that all tree-type aspen will revert to shrub-aspen.

To test this hypothesis, we used historical photographs to locate early aspen clones on the park's northern range and then visited those sites to determine what proportion were still occupied by shrub-aspen. This also allowed us to compare the area occupied by early aspen stands with the area covered by shrub-aspen today. During the course of this research, the 1988 fires burned several of the shrub-aspen sites we had previously identified. This permitted us to measure the response of those communities to fire.

Our study was funded by the Rob and Bessie Welder Wildlife Foundation (Contribution No. 451), the Quest For Truth Foundation, Wyoming State Grazing Board No. 4, and Utah State University's Ecology Center.

Study Area

Our work was conducted on the winter range of Yellowstone's northern elk herd. Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range.

Methods

We searched archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological

Survey's Denver Photographic Library for historical photos of the northern range. We reviewed approximately 50,000 images taken in the park and throughout the Yellowstone area. Only a small portion of these were taken on the northern range, and a still smaller number contained views of aspen. During 1986-88, we rephotographed the locations in the historical pictures to form sets of comparative photos, a process called repeat photography (Rogers et al. 1984).

By field examination, we determined if the aspen clones shown in historical photos were still represented by aspen trees, shrub-aspen, or had completely died out. If shrub-aspen was present, we estimated the area occupied by the original aspen clone, as depicted in the historical photograph, and compared that estimation to the area supporting shrub-aspen at the time of our study. We then randomly placed a single 2x30 m belt transect in each of the shrub-aspen communities and counted the number of aspen stems present. We also recorded the height of each aspen stem and aged a representative sample by cutting the suckers at ground level and counting annual growth rings. Photographs were taken of each shrub-aspen community and of each belt transect, but the plots were not otherwise marked.

After the 1988 fires, our earlier photographs allowed us to establish permanent 2x30 m belt transects as close to the original sites as possible in five of the shrub-aspen communities we had previously measured. The number of aspen stems on those transects was recorded in 1989, 1991, and 1992 as was the height of each sucker. During 1989, we also measured the width of the largest leaf on a sample of shrub-aspen stems to determine if burning had stimulated juvenile-type growth as commonly occurs when tree aspen are subjected to killing fire. A study was also instituted on 131 tree-type aspen clones burned during 1988 to measure the ability of those stands to regenerate via root suckering. Those data, however, will not be reported here except to compare initial sucker density, height, and leaf width with that recorded on shrub-aspen plots.

Where appropriate (Hurlbert 1984), sample means were compared using Student's *t* test (Sokal and Rohlf 1981).

Results and Discussion

We made 81 repeat photosets of aspen communities on Yellowstone's northern range dating to 1871 (Kay 1990). Only two-thirds of aspen clones depicted in early photos, and which today lack aspen trees, are now represented by shrub-aspen; i.e. a third of the aspen clones have completely died out. There was no correlation between slope, aspect, elevation, distance from surface water, or surrounding vegetation and whether clones either went extinct or reverted to shrub-aspen.

Where shrub-aspen was found, it occupied, on average, only 20% of the area covered by the early aspen clones. Many stands that once contained thousands of aspen trees are now represented by only relatively small numbers of aspen suckers. On 22 shrub-aspen plots measured before the 1988 fires, densities ranged from 1,500 to 56,511 stems per ha and averaged 22,551. Individual shrub-aspen stems are also short-lived. The majority were less than four years old while the oldest stem we found was only 15. These results are similar to those reported for the longevity of aspen suckers in tree-type clones on Yellowstone's northern range (Kittams 1952a, 1952b).

Burning did not significantly stimulate shrub-aspen stem density (Table 1); 18,004 per ha before the fires versus 19,170 in 1989. One year after they were burned, tree-type aspen killed by the fires produced sucker densities ranging from 68,847 to 199,040 stems per ha with a mean of 120,941 (Kay unpub. data). This was significantly greater than the density recorded in shrub-aspen communities ($t=22.62$, $p<.001$), and is probably related to clonal vigor; i.e., tree-type aspen is in better condition than shrub-aspen (Bailey et al. 1990).

Burning also did not stimulate shrub-aspen height growth (Table 2). Following fire, mean height growth fell from 41.2 cm to 20.9 cm ($t=3.55$, $p<.01$). In comparison, aspen suckers that sprouted on tree-type, fire-killed aspen plots averaged 70.5 cm ($n=818$) in 1989 (Kay unpub. data), which was significantly taller than what we recorded for shrub-aspen ($t=37.96$, $p<.001$). The 1989 height measurements were recorded before those plants were browsed, as most browsing occurs during winter when animals move on to Yellowstone's northern range. By 1992, however, shrub-aspen on the burned plots were approximately as tall as they had been prior to the 1988 fires. Long-term average aspen sucker height on Yellowstone's northern range appears to be more a function of variable snow depth limiting elk browsing than other factors (Kittams 1952a, 1952b; Barmore 1981).

Table 1. Density of shrub-aspen stems on Yellowstone's northern range before and after the 1988 fires.

Plot	Year — Stems per ha			
	1986	1989	1991	1992
SC-1	34,173	42,008	30,006	20,337
SC-2	23,171	20,504	20,671	14,836
SC-3	20,171	11,669	7,668	4,668
A-8	3,667	833	500	667
SC-10	8,668	21,171	13,169	12,336
Mean	18,004	19,170	14,336	10,502
SEM	5,501	6,835	5,168	3,667

Table 2. Mean height (cm) of shrub-aspen stems on Yellowstone's northern range before and after the 1988 fires.

Plot	Year — Mean (SEM) height			
	1986	1989	1991	1992
SC-1	33.7 (0.9)	16.8 (0.6)	16.3 (0.6)	30.2 (1.0)
SC-2	30.9 (0.8)	22.7 (0.7)	22.2 (0.6)	30.7 (0.8)
SC-3	46.7 (2.6)	30.8 (1.8)	31.3 (1.5)	42.6 (2.8)
A-8	42.9 (2.9)	23.6 (7.4)	34.7 (7.4)	49.6 (2.6)
SC-10	51.7 (6.8)	11.0 (0.4)	38.0 (1.7)	43.5 (6.0)
Mean	41.2	20.9	28.6	39.3
SEM	3.9	3.3	4.0	3.8

Measurements of aspen leaf widths further indicate that fire did not stimulate shrub-aspen. The width of the largest leaf on aspen suckers that sprouted in burned tree-type aspen the first year after Yellowstone's fires averaged 79 mm (n=127) while that of shrub-aspen averaged 26 mm (n=159) ($t=34.71$, $p<.001$). There was also no indication that burning stimulated the spread of the shrub-aspen clones. Instead, declining stem-densities (Table 1) suggest the opposite trend. This is not surprising since other research in Yellowstone has shown a positive correlation between above-ground aspen biomass and aspen suckering following fire (Renkin and Despain 1991). Aspen stands with the lowest above-ground biomass, such as shrub-aspen, produced the lowest amounts of sucker biomass after they were burned (Renkin and Despain 1991).

Recently, Park Service biologists have attributed the demise of aspen in Yellowstone National Park to a drying climatic trend unrelated to ungulate use of the northern range. There is no evidence, however, to support that contention especially since aspen located inside long-term, ungulate-proof exclosures has expanded and replaced grasslands (Kay 1990). Moreover, shrub-aspen located along streams or in other areas with supplemental moisture have not achieved tree status. In addition, with the loss of aspen trees, soil chemistry often is modified to such an extent that normal aspen communities may not be able to become reestablished even if grazing is excluded (Cryer and Murray 1992). This suggests that it may be difficult to restore aspen to its former status in the park. Moreover, aspen seedlings which grew after Yellowstone's 1988 fires will not reverse this trend because ungulate browsing is limiting aspen seedling height growth and will probably prevent any of those plants from growing into trees, let alone establishing new clones (Kay 1993). This is not surprising since others

have shown that elk (Bartos et al. 1991, 1994) or cattle (Fitzgerald and Bailey 1984, Fitzgerald et al. 1986, Walker 1993) can prevent regeneration of even burned tree-type aspen.

Conclusions

These data indicate that Yellowstone's shrub-aspen is not a persistent vegetation type. Instead, the decline of aspen on Yellowstone's northern range, including the creation of shrub-aspen, is indicative of retrogressive plant succession caused by repeated ungulate browsing. Based on vegetation changes in long-term ungulate-proof exclosures (Kay 1990), the only known way for shrub-aspen to grow back into the types of aspen communities that existed on Yellowstone's northern range ca. 1870-1890 is if all ungulate browsing were excluded for 100 years or longer. These data do not support current "natural regulation" management.

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Large Mammal Mortality in the 1988 Yellowstone Fires

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Abstract There were 396 confirmed deaths of large mammals from fire-related causes within the Yellowstone ecosystem during the fire season of 1988: 333 (84.1%) elk (*Cervus elaphus*), 36 (9.1%) mule deer (*Odocoileus hemionus*), 12 (3.0%) moose (*Alces alces*), 9 (2.3%) bison (*Bison bison*), and 6 (1.5%) black bears (*Ursus americanus*). The primary cause of death appeared to be from smoke inhalation. Only a small number of animals died as a result of burns. Extensive wildland fires have a significant influence on population numbers of some large mammals through habitat alterations, but large mammals appear to be adept at avoiding injury and death in wildland fires. However, certain fire characteristics such as wide and fast moving fronts, canopy burns, and thick ground smoke, could place some animals at risk, especially in large groups. Even under the extreme fire conditions of 1988, large mammal populations in the Yellowstone ecosystem suffered <1% reduction from fire-associated mortality.

Keywords: Fire; Large mammals; Yellowstone ecosystem; Mortality.

Introduction

The immediate effects of wildland fires on vegetation are relatively easy to document, such as the total burn area, the classification of burns, and the habitat types involved. It is more difficult to access the direct impacts to wildlife and there is little documentation of large mammals dying in fires (Howard et al. 1959, Bendell 1974).

The Yellowstone fires of 1988 involved approximately 4.8 million ha of mostly public land in and around Yellowstone National Park and provided a unique opportunity to investigate the impact of fire on large mammal mortality. The fires were often associated with wide storm fronts, allowing fires to advance up to 16 km/day (Schullery 1989) through land that contained large numbers of free-ranging animals.

Methods

Throughout the summer of 1988 we remained in the Yellowstone ecosystem as part of an ongoing ecological study of grizzly bears (*Ursus arctos horribilis*) and observed the reaction to fire of grizzly bears and other large mammals, such as bison (*Bison bison*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), black bears (*Ursus americanus*), coyotes (*Canis latrans*) and moose (*Alces alces*). We also monitored some radio-instrumented grizzly bears by ground with a Telonics receiver and a hand-held Yagi antenna.

To document grizzly scavenging activity we surveyed burned areas by ground and from the air to make a census of dead animals. Helicopters were used to survey areas where extensive, fast moving fire fronts occurred. Additional areas were surveyed by ground. We recorded the location, age and sex class, type of scavenger activity and percent consumption for each animal. The upper airway was removed from 31 animals to determine the cause of death. Some carcasses were reexamined at a later date to determine scavenger activity.

Results

Animal Behavior

We observed no large mammals fleeing a fire front and most appeared indifferent to fires even when fire canopy fires were nearby. Some appeared curious, approaching a fire front and watching trees burn. One black bear was observed to stick its paw into the flames of a burning log. Most animals continued foraging even in thick smoke associated with fire fronts.

Two radio-instrumented female grizzly bears were monitored by ground as a wide fire storm approached. An adult female with 2 cubs-of-the-year avoided the fire by moving around the leading edge and left the area. During the next 12 hours they traveled more than 20 km.

A single adult female remained directly in the path of the fire storm and continued foraging in the burned areas for several days.

Census of Fire-Killed Animals

Two hundred and fifty-nine large mammals killed by the fires were found in Yellowstone National Park and an additional 137 were discovered immediately outside the park in Montana and Wyoming (Singer et al. 1989) (Table 1). There were no known grizzly bear deaths. Two radio-instrumented grizzly bears were listed as probable deaths (Blanchard and Knight 1990), but one of these bears was re-trapped in 1993 (Richard R. Knight, biologist, U.S.D.I. National Park Service, pers. commun.).

The largest group of dead animals found contained 144 elk: 74 adult females, 9 adult males, 18 yearling males, 8 yearling females, and 37 calves. Two were in a burned meadow 40 and 150 m respectively from the forest edge. The remaining 142 carcasses were clustered in an area of about 120 m diameter just within the forest.

This area had been subjected to a canopy fire in early September approximately one month before our discovery. The trees were extensively charred and branchless, and no ground cover remained. The forest floor consisted of a uniform layer of fine ash about 5-10 cm thick. Carcasses were evenly distributed within this roughly circular area with some lying on top of one another and some under fallen trees. Antlers, teeth, and distal extremities were burned and shattered, and hides were singed and burned to a hard leathery texture. Soft tissues were partially or completely cooked, and the typical decaying process was absent, including foul odor.

Thirty-five of the 144 carcasses had definitive evidence of bear feeding activity and 7 had possible bear feeding activity. Six carcasses were buried. Both black and grizzly tracks were found in the ash. During revisits to this area we observed grizzly bears, black bears, coyotes, bald eagles (*Haliaeetus leucocephalus*), golden

eagles (*Aquila chrysaetos*), and ravens (*Corvus corax*) feeding on the carcasses. More than 500 ravens were observed feeding on the carcasses each day this site was monitored.

Tissue Sampling

The airway from the oropharynx to the mid-trachea were removed from 31 dead animals surveyed. Five airways were extensively burned but the remaining 26 contained a thick layer of soot extending from the oropharynx down past the vocal cords into the tracheae. These findings were observed in both burned and unburned carcasses.

Discussion

The most reliable clinical test in diagnosing fatal smoke inhalation is the presence of soot below the level of the vocal cords (Heimback and Waeckerle 1988, Herndon 1984, Moylan 1980, Trunkey 1978, Walker et al. 1981). Based upon this criteria, 26 of the 31 animals we surveyed (84%) probably died of smoke inhalation. Smoke inhalation induces death by the direct toxic effects of smoke on pulmonary physiology and/or carbon monoxide poisoning (Cohen and Guzzardi 1983, Fisher 1969, Nieman 1980, Zikria et al. 1972).

Singer et al. (1989) reported that an elk and bison died as a result of burns during the 1988 Yellowstone fires. We suspect that there were probably a small number of other large mammals that did as well. Five of the animals we sampled may have died from burns, but the samples were inconclusive since the tracheal lining was completely burned.

Seventy-five percent of the animals killed in Yellowstone National Park were in three groups of 18, 33, and 144 animals respectively, and were apparently killed in the same fire storm that was wide, fast moving, and had a thick, low-lying cloud of smoke in advance. Most of these animals were elk and appeared to be harem groups that joined together in panic where they died of smoke inhalation before the fire front arrived.

Most of the carcasses were extensively burned and the typical decaying process that leads to odor and detection by bears and other scavengers was significantly suppressed. Airborn scavengers were probably the first to detect many of the carcasses and the circling behavior of large numbers of ravens observed at one site probably attracted bears and coyotes.

We observed little carcass-burying activity by bears at the site containing 144 elk carcasses. Bears will often bury a carcass, possibly to reduce its attraction to other scavengers. The unusual circumstances at this site may have made burying behavior a waste of time and energy, but burying may have served to "claim" a certain carcass

Table 1. Species and Location of the 396 Large Mammals Killed by the Yellowstone Fires in 1988.

	Species				
	Elk	Moose	Bison	Mule Deer	Black Bear
Yellowstone National Park	244	2	9	4	0
Surrounding National Forests	89	10	0	32	6
Total	333	12	9	36	6

after a bear had begun feeding on it. Another possibility is that burying behavior is advantageous for a single carcass, but not when multiple carcasses are present.

Animals of some species probably survived the fires because of habitat preferences. Bighorn sheep (*Ovis canadensis*) generally remained in alpine environments during the summer, and pronghorn (*Antilocapra americana*) preferred large open grasslands. Species like mountain lion (*Felis concolor*) and whitetail deer (*Odocoileus virginianus*) were rare in this ecosystem, and detection of individuals killed by fire would have been unlikely.

Large mammals appear to be adept at avoiding injury or death in wildland fires. However, certain fire characteristics such as wide and fast moving fronts, canopy burns, and thick ground smoke, could place some animals at risk, especially in large groups.

The summering population of elk in Yellowstone National Park was about 31,000 (Singer et al. 1989), but only 244 elk deaths were documented. During the summer of 1988 the bison population was between 3200-3300 (Mary Meagher, biologist, U.S.D.I. National Park Service, pers. commun.) and only 9 bison deaths were documented. Both populations suffered <1% reduction from fire-associated mortality even under the extreme fire conditions of 1988. Extensive wildland fires have a significant influence on population numbers of some large mammals through habitat alterations, but apparently do not kill significant numbers of animals in free-ranging populations.

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Effects of Wildfire on Grizzly Bear Movements and Food Habits

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Abstract. Forty-four radio-telemetered grizzly bears (*Ursus arctos horribilis*) were located 867 times during 1989-92 within Yellowstone National Park following extensive wildfires in 1988. Pooled locations indicated avoidance of burned sites during 1989, especially by females with cubs-of-the-year, but not during subsequent years. On the average, individual grizzly bears were located in burned and unburned habitats in proportion to their availability within each bear's annual range. Rates of movement were lower than those recorded prior to the fires, indicating adequate native food supplies. Feeding habits at burned sites differed significantly from those recorded at unburned sites. Short-term effects of the fires were beneficial to grizzly bears largely because of increased production of diet items such as forb foliage and tuberous root crops in burned habitats.

Keywords: fire, food habits, grizzly bear, movements, Yellowstone National Park.

Introduction

Wildfires during 1988 burned approximately 12% of the 4.8 million-ha Greater Yellowstone Area which includes Yellowstone National Park and contiguous portions of 6 national forests, 2 national parks, 2 national wildlife refuges, state land, and land in private ownership (Schullery 1989). The burned area was entirely contained within the range of the Yellowstone grizzly bear population. Effects of altering grizzly bear habitat by timber harvest and fire have been studied in northwest Montana (Mealey et al. 1977, Zager et al. 1983, Holland 1986), but not in the Yellowstone area. Results of those studies cannot be directly applied to Yellowstone because habitat and cover types are not similar (Knight et al. 1984). Food habits of grizzly bears also differ substantially between the two areas (Mattson et al. 1991).

The primary immediate effect of the fires on Yellowstone grizzly bears was increased availability of

elk carrion during the fall of 1988 through fire-related deaths (Blanchard and Knight 1990). We tested the hypotheses that the fires had no significant deleterious effects on grizzly bear movements or feeding habits during 1989-92.

Funding for this study was provided by the National Park Service, U.S. Fish and Wildlife Service, U.S. Forest Service, and the states of Idaho, Montana, and Wyoming. Technical support was provided by Yellowstone National Park and the 3 states. Aerial radio-tracking was skillfully performed by D. and R. Stradley. We thank P. Gogan for reviewing the manuscript.

Methods

Three data sets were used in the analysis: (1) aerial radio-telemetry locations of instrumented grizzly bears, (2) grizzly bear feeding sites, and (3) scat contents. Grizzly bears were captured and fitted with neck collar transmitters (Blanchard 1985). Randomly selected locations of instrumented bears were investigated for evidence of feeding activity and plant communities at the sites were recorded. Community plots were variable in size, being large enough to adequately represent the vegetative association (Blanchard 1985). Cover of plant species, and total grasses, forbs, shrubs, and forest were visually estimated. Heights of grasses, forbs, and shrubs were measured. Scats were collected at radio-telemetry locations and en route to and from those sites. Scat contents were determined by visually estimating percent volume of each diet item which were identified to the finest taxonomic resolution possible (Mattson et al. 1991).

Burned areas were determined from aerial photo interpretation of Landsat imagery and ground truthing. Areas were categorized as unburned or 1 of 4 burn types (Despain et al. 1989). Canopy burns were characterized by burned forest overstory and ground cover; mixed burns contained both burned and unburned trees; nonforested burns included burned shrublands, grass-

lands, and meadows; undifferentiated burns were burned areas that could not reliably be classified in another burn type.

Locations of radio-marked bears and feeding sites were assigned to a burned or unburned category using Geographic Resource Analysis Support System (GRASS) software. Analyses were restricted to within the boundaries of Yellowstone National Park by availability of digitized mapping data.

Seasons were spring (Mar-Jun), summer (Jul-Aug), and fall (Sept-Nov). Adults were 5 years and older. Cohorts included females with cubs-of-the-year (COY), other adult females, subadult females, subadult males, and adult males. Rates of movement were calculated from harmonic mean distances between successive location, and range sizes were estimated by the minimum convex polygon method (Blanchard and Knight 1990). Instrumented bears were located from the air approximately once a week. To ensure independence of observations, only one location per day and one den location per season per animal was used (Swihart and Slade 1985). Sites to which bears were transported during management actions were excluded as were capture sites.

Data recorded as percentages were converted by arcsin transformation prior to statistical testing since percentages form binomial rather than normal distributions (Zar 1984). Depending on sample size, the Chi-square test or Fisher's Exact Test (FET) was used to determine if there was a significant difference between the observed frequency of burn type use (locations of radio-marked bears) and the expected use based on availability. Bonferroni confidence intervals were used to determine which burn types were being "preferred/avoided" when $P < 0.05$ (Byers et al. 1984). Burned categories were combined for analysis of seasonal and cohort stratifications due to limited sample sizes.

Results

Forty-four individual radio-telemetered grizzly bears were located 867 times during 1989-92. Bears were located in burned and unburned habitats in proportion to

their availability except during 1989 ($P = 0.001$, $X^2 = 19.878$, $df = 4$) (Table 1). That year, bears were located in unburned habitats more often than expected by chance and in canopy and mixed burns less often. During 1989, females with COY used burned habitats significantly less than expected during spring ($P = 0.032$, $X^2 = 4.622$, $df = 1$), summer ($P = 0.001$, $X^2 = 10.306$, $df = 1$), and fall ($P = 0.003$, $X^2 = 9.017$, $df = 1$). That year, other adult females also used burned habitats less than expected during fall ($P = 0.034$, $X^2 = 4.500$, $df = 1$). Subadult males used burned habitats less than expected during spring of 1989 (FET: $P = 0.045$) and 1991 ($P = 0.048$, $X^2 = 3.900$, $df = 1$). Other cohorts used burned and unburned habitats in proportion to their availability during all seasons each year.

Data were available to estimate annual ranges for 27 grizzly bears during 1989-92, including 7 females with COY, 10 other adult females, 2 subadult females, 4 subadult males, and 4 adult males. The majority of bears were located in burned or unburned habitats in proportion to their availability within each individual's annual range. Twenty-eight percent of the 501 locations associated with these 27 annual ranges were within a burn, and 35% were within 50 m of a burn. The average availability of burned area within these annual ranges was also 28% (range: 2-69%). The observed numbers of locations within burns differed significantly from the proportion of burned habitat within each annual range for only 2 bears. During 1990, 1 subadult male was located in burned habitats (i.e. canopy burns) more than expected (FET: $P = 0.001$). During 1991, 1 adult female was located in burned habitats of all burn categories more than expected (FET: $P = 0.049$).

The relative area of unburned habitat was significantly greater within female annual ranges (mean = 0.788) compared to male annual ranges (mean = 0.554) ($P = 0.002$, $t = 3.283$, $df = 25$). This can largely be explained by the significantly larger ranges of males (M: 915 km², F: 321 km²; $P = 0.021$, $t = 2.134$, $df = 25$).

Three individuals were radio-tracked for more than 1 year - 2 adult females for 3 and 2 consecutive years, and a subadult female for 2 years. These individuals were located in burned and unburned habitats in proportion to

Table 1. Observed and expected occurrence of locations of radio-marked grizzly bears within burns in Yellowstone National Park, 1989-92.

Burn category*	Area (ha)	Relative area	1989		1990		1991		1992	
			Expected usage	Observed usage	Expected usage	Observed usage	Expected usage	Observed usage	Expected usage	Observed usage
Canopy	130,889	0.154	47	22 ^b	25	30	34	21	28	24
Mixed	113,860	0.134	41	22 ^b	22	11	29	21	24	27
Nonforest	20,772	0.025	8	5	4	5	6	3	5	4
Undifferentiated	15,068	0.018	6	8	3	1	4	2	3	5
Unburned	568,533	0.670	203	246 ^b	111	118	147	172	121	120

* Canopy = forest overstory and ground cover burned. Mixed = forest overstory not burned uniformly. Nonforest = burned shrublands, grasslands, and meadows. Undifferentiated = burned areas that could not be classified.

^b Simultaneous confidence indicate a difference at the 0.05 level of significance.

their availability within their annual ranges with one exception. One adult female with yearlings used burned habitats more often than expected during 1991.

Movements

Mean seasonal rates of movement were consistently lower during 1989-92 compared to the 13-year average (1975-87) (Blanchard and Knight 1991) for all cohorts (Figure 1). Differences were statistically significant for females with COY during spring, and all other adult females and adult males during spring and summer. Mean annual range sizes of cohorts differed significantly from that recorded 1975-87 only for females with COY (Table 2) who had smaller ranges 1989-92 ($P = 0.034$, $t = 2.222$, $df = 6$).

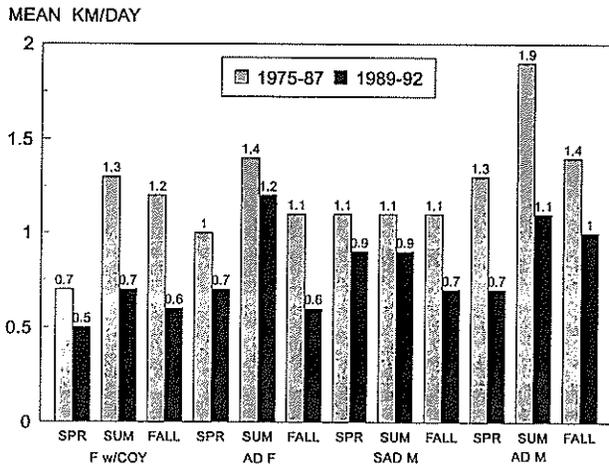


Figure 1. Seasonal rates of movement of female grizzly bears with cubs-of-the-year (Fw/COY), adult females (ADF), subadult males (SAD M), and adult males (ADM) 1989-92 compared to 1975-87 in the Yellowstone ecosystem.

Feeding Activity

Feeding activities were recorded at 891 feed site examinations during 1989-92 (Table 3). Twenty-four percent of the sites occurred at burned sites. Types of feeding activities varied by season, habitat (forest or nonforest), and whether the site was burned.

During spring, types of feeding activities differed significantly between burned and unburned sites in forested habitats ($P = 0.000$, $X^2 = 25.479$, $df = 5$), but not in nonforested habitats ($P = 0.086$, $X^2 = 8.160$, $df = 4$). During summer, feeding activities differed significantly between burned and unburned sites in both forested ($P = 0.000$, $X^2 = 58.620$, $df = 5$) and nonforested ($P = 0.032$, $X^2 = 10.547$, $df = 4$) habitats. During fall, feeding activity frequencies differed significantly between burned and unburned sites in forested habitats (FET: $P = 0.002$), but not in nonforested habitats (FET: $P = 0.303$).

Grazing was consistently recorded more frequently at burned forested sites during spring and summer of all years and included both graminoids and forbs. Species of grazed forbs differed at burned and unburned sites (FET: $P = 0.014$). Grazing on fireweed (*Epilobium angustifolium*) accounted for 29% of forb grazing at burned sites compared to no such instances at unburned sites. Horsetail (*Equisetum* spp.) comprised 27% of forb grazing at unburned sites compared to 13% at burned sites. Height of foliage (graminoids and forbs) and forb cover did not differ at burned and unburned sites. However, cover of graminoids was significantly different ($P = 0.000$, $t = 4.113$, $df = 95$) with an average of 9.7% cover at burned sites ($SD = 6.0$, $n = 61$) and 16.3% at unburned sites ($SD = 10.0$, $n = 36$). Analysis of scat contents revealed no difference in percent volume of graminoid foliage during 1989-92 (30%) compared to the 1977-87 (24%) average. However, volume of forb foliage during spring and summer increased annually to a high in 1992 of 20% in spring and 45% in summer compared to the 1977-87 average of 13% and 22%, respectively (Figure 2). Volume of clover (*Trifolium* spp.) increased from 0% in spring of 1989 to 6% in spring of 1992, and from 4% in summer of 1989 to 27% in summer of 1992 compared to the 1977-87 average of 3% in spring and 4% in summer (Figure 3). Volume of fireweed foliage increased during summer from 3% in 1989 to 10% in 1991, then returned to 3% by 1992 compared to the 1977-87 average of 1% (Figure 4).

Other types of feeding activities also differed at burned and unburned habitats. Use of ungulate carcasses was consistently recorded more frequently at unburned forested sites during spring of all 4 years (range: 0.24-0.78). Searching for insects (primarily ants) was consis-

Table 2. Mean annual range size of grizzly bear sex-age groups 1989-92 compared to 1975-87 in Yellowstone National Park. Range sizes were minimum convex polygons (MCP) in km².

	1989-92			1975-87			P	t	df
	n	MCP	SD	n	MCP	SD			
Adult females	17	254	389	48	281	196	0.291	0.562	16
Females with COY	7	117	74	14	231	136	0.034	2.222	6
Subadult males	4	1,353	1,196	8	698	598	0.058	2.190	3
Adult males	4	476	250	28	874	630	0.148	1.263	3
Lone adult females	7	223	169	17	236	114	0.389	0.296	6
Subadult females	2	891	196	15	365	191	0.080	3.891	1

Table 3. Grizzly bear feeding activities recorded at feed site examinations in the Yellowstone ecosystem, 1989-92.

Habitat	Season ^a	Burn ^b	Feed sites	Feeding activities							Total
				Grazing	Ungulates	Insects	Roots	Rodents/ caches	Whitebark pine seeds	Other	
Nonforest	Spring	B	48	22	2	4	18	8	0	0	54
		U	152	45	19	8	47	44	0	0	54
	Summer	B	64	12	2	5	51	2	0	3	75
		U	168	34	8	33	99	18	4	2	198
	Fall	B	5	1	1	0	3	0	0	0	5
		U	21	3	1	0	18	1	0	1	24
Forest	Spring	B	51	31	9	6	1	1	0	2	50
		U	70	12	26	10	2	1	8	4	63
	Summer	B	38	23	4	4	3	1	2	3	40
		U	123	9	8	58	8	1	28	18	130
	Fall	B	3	1	0	0	0	0	0	2	4
		U	148	1	3	18	2	3	115	7	149

^a Spring: March-June, Summer: July-August, Fall: September-November.

^b B: burned, U: unburned.

tently recorded more frequently at unburned forested sites during summer (range: 0.10-0.62). Within unburned forested habitats, digging for roots was consistently recorded more often at unburned sites (42% of 232 feed sites) during all 4 summers compared to burned sites (22%). Species of roots dug differed between burned and unburned sites ($P = 0.000$, $X^2 = 15.673$) with yampa (*Perideridia gairdneri*) dug more frequently at burned sites (82%) compared to unburned sites (44%). Biscuitroot (*Lomatium* spp.) was dug more frequently at unburned sites (56%) compared to burned sites (18%). Searching for seeds of whitebark pine was the most frequent feeding activity at unburned forested sites during fall of all 4 years (range: 0.46-0.93). No instances of this activity were recorded at burned forested sites.

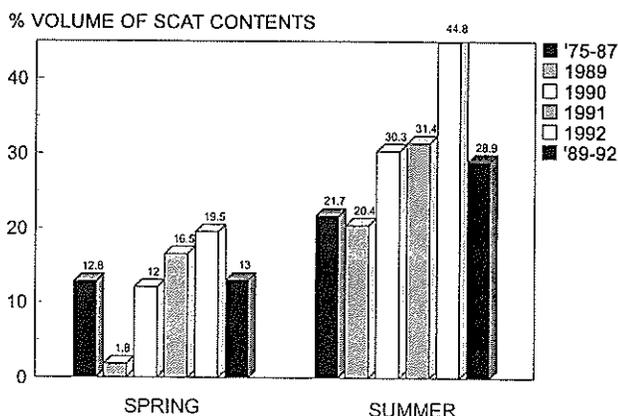


Figure 2. Percent volume of forb foliage in spring and summer grizzly bear scat 1977-87 and 1989-92 in the Yellowstone ecosystem.

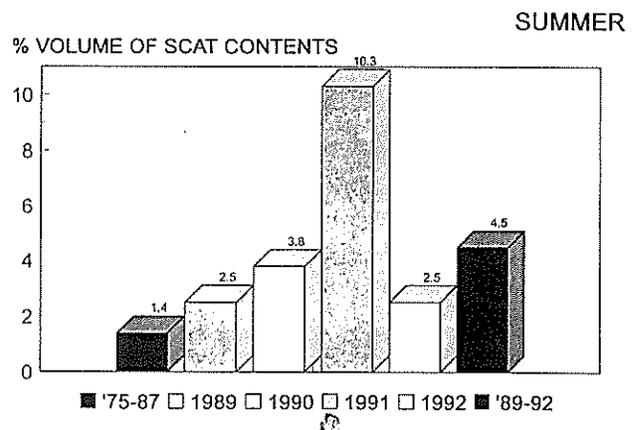


Figure 3. Percent volume of *Epilobium* foliage in summer grizzly bear scat 1977-87 and 1989-92 in the Yellowstone ecosystem.

Discussion

We failed to reject the hypothesis that the wildfires had no deleterious effect upon the subsequent movements of Yellowstone grizzly bears. Annual range sizes remained similar to those recorded prior to the fires, except for smaller ranges for females with COY after the fires. Seasonal rates of movement were generally lower, especially for females with COY, other adult females, and adult males. Low rates of movement (km/day) and small ranges are characteristic during seasons of plentiful native foods, whereas bears range more widely in search of alternate food sources during seasons of low native food abundance (Blanchard and Knight 1991).

We also failed to reject the hypothesis that the fires had no deleterious effect on food habits. However, types of feeding activities differed significantly between burned and unburned sites. Grazing was consistently recorded more frequently during spring and summer at burned forested sites compared to similar unburned sites. This

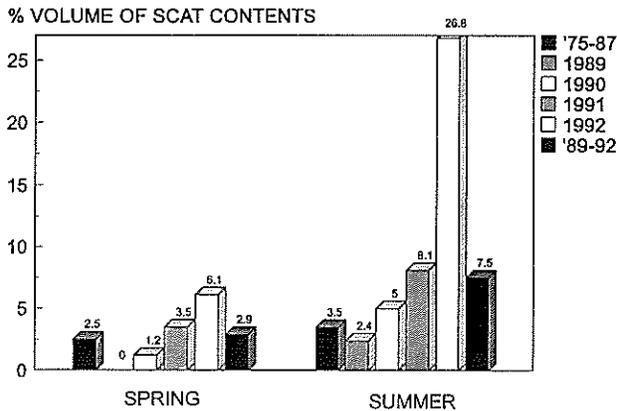


Figure 4. Percent volume of *Trifolium* in spring and summer grizzly bear scats 1977-87 and 1989-92 in the Yellowstone ecosystem.

activity was focused primarily on forb foliage, especially clover and fireweed. Greater forb production in burned habitats was very likely a result of both reduced canopy cover and increased soil nutrients released by the ash. Fireweed is known to proliferate following fires and is relatively high in protein (22% [Hamer et al. 1979]). Clover contains approximately 20% protein compared to 13% for graminoid foliage (Mealey 1975). In addition, fire has been documented to produce significant increases in foliage protein content even after 2 years (DeWitt and Derby 1955).

More frequent digging for yampa roots in burned nonforested habitats during summer was also likely due to increased soil nutrient levels and resulting increased production of root crops. The fact that biscuitroot was dug more often at unburned sites was very likely due to site characteristics. Biscuitroot generally grows on higher elevation, dry ridge tops with sparse vegetation that most often would not burn as intensely as the more abundant vegetation characteristic of the lower elevation mesic meadows where yampa grows (Knight et al. 1984).

Unburned forested sites were favored for feeding on ungulate carcasses in spring, insects during summer, and whitebark pine seeds during fall. Grizzly bears during 1975-83 generally favored forest cover for use of winter-killed and weakened ungulates during spring (Knight et al. 1984). Unburned forested sites very likely provided more cover security for carcass consumption than burned sites. Grizzly bears typically search for ants in moderately to well-decomposed logs within late successional lodgepole and spruce-fir cover types (Mattson 1992). This type of downfall was generally destroyed within burned forested habitats, as were many cone producing whitebark pines.

Fires benefitted grizzly bears in northwestern Montana largely because of increased productivity in a variety of berry-producing shrubs (Martin 1983, Holland 1986, and others). Those bears consume large volumes of berries when available, whereas berries compose a minor

portion of Yellowstone grizzly bears' diets (Mattson et al. 1991). Habitat types are more austere in Yellowstone and do not support the variety and quantity of berry-producing shrubs characteristic of northwestern Montana (Knight et al. 1984).

Potentially the most important and long-term affect of the fires to grizzly bears was destruction of substantial numbers of cone-producing age whitebark pine. Seeds of these trees are by far the single most important source of fat for Yellowstone grizzly bears which consume these seeds to the near exclusion of other food items when available (Mattson et al. 1991). Approximately 30% of the most productive whitebark habitat types were burned within Yellowstone National park in 1988 (D. G. Despain, Natl. Biol. Serv., pers. comm.). The thin bark of whitebark pine makes it vulnerable to damage by fire and its natural regeneration period is at least 50 years (Eggers 1986). Significant cone crops are not produced until about 100 years and may persist for 200-300 years (Mattson and Reinhart 1994). All stands in Yellowstone used by bears to obtain whitebark pine seeds were mature to over-mature in mid-successional to climax stage (Mattson and Jonkel 1990).

Persistence of whitebark pine, a seral species, appears dependent on stand-replacement fires for successful regeneration (Morgan and Bunting 1990). Given the long period until significant cone production of (ca. 100 years), researchers have recommended stand-replacement fires every 300 years of approximately 3% each decade to promote regeneration and sustain productivity for wildlife dependent on the seeds (Mattson and Reinhart 1994).

During 1989-92, cone production was abundant and bears were able to obtain sufficient amounts to preclude searching for alternate food sources often associated with human activities. During years of low to moderate cone production, the loss of whitebark pine burned in 1988 may become more critical.

In summary, the 1988 fires had no apparent harmful short-term affects upon Yellowstone grizzly bears, and were in fact likely beneficial, largely due to increased production of grizzly bear diet items such as forb foliage and tuberous root crops. The long-term affects of substantially reduced numbers of cone producing whitebark pine many prove to be deleterious as bears come into conflict with humans in search for alternate food sources during years of low cone production.

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Pronghorn Migration and Habitat Use Following the 1988 Yellowstone Fires

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Abstract. The genetically-unique Yellowstone pronghorn (*Antilocapra americana*) occupies a limited geographic range within and near Yellowstone National Park. Objectives of our study were to determine if the large 1988 Yellowstone fires affected pronghorn migrations and if there were a lasting (five year) effect on pronghorn preference for, or avoidance of, previously-burned habitat. We used historic and recent pre-fire sightings of pronghorns to delineate their normal migration patterns and summer range habitat. We captured 73 pronghorns and equipped them with radiotelemetry equipment so we could monitor their post-fire habitat use. We also made extensive visual observations of pronghorn habitat use as we traveled along roadways. LANDSAT data and GRASS GIS software were used to map seven major vegetation-burn habitat types on the pronghorn summer range, and we statistically compared pronghorn use of those habitats versus the amount of area in each. Pronghorns migrated to a number of unusual places in and out of the park following the fires. For all seven pronghorn summer range units combined that were frequently used, pronghorns avoided forested areas and used burned and unburned nonforest equally. There were three individual units where pronghorns preferred burned nonforest to unburned. Forest burns on the summer range were probably beneficial to pronghorns because they may have cleared new feeding areas or opened corridors to isolated rangeland habitat. Pronghorns wintered on the unburned Yellowstone permanent range between Mammoth and Reese Creek and depended upon big sagebrush (*Artemisia tridentata*) for food. Since the shrub has been declining in this area, large fires should be excluded unless restoration of the permanent range takes place or ungulate browsing intensity is reduced.

Keywords: Pronghorns; Fires; Habitat use; Migration.

Introduction

It is known that, in the months following rangeland fires, pronghorn antelope may move to such areas and feed on resprouted, nutritious forbs and grasses (Allen 1842, Roosevelt et al. 1908, Deming 1963, Page 1975, Autenrieth 1978). However, it is not known if vegetative regrowth after large fires may affect established annual pronghorn migration patterns, or if fires cause changes in vegetation that have a long-term effect on pronghorn habitat use.

Following the very large fires in and around Yellowstone National Park in the summer and fall of 1988 (Figure 1), a fire mapping team determined that 8 major fires burned 321,409 ha within Yellowstone boundaries (Despain et al. 1989, Schullery 1989). Some of these fires burned into rangeland habitats along the Yellowstone and Lamar Rivers, as well as the large Blacktail Deer Creek drainage (Minshall et al. 1989). These areas are in the northern 1/5 of the park, and have been known to be preferred pronghorn habitat for well over 100 years (Norris 1878).

Rugged mountains surround the entire range used by the Yellowstone pronghorn population. Apparently, the herd is geographically isolated and genetically distinct from all other herds (Scott 1990, Lee et al. 1994). Since Yellowstone pronghorn habitat is quite restricted, we wanted to investigate if the large 1988 fires affected the way the animals used their habitat. Specifically, we had two main objectives: a) find out if there were changes in migratory patterns the next spring following the autumn fires, and b) determine, after shrub regrowth was well underway, if there were a lasting (5+ years) effect on pronghorn preference for, or avoidance of, previously-burned habitat.

This research was partly funded by the National Park Service, Yellowstone National Park, but would not have been possible without considerable volunteer labor by the authors and many others. We would like to especially

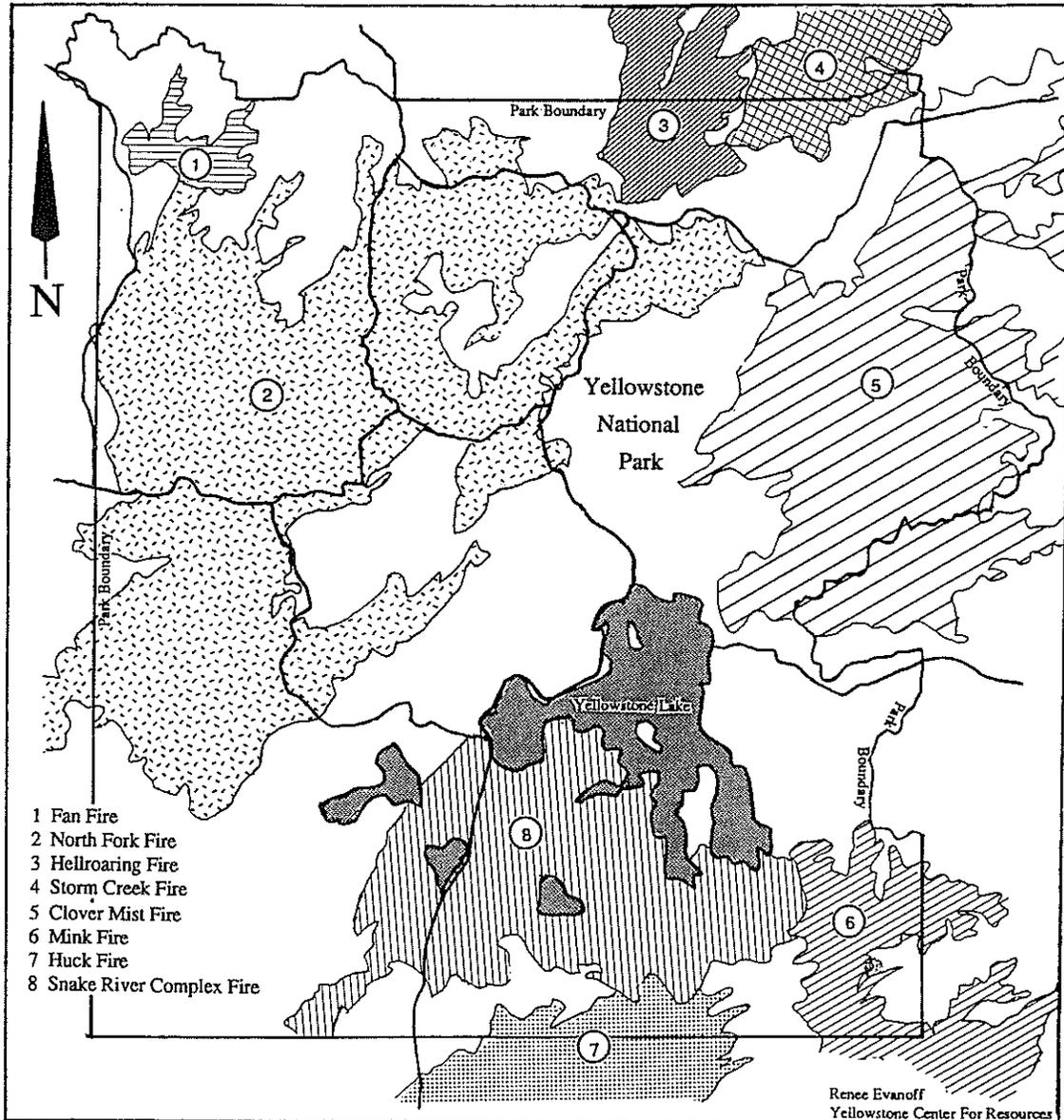


Figure 1. Eight major fires that burned in Yellowstone National Park in the late summer of 1988.

thank R. T. Myers and J. G. Scannell for extensive help in locating pronghorn groups on summer range in the summer of 1993. D. G. Despain provided much-appreciated assistance with the G.I.S. analysis of fire mapping data.

Study Area

The Yellowstone pronghorn herd occupied some land year-round (called the permanent range), and used other areas (termed summer range) only during part of the year (Murie 1940:89, M. D. Scott, Natl. Park Serv., unpubl. data). We determined the extent of the permanent range by plotting locations of pronghorn individuals and groups recorded on over 200 pre-1988 "natural history field

observation" cards, which were filed by park rangers and other Yellowstone personnel from 1890 through 1987. During January 1988 through August 1993, over 500 records from aerial surveys, and over 7,500 records from ground surveys by Scott and helpers were used to further refine the boundaries of the permanent range. Area 16 (Figure 2) contained all of the 1890-1993 sightings of pronghorn individuals and groups on permanent range. About 80% of the entire pronghorn herd remained year-round on this range (M. D. Scott, Natl. Park Serv., unpubl. data), which was generally north and downslope of park headquarters at Mammoth Hot Springs. Elevations on the permanent range varied from 1,574 to 2072 m, and pronghorns used the entire area unless winter snowpack deeper than about 10 cm forced them to concentrate on the lower portion. During the winters of

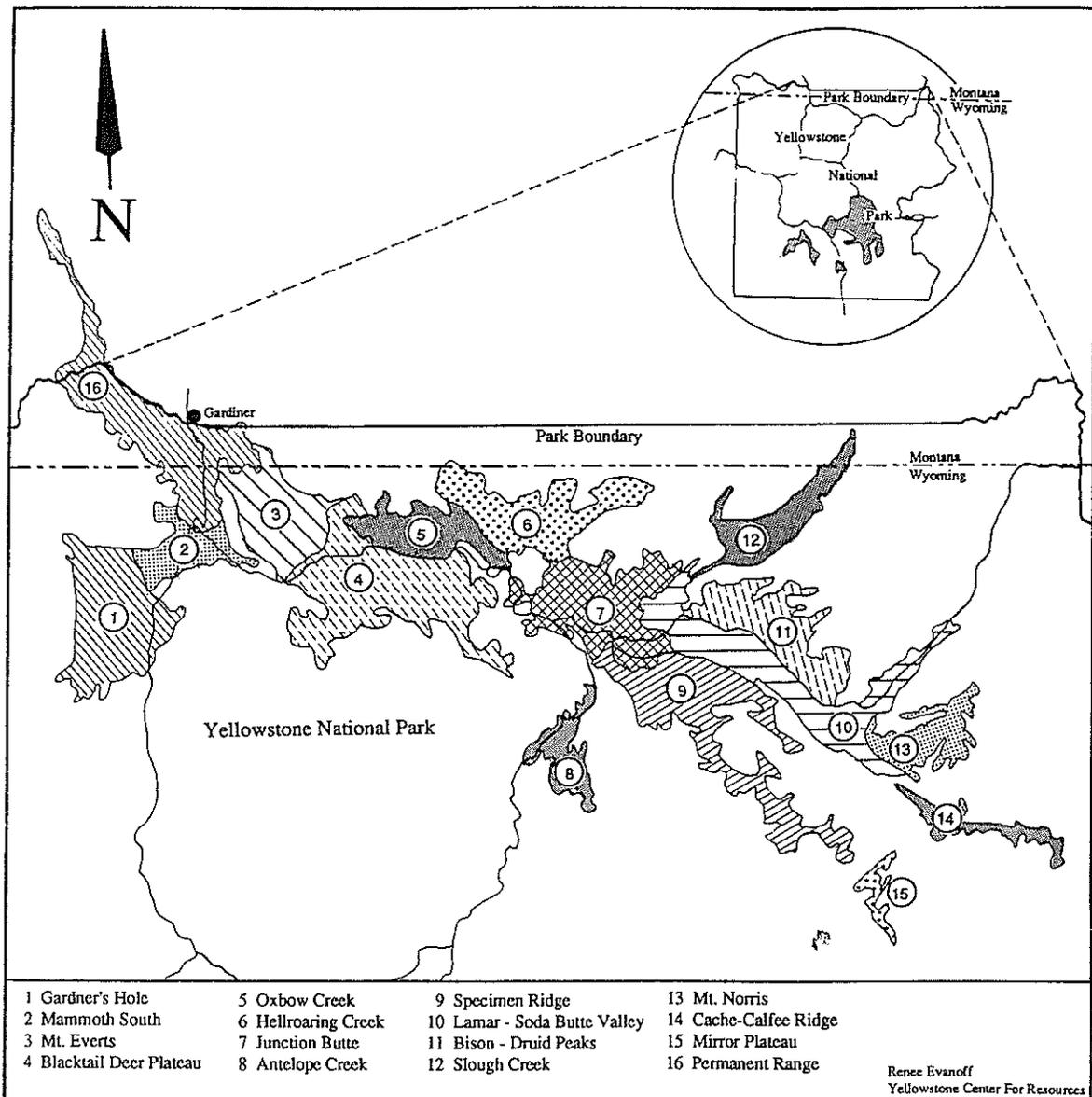


Figure 2. Summer and permanent pronghorn range units in and near Yellowstone National Park. Unit 16 was the only permanent range and was not burned.

1988 and 1989, snow depths at 1,586 m elevation ranged from 0.0-10.0 cm, and depths were 14.0-76.0 cm at 2,167 m (Scott 1992).

In spring of each year, about 20% of Yellowstone's pronghorns left the permanent range and migrated mostly east and upslope from Mammoth to valleys and nearby ridges close to the Yellowstone and Lamar Rivers. At least part of this "summer range" was occupied from about mid-March to mid-November (Murie 1940:89, M. D. Scott, Natl. Park Serv., unpubl. data). The general summer range area occupied by the pronghorns was determined from 3 sources: pre-1988 "natural history field observation" cards (113 records), distribution of 126 groups and individuals found during aerial surveys made from March 1988 through April, 1993, and distribution

of 174 groups and individuals found during ground vehicle surveys made during June 1988 through November 1990 by Scott and helpers. One hundred thirteen of the 300 aerial and ground survey sightings were made before the 1988 fires started. For convenience, the summer range, as determined from pre-fire records and sightings, was divided into 15 units which were named according to some prominent local geographic feature (Figure 2). Only 14 additional records, from the nearly 100 years of sightings data before 1988, were located in remote areas outside the currently-delineated summer range units. Most of these unusual records were sightings by park rangers of only 1-3 animals, or rumors of "small bands" as reported by Young (1907).

Elevations on the summer range varied from 1,829 m to 2,835 m. A large January - April accumulation of snow, with 15-year mean depths of from 50 to 90 cm, depending on month, (Dirks and Martner 1982, Lupine Creek snow course at 2,225 m elevation) likely was the ultimate factor encouraging pronghorns to leave the summer range each fall.

Pre-fire location data showed that pronghorns almost always preferred non-forested rangeland or mountain meadow habitats. The most common shrub on the 15 summer range map units was mountain big sagebrush (*Artemisia tridentata vaseyana*), while Wyoming big sagebrush (*A. tridentata wyomingensis*) and rubber rabbitbrush (*Chrysothamnus nauseosus*) dominated the permanent pronghorn range in unit 16 (C. L. Wambolt, Montana State Univ., Pers. Commun.). Typical grasses in all units were Idaho fescue (*Festuca idahoensis*) and bearded wheatgrass (*Agropyron caninum*), while at lower elevations bluebunch wheatgrass (*Agropyron spicatum*) and needle-and-thread (*Stipa comata*) were common. The most common forbs on summer range units, both before and after they burned (S. A. Scott, Natl. Park Serv., Pers. Commun.), were yarrow (*Achillea millefolium*), wild strawberry (*Fragaria virginiana*), starry solomon-plume (*Smilacina stellata*), and graceful cinquefoil (*Potentilla gracilis*). Typical forbs on the permanent range (which did not burn) were Hood's phlox (*Phlox hoodii*), rosy pussy-toes (*Antennaria microphylla*), goatsbeard (*Tragopogon pratensis*), and yellow sweet-clover (*Melilotus officinalis*). Douglas-fir (*Pseudotsuga menziesii*) forest, with occasional stands of lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*), generally bordered, or formed small islands in, the range used by pronghorns. Forest, shrub and grassland habitat types were described in more detail by Despain (1990).

Methods

Migration

By examining over 80 historic spring and fall migration records, and 105 of our group locations plotted in spring and early summer of 1988, we knew the usual migration route of Yellowstone pronghorns before fires started growing rapidly in July (Schullery 1989). However, 14 historic records in the pre-1988 years indicated that pronghorns could be found rarely almost anywhere in the park, even if they had to cross considerable amounts of forest to get there. Since a regular, systematic search of the entire 890,000-ha park for migrating pronghorns could not be done, we relied upon sightings of pronghorns in unusual places made by other Yellowstone National Park personnel. We placed notices in the "Yellowstone News", an employee newsletter reaching over 400 seasonal and permanent employees

working throughout the park, including the backcountry, asking them to contact us by telephone or send us a written sighting form if they saw pronghorns in unusual places.

Use of Burned Versus Non-burned Habitat

From January, 1992 to February, 1993, 33 adult or yearling pronghorns were captured with the aid of 4-barrelled netguns deployed from trucks or a helicopter (Firchow et al. 1986, Scott 1994). Animals were equipped with radiotransmitter packages operating in the 166-167 MHz range, as an aid in locating the animals. Each pronghorn was radiolocated 2-4 times per week and, after direct visual contact was made, the location of the animal or its group was plotted on U.S.G.S. 7.5-minute topographic maps. Because map locations of animals were not determined solely by triangulation, "error polygons" (Saltz 1994) were avoided.

During May and June of 1991, 1992, and 1993 40 newborn pronghorn kids were captured with long-handled dip nets and also equipped with radiotransmitters (Barrett 1981, Trainer et al. 1983). They were located in the same manner as the adults.

Many other pronghorns were not instrumented, and we plotted the map locations of those individuals or groups after they were found through the use of spotting scopes and binoculars while we traveled along roadways.

At the same time pronghorns were located, we recorded the general major type of vegetative habitat in which the animals were located, and whether or not the site had burned in 1988. The seven habitat categories we used (Table 1) corresponded to the seven that were mapped from 50x50-m resolution LANDSAT satellite data from a two October, 1988 flyover (Despain et al. 1989). After groundtruthing with aerial photographs to a resolution of 5.0 acres (2.0 ha), satellite data from recently-burned areas could be used to differentiate burned from nonburned vegetation (Despain et al. 1989). During our study of the same habitat five years later, however, burned range or meadow sites were obscured by new growth of shrubs and grasses. We used the presence of standing dead, blackened stems of shrubs like big sagebrush or shrubby cinquefoil (*Potentilla fruticosa*) as indicators of 1988 burning.

Not all known pronghorn habitat (determined before the large fires started) was visible from roads, yet most of our habitat use data from this study were obtained along roads. In order to correct for this possible source of bias, we mapped all of the known pronghorn habitat that was visible from the roads, and then confined most of our habitat preference analysis just to the visible areas. When sufficient telemetry data were available, habitat use in entire mapping units was analyzed.

LANDSAT plant cover and burn data were compiled and statistically analyzed with GRASS geographic infor-

Table 1. Major Yellowstone vegetation-burn habitat types determined from LANDSAT imagery data after the 1988 fires^a.

Type	Description
Burned areas	
Canopy burn	Forest overstory and ground cover - 100% burn
Mixed burn	Mixture of burned and unburned forest overstory and ground cover - 50% burn
Nonforest burn	Rangeland, wet and dry meadows, alpine tundra - 80% burn
Undifferentiated burn	Areas that could not be reliably categorized as forested or nonforested; bare earth, burned tree islands surrounded by nonforest, edges between forest and nonforest, burned nonforest and scattered trees in a savanna
Water	
	Ponds, lakes, and large streams
Unburned areas	
Forest	Forest canopy and ground cover unburned
Nonforest	Rangeland, wet and dry meadows, alpine tundra
Savanna	Mosaic of trees and nonforest - mostly unburned

^aFrom Despain et al. 1989.

mation system (GIS) software (U.S. Army Corps of Engineers 1991). We then compared pronghorn use of burned and unburned portions of the 7 vegetation habitat types versus the availability of those burned or nonburned habitats to estimate pronghorn preference for or avoidance of burned areas. Standard programs for X² analyses (Ashton-Tate, dBase III Plus, Torrance, Calif., 1987), with simultaneous Bonferroni confidence intervals (Byers and Steinhorst 1984), were used.

Results

Migration

Pronghorns migrated to at least nine unusual places in the spring and summer of 1989 (Figure 3). Eight of the sightings were in locations entirely outside of the typical pronghorn permanent or summer range. The most remarkable sighting was that of a doe antelope swimming south across the 2 km-wide channel between West Thumb and the main body of Yellowstone Lake. The animal

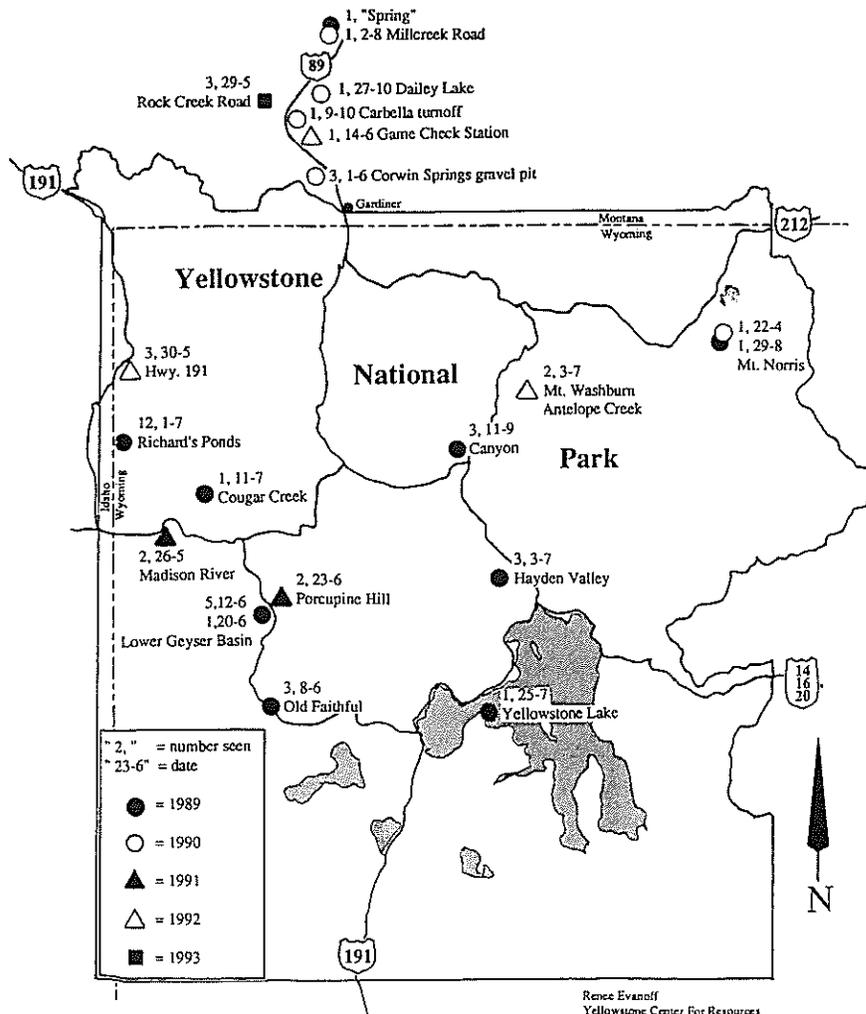


Figure 3. Unusual locations where migratory pronghorns were seen in and near Yellowstone - 1989-1993.

reached land at Breeze Point, and ran into the forest. With the exception of this animal and a doe that we saw 61 km north of the park in Paradise Valley, all unusual sightings of pronghorns in 1989 were in areas that had burned.

The Paradise Valley doe was 21 km south of a resident pronghorn herd that lived just east of Livingston, Montana. However, easy access to the Livingston herd appeared to be blocked by the narrow Allenspur canyon at the north end of the valley, since weekly surveys during the last seven years found no other antelope in the northern 2/3 of the valley (M. D. Scott, Natl. Park Serv., unpubl. data). We observed this doe in 1990 in almost exactly the same place it had been seen in 1989. It appeared habituated to human presence, as are many Yellowstone pronghorns, and allowed two people to walk within 50 m of it. The Livingston pronghorns were hunted, and did not commonly exhibit such tame behavior.

Three other pronghorns were found outside the park in 1990 in southern Paradise Valley. Only one animal was found on a burned area inside the park that year. In 1991 and 1992, three of four unusual sightings inside the park were in burned areas.

Sightings of pronghorns in unusual locations declined from nine in 1989 to one in 1993.

Use of Burned Versus Unburned Habitat

None of the permanent pronghorn range (unit 16, Figure 2) burned. On the summer range, much of which burned, the relative proportions of the seven major vegetation-burn habitat types were different when we compared the entire area within all 15 units to the area that was visible from the road in 13 units (Table 2). Generally, whether burned or not, proportionately more rangeland and less forest were visible along roads. Because of this, our initial habitat preference analysis was mostly restricted to habitats visible from the road, and limited to only those summer range units where we recorded ≥ 10 locations of pronghorn individuals or groups in the entire unit (3, 7, 10, and 11, Figure 4). This analysis also included, however, three entire units (1, 4, 9) where all the habitat was subject to sampling because of frequent radiolocations there or because we commonly searched the areas on foot.

We termed these seven partial and whole units the "core analysis area." The core analysis area contained 463 (97.3%) of the total 476 sightings we made of habitat use by pronghorn groups or individuals. Only two of the 476 sightings were outside the areas that we had previously determined to be summer range. We compared the proportion of the groups of pronghorns found on burned versus unburned sites to the amounts of the core analysis area that was burned or not burned (Table 3). Combining all areas, Yellowstone pronghorns did not appear to prefer either burned or unburned sites.

Table 2. Vegetation-burn habitat types on the entire 15-unit pronghorn summer range versus types on the portions of 13 units that were visible from roads. (Units in ha.) Relative amounts for each habitat type are different when comparing the 2 areas ($P < 0.001$).

Habitat type	Total area	%	Visible area	%
Canopy burn	1,069	2.4	79	0.7
Mixed burn	1,083	2.4	148	1.3
Nonforest burn	10,185	22.7	3,484	31.4
Undifferentiated burn	1,006	2.2	118	1.1
All burned areas	13,343	29.7	3,829	34.5
Water	38	0.1	19	0.2
Unburned forest	4,771	10.6	486	4.4
Unburned nonforest	21,750	48.5	6,354	57.3
Savanna (mosaic)	4,970	11.1	401	3.6
All unburned areas	31,527	70.3	7,260	65.5
Total	44,870	100.0	11,089	100.0

We then analyzed pronghorn preference for each individual vegetation-burn habitat type (Table 4). Pronghorns showed a high amount of use of both burned and unburned nonforest. Their preference for these two types was largely the result of avoidance of any habitat type that contained trees. A separate comparison of pronghorn use of burned versus unburned nonforest revealed the two habitats were equally preferred ($P = 0.97$, 2x2 contingency table, with correction for continuity), when the core analysis areas for all summer range units were combined.

Besides the core analysis area, we also examined pronghorn sightings in just what we termed the "visible core analysis area." This was smaller than the core analysis area, as only those portions of the summer range units that both were visible from a road and contained ≥ 10 data points were analyzed. Portions of summer range units 1, 3, 4, 7, 10, and 11 met these criteria, and $n = 429$. Habitat use data from telemetry work or walking searches were not used in this particular analysis if they were obtained in areas not visible from roads.

Another data subset we analyzed consisted of only those summer range units with road-visible portions that contained ≥ 25 sightings (from all sources) of pronghorn individuals or groups. Areas 4, 7, and 10 met these criteria, and $n = 395$. We termed this the "heavy use analysis area." Bonferroni analysis of the same seven vegetation-burn habitat types for each of these two smaller data sets confirmed that pronghorns significantly avoided unburned nonforest and savanna ($P = 0.05$). Neither set confirmed a preference for burned or unburned nonforest.

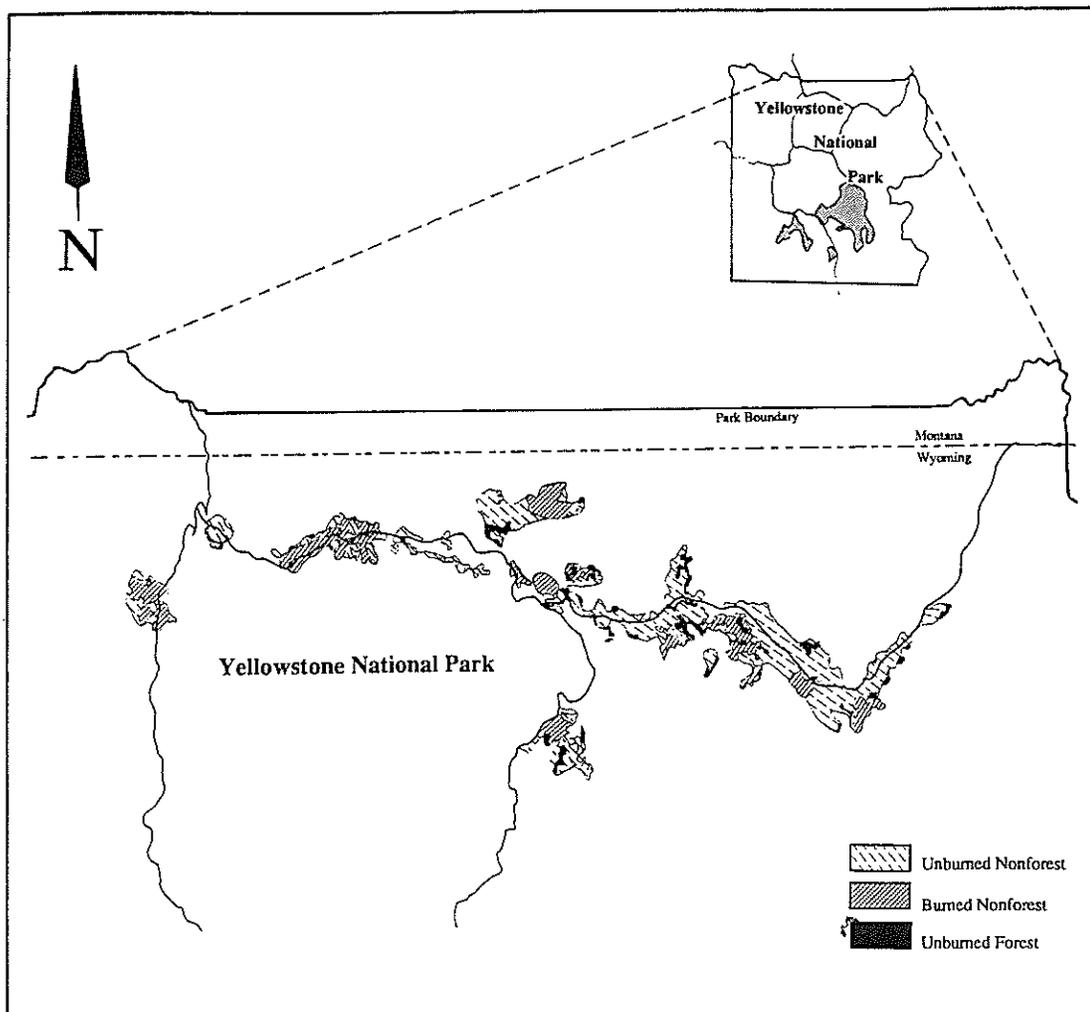


Figure 4. Portions of pronghorn summer range units that were visible from roads. Clear areas were unburned nonforest, gray areas were burned nonforest, and black areas were primarily unburned forest.

Lastly, we analyzed pronghorn preferences for vegetation-burn habitat types in individual summer range units (Table 5). We looked at entire areas for units 1, 4, and 9, which included all the habitat and all visual and telemetry data ($n = 94$), and each unit of the heavy use analysis area (portions visible from roads only), consisting of areas 4, 7, and 10, where $n = 395$.

When analyzing entire summer range units, pronghorns preferred burned nonforest in areas 1 (Swan Lake) and 9

Table 3. Observed versus expected pronghorn use of burned and non-burned habitats for the entire core analysis area in Yellowstone National Park ($P = 0.98$).

	Area (ha)	No. of sightings n	%	Expected No. sightings n	%
Burned	7,799	164.0	35.4	165.4	35.7
Unburned	14,032	299.0	64.6	297.6	64.3
Total	21,831	463.0	100.0	463.0	100.0

Table 4. Simultaneous Bonferroni confidence intervals for pronghorn preference of major vegetation-burn habitat types in Yellowstone National Park.

Habitat type	Expected use	Actual use	Bonferroni interval for actual use	Signif. ^a
Canopy burn	0.037	0.007	$0 \leq P \leq 0.017$	Avoid
Mixed burn	0.023	0	-	b
Nonforest burn	0.279	0.343	$0.283 \leq P \leq 0.404$	Prefer
Undifferentiated burn	0.019	0.004	$0 \leq P \leq 0.013$	Avoid
Water	0.001	0	-	-
Unburned forest	0.076	0.009	$0 \leq P \leq 0.020$	Avoid
Unburned nonforest	0.517	0.626	$0.567 \leq P \leq 0.688$	Prefer
Savanna (mosaic)	0.050	0.011	$0 \leq P \leq 0.024$	Avoid
Total	1.00	1.00		

^a Differences at the 0.05 level of significance.

^b No actual use of mixed burn sites, so the Bonferroni analysis could not be done. If there had been just one sighting, there would have been significant avoidance of this habitat type.

Table 5. Pronghorn preference for vegetation-burn habitat types on individual units of the pronghorn summer range.

Habitat type	Entire units ^a			Heavily used units (road-visible parts)		
	1	4	9	4	7	10
Canopy burn	Ns ^b	Ns	Ns	Ns	Ns	Ns
Mixed burn	Ns	Ns	Ns	Ns	Ns	Ns
Nonforest burn	Pr*** ^c	Ns	Pr*	Ns	Av***	Pr***
Undifferentiated burn	Ns	Ns	Ns	Ns	Ns	Ns
Unburned forest	Ns	Ns	Ns	Ns	Ns	Av**
Unburned nonforest	Av*	Pr*	Ns	Ns	Pr***	Av**
Savanna (mosaic)	Ns	Ns	Ns	Ns	Ns	Av*

^a These were units where there were sufficient telemetry or sighting locations away from roads to allow analysis of the whole area.

^b Ns = not significant, Pr = prefer, Av = avoid.

^c * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

(Specimen Ridge), and no marked avoidance of forested areas was seen. For area 4 (Blacktail Deer Creek) there was a moderate preference for unburned nonforest (Table 5). However, this may have been a result of the fact that pronghorns showed a tendency to avoid burned forest canopy ($P = 0.06$), and also unburned forest ($P = 0.14$) in this area. On heavily-used portions of units that were visible from roads, pronghorns showed no significant habitat preferences on area 4. In area 10 (Lamar-Soda Butte Valley), they strongly preferred burned over unburned nonforest (Table 5). The reverse was true in unit 7 (Junction Butte).

Discussion

Migration

Barmore (1980:92) felt a number of pronghorns left Yellowstone for the Paradise Valley in the "severe" winter of 1967-1968, but he provided little data. Other than this, the Yellowstone research files contain no data before 1988 on pronghorns leaving the park for Paradise Valley. Since neither the Yellowstone permanent pronghorn range or the Paradise Valley burned in 1988, it is debatable if nearby park fires triggered pronghorn exploration of the valley. The 1988 drought (Schullery 1989) may have been responsible for pronghorns seeking more forage outside the park that winter. One to three animals returned to the valley in three of the next four years, but these may have been just the few that learned about the area in 1988-1989.

Most of the unusual places pronghorns migrated to after the 1988 fires were not entirely new, according to the natural history field observation cards. Two pronghorns were seen in Hayden Valley in the summer of 1954 by L. Coleman. In 1935 3 were seen there (Murie 1940:89),

and Superintendent Young (1907) said small remnant bands were seen in Hayden Valley, Pelican Valley, and the meadows bordering the Yellowstone River between Yellowstone Lake and the Upper Falls.

Pronghorns were last seen in the Antelope Valley area on 30 May 1946. Pronghorns were previously observed in the Lower Geyser Basin on 1 July 1986. Pronghorns were seen in several places along the Madison and Gibbon Rivers in June of 1969. They were also seen at Madison Junction on 16 November 1967. Pronghorns were last reported from the top of Mt. Norris in June 1938. The Canyon area had pronghorns sighted in July 1936. Although most sites had been visited during the last 40-50 years, pronghorn exploration of the park interior was evidently very sporadic.

The aftermath of the 1988 fires seemed to produce a flurry of exploration activity by Yellowstone pronghorns. This may have been encouraged because of the opening up of the forest by fire, producing migration routes more suitable to pronghorn preferences. The North Fork Fire (Figure 1) was especially important in clearing travel corridors. Specifically, this fire burned the high ridges between Tower Falls and Canyon, which removed trees from a natural route between current pronghorn summer range in the Lamar Valley and potential summer range in Hayden Valley. The North Fork Fire also burned much of the forest between West Yellowstone, Madison Junction, and the geyser basins. Much of this was relatively flat land along the Old Fountain Pack Trail, southwest of Madison Junction, and would provide a convenient corridor for pronghorns from the Hebgen Lake - Madison Valley population outside the park to reach the geyser basin meadows. Once in the Lower Geyser Basin, Madison Valley pronghorns could then travel east through the meadows along Nez Perce Creek, and reach Hayden Valley. Thus, Hayden Valley could be a mixing site for pronghorns from the Yellowstone and Madison Valleys.

Romme and Despain (1989) studied fire history in a 129,600 ha area that included much of the burned area southwest of Madison Junction, and found that the last major fire that cleared most of this area occurred in about 1700. Although several small fires burned parts of this area during the intervening years (Romme and Despain 1989), by 1988 the closed forest was dominated by older lodgepole pine with an understory of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), preventing easy pronghorn access to the geyser basin meadows. Periodic large fires were considered part of the normal environment of Yellowstone (Romme and Despain 1989), and it is probable that pronghorns are adapted to exploring and occupying newly cleared areas, or at least using them as corridors to more permanent meadows and rangeland until the forest closes in once more.

The amount of meadow and major valley habitat in the center of Yellowstone that fires can make available to pronghorns is significant. The entire current prong-

horn summer range (Figure 2) is 44,870 ha. Potential summer range in the geyser basins, Hayden Valley, Pelican Valley, and meadows around Lake totals 13,411 ha, which would be a 30% increase in summer range. Past availability of this range may be one reason why Young (1907) reported Yellowstone once had about 2,000 pronghorns, whereas there are now only about 400 (M. D. Scott, Natl. Park Serv., unpubl. data).

Use of Burned Versus Unburned Habitat

Analysis of vegetation-burn habitat types confirmed that pronghorns generally avoided forested or partly forested habitats and preferred nonforested areas. When all summer range units were combined, the animals seemed to show no preference for burned versus unburned nonforest, but this masked some important differences between units. Pronghorns preferred burned nonforest in summer range units 1, 9, and 10. In all three cases, unburned nonforest was nearby, so the pronghorns made a clear choice in their habitat preferences.

In unit 4, pronghorns mildly preferred unburned nonforest, but this may have been because they were avoiding nearby forested sites. The only strong preference for unburned nonforest was in unit 10. Analysis of the burn pattern in unit 10 that was visible from the road (Figure 4) showed that most of the nonforest burn in this unit was in the Pleasant Valley - Yancey's Hole area. This area received almost continuous use by a park concessioner for stagecoach rides, barbecues, and long strings of horseback riders. Past observations (M. D. Scott, Natl. Park Serv., unpubl. data) showed that pronghorns seldom stayed in this small valley, probably due to human and livestock disturbance. This may have concentrated pronghorn use on the unburned habitat in the eastern part of the unit, causing the apparent preference.

Partly due to firefighting efforts, not one ha of the Yellowstone pronghorn permanent range (unit 16) burned. The entire pronghorn herd winters on the permanent range and during that season big sagebrush is the most important food, partly because it projects above the snow (Skinner 1924, Murie 1940:87, Barmore 1969, O'Gara and Greer 1970, Singer and Norland 1995, M. D. Scott, Natl. Park Serv., unpubl. data).

Abundance and cover of big sagebrush has been steadily declining in the park area where pronghorns winter (Murie 1940:88,179, Houston 1982:128,415), as well as nearby areas outside the park (C. L. Wambolt, Montana State Univ., Pers. Commun.). These people agreed the decline was caused by heavy browsing by native ungulates. The percentage of the Yellowstone pronghorn herd that left the park each winter steadily increased in the late 1980's (Scott 1991), and this was likely at least partly due to the declining sagebrush in the park wintering area. Preferred foods on the private lands

included Wyoming big sagebrush and domestic hay species. Pronghorn consumption of hay stubble led to crop damage complaints by a large landowner which, in turn, resulted in the Montana Department of Fish, Wildlife and Parks opening an unprecedented regular hunting season on Yellowstone antelope in 1991.

Big sagebrush is readily consumed by fire. Severely burned sagebrush plants seldom resprout, and new plants may or may not easily return from seed stored in the soil (Harniss and Murray 1973, Wright et al. 1979, Fraas et al. 1992). Since sagebrush is already declining on the Yellowstone pronghorn wintering area due to heavy browsing, it is very unlikely that this shrub would be able to reestablish itself soon after a fire. Thus, if park managers hope to preserve critical winter food for pronghorns inside the park, and help prevent conflicts and loss of animals outside the park, it is advisable to suppress fires that threaten large stands of sage on the pronghorn permanent range between Mammoth and Reese Creek. Smaller prescribed fires covering perhaps 100 to 200 ha might, however, benefit sagebrush communities used by Yellowstone pronghorns since young plants might be more nutritious and easier to reach. For such a program to work, however, the burned areas would have to be protected for several years from current heavy browsing by abundant native ungulates.

Management Implications

The pronghorn may be thought of as a fire-follower animal species. Fires on the summer range may open up forested areas and provide additional feeding habitat or migration corridors to suitable habitat. Even 5 years after the 1988 fires were out, we were able to detect pronghorn preferences for some burned areas. Park managers may allow prescribed fires in pronghorn summering areas and expect pronghorns to benefit. If shrublands on the Yellowstone pronghorn wintering area were much larger and healthier, uncontrolled fires might provide a mosaic of habitats that could benefit the animals. However, given the small amount of big sagebrush available to pronghorns wintering in the park, it is not advisable to allow large fires to burn in this area at this time. In the future, skilled managers may restore the former cropland in this area to native shrubland, allowing more flexibility in prescribed burning of small areas for enhancement of sagebrush communities.

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Physiological Responses of Yellowstone Elk to Winter Nutritional Restriction Before and After the 1988 Fires: A Preliminary Examination

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Abstract. We assessed nutritional restriction of elk (*Cervus elaphus*) on the Northern and Madison-Firehole Ranges in Yellowstone National Park during winters 1987-88 (13 Jan-30 Mar), 1988-89 (1 Dec-6 Apr), and 1989-90 (29 Nov-26 Mar). Physiological responses to nutritional restriction were examined via sequential collections (4-5 collection periods per winter) and chemical analyses of urine suspended in snow. During each winter, 688-726 and 173-233 urine samples were collected from cow groups on the Northern and Madison-Firehole ranges, respectively. The Northern Range was divided west to east into lower, middle, and upper elevational sampling areas to facilitate consistent sampling of elk across this range.

Because elk calves are more predisposed to the adverse effects of winter nutritional restriction than cows, insight into calf:cow ratios of sampled groups was important to physiological data comparisons. Thus, we calculated a weighted calves:100 cows ratio (calves:100 cows_w) for each elk group sampled based on the observed calf:cow ratio, the number of samples collected from that group, and the total number of samples collected per collection and sampling area. The weighted calves:100 cows usually were well below actual calf:cow ratios; their value was in permitting a more valid analysis of the potential influence of calf:cow ratios on physiological data and their interpretation. During winter 1987-88, there was a significant ($P < 0.0003$) collection number by winter range interaction for mean calves:100 cows_w, and this ratio varied ($P = 0.006$) on the Northern Range (Figure 1). Mean ratios also varied ($P = 0.037$) during winter 1988-89 on the Madison-Firehole Range (Figure 1). However, despite some variation, mean calves:100 cows_w ratios were low in sampled groups during all 3 winters (Figure 1), and thus, we feel confident cows were being physiologically assessed primarily.

Nutritional restriction was most severe immediately

following the fires during winter 1988-89, with a recovery clearly evidenced by winter 1989-90; nutritional stress was comparatively mild during pre-fire winter 1987-88. Progressive winter nutritional restriction was indicated by significant ($P = 0.0001$) declines of urinary potassium:creatinine (K:C) ratios on the Northern Range during all 3 winters (Figure 2). In Madison-Firehole elk, K:C ratios reflected similar patterns of nutritional deprivation during winters 1987-88 and 1989-90 (Figure 2). However, by the third urine sample collection of the first winter post-fire (1988-89), increasing urinary K:C values (and supportive evidence) reflected muscle cell breakdown, K leakage, and a more extreme nutritional deterioration of elk (Figure 2). During the fourth and fifth urine sample collections, sampled elk were being supplementally fed by residents in the Duck Creek area of the Madison-Firehole Range, and the subsequent dramatic increase in K:C was attributable to increased dietary K.

Urinary urea nitrogen:creatinine (U:C) ratios of elk varied ($P = 0.0001$) also on both winter ranges and during all 3 winters (Figure 3). During winters 1987-88 and 1989-90, declining trends of urinary U:C during the early part of the season in Northern Range and Madison-Firehole elk were suggestive of an early phase of under-nutrition associated with increased urea reabsorption and recycling. Subsequent increasing trends were indicative of the progressive dietary energy deficiency and accelerating net protein catabolism; however, mean values remained well below a threshold (U:C ≥ 3.5 mg:mg), derived from winter-killed elk, indicative of severe nutritional restriction. The relatively mild nutritional deprivation of these winters was supported by the low percentage of sampled elk exhibiting U:C ratios beyond this threshold of severe restriction (Figure 4).

During winter 1988-89, the steadily increasing trend of urinary U:C in Northern Range elk to a mean value beyond the 3.5 mg:mg threshold indicated more severe progressive nutritional restriction than during the winter pre-fire and the second winter post-fire (Figure 3). This was evidenced further by the increasing percentage of elk

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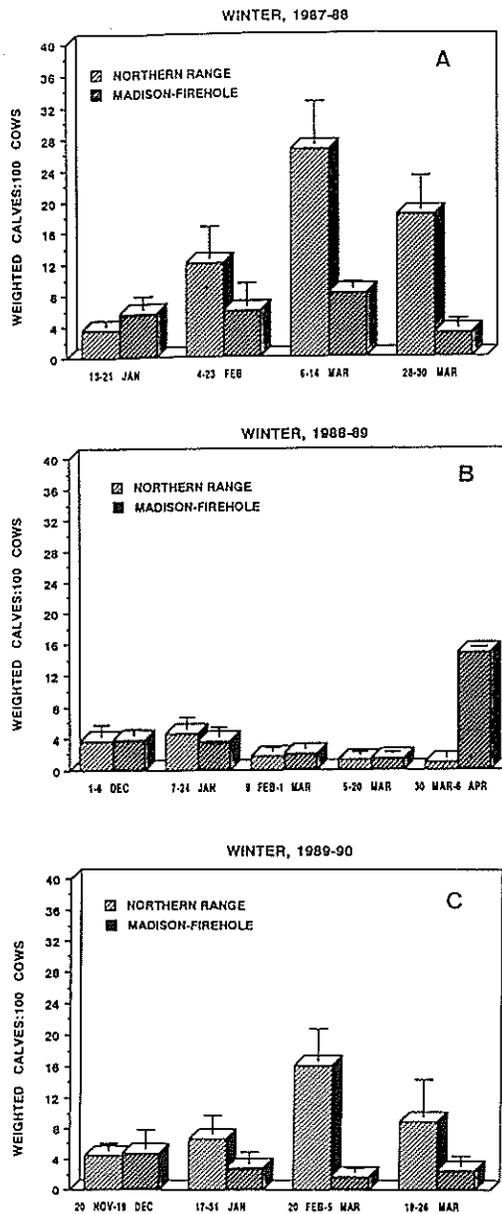


Figure 1. Mean (+SE) ratios of weighted calves:100 cows of elk groups sampled for urine (suspended in snow) on the Northern Range and Madison-Firehole Range, Yellowstone National Park, Wyoming, winters 1987-88 (A), 1988-89 (B), and 1989-90 (C). (Sample sizes per collection were 3-10, 7-16, and 6-11 elk groups for the Northern Range and 5-7, 1-10, and 3-8 elk groups for Madison-Firehole during the 3 winters, respectively.)

exhibiting U:C ratios ≥ 3.5 mg:mg from early December (8%) to late March-early April (60%) (Figure 4), while K:C ratios continued to decrease. Nutritional restriction appeared to be even more severe for Madison-Firehole elk; mean values of U:C were above 3.5 mg:mg from early December through 1 March, and the percentage of elk exhibiting U:C ratios indicative of severe dietary energy restriction ranged from 12-39% during this time (compared to 23% on the Northern Range by 1 March).

The severe nutritional restriction reflected by the physiological responses of Northern Range and Madison-Firehole elk during winter 1988-89 appeared to agree with the elevated winter mortality estimates (24-27% and 50%, respectively) that have been reported. Beyond 1 March, high and increasing U:C ratios in Madison-Firehole elk, again, reflected increased nutrient availability associated with the supplemental feeding that had been initiated.

Overall, mean urinary U:C ratios exhibited by Northern Range and Madison-Firehole elk during the first winter post-fire were 133% and 364% greater than their values during the winter pre-fire, respectively. If one considers that much, if not all, of the difference in U:C

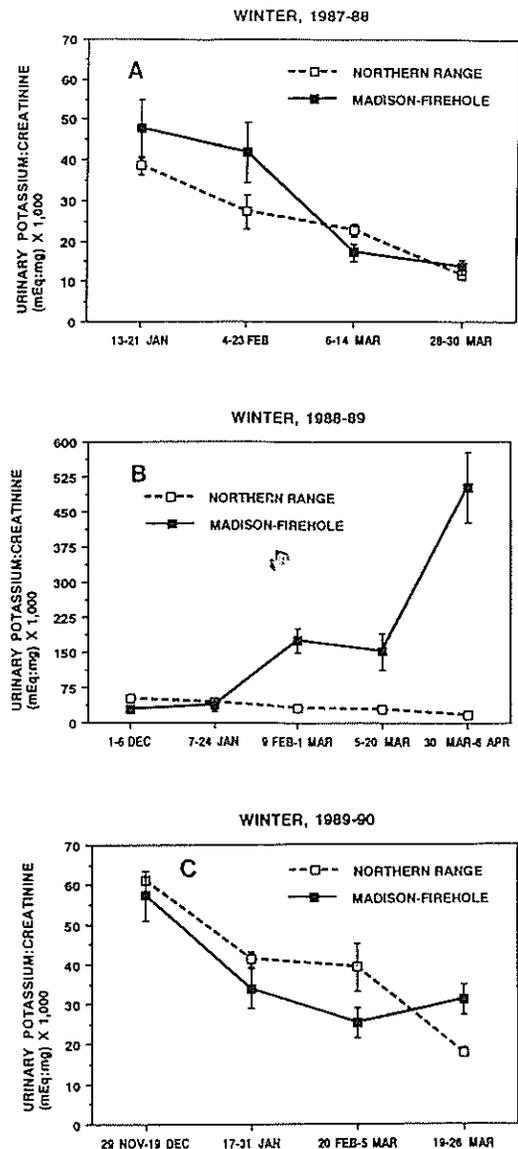


Figure 2. Mean (\pm SE) potassium: creatinine ratios in elk urine suspended in snow on the Northern Range and Madison-Firehole Range, Yellowstone national Park, Wyoming, winters 1987-88 (A), 1988-89 (B), and 1989-90 (C). Sample sizes per collection were 154-185, 92-186, and 112-212 urine samples for the Northern Range and 52-63, 28-59, and 25-70 urine samples for Madison-Firehole during the 3 winters, respectively.

ratios between these two winters may very well have been attributable to an increase in net catabolism of endogenous protein, an illustration of how such differences may translate into body condition deterioration is worthwhile. For example, at Madison-Firehole, the difference in mean U:C ratios of temporally corresponding sample collections of winters 1987-88 (collections 1) and 1988-89 (collections 2) was 4.9 mg:mg. Assuming this increased loss of urinary urea nitrogen was attributable to protein catabolism; it converts to 123 mg of lean tissue loss per mg of urinary creatinine excreted. Using a 227 kg (500 lb) cow elk as a model, excreting 5.96 g of creatinine daily (rate of 0.1 g/kg^{0.75}/day), this cow would lose 0.730

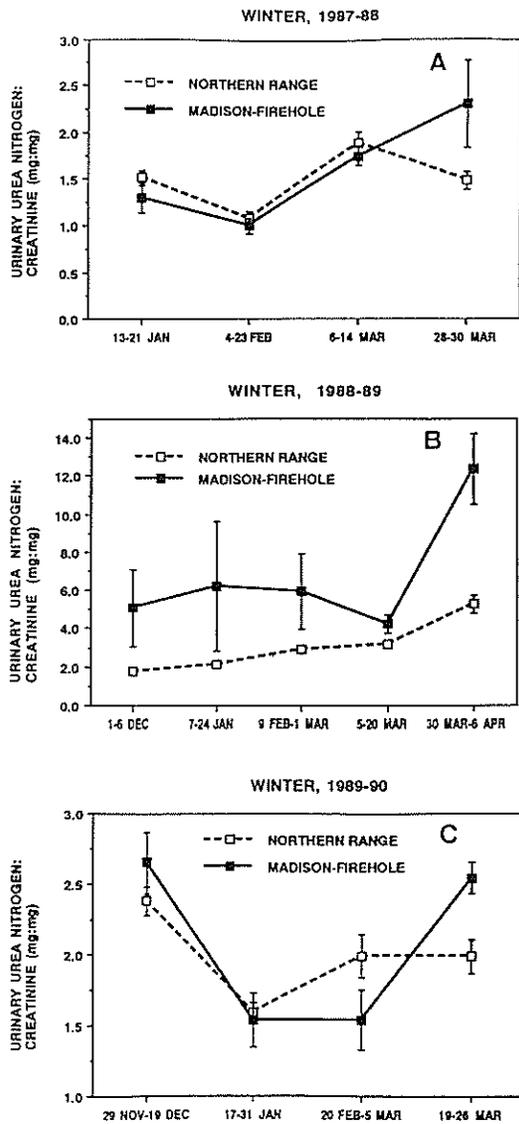


Figure 3. Mean (\pm SE) urea nitrogen:creatinine ratios in elk urine suspended in snow on the Northern Range and Madison-Firehole Range, Yellowstone National Park, Wyoming, winters 1987-88 (A), 1988-89 (B), and 1989-90 (C). (Sample sizes per collection were 154-184, 92-186, and 112-212 urine samples for the Northern Range and 51-63, 28-59, and 24-70 urine samples for Madison-Firehole during the 3 winters, respectively.)

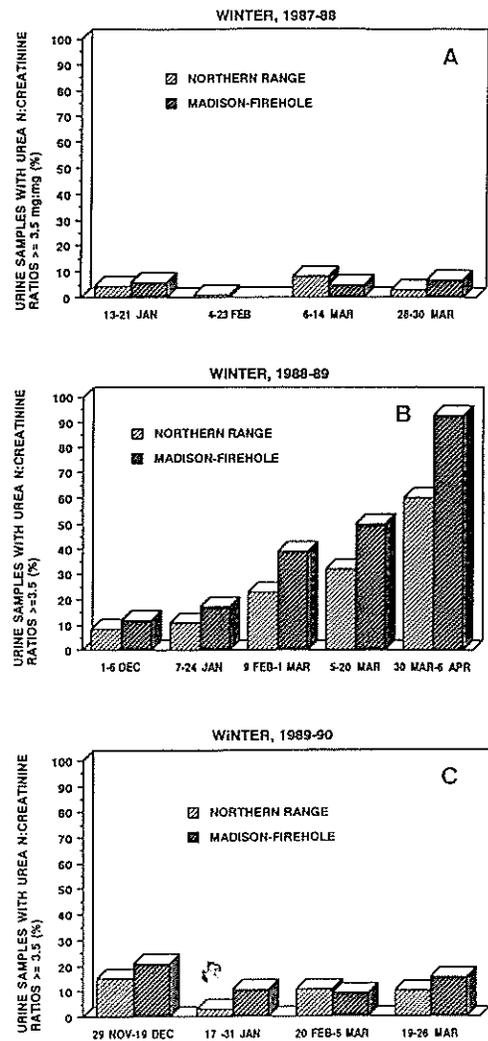


Figure 4. Percentage of elk urine (suspended in snow) samples with urinary urea nitrogen:creatinine ratios \geq 3.5 mg:mg on the Northern Range and Madison-Firehole Range, Yellowstone National Park, Wyoming, winters 1987-88 (A), 1988-89 (B), and 1989-90 (C). (Percentages for the last 2 sample collections at Madison-Firehole, winter 1988-89, were influenced by supplemental feeding of elk by area residents.)

kg of lean tissue alone in a 24-h period. This does not include the more accelerated simultaneous loss of adipose tissue. Elk mobilize endogenous protein along with fat reserves during nutritional restriction; however, they can tolerate a loss of only 33% of their body protein. If such a high rate of protein loss, occurring as early as mid-January, were sustained, prospects for the elk's survival would certainly be grim. It is noteworthy that the difference in mean U:C continued at 4.9 mg:mg between the next set of temporally corresponding urine collections (no. 2 for 1987-88 and no. 3 for 1988-89) on the Madison-Firehole Range. Presumably, the occurrence of such high U:C ratios during early winter has biologically significant adverse implications related to elk survival and reproduction.

Post-fire Effects on Coarse Woody Debris and Adult Trout in Northwestern Wyoming Streams

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Abstract. Following fire, streamflow changes in burned watersheds may alter channel morphology and mobilize coarse woody debris. In 1990 and 1991, we measured characteristics of coarse woody debris and riparian trees in Jones Creek, a watershed burned in 1988, and Crow Creek, an old-growth watershed. Tagged debris in Jones Creek was 3 times as likely to move and moved over 4 times as far as such debris in Crow Creek. In Jones Creek, the probability of movement was higher for pieces in contact with the stream surface. Larger pieces tended to be more stable in both streams. A greater duration of high spring flows following snowmelt, or occasional high summer flows following thunderstorms, apparently displaced much of this debris; one instance of the latter caused a fish kill in Jones Creek on 17 August 1990. We observed suspended sediment concentrations of 9680 mg/L following a debris torrent, and collected numerous dead trout displaying symptoms of suffocation the following day. Debris transport and suspended sediment concentrations will probably decline as terrestrial vegetation in Jones Creek becomes re-established.

Keywords: Coarse woody debris; Fish kill; Fire; Suspended sediment.

Introduction

Forest fires can cause immediate and extensive changes in the terrestrial landscape. As a consequence of the links between streams and their valleys (Hynes 1975), fires may also affect the hydrology, water chemistry, and geomorphology of aquatic ecosystems (Tiedemann et al. 1979, Schindler et al. 1980, Minshall et al. 1989). One consequence of fire is that spring snow-melt flows often increase and summer storm flows may be abnormally high (Bolin and Ward 1987, Minshall and Brock 1991). Such flows can alter channel morphology, mobilize

coarse woody debris, and transport sediment. And depending on the concentration and duration of exposure to suspended sediment, fish may suffer physiological stress, reduced growth, or death (Newcombe and MacDonald 1991).

The interaction between coarse woody debris and stream channels is complex; debris affects sediment storage and transport, flow erosivity, channel morphology, and fish habitat (Bisson et al. 1987). Though individual pieces of coarse woody debris may occupy a channel for over a century (e.g., up to 220 years; Swanson and Lienkaemper 1978, Keller and Tally 1979), less is known about the movement of coarse woody debris (but see Grette 1985, Lienkaemper and Swanson 1987, Benke and Wallace 1990). In this paper, we contrast the characteristics and movement of coarse woody debris in a stream flowing through a recently burned watershed with those of debris in an adjacent stream unaffected by recent fire.

While conducting the study on coarse woody debris, we observed a fish kill in the burned watershed that occurred two years after fire. During the 1988 fires in the Greater Yellowstone Ecosystem, Minshall et al. (1989) observed fish kills in streams, but the extent and causes of mortality were not reported. Our second objective is to describe aspects of this post-fire fish kill, and relate them to hydrologic conditions in this stream and to those in a nearby, unburned watershed.

Study Area

We studied two tributaries of the North Fork Shoshone River in the North Absaroka Wilderness Area adjacent to the eastern border of Yellowstone National Park in the Absaroka Mountains of northwestern Wyoming. Crow Creek (mean gradient 5.5%, mean low-flow wetted width 7.0 m in the study reach) drains a 4,946-ha watershed that

has been largely unaffected by recent fire. Jones Creek (mean gradient 4.1%, mean low-flow wetted width 6.4 m in the study reach) drains a 6,423-ha watershed immediately to the north of Crow Creek, has similar topographic relief and watershed orientation, and had similar vegetation, but was almost completely burned in 1988. Both drainages contain numerous high-gradient tributaries and steep ephemeral chutes, and consist of geologically young and highly erodible soils derived from Absaroka Volcanic rock (G. S. Bevenger, U.S. For. Serv., Cody, Wyo., pers. commun.). Instantaneous peak flows in 1991 were 11.0 m³/s in Jones Creek and 9.2 m³/s in Crow Creek (U.S. Geological Survey 1991). For 1989 through 1991, the average maximum and minimum mean daily flows in Jones Creek were 7.8 m³/s and 0.3 m³/s, and in Crow Creek were 6.1 m³/s and 0.2 m³/s (U.S. Geological Survey 1989, 1990, 1991).

Methods

Coarse Woody Debris

In August 1990, we sampled a 918-m reach of Jones Creek and a 1223-m reach of Crow Creek; each reach began at the stream mouth. With a tape and rod, we measured all woody debris at least 2.0 m long with a mean diameter \geq 15 cm that was in or suspended over the wetted width of the stream channel. The volume of a piece was estimated by calculating the volume of a cylinder with that total length and mean diameter.

To assess the influence of stream channels on coarse woody debris, we evaluated the anchoring and stream contact of each piece. To determine anchoring, we counted the number of ends and sides buried in either the bank or the stream. We considered pieces with no buried ends the least secure and those with at least 1 side buried the most secure. Finally, we noted whether each piece of debris was in contact with the stream surface at low flow.

Every third piece of coarse woody debris in the Jones Creek (60 of 180 pieces) and Crow Creek (100 of 300 pieces) study reaches was marked with a numbered aluminum tag near both ends. To detect movement of the tagged pieces, we noted the distance and compass bearing to tagged reference trees in the riparian zone. Furthermore, we photographed each tagged piece and its reference tree. In September 1991, we relocated all the reference trees, identified the original locations of tagged debris, and inspected all instream debris for tags. If a tagged piece was found, we measured the distance to its reference tree; otherwise, pieces were noted as missing. A relocated piece was considered mobile if the distance to the reference tree had changed by at least 0.5 m.

We recorded the species composition and diameter of standing trees (living and dead) along each reach. At the downstream end of every fifth channel unit i.e., pool or

riffle, we used the point-centered quarter method (Cottam and Curtis 1956) to estimate the density of trees greater than 20 cm dbh. If no trees of this size could be found in a quarter circle within 50 m of the channel, we calculated a correction factor to account for missing data (Warde and Petranka 1981). The species sampled included lodgepole pine (*Pinus contorta* Dougl.), Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and cottonwood (*Populus* sp.).

All analyses were performed with SPSS/PC+ 4.0 (Norusis 1990). We analyzed categorical variables (or continuous variables converted to categories) by using G-tests (Zar 1984). Distributions of the length, mean diameter, and volume of coarse woody debris in each stream were tested for normality by using a 1-sample Kolmogorov-Smirnov test (Zar 1984). Because 5 of the 6 distributions were found to be non-normal, comparisons involving these variables relied on Mann-Whitney U-tests (Zar 1984). For consistency, the comparison of the mean distance moved by debris in each stream and comparisons of riparian tree diameters and point-center distances between streams were also evaluated by using the Mann-Whitney U-test. We used Pearson correlation to determine whether physical dimensions of coarse woody debris were related to the distance each piece traveled. For all statistical tests, $P \leq 0.05$ indicated significance.

Fish Kill

On 17 and 18 August 1990, we surveyed 1774 m of the stream channel and lower and upper banks of Jones Creek for dead fish following storm flows that had been caused by rain that began at 1600 hrs on 16 August. Fish were identified, measured, and examined to determine possible causes of death. We examined the external anatomy of the fish, including the skin, eyes, and gills, as well as the stomachs of several fish.

Suspended sediment and discharge data from April to September 1990 were obtained from continuous remote sampling stations operated by the U.S. Geological Survey (U. S. Geological Survey 1990). Suspended sediment concentrations are daily means based on two to four samples per day; mean daily discharge was based on hourly observations. On 17 August, we collected two grab samples from Jones Creek to quantitatively assess the unusually high concentration of suspended sediment observed during the storm. Samples were collected at mid-depth in 0.5 m of water. We analyzed the grab samples for total suspended sediment by filtering them through Whatman grade 934AH fiberglass filters (1.5 μ m effective pore size), oven-drying them for one week to constant weight, and then measuring them and averaging the results to determine the total concentration of suspended sediment (American Public Health Association 1989).

Results

Coarse Woody Debris

In comparisons of all debris (both tagged and untagged), pieces in Crow Creek were more frequently in contact with the stream surface (55% vs. 41%, $P = 0.004$), were longer (8.5 m vs. 7.5 m, $P = 0.037$), and had a smaller mean diameter (24 cm vs. 27 cm, $P = 0.002$) than pieces in Jones Creek. Mean debris counts per 100 m of channel were 32 pieces in Crow Creek and 15 in Jones Creek.

Furthermore, the proportion of the tagged sample that moved or was buried was significantly greater in Jones Creek than in Crow Creek (58% vs. 18%, $P < 0.001$). Of the tagged pieces that moved or were buried, a significantly greater proportion could not be relocated in Jones Creek than in Crow Creek (66% vs. 28%, $P = 0.008$). And the mean distance traveled by tagged pieces that were relocated was significantly greater in Jones Creek than in Crow Creek (95.3 m vs. 21.9 m, $P = 0.01$). Measures of debris size were not correlated with the distance each piece traveled in either stream.

There were several significant differences between stable and mobile pieces of tagged debris in each stream. In Jones Creek, stable debris was significantly greater in volume (0.98 m³ vs. 0.38 m³, $P = 0.045$) and less likely to be in contact with the stream surface (20% vs. 54%, $P = 0.006$) than was mobile debris. Similarly, stable debris in Crow Creek was significantly longer (8.5 m vs. 3.9 m, $P = 0.002$) and greater in volume (0.47 m³ vs. 0.15 m³, $P = 0.002$) than mobile debris, but was also more likely to have some portion buried (82% vs. 44%, $P = 0.002$). Mobile debris in Jones Creek was significantly greater in volume (0.38 m³ vs. 0.15 m³, $P = 0.045$) than mobile debris in Crow Creek, and stable debris in Jones Creek was significantly larger in diameter (29 cm vs. 23 cm, $P = 0.010$) and less commonly in contact with the stream surface (20% vs. 50%, $P = 0.006$) than stable debris in Crow Creek.

The density and diameter of standing riparian trees also varied between the two streams. The mean distance from point-centers to trees was greater along Jones Creek than along Crow Creek (12.6 m vs. 7.7 m, $P < 0.001$); mean density of trees per 1000 m² was 6.3 along Jones Creek and 16.8 along Crow Creek. Also, the mean diameter of riparian trees was greater near Crow Creek than near Jones Creek (38.2 cm vs. 35.2 cm, $P = 0.021$). Nearly 1/4 of the riparian trees adjacent to Crow Creek were 50 cm DBH or greater (estimated to be from 225 to 400 years old; B. Spanogle, U.S. For. Serv., Cody, Wyo., pers. commun.), but less than 1/6 of these trees were this large adjacent to Jones Creek.

Fish Kill

On 17 and 18 August 1990, one rainbow trout (*Oncorhynchus mykiss*), four Yellowstone cutthroat trout (*O. clarki bouvieri*), 11 brook trout (*Salvelinus fontinalis*), and two Yellowstone cutthroat trout X rainbow trout hybrids, all ranging from 190 to 410 mm total length, were found dead during surveys of Jones Creek. We found fish only in or near obstructions to flow (e.g., debris accumulations and boulders), thus our survey probably overlooked dead fish that had been transported downstream or buried in newly formed bars. We believed that fish collected on 17 August had died recently because rigor mortis had not set in. Fish collected the following day were rigid and had started to dry; we suspect these had also succumbed on 17 August. Surveys on seven other occasions on Jones Creek (including 16 August) and 8 other occasions on Crow Creek failed to reveal any moribund fish.

Each fish we examined appeared to have been asphyxiated by sediment. Typically, sediment completely embedded the gills of each fish and individual lamellae were often difficult to see (cf. Cordone and Kelley 1961:192). The eyes and skin appeared to be relatively normal, and fish lacked contusions and lacerations. The stomachs we examined appeared normal, and all contained recently consumed invertebrates.

The timing of the fish kill coincided with storms that began on 16 August and continued into the early morning of 17 August. Nearly 23 mm of rain was recorded on 16 August, followed by an additional 7 mm the next day. Though discharge in Jones Creek peaked on 16 August, the concentration of suspended sediment did not appear to peak until 17 August (Figure 1). And though suspended sediment concentrations on 17 August were the highest recorded from April to September 1990 (U. S. Geological Survey 1990), the concentration of suspended sediment in the grab samples (9680 mg/L) was more than an order of magnitude higher than the daily mean concentration (587 mg/L) recorded for that date. Because the continuous remote sampling station collects samples at intervals, it is likely that the automated sampling missed the instantaneous peak concentration of suspended sediment. Likewise, it also is possible that our grab samples did not represent the instantaneous peak concentration.

Discussion

Coarse Woody Debris

Debris movement in Jones Creek was much greater than that observed in Crow Creek or reported elsewhere. Though Bilby (1984) stated that about 60% of the debris moved during the first winter storm flow (6.8 m³/s) in a Washington stream, many of these pieces had been

intentionally destabilized during stream cleaning following logging; a later, larger ($12.4 \text{ m}^3/\text{s}$) storm flow only moved 35% of the debris. After one year and exposure to a peak flow of $4.7 \text{ m}^3/\text{s}$, 36% of the debris dams affecting the low-flow channel of an English stream had moved, but the minimum size of debris was not reported (Gregory et al. 1985). In contrast, 79% of the tagged debris exposed to low flow in Jones Creek had moved, as did 24% in Crow Creek.

Estimates of annual transport of debris in other regions are similar to those for unburned Crow Creek. For lower-gradient (0.5-2.0%) streams with smaller watersheds (340-1240 ha) in northwestern Washington, Grette (1985) reported that the mean proportion of mobile debris was 18% annually. After 19 months and exposure to a peak flow of $300 \text{ m}^3/\text{s}$, 17% of the debris in a low-gradient (0.02%) southeastern U.S. river had moved (Benke and Wallace 1990). We also observed that much of the debris that was transported in Crow Creek was captured by downstream debris accumulations; two such accumulations both contributed and received tagged pieces (cf. Bilby 1984:610; Lienkaemper and Swanson 1987:153). Though debris size appeared to determine whether a piece moved, the spacing of channel roughness elements may have outweighed the importance of debris size in determining the distance that pieces moved (in contrast to Bilby 1984, Swanson et al. 1984).

Others have reported extensive debris movement, but often over undefined periods of time. McDade et al. (1990) noted that they could not find the source for nearly half the debris they encountered in 39 stream reaches; these pieces could have originated only from breakage of existing pieces or standing snags, or by transport from upstream. Murphy and Koski (1989) apparently could not identify the source for about 80% of the instream debris. And Lienkaemper and Swanson (1987) determined that from less than 10% to over 50% of the debris was mobile in five Pacific Northwest streams over a seven- to nine-year period. These findings emphasize the potential magnitude of stream transport of coarse woody debris in forested watersheds.

We did not sample either of these streams before the fire, thus can only speculate on pre-fire conditions in both watersheds. However, significant differences in the mean diameter of standing riparian trees between the two streams implied that pre-fire stands were not alike. The post-fire contribution of small snags to Jones Creek should have exceeded the contribution of larger snags (small snags fall sooner than large snags; Lyon 1984), thus the mean diameter of instream debris potentially should have been smaller in Jones Creek. But the greater mean volume of coarse woody debris in Jones Creek suggested that much of the small debris in and along Jones Creek had been transported downstream.

After the fire, the addition of snags to Jones Creek may have escalated due to blowdown (Lyon 1984) and

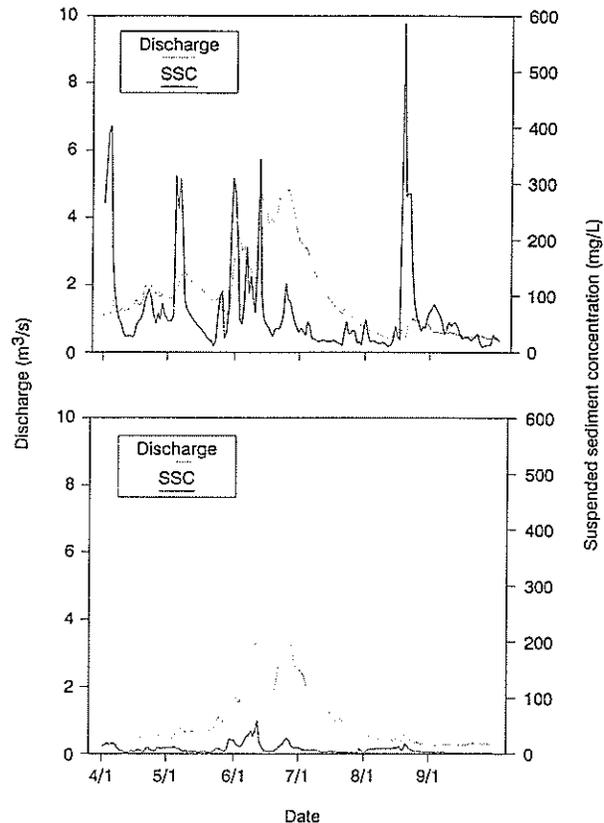


Figure 1. Discharge (m^3/s) and suspended sediment concentrations (mg/L) from April through September 1990 in Jones Creek (above) and Crow Creek (below), Wyoming (U.S. Geological Survey 1990). The peak in suspended sediment in Jones Creek on 17 August coincides with the fish kill.

lateral channel movement (Minshall et al. 1989). Despite this potential increase in debris loading in Jones Creek, the abundance of debris may have declined even faster because some spring peak flows (and their duration; G. Bevenger, U.S. For. Serv., Cody, Wyo., unpubl. data) and some summer storm flows apparently increased (Bozek and Young 1994; also see Bolin and Ward 1987, Campbell and Morris 1988, Baker 1990, and Beschta 1990 for data on flow increases following fire) and probably accelerated debris transport. Also, banks lacking living vegetation may have become less stable (Sullivan et al. 1987), and declined in ability to retain partially buried debris or to capture transported debris (C. A. Troendle, Rocky Mt. For. Range Exp. Stn., Ft. Collins, Colo., pers. commun.). These fire-influenced flows and the concomitant debris movement will probably decline as terrestrial vegetation becomes re-established (Likens and Bilby 1982, Minshall et al. 1989).

Few studies have evaluated stream/debris relations in the Rocky Mountains, but such studies have been conducted elsewhere. Bilby and Ward (1989) developed equations for predicting the geometric mean length, diameter, and volume of coarse woody debris, based on the bankfull width of 22 western Washington streams in

old-growth watersheds. We applied these equations to Crow Creek (using a conservative estimate of bankfull width of 10 m), and calculated values for geometric mean length, diameter, and volume of 7.9 m, 48 cm, and 1.63 m³, whereas the measured values were 6.6 m, 22 cm, and 0.25 m³. These differences suggest that in western Washington either: (1) coarse woody debris is larger (see Harmon et al. 1986); (2) riparian trees are larger (see Burns and Honkala 1990); (3) discharge per unit stream width is higher; or (4) some combination of these. Consequently, regionally specific models will probably be necessary to predict debris characteristics in streams in old-growth watersheds (cf. Bilby and Wasserman 1989).

Another series of models has attempted to relate riparian characteristics to debris abundance in streams, but an acknowledged weakness of these models is the lack of information on the fate of debris once it enters the channel (Murphy and Koski 1989, Robison and Beschta 1990, Van Sickle and Gregory 1990). Further studies of debris movement may enhance the precision of estimates of the steady-state debris load in streams. If this problem is overcome, managers may be tempted to use such models to determine the minimum number of trees to retain near (typically < 30 m; McDade et al. 1990) the channel. But because these models also ignore channel migration, they should be applied with caution. Between 1990 and 1991, Jones Creek laterally shifted over 100 m in some locations (M. Young, pers. obs.). Failing to conserve an adequate density of sizeable trees in the stream valley away from the immediate riparian zone could disrupt the future interaction between coarse woody debris and the stream channel.

Fish Kill

Suspended sediment is known to be lethal to salmonids, but usually at higher concentrations or for longer exposures (Redding et al. 1987, Newcombe and MacDonald 1991) than we observed in Jones Creek. For example, Newcomb and Flagg (1983) calculated that a 36-hr exposure to a suspended sediment concentration of 9,400 mg/L would kill 50% of juvenile chinook salmon (*O. tshawytscha*) and sockeye salmon (*O. nerka*). However, the lethal effects of suspended sediment may be more pronounced in the field than in the laboratory. In live-box tests in streams affected by ashfall from Mount St. Helens, concentrations of suspended sediment as low as 488 mg/L killed 50% of chinook salmon smolts after a 96-hr exposure (Stober et al. 1981). But in comparable laboratory tests, it required a concentration of 19,364 mg/L to produce the same mortality rate (Stober et al. 1981). Clearly, the suspended sediment concentrations in Jones Creek were stressful for trout. For the 24 hours beginning at 1600 on 16 August 1990, we estimated a minimum stress index (exposure to a given suspended sediment

concentration per unit time) of 11.3 mg/hr/L (Newcombe and MacDonald 1991), which is near the value associated with lethality in adult salmonids (12 mg/hr/L; C. P. Newcombe, B.C. Minist. Environ., Victoria, B.C., pers. commun.).

Other factors may have contributed to the fish kill in Jones Creek. Newcombe and MacDonald (1991) suggested that high or fluctuating temperatures may increase the sensitivity of trout to suspended sediment. In Jones Creek, water temperature varied from 10.1 to 17.3°C on 17 August (U. S. Geological Survey 1990), but these temperatures are largely within the range of those reported for other tests (e.g., Newcomb and Flagg 1983, 15-17°C; Redding et al. 1987, 12.5-13.5°C). Temperature fluctuation alone was unlikely to produce mortality, because the 7.2°C change was equaled or exceeded on 70 of the 137 monitored days. Nonetheless, temperature fluctuations, either alone or combined with unmeasured changes in water chemistry (e.g., reduced dissolved oxygen), could have coincided with high suspended sediment concentrations and exacerbated mortality.

Tiedemann et al. (1979) indicated that landslide activity in steep drainages increased after wildfires. In Jones Creek, a debris torrent down a tributary, apparently caused by heavy rainfall on unstable burned slopes, may have produced the high concentrations of suspended sediment on 17 August. After surveying farther upstream on subsequent days, we found a fresh debris and mud jam in Jones Creek near the mouth of a severely eroded tributary. Possibly because the stream was downcutting through this material, concentrations of suspended sediment remained high for several days (Figure 1). Once activated by the rainfall, numerous other ephemeral channels also carried silt-laden water for several days, but in concentrations visibly less than the peak concentration observed in Jones Creek.

The effects of fires on streams include increases in discharge and suspended sediment (Tiedemann et al. 1979, Schindler et al. 1980), and these differences seem evident in the comparison between the burned Jones Creek and the unburned Crow Creek watersheds. Discharge and suspended sediment concentrations in Jones Creek were relatively high and erratic throughout the 137-day sampling period (Figure 1). During this time, the daily mean concentration of suspended sediment averaged 73.9 mg/L (U. S. Geological Survey 1990). Though concentrations of total suspended sediment often increased with stream discharge (e.g., during spring runoff), pronounced episodic peaks in the concentration of suspended sediment also occurred during lower discharges, apparently associated with summer rainfall (e.g., as seen from 16-21 August).

In contrast, discharge and suspended solid concentrations in the unburned Crow Creek watershed were markedly lower and more stable (Figure 1). As in Jones Creek, suspended sediment increased during snowmelt and storm

events, but changes appeared more proportional to increases in discharge. Daily mean concentrations of suspended sediment averaged 8.2 mg/L and the maximum daily mean concentration recorded (59 mg/L) was less than the Jones Creek average for the entire sampling period. Unfortunately, though the contrast between the responses of both watersheds was quite marked, the lack of pre-fire hydrologic data makes it difficult to conclude that this contrast was the result of fire. However, during observations made on both streams for four weeks over two years, we did not witness high concentrations of suspended sediment or a fish kill in either stream. At least circumstantially, it appears that the fish kill was related to the unusually large hydrologic event associated with a rainstorm in the Jones Creek watershed.

The fish kill that we observed was notable because it occurred two years after the fire and appeared to result from an acute exposure to sediment. The extent and frequency of lethally acute concentrations of suspended sediment, as well as their effect on entire fish populations, is unknown. Previous fires in the Yellowstone area in the 1700's were at least as intense as those that occurred in 1988 (Romme and Despain 1989) and may also have produced slope instability, high suspended sediment concentrations, and consequently, fish kills. In both Jones and Crow creeks, we found remnants of the toes of landslides and the termini of debris flows that may have resulted from past fires. Because fire is a natural disturbance that will recur, further investigations are needed to gain a better understanding of the effects of fire and how watersheds, streams, and fish populations respond immediately and during the successional recovery of adjacent terrestrial vegetation.

Acknowledgments. We thank K. Benson, J. Blake, J. Hansen, and J. Krajewski for assisting with field work, G. Laidlaw for access to the U.S. Geological Survey data, and A.J. Cordone, K.D. Fausch, G.W. Minshall, C.P. Newcombe, A.D. Richmond, R.B. Rader, E.G. Robison, F.J. Swanson, R.J. Zubik, and two anonymous referees for reviewing portions of earlier versions of the manuscript.

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Monitoring the Impacts of the 1988 Wildfires on Yellowstone's Major Lakes

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The fires that burned the Greater Yellowstone Area (GYA) during the summer of 1988 were the largest ever recorded for that area, burning a total 562,000 ha. In addition to its obvious direct effects on forest ecosystems, wildfire can have profound indirect effects on aquatic ecosystems. Fire disturbance by freeing nutrients otherwise immobilized in biomass or soils increases the release of ions and nutrients from the uplands to downstream aquatic ecosystems. Until post-fire vegetation is sufficiently established, the reduction in canopy cover can result in increased sediment erosion and runoff. The extreme severity of the summer of 1988 fire season presented a unique natural experiment to examine land-water linkages for several coupled watershed-lake basins. Twenty five percent of the Yellowstone Lake and 26% of the Lewis Lake watersheds were affected by the fires to some degree. Jackson Lake in Grand Teton National Park had 26% of its watershed burned.

The long-term water quality monitoring program operated by the U.S. Fish and Wildlife Service provided critical data on the pre-fire and post-fire status of Yellowstone and Lewis Lakes. Statistical comparison (Wilcoxon rank-sum test) of the pre-fire (1976-1984) and post-fire (1989-1991) data sets showed that there has been some measurable change in the water quality of Yellowstone's major lakes (Lathrop 1993). Secchi disk transparency, Ca, Cl, and SO₄ have generally all decreased. Conductivity, pH, total dissolved solids, Na, and K have generally increased. However, due to the great intra- and inter-annual variability that naturally occurs in the measured parameters, only several parameters show statistically significant differences (at an alpha = 0.05).

As with many other complex environmental systems, it is hard to definitively link cause and effect with strictly observational data. Several other environmental processes have a potential role in determining lake water quality. Analysis of the atmospheric deposition data from the National Atmospheric Deposition Program (NADP) sampling station located at Tower Falls (in Yellowstone

National Park) showed a decrease in concentrations of Ca, SO₄ and an increase in pH during the same time period; mirroring the trends found in the lake water quality record. Thus the measured changes in the water chemistry of Yellowstone's major lakes may be due to changes in atmospheric deposition rather than increased fire-mediated inputs from the upland watersheds. The significant but variable inputs from Yellowstone Lake's hydrothermal springs or other nearby geothermal features may also have a major impact on water quality.

Jackson Lake appears to be receiving a higher input of suspended sediment but with unknown consequences on the lake system due to the lack of systematic pre- and post-fire monitoring data (Lathrop et al., 1993). Analysis of USGS monitoring records for the Flagg Ranch station on the Upper Snake River (approximately 8 km upstream of Jackson Lake) show a large post-fire pulse of sediment. This increase is substantiated by the analysis of satellite remote sensing imagery from the pre-fire (1987 and 1988) with the post-fire (1989 and 1990) period which shows the magnitude of the Snake River sediment plumes in Jackson Lake, a normal occurrence during the spring freshet period, were enhanced in the post-fire period.

Overall, the measured effects for Yellowstone and Lewis Lakes are quite subtle and do not qualify as a gross or major shift in water quality. At least in the short-term, Yellowstone and Lewis Lakes appear to be relatively unaffected from fire disturbance of approximately a quarter of their watershed. The large size of these lakes in comparison to their watersheds appears to be diluting the effect of any increased inputs. However, many burned areas have not fully revegetated and nutrient export from the uplands is likely still occurring. Longer term effects are still possible. Due to the large volume of Yellowstone lake and its long water renewal time (the time it takes for the entire lake to be replaced by new water, in this case approximately 10 years), the maximum effect may lag behind maximum yield from the stream inputs by several years. Compared to Yellowstone Lake,

Jackson Lake has a much larger watershed area in comparison to its volume, therefore it has less capability to dilute increased inputs from the land surface. With its shorter water renewal time (approximately three years), Jackson Lake should respond more quickly (shorter lag time) to events such as fire disturbance in its watershed. Conversely, a shorter water renewal rate also means that any increased inputs are flushed from the lake at a faster rate.

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Habitat Requirements for the Reestablishment of Litter Invertebrates Following the 1988 Yellowstone National Park Fires

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Abstract. Litter invertebrate richness, density, diversity, and evenness were studied for two years following the 1988 Yellowstone National Park fires. The extent fire disrupted the invertebrate community depended on fire intensity. Fire damage ranged from total destruction of pine seedlings, herbaceous cover, and litter to slight singeing and little damage to the litter layer. Invertebrate reestablishment correlated with the percentage herbaceous recovery, log debris density, amount of litter left from fire events, and pine seedling density. Reestablishment was detected with a minimum of 10% herbaceous cover, 10 pine seedlings/m², and log debris of 14/ha².

Keywords: Invertebrates

Introduction

Studies have shown the role of invertebrates in ecosystems. These roles include organic matter decomposition, nutrient cycling, and seed dispersal (Schowalter et al. 1991, Christiansen et al. 1989, Lavigne and Kumar 1974).

Fire can alter habitat structure. An invertebrate community especially could be changed due to habitat alteration or disturbance (Christiansen et al. 1992 and Schowalter et al. 1991). Litter invertebrates may require particular habitat characteristics in burned pine forests before the reestablishment of the invertebrate community structure.

We studied litter invertebrate community structure and recovery after the large-scale fire event which occurred in Yellowstone National Park during 1988. Objectives of this study were to a) determine the effects of fire on habitat structure, b) investigate the effect of fire on invertebrate richness, density, diversity, and evenness, and to c) study the reestablishment of invertebrate community structure in burned pine stands.

Methods and Materials

Yellowstone National Park occupies 8,995 km² in northwestern Wyoming, with small sections in Montana and Idaho. Topography ranges from grasslands to alpine habitats. Forested areas occupy 79% of the park. Lodgepole pine (*Pinus contorta* Dougl. ex Loud) stands, in which this research was conducted, comprises 81% of the forested area at elevations from 2300 to 2600 m (Houston 1982).

Lodgepole pine stands were considered intensively burned if fire a) created boles without branches, b) completely ashed the litter organic layer, and c) hollowed log debris. Lodgepole pine stands were considered lightly burned if fire a) scorched trees but left branches and needles on boles, b) burned the top half-inch of the litter layer but left much of the layer intact, and c) scorched log debris but did not burn into the debris. Lightly burned stands were classified by forest personnel as being in the halo of the more intensely burned stands. Reference lodgepole pine stands did not sustain fire damage of any degree.

Nine randomly chosen undisturbed forest stands of at least eight ha. were paired with adjacent nine intensively disturbed forest stands of eight ha. and five lightly disturbed forest stands of at least eight ha. These stands were randomly chosen from a large pool of forest stands, reference and fire disturbed, which had similar characteristics. The chosen stands were located along a line from the southern section of the park to the northern section of the park.

Invertebrates (insects, spiders, mites, millipedes, centipedes, and some annelids) were collected beginning in July of the first post-fire year (1989) and continued to snowfall in mid-September. The second post-fire year's collection began in late May (snow melt) and continued until snowfall in mid-October 1990. Litter, if present, or ashed material for invertebrate extraction was collected every 10 days from five 0.5 m² quadrates every 20 m

along two of three permanently placed 150m² transects in each stand. Starting points along each transect and each two transects, for a total of 10 samples per stand per sampling date, were chosen from a random numbers table. Litter or ashed material was placed into Tullgren funnels for 24 hours to extract invertebrates. The Tullgren funnel technique was proper for doing population studies (Crossley et al. 1991). Extracted invertebrates were stored in 70% ETOH until identification and enumeration were completed.

Forest stand characteristics included tree density (height > 2m), seedling (height < 15 cm), and sapling density (height > 15cm and less than 2m). Tree height and density may be an indicator of habitat cover. Seedling density was used as both an indicator of stand recovery and habitat cover. Herbaceous cover (%/m²), density of log debris (no./ha²), and litter weight (g/m²) were also determined for each stand. Stand characteristics were determined along a 1-m swath along each transect in each stand twice a sampling season.

Invertebrate community variables of density, species richness, Shannon diversity, and evenness (H') were determined from each extracted litter sample. Principle component analysis (Statistical Analysis System 1988) was employed to determine which habitat and invertebrate variables showed the best possible relationships. Simple linear regression (P<0.05) was then used to examine possible relationships between the selected habitat variables and invertebrate community variables. Student's t-test was also used for determining if statistically significant differences existed between habitat variables for reference, lightly disturbed and intensively disturbed pine stands.

Results

As expected, fire disturbed stands contained significantly lower litter weight, sapling density, seedling density, percent herbaceous cover, and log debris density than found in reference stands (Table 1). Two years after the fires, lightly disturbed stands contained significantly lower seedling density and herbaceous cover than intensively disturbed stands.

Data for invertebrate communities in both disturbed and reference pine stands were analyzed from the first spring after the 1988 fires so as to have a starting reference for comparisons over time. Reference stands contained greater densities, richness, and diversity than found in disturbed stands (Table 2). Litter insects had a slightly higher species evenness index than other litter invertebrates.

Lightly burned stands supported greater non-insect than insect densities, richness, and diversity (Table 2). However, insect communities were more evenly composed than noninsect communities as indicated by the

Table 1. Habitat variables in reference, lightly burned, and intensively burned lodgepole pine habitats in Yellowstone National Park, 1990. (n = 27 transects).

Habitat Variable	Fire Intensity		
	Reference	Light	Intensive
Litter Weight (g/m ²)	153.20a ¹	123.60a	57.80b
Tree ²	42.82a	45.20a	0.00b
Sapling ³	40.50a	0.00b	0.00b
Seedling ⁴	24.42a	7.80b	17.64a
Standing Dead ⁵	12.09a	14.20a	33.08b
Log Debris	38.11a	29.00a	26.73b
Herbaceous Cover (%/m ²)	50.19a	1.90b	7.24b

¹Means in the same row followed by different letters differ at the P<0.05 level of significance. (Student's t-test).

²Tree boles taller than 2.00 m.

³Tree boles with heights between 15 cm and 2.00 m.

⁴Tree boles less than 15 cm.

⁵Standing dead boles over 61 cm in diameter.

slightly higher evenness value (Table 2). Initially, lightly burned stands contained greater richness and evenness values than intensively burned stands, but contained significantly lower densities and diversities. Richness was lower in lightly burned stands than in either reference or intensively burned stands.

Intensively burned stands contained higher noninsect densities, richness, and diversity than insect densities, richness, and diversity. Insect density was higher in intensively burned stands than in lightly burned stands.

High invertebrate density and low diversity were correlated with lightly burned stands which contained greater than average litter weight found in lightly burned stands. Regression analysis showed that two years after the 1988 fires, invertebrate density (insect and non-insect densities were combined) was correlated with seedling density and log debris density in intensively burned stands. Low invertebrate density and diversity were found in sites containing higher than average seedling densities and higher than average log densities in lightly

Table 2. Baseline data of insect and non-insect invertebrates in reference, lightly burned, or in intensively burned lodgepole stands in Yellowstone National Park, 1990 (n = 540 litter samples/ fire intensity).

Community Variable	Fire Intensity			
	Reference	Light	Intensive	
Insects ²	Richness	18.80a ¹	7.00b	6.10b
	Density	154.70a	13.00b	19.40b
	Evenness	0.82a	0.97b	0.87b
	Diversity	2.39a	0.82b	1.43c
Non-insects ³	Richness	27.80b	8.00b	9.40b
	Density	222.70a	25.00b	74.10c
	Evenness	0.76a	0.78a	0.75a
	Diversity	2.52a	0.87b	1.70a

¹Means in a row followed by different letters differ at the P<0.05 level of significance (Student's t-test).

²All insects except ants.

³Includes mites, centipedes, millipedes, segmented round worms, and spiders.

burned stands. Low diversity in reference stands was also correlated with high seedling density.

Mites and springtails comprised both the highest density and richness, as compared to other invertebrates, in all reference and fire disturbed stands (Table 3). Two years after the fire event, mite communities in burned stands had 10% of the density and 20% of the richness as compared to adjacent reference stands (Christiansen et al. 1992). Mite community evenness was lower in lightly burned stands than in intensively burned stands. More changes occurred in mite density, richness, and diversity in lightly burned stands than in intensively burned stands.

Mite density, two years post-fire, was found to be significantly greater in burned stands containing a minimum of 10 pine seedlings/m², 14 logs/ha², and 45 grams litter weight/m² (litter accumulated from falling bark as well as from dead needles which fell off of pine trees) than in burned stands which contain fewer seedlings, logs, and lower litter weight. A 40% herbaceous cover (grasses and broadleaf plants) was necessary before density became significantly different among burned stands.

Springtail density was lower in intensively burned stands than in either lightly burned or reference stands. However, their percentage of total richness increased in burned stands over the two years. Springtail density and richness were greater in burned stands which contained at least 10 pine seedlings/m², 12 logs/ha², 36 saplings/ha², and at least 50 g of litter/m² than in burned stands which contained lower amounts of habitat variables.

Discussion

Comparisons of invertebrate density, richness, diversity, and evenness in reference stands to burned stands helped to explain some of the habitat requirements nec-

Table 3. Baseline data of community composition (%) of mite, springtail, and other invertebrates collected in reference, lightly burned, or in intensively burned lodgepole pine stands in Yellowstone National Park, 1990. (n = 540 samples/fire intensity).

Invertebrate	Fire Intensity		
	Reference	Light	Intensive
		Density	
Mites	63Aa ¹	61Aa	85Ab
Springtails	24Ba	31Ba	5Bb
Others ²	13Ca	8Ca	10Ba
		Richness	
Mites	52Aa	46Aa	54Aa
Springtails	25Ba	31Bb	30Bb
Others	23Ba		16Cb

¹Means followed by different letters differ at the P<0.05 level of significance. (Student's t-test). Capital letters compare across invertebrate groups within each fire intensity. Small letters compare invertebrate groups across fire intensities.

²Invertebrates excluding ants.

essary for litter community reestablishment. Data indicated the significance of canopy cover, log cover, and litter cover to invertebrate communities. Many litter invertebrates, such as some mites and springtails, are sensitive to moisture differences which are found in open habitats. This sensitivity may have helped restructure some of the invertebrate community.

Studies by Schulz (1960) and Pontaiiller (1979) described soil surface moisture fluctuations due to forest gaps. Reference stands which contained higher than average seedling densities contained lower invertebrate diversity. These stands had lower average mature tree density which would indicate that canopy cover could have been low. Burned stands which did not have either canopy cover or litter cover contained low invertebrate diversities.

Further data also indicated the importance of habitat cover for invertebrate community reestablishment. Higher invertebrate diversity, in reference stands, was found in stands containing high amounts of litter and enclosed canopies. Studies by Schowalter et al. (1991) and Seastedt and Crossley (1981) showed that many invertebrates were more abundant with an increase in litter and log debris.

The non-insect community contained greater richness, density, and diversity than insect communities in lightly burned stands. Non-insect communities may reestablish more quickly than insect communities in lightly burned stands or perhaps non-insect communities were not as disrupted as insect communities during the fire.

Mites, a non-insect, are important, directly or indirectly, in litter processes such as decomposition and nutrient cycling. Due to their thick cuticles, mites may withstand dry conditions. This morphological advantage may have resulted in mites being dominant in lightly burned stands as well as in reference stands. Minimum habitat requirements for mites may not have been met in the intensively burned stands. Mite communities were not well reestablished in burned stands two years after the fire.

Springtails are also a major component in the litter system. These insects feed upon detritus, fungi, and bacteria which in turn may regulate forest productivity (Dindal 1990). The springtail community was being reestablished by the second year in intensively burned stands which contained logs and seedlings which could have provided cover for springtail reestablishment.

Many litter invertebrates had not become reestablished, as compared to reference stands, two years after the fires. Succession and reestablishment will occur as additional litter from plant regrowth is added to the burned stands. The reestablishment by natural or artificial means of invertebrate litter communities will help in the recovery of ecosystem processes such as nutrient cycling and organic decomposition.

Further studies may show the possibility of artificially reestablishing invertebrate communities by placing minimum amounts of biotic materials such as litter and log debris within fire disturbed habitats. This reclamation work would help in forest management of fire disturbed pine stands.

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Bark Beetle Activity and Delayed Tree Mortality in the Greater Yellowstone Area Following the 1988 Fires

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Abstract. After the 1988 Greater Yellowstone Area fires two studies were begun to monitor beetle activity in burned and unburned conifers and to evaluate the susceptibility of fire-injured trees to bark beetle attack. An intensive survey was conducted annually from 1989 through 1992 on 24 permanent plots located in or near stands burned by surface fire. Stands were located adjacent to areas of extensive crowning and torching. By August 1992, 79% of the 125 Douglas-fir had been infested by bark beetles (primarily by the Douglas-fir beetle) and wood borers; 62% of the 151 lodgepole pine were infested (primarily by the pine engraver); 94% of the 17 Engelmann spruce were infested (primarily by the spruce beetle); and 71% of the 17 subalpine fir were infested (primarily by wood borers). Fire injury combined with subsequent insect attack killed 77% of the Douglas-fir, 61% of the lodgepole pine, 94% of the Engelmann spruce, and all of the subalpine fir. An extensive survey was conducted in 1991 and 1992 on 519 randomly located plots throughout the area. Plots were located in unburned and surface fire-burned areas. Insects killed 13% of the 1,012 Douglas-fir, 18% of the 4,758 lodgepole pine, 7% of the 439 Engelmann spruce, 8% of the 134 subalpine fir, and 3% of the 144 whitebark pine. For all species, insect infestation increased with the percent of the basal circumference killed by fire, except for Engelmann spruce where infestation was greatest with 40 to 80 % of the basal circumference girdled. Infestation in Douglas-fir, lodgepole pine, and Engelmann spruce increased with time. The high level of infestation suggests that insect populations increased in fire-injured trees and then spread to uninjured trees. Increases from 1991 to 1992 suggest that additional tree mortality will occur in 1993, and that a major outbreak could occur in Engelmann spruce. Delayed tree mortality attributed to fire injury accounted for more mortality than insects. Both types of mortality greatly altered the original mosaics of green trees and dead trees that were apparent immediately after the 1988 fires.

Keywords: *Abies lasiocarpa*; Buprestidae; Cerambycidae; *Dendroctonus ponderosae*; *Dendroctonus pseudotsugae*;

Dendroctonus rufipennis; *Ips pini*; *Picea engelmannii*; *Pinus albicaulis*; *Pinus contorta*; *Pseudotsuga menziesii*.

Introduction

Conifer survival following fire depends on the type and degree of tree injuries, initial tree vigor, and the postfire environment. Postfire environment includes the influence of insects, diseases, and weather on tree survival. As fire injury increases, the probability of death due to one or more causes increases (Peterson and Arbaugh 1986, Ryan and Reinhardt 1988, Ryan and Amman 1994). Delayed mortality associated with fire injuries and subsequent insect infestation significantly alters forest structure.

In 1988 crown fires in the Greater Yellowstone Area (GYA) burned roughly 350,000 ha, while surface fires burned an additional 200,000 ha (Greater Yellowstone Post-Fire Resource Assessment Committee, Burned Area Survey Team 1988). Crown fires badly charred trees, instantly killing most of them. Surface fires caused varying degrees of crown and bole injury, increasing susceptibility to insect attack. Increases in insect populations in fire-injured trees create the possibility insects can spread to unburned trees. After the 1988 fires, we began 2 surveys to improve our understanding of fire injury and insect interactions in the GYA. The first study began in 1989 and focused on determining the species of insects associated with varying degrees of fire injury and the way insect attack and tree survival changed over time. In 1991 a second study was begun to cover a larger area and assess the potential for build-up of bark beetle populations and their spread to adjacent unburned trees. The objectives of the second study were to determine delayed tree mortality resulting from fire injury, bark beetles, and wood borers; and to assess if the build-up of insects in fire-injured trees led to subsequent infestation of uninjured trees.

Methods

Intensive Survey

Canopy fires usually completely burned or severely scorched the phloem and cambium, especially in thin-barked trees. Because bark beetles feed on the phloem and cambium, such trees were no longer suitable for bark beetle infestation. The intensive survey focused on sampling in stands along the boundary between unburned forests and forests burned by surface fires. We made observations on 24 Bitterlich point-sample plots (Avery 1967) using a 2.23 m²ha⁻¹ basal area factor prism. Plots were located within the North Fork, Snake River, Huck, and Hunter fires. Fuel (Hartford and Rothermel 1991), weather (Bushey 1989), and fire behavior (Rothermel et al. 1994) conditions have been previously described for the GYA. Plots were located in lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests between 2,000 and 2,500 m elevation, and within a few hundred meters of roads. In addition to lodgepole pine and Douglas-fir, we encountered a few Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Measurements were made of tree diameter at breast height, crown scorch, and the percentage of the circumference killed at the base. Crown scorch was estimated visually and expressed as the percentage of the prefire crown volume killed. We determined cambium injury by removing small sections of bark and visually inspecting tissues. We classified insects attacking trees as primary (those that can infest and kill healthy trees) or secondary bark beetles (those commonly attracted to weakened or recently killed trees), wood borers of the families Buprestidae and Cerambycidae, or other insects (Table 1). Observations of insects were restricted to the lower 2 m of the bole. We detected insect attack by inspecting for boring dust and for insect entrance and exit holes. Insect species were identified by removing a small

portion of bark, exposing the phloem and cambium. Annual observations were made of insect attack and tree mortality from 1989 through 1992. Trees were classified as alive or dead based on the presence or absence of living foliage. Additional details on plot location, measurements, and preliminary observations are contained in Amman and Ryan (1991) and Ryan and Amman (1994).

Extensive Survey

An extensive survey for bark beetle activity was conducted in 1991 and 1992. Plots were located throughout the burned/unburned mosaic at random distances along the roads in Yellowstone Park and the Rockefeller Memorial Parkway. Plots were in unburned or lightly burned forests primarily between 2,000 and 2,500 m elevation. To be included in the study, a plot had to contain green trees. In 1991, 321 plots were examined, in 1992 198 were examined. Additional details of plot locations and descriptions are outlined in Rasmussen et al. (1996). The survey consisted of 4,758 lodgepole pine, 1,012 Douglas-fir, 439 Engelmann spruce, 134 subalpine fir, and 144 whitebark pine (*Pinus albicaulis*). Sampling was conducted on variable radius plots as outlined in the intensive survey. All trees in the plot were examined and classified as alive, fire killed, or insect killed, based on the presence or absence of living foliage, the degree of girdling by the fire, and degree of insect infestation. Fire injury was grouped into six classes based on the percent of the circumference girdled by heat: unburned, 1 to 20 %, 21 to 40 %, 41 to 60 %, 61 to 80 %, and 81 to 100 %.

Observations of each tree included species, diameter at breast height, presence or absence of insect attack, insect species, and the percentage of basal circumference in which the cambium was killed by fire. Trees in which the cambium was killed for 100 percent of the basal circumference (completely girdled), were considered to have been killed by the fire. Those that were not com-

Table 1. Bark beetles and wood borers infesting trees in the Greater Yellowstone Area after the 1988 fires

Host	Bark beetles		Borers	Other
	Primary	Secondary		
Lodgepole pine	<i>Dendroctonus ponderosae</i>	<i>Ips pini</i> <i>Dendroctonus valens</i> <i>Pityophthorus</i> spp. <i>Pityogenes</i> spp.	Buprestidae Cerambycidae	Ambrosia <i>Hylurgops</i> spp. <i>Hylastes</i> spp.
Whitebark pine	<i>Dendroctonus ponderosae</i>	<i>Ips</i> spp.	Buprestidae Cerambycidae	
Douglas-fir	<i>Dendroctonus pseudotsugae</i>	<i>Pseudohylesinus</i> spp.	Buprestidae Cerambycidae	
Engelmann spruce	<i>Dendroctonus rufipennis</i>	<i>Ips pilifrons</i> <i>Scierus</i> spp.	Buprestidae Cerambycidae	Siricidae Ambrosia
Subalpine fir			Buprestidae Cerambycidae	

pletely girdled but became infested by bark beetles or wood borers were attributed to insect mortality. Cambium injury and insect attack were determined using procedures outlined in the intensive survey methods. The build-up of insects in fire-injured trees and the subsequent increase in infestation of unburned trees were determined by relating infestation to the year of its occurrence. Dating the year of insect attack for 1989 and 1990 was estimated from foliar characteristics criteria described in Rasmussen et al. (1996). Dates for the next two years were based on the actual observation of infestation of green trees.

Results

Intensive survey

Detailed descriptions of fire injury and preliminary results of the intensive survey were reported in Amman and Ryan (1991) and Ryan and Amman (1994). The results presented here are the final insect attack and tree mortality observations.

Douglas-fir

By 1992, 79% of the 125 Douglas-fir in the intensive survey were attacked by 1 or more species of insects, and 77% had died (Tables 2, 3). Both live and dead Douglas-fir were similar in size and, therefore, resistance to fire injury. However, dead trees suffered greater crown and bole injury, indicating that these trees experienced more extreme fire behavior. Seventy-one percent of the insect attacks were by the Douglas-fir beetle (*Dendroctonus pseudotsugae*). Of the dead Douglas-fir, 83% were attacked by insects (Table 2), primarily Douglas-fir beetles (n = 73). Larvae of Buprestidae and Cerambycidae wood borers infested 23% of the Douglas-fir. Dead trees that

Table 2. The number of trees that were alive or dead and whether they had been infested by insects or not.

Species/status	Alive	Dead	Total
Douglas-fir			
Infested	19	80	99
Noninfested	10	16	26
Total	29	96	125
Engelmann spruce			
Infested	1	15	16
Noninfested	0	1	1
Total	1	16	17
Lodgepole pine			
Infested	13	80	93
Noninfested	46	12	58
Total	59	92	151
Subalpine fir			
Infested	0	14	14
Noninfested	0	3	3
Total	0	17	17

Table 3. Cumulative percent insect attack and mortality by year for the intensive survey.

Species/status	Year			
	1989	1990	1991	1992
Douglas-fir (n = 125)				
Infested	24	62	76	79
Dead	12	37	52	77
Engelmann spruce (n = 17)				
Infested	65	82	82	94
Dead	12	82	82	94
Lodgepole pine (n = 151)				
Infested	24	44	58	62
Dead	18	48	58	61
Subalpine fir (n = 17)				
Infested	37	65	71	71
Dead	76	100	100	100

were not attacked by Douglas-fir beetles were generally small diameter and too severely burned to make suitable habitat for the beetles. Two-thirds of the surviving trees were attacked. These were primarily "strip" attacks (narrow vertical areas of infestation) of Douglas-fir beetles (n = 15) in green phloem and wood borer attacks (n = 9) in dead phloem. The average basal girdling of surviving burned Douglas-fir was 59% of the circumference. Except in the smaller diameter trees, injury to the phloem and cambium was restricted primarily to narrow bands near the root crown. This resulted when duff concentrations beneath the trees burned.

Douglas-fir beetles preferred trees with more than 50% basal girdling, ample green phloem, and less than 75% crown scorch (Table 4). Wood borers initially attacked phloem that was not suitable for Douglas-fir beetles or delayed attack until those beetles were well established. The role of other beetles in Douglas-fir was minor and usually associated with Douglas-fir beetles. Douglas-fir beetles initially attacked severely injured trees, then attacked more lightly injured trees during 1991 and 1992. The major increase in cumulative insect attack occurred in 1990, when 38% of the trees were attacked, compared with 14% in 1991 and 3% in 1992 (Table 3). Mortality was substantially higher in trees with more than 50% crown scorch or more than 75% basal girdling (Table 4). Most trees that died in 1989 suffered both severe crown and severe bole injury. The majority of subsequent mortality occurred among trees that suffered little crown injury but had more than 50% basal girdling.

Table 4. Number of trees, percent mortality, and number of trees infested by insects by species and fire injury.

Species	Crown scorch (%)	Basal girdling (%) ^a			
		0-25	26-50	51-75	76-100
Douglas-fir (n = 125)	0-25	11(82) 8 ^b	14(64)12	13(46)11	17(76)17
	26-50	-	6(33) 6	4(50) 4	5(100) 5
	51-75	1(100) 1	3(0) 2	4(75) 4	12(100)12
	76-100	-	8(88) 4	1(100)1	26(100)15
Engelmann spruce (n = 17)	0-25	1(0) 0	-	-	4(75) 4
	26-50	-	-	-	3(100) 3
	51-75	-	-	-	5(80) 5
	76-100	-	-	-	4(100) 4
Lodgepole pine (n = 151)	0-25	30(13) 2 ^c	15(13) 5	15(13) 4	59(88)54
	26-50	-	-	-	8(100) 6
	51-75	-	-	-	6(100) 4
	76-100	-	-	1(100) 1	17(100)14
Subalpine fir (n = 17)	0-25	-	1(100) 1	-	4(100) 4
	26-50	-	-	-	1(100) 1
	51-75	-	-	-	1(100) 1
	76-100	-	-	-	10(100) 9

^aThe first number is the number of burned trees in the survey, the number in parentheses is the percentage of trees that died, and the third number is the number of trees infested by insects.

^bIncludes nine trees from an unburned patch of forest. Six of these were attacked by Douglas-fir bark beetles and died.

^cIncludes 25 unburned trees, two of which died. These trees were not attacked by insects and their deaths appear unrelated to the fires.

Lodgepole Pine

Of the 151 lodgepole pine in the intensive survey, 62% were attacked by one or more species of insects, and 61% died (Tables 2, 3). The majority of dead trees were extensively fire girdled (greater than 75% of the circumference) and heavily insect infested (Table 4). Both live and dead trees were similar in size, but dead trees had suffered greater fire injury. Surviving trees received less than 25% crown scorch. Burned living trees averaged 56% basal girdling. Because lodgepole pine is a thin-barked species, severe crown injury was associated with severe bole injury. Severely injured bole tissues were not suitable for bark beetles. The dominant fire injury to sample trees was to the phloem and cambium in the lower 0.5 m of the bole. Frequently, only a 2- to 4-cm high band at the root crown was killed. Of the 25 unburned lodgepole pine in the survey, two trees died. Their deaths appear to be unrelated to the fires.

The majority of insects attacking lodgepole pine (Table 2) were pine engravers (*Ips pini*). Of the 70 trees attacked by pine engravers, 62 died. Most trees infested by pine engravers had more than 75% basal girdling but less than 50% crown scorch. The twig beetle (*Pityophthorus confertus*) attacked 18 trees, while mountain pine beetle (*D. ponderosae*) attacked eight trees. Seven of these pines died. However, mountain pine beetle attack densities appeared to be low. Red turpentine beetle (*D. valens*) attacked two trees and one died. Wood borers attacked 21 of the fire-injured lodgepole pine. Five of these pines lived and 16 died. The lodgepole pine that survived attacks primarily experienced strip attacks. When insect attacks occurred above the ungirdled portion of the bole, the tree generally died. The cumulative percent of lodgepole pine infested by insects increased by 20% between 1989 and 1990, by 14% between 1990 and 1991, and by 4% between 1991 and 1992 (Table 3). Cumulative mortality followed a similar trend (Table 3).

Engelmann Spruce and Subalpine Fir

We encountered only 17 Engelmann spruce and 17 subalpine fir in the intensive survey because we focused on Douglas-fir and lodgepole pine forests. By August 1992, all but 1 spruce had died (Table 2). The 14 spruce trees that died before 1991 were completely girdled. The 2 trees that died between 1991 and 1992 were 90% girdled and heavily infested with spruce beetle (*D. rufipennis*) in 1991. Spruce beetle infested 24% of the spruce. Thirteen of the subalpine fir suffered basal girdling in excess of 75% of the circumference and died by 1989. All of the subalpine fir died by 1990. Wood borers infested 74% of the spruce and fir.

Extensive Survey

By 1991, when the extensive survey began, most trees that suffered severe crown scorch or severe bole injury had died. Subsequent bark beetle infestation of less severely burned and unburned trees resulted in considerable delayed mortality. Delayed mortality from fire injury and insects in the tree species represented in this study ranged between 41 and 64%. This mortality altered the visual appearance of the stands during the years after the 1988 fires. Infestation by insects was positively related to the percentage of the basal circumference of the tree that had been killed by fire in Douglas-fir, lodgepole pine, and Engelmann spruce (Figure 1). Meaningful relationships were not established for subalpine fir and whitebark pine because of the small numbers of those species in our sample. For uninjured trees, insects attacked 22% of the lodgepole pine, 18% of the Douglas-fir, 11% of the subalpine fir, 10% of the Engelmann spruce, and 3% of the whitebark pine (Figure 1).

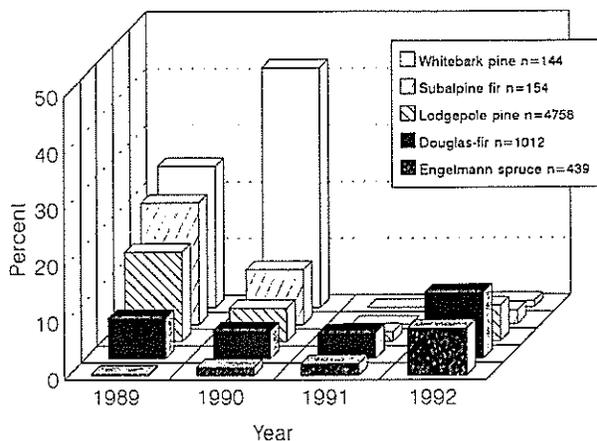


Figure 1. Percentage of trees infested by insects for five conifer species and percentage of basal circumference killed. Data are from the extensive survey of the 1988 Greater Yellowstone Area fires.

Douglas-fir

Of the 1,012 Douglas-fir examined, 32% were dead. Almost one-third of the Douglas-fir that were green and appeared to be alive following the 1988 fires died from the delayed effects of fire injury or were killed by insects. Of the delayed mortality, 19% was attributed to fire injury, while 13% was attributed to bark beetle and wood borer infestation. The cause of death could not be identified in 1% of the trees (Figure 2). Most infestation was by the Douglas-fir beetle. Additional mortality, especially of small diameter trees, was associated with Douglas-fir pole beetle (*Pseudohylesinus nebulosus*) and wood borers.

An average of 42% of the Douglas-fir in all fire-injury classes combined was infested by insects. Infestation increased from 18% in the unburned class to 80% in trees with 81-100% of the basal circumference girdled by fire (Figure 1). Douglas-fir beetle accounted for most of the infestation, which ranged between 16% of the trees in the uninjured class to 47% in the 81-100% basal injury class.

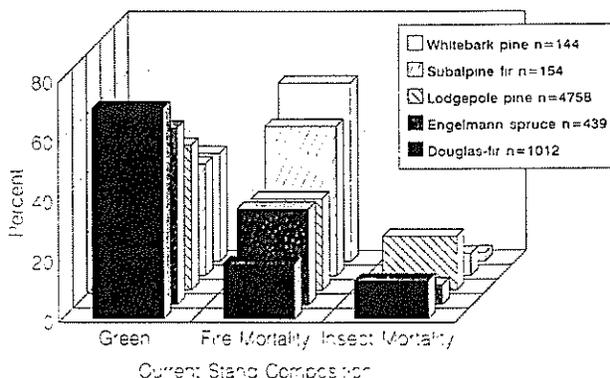


Figure 2. Percentage of healthy (green) trees versus fire-killed and insect-killed trees for the extensive survey of the 1988 Greater Yellowstone Area fires.

The second most common bark beetle infesting Douglas-fir was *P. nebulosus*; wood borers were the next most common insect infesting Douglas-fir.

In Douglas-fir, insects, particularly Douglas-fir beetles, began infesting uninjured trees the first year after the fire. Infestation of uninjured trees declined somewhat in 1990 and 1991. Then the infestation increased from 4% in 1991 to 12% in 1992 (Figure 3). Most of this was due to Douglas-fir beetle.

Lodgepole Pine

Lodgepole pine mortality was 52% of the 4,758 sampled trees. Of tree mortality, 31% was due to fire-injury, 18% was due to insects, and 3% was due to unidentified causes (Figure 2). Because of green foliage after the 1988 fires, many of these trees appeared to have survived the fires. However, almost two-thirds of the lodgepole pine that subsequently became infested and died had been completely girdled by light ground fires. The foliage on many of these trees did not fade until they were infested by pine engravers or twig beetles (*Pityophthorus confertus* and *Pityogenes knechteli*) three or four years after the fires. Of the dead lodgepole pine, 44% were infested by pine engravers. Total insect infestation ranged from a low of 22% of lodgepole with no injury to 67% of lodgepole with 81-100% of their basal circumference girdled by fire (Figure 1). Pine engravers accounted for most lodgepole pine infestation, ranging from 17% of trees in the uninjured class to 45% of trees in the 81-100% basal injury class. Twig beetles were the next most common, with the wood borers infesting a few trees. Mountain pine beetles infested less than 1% of the lodgepole pine and did not show much preference for any fire-injury class.

In lodgepole pine, infestation of uninjured trees increased from 2% in 1991 to 7% in 1992. Most of this was attributed to pine engravers. The pattern of infestation by year is similar to that in Douglas-fir. Infestation of lodgepole was high in 1989, then declined through 1991. A substantial increase occurred in 1992 (Figure 3).

Engelmann Spruce, Subalpine Fir, and Whitebark Pine

Mortality of Engelmann spruce totaled 41% of the 439 trees in the sample. Of these, 32% were killed by fire injury, 7% by insects (Figure 2); 2% died from unidentified factors. Spruce beetles killed almost half of the spruce that were killed by insects. Other insects that killed spruce were the pine engravers (*Ips pilifrons*) and wood borers.

Across all basal injury classes, 29% of the Engelmann spruce were infested by insects. Infestation ranged from 10% of the uninjured class to 54% of trees having 41-60% of their basal circumference girdled by fire (Figure 1). Spruce beetles accounted for almost half of the infested trees (14%). Infestation by spruce beetle ranged between 6% of the uninjured class to 39% of trees having 41-60% basal girdling.

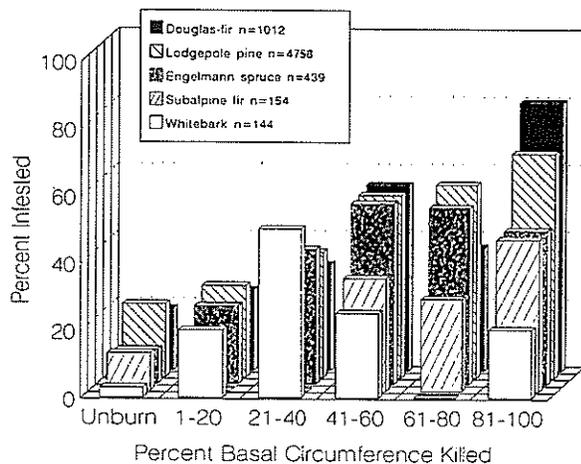


Figure 3. Percentage of trees infested by insects for 5 conifer species in the Greater Yellowstone Area for 4 years after the 1988 fires. Data are from the extensive survey of the 1988 Greater Yellowstone Area fires.

Mortality of the 134 subalpine fir totaled 63%. Fire injury accounted for 50% of the mortality, whereas insects accounted for 8% and unidentified causes accounted for 5% of the mortality (Figure 2). Wood borers accounted for most of the insects attacking subalpine fir.

Of the 144 whitebark pine in the extensive sample, 64% died; 60% died from fire injury, 3% died from insect attacks, and 1% died from unidentified causes (Figure 2). Mountain pine beetle and a pine engraver, probably *Ips montanus*, were the most common insects killing whitebark pine.

Our samples of subalpine fir and whitebark pine were too small to draw meaningful conclusions about insect response to different fire-injury classes. However, it appeared that insects consisting mostly of wood borers preferred the more severely injured subalpine fir (Figure 1). No strong relationship between fire injury and infestation existed in the whitebark pine data (Figure 1).

Discussion

The results of both the intensive and extensive surveys indicate that several insect species were attracted to trees stressed by fire injury. These attacks contributed to delayed mortality throughout the GYA. Few of the burned trees had more than half of their crown injured by fire. Many had no crown injury at all. In an analysis of the mortality of seven western conifers, including all of the species in this study except whitebark pine, Ryan and Reinhardt (1988) found little difference in mortality among species due to crown scorch. With less than 70% crown scorch, and in the absence of bole or root injury, trees of normal vigor are more likely to live than die (Ryan 1990). Studies of girdling by mechanical means

(Noel 1970) and heat (Ryan and Frandsen 1991, Ryan 1993) indicate that trees have a high probability of surviving until nearly all of the phloem is severed. Ryan (1993) found basal girdling up to 80% of the circumference had no effect on seasonal water relations and only minor effects on allocation of carbon to growth. The high mortality in trees with minor crown and bole injury indicates that insects contributed to significant mortality in the GYA. The relatively high infestation of unburned trees in 1991 and 1992 compared to endemic attack rates further demonstrates that insects contributed to increased mortality after the 1988 fires.

We observed few trees infested by mountain pine beetles and those that were infested appeared to have few beetles. The lack of significant mountain pine beetle activity may be due to low population levels or habitat preference. Populations of mountain pine beetles were low in the GYA in 1988 (Knapp et al. 1988, Gibson and Oakes 1989). Also, mountain pine beetles do not prefer trees stressed by fire or drought (Rasmussen et al. 1996). Although some mountain pine beetles were present in the GYA during this study, populations did not increase in the stressed trees. Schmitz (1988) observed mountain pine beetles infesting diseased lodgepole pine when beetle populations were at an endemic level; brood production was very low, preventing the beetle population from building up. Population build-up and a full-scale outbreak appears to require faster growing trees with thicker phloem, the larvae's food source.

Although we did not sample Douglas-fir beetle populations by removing bark, Pasek and Schaupp (1992) did remove bark in areas of the Clover Mist Fire in the Shoshone National Forest adjacent to Yellowstone National Park. They observed that broods were reduced from 1990 levels; they attributed the reduction to prolonged, extremely cold temperatures. Reduced brood survival could account for low infestation in 1991. The large increase in Douglas-fir infestation in 1992 (Figure 3) is close to the upper limit of the 1.5- to 3-fold increase predicted by Pasek and Schaupp (1992), based on their sampling of Douglas-fir beetle populations. Infestation figures for 1992 are higher than those for 1991, but we don't know that all of these infested trees will die. However, it appears that fewer fire-injured trees are available for infestation, increasing infestation of uninjured trees. The attack trends from the extensive survey suggest increased infestation in 1993. However, Douglas-fir beetle outbreaks generally coincide with periods of drought. Increased precipitation in 1993 could alter the apparent trend.

In Engelmann spruce, infestation steadily increased in each of the four years after the fire (Figure 3). Spruce beetles accounted for most of this infestation. The large increase from about 2% in 1991 to 8% in 1992 suggests that beetles probably built up in fire-injured trees and are now infesting more of the uninjured trees. The steady

increase in infestation of uninjured spruce indicates that the spruce beetle population could be poised for a major outbreak. Because the spruce beetle has a 2-year life cycle, the large increase in 1992 would be the result of populations surviving in trees infested in 1990. Should survival be as high in the spruce infested in 1991 beetles could infest a higher percent of the uninjured spruce than they infested in 1992. With good survival, beetles emerging in 1994 could continue the high level of infestation.

Delayed mortality resulting from lethal underburning and the subsequent insect-caused mortality in surviving underburned and adjacent unburned forests changed the 1988 postfire forest mosaic. Delayed mortality creates diverse habitats for fauna (McEneaney 1996), affects regeneration (Anderson et al. 1996) and nutrient cycling, and confounds efforts to survey burned forests using remote sensing (White et al. 1994). Recent evidence suggests that 60% of the area burned in stand-replacement fires in the Selway-Bitterroot Wilderness in Idaho and Montana occurred as lethal understory fires, with the remainder occurring as crown fires (Brown et al. 1994). Our surveys were not designed to quantify the area of delayed mortality in the GYA. However, photographs taken periodically since 1988 and our survey data suggest that delayed mortality was extensive.

Conclusions

The results of both the intensive and extensive surveys indicate that stress resulting from fire injury led to increased bark beetle activity in the GYA. Lethal basal girdling coupled with insect attacks of unburned and lightly burned trees caused considerable delayed mortality. Delayed mortality altered the visual appearance of the burn mosaic. Lethal underburning alters a number of ecosystem processes that can have long-lasting effects on forested ecosystems. Additional research is needed to better understand how fires of varying severity alter forest structure and insect ecology.

Trees with severe crown scorch tended to have more heat-killed cambium and to succumb more rapidly. These trees tended to not be favorable habitat for bark beetles but frequently were attacked by wood borers. In contrast, trees with light crown scorch and basal girdling were attacked more frequently first by primary and secondary bark beetles and were later attacked by woodborers. Bark beetle infestation increased with the percent of basal circumference killed by fire. The relative importance of factors affecting beetle response such as insect populations before the fire, trees' reduced resistance to attack, increased nutritional value of phloem, weather after the fire, and predation are unknown.

Bark beetle populations appear to have increased in fire-injured trees and then infested uninjured trees.

Whether some beetle species will continue to spread to unburned forests is uncertain. However, historic evidence from other fires suggests major epidemics are unlikely in the absence of additional stress from drought or other sources.

Acknowledgments. The authors gratefully acknowledge Kenneth E. Gibson, A. Steven Munson, Robert D. Oakes, Lynn A. Rasmussen, and James C. Vandygriff for their efforts in collecting the extensive survey data and the two anonymous reviewers.

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Responses of Elk to the 1988 Yellowstone Fires and Drought

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Abstract. We had 13 bull and seven cow elk radio collared prior to the fires in 1988. There were no mortalities directly related to the fires. Fires burned 0% to 60% of summer home ranges but did not affect home range size or timing of migration compared to 1987. Fires burned between 0% and 82% of winter home ranges and affected winter home range location and movements of 12 animals, though differently among sex-age classes. Diets were more fibrous and consisted of more trees and less grasses and forbs than in previous winters, indicating lower nutrition during 1988-1989. Winter mortality during 1988-1989 was 57% for cows, 17% for subadult bulls, and 86% of bulls ≥ 6 years old. Mortality was significantly related to animal age and proportion of winter home range burned, though not to proportion of summer range burned. We had no index to animal condition prior to winter, but it was probably lower than the previous two years due to drought effects on plants. Poorer pre-winter condition probably contributed to mortality. Activity during the 1988-1989 winter was less than during the winters of 1986-1987 and 1987-1988, though lower temperatures partially contributed to reduced activity time. The surviving eight elk did not show any selection for burned habitats during the summer of 1989; ratios of percent of locations in burned habitats to percent of burned area available within summer home ranges were 0.78 to 1.65.

Keywords: Elk; Fire; Home range; Diet composition; Activity; Mortality.

Introduction

Bendell (1974), Kelsall et al. (1977), and Lyon et al. (1978) have reviewed the effects of wildfire on large mammals. Studies have primarily reported population responses after fires (Kruse 1972, Peek 1974, Martinka 1976, Crowner and Barrett 1979, Peek et al. 1985, Klinger et al. 1989), and a few have described immediate

responses by individuals (Komarek 1969, Gasaway and Dubois 1985). Purcell et al. (1980) determined that radio-collared mule deer (*Odocoileus hemionus*) did not abandon or extend their home ranges as a result of fires. Six of seven radio-collared meadow voles (*Microtus pennsylvanicus*) survived a prescribed grassland fire (Geluso et al. 1986). The Yellowstone fires had no apparent effects on annual range size or mean rate of movement of grizzly bears (*Ursus arctos horribilis*) (Blanchard and Knight 1990). Though extensive prescribed burning is done to improve elk habitat, information on the response by individual elk to fire is lacking. The 1988 Yellowstone fires offered an opportunity to examine the short-term responses of 18 elk that were radio-collared January 1987, and two in September 1987. The elk were collared for another research study, but the uniqueness of the large-scale events in 1988 prompted us to separately report their effects on the collared elk.

Drought affects wildlife by increasing mortality (Hillman and Hillman 1977, Caughley et al. 1985, Walker et al. 1987), altering habitat use (Marcum and Scott, 1985), movements (Purcell et al. 1980), or diets (Anthony 1976, Stephenson et al. 1985). Northern Yellowstone elk (*Cervus elaphus*) are migratory (Skinner 1925, Craighead et al. 1972) and can respond to changes in forage by either changing diets or moving to new areas in search of better food (Morgantini and Hudson 1989). Elk typically migrate from summer to winter ranges when snow accumulates on summer range (Anderson 1958, Lovaas 1970, Adams 1982, Morgantini and Hudson 1988, Boyce 1991). In Yellowstone, fall migrations occur between September and late November in response to snow (Skinner 1925, Houston 1982), with most elk arriving on the winter range in November (Craighead et al. 1972).

Our objectives were to: 1) document the immediate effects of summer range fires on elk. The null hypothesis was that if elk were not affected by fires they would remain within their summer home range and not use areas outside of it. The alternative hypothesis was that as more

of their home range was burned, elk would venture outside the boundary of their home range in search of needed resources. We tested this by determining if the change in size of the 1988 summer home range compared to the 1987 home range was directly related to extent of burning within the home range. We further hypothesized that those elk affected by fire would migrate to their winter range no earlier than those whose summer range was not affected by fire. If these hypotheses were not rejected, elk did not move outside of their summer home range to escape advancing fire or search for additional food sources while on summer ranges; 2) describe shifts in winter home range during 1988-1989; 3) describe mortality patterns during the winter 1988-1989; 4) test for differences in winter diet composition and quality between two winters prefire and winter 1988-1989; 5) test for differences in activity patterns between the 2 winters prefire and winter 1988-1989; and 6) assess elk selection for burned habitats during summer 1989.

Study Area

Radio-collared elk were located throughout much of Yellowstone National Park in northwestern Wyoming in areas that were burned and unburned (Figure 1). Forest vegetation on summer ranges was mostly lodgepole pine with some Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Winter range also contained Douglas-fir (*Pseudotsuga menziesii*), whitebark pine (*Pinus albicaulis*), and Rocky Mountain juniper (*Juniperus scopulorum*). Winter range vegetation was primarily sagebrush (*Artemisia* spp.)-grass (*Stipa*, *Festuca*, *Agropyron*, *Oryzopsis*, *Poa*, *Agrostis*, *Bromus*, *Koeleria*, *Elymus*, *Danthonia*, *Deschampsia*, *Phleum*, and *Muhlenbergia*), mixed grass-forb, or sedge (*Carex*, *Typha*, *Juncus*) meadows.

Elk were located at elevations ranging 2100 to 3100 m during summer and at 1700 to 2900 m during winter. Normal monthly precipitation during June, July, and August for Yellowstone National Park between 1951 and 1980 was 49, 32, and 35 mm, respectively (NOAA 1989). Normal monthly temperatures during June, July, and August for the same period were 12.1, 16.1, and 15.1 °C (NOAA, 1989).

Methods

Cow elk and two bulls were captured during winter using clover traps (Clover 1954, McCullough 1975, Thompson et al. 1989) baited with alfalfa. Traps were located within 200 m of roads because of their size, weight, and difficulty moving them over snow. In addition bulls were free-darted opportunistically from a vehicle and immobilized with 2.55 to 3.00 mg carfentanil.

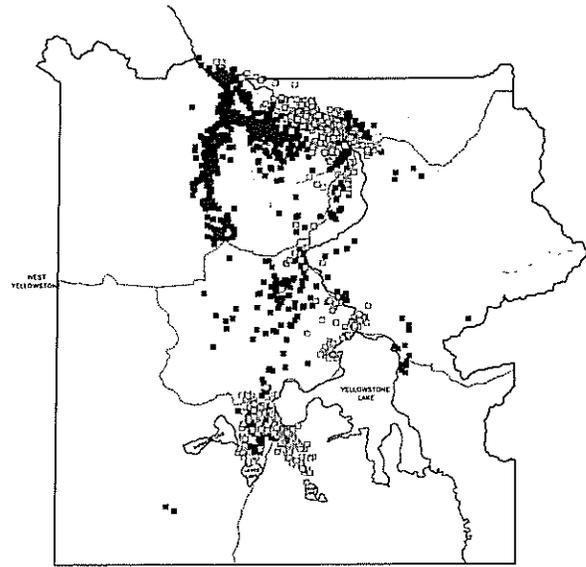


Figure 1. Locations of radio-collared elk in Yellowstone National Park 1987-1989. Dark squares are bull locations, lighter squares are cow locations.

Elk were fitted with Telonics MOD 500 motion-sensitive radio collars. During January to March 1987, seven cow, five adult bulls ≥ 6 years old, and six subadult bulls aged one to four years were collared. One adult bull and one subadult bull were collared during September 1987.

Radio-collared elk were primarily located by aerial telemetry from a Super-Cub. Collared elk were seen $\geq 60\%$ of the time from the aircraft. No aerial telemetry flights were possible between 7 August and 19 September, 1988, the most intense burning period. Ground telemetry using a hand-held "H" antenna and visual locations supplemented aerial locations when flights were restricted because of smoke or congested air traffic. During the study aerial telemetry comprised 38% of locations, ground visuals 32%, and ground telemetry 24%.

Migration date was defined as the median date between the last location an animal was within its seasonal home range and the next location when the animal was not on its seasonal home range. Migration of an individual was obvious and rapid once the animal began to move. Migration from summer to winter range for any individual was usually accomplished in two to five days.

Home ranges were delineated using minimum convex polygon (Mohr 1947; MCP) and harmonic mean (Dixon and Chapman 1980) methods using program HOME RANGE (Ackerman et al. 1990). Prefire home ranges were based on 12 to 53 locations per home range; annual summer home ranges were based on eight to 52 locations per animal. Home ranges calculated with MCP based on small sample sizes may be biased small (Jennrich and Turner 1969), but a variety of logistic factors prevented us from obtaining more locations.

Burned areas within home ranges were determined using digitized data obtained from fall 1988 LANDSAT multispectral imagery with 0.06 ha minimum map unit size. Burn type signatures were verified by comparison with aerial photography (two ha resolution) and ground truthing at selected sites (Despain et al. 1989). Area of home ranges burned were obtained using Geographic Resources Analysis Support System (GRASS).

Diet composition during winter was determined from microhistological analysis of fecal samples (Sparks and Malecheck 1968) at the Composition Analysis Laboratory, Colorado State University. Chemical analysis of fecal samples for crude protein, neutral detergent fiber, acid detergent fiber, and lignin were done at the Nutritional Analysis Laboratory, Colorado State University. Composite samples were collected every other month November to April in areas frequented by bulls (three areas - Lava Cr., Elk Cr., Tower Jct.) and cows (five areas - Phantom Lk., Geode Butte, Hellroaring Trailhead, Floating Island Lk., and Junction Butte). We observed groups of elk of the desired sex-age class in sample areas before collecting fecal pellets to ensure the samples were obtained from bulls or cows. Three pellets from a minimum of 15 fecal groups (usually more, up to 70 groups) were collected for each sample.

We used mechanical strip-chart recording devices connected to a digital processor (digital to analog conversion) to record radio signals from collared animals. All elk except two cows were equipped with motion-sensitive instantaneous tip-switches that permitted interpretation of head down and head up behavior. Three animals were simultaneously sampled using three receiving stations. Activity of animals was continuously monitored, providing complete 24-hour records of activity. Only complete 24-hour periods (0000-2400) were used in calculating average number of minutes active per day per month by sex-age class. Active periods were identified when transmitter pulse rate and signal strength were both variable. In most cases signals from active animals could be easily distinguished from signals from inactive bedded animals.

We used linear regression to test short-term responses of change in home range size and migration timing to proportion of the prefire home range burned. Analysis of variance was used to test diets and activity among years and sex-age classes. Stepwise logistic regression was used to identify variables determining mortality. Chi-square was used to test selection for burned habitats (Neu et al. 1974). Power for simple t-tests was calculated using STPLAN (Brown et al. 1993). Power for analysis of variance and regression was calculated using the methods outlined by O'Brien and Muller (1993). Power for the chi-square test was calculated following Cohen (1988).

Results and Discussion

Short-term Effects

None of the 20 radio-collared elk died in the fires. Fire did not burn within the home ranges of two elk, four had 1% to 10% burned, and 14 had more than 20% of their prefire summer home range burned (Table 1). Changes in summer home range size between 1987 and 1988 ranged from -65% (smaller) to +268% (Figure 2a). All but one collared elk migrated earlier in 1988 than in 1987 (Figure 2b).

There were no differences among sex-age classes in percent of summer home range burned ($P = 0.81$, $n = 20$, power = 0.08) or percent change in home range size between 1987 and 1988 ($P = 0.21$, $n = 18$, power = 0.31). Power for both tests was low due to similar means among sex-age classes and large variation within sex-age classes. The number of animals needed to obtain a power of 0.80 would be 450 for the percent of home range burned and 51 for the change in home range size analyses.

Adult bulls migrated nine days earlier in 1988 than in 1987, subadult bulls 14 days earlier, and cows 31 days earlier, differing among sex-age classes ($P = 0.049$, $n = 16$). We expected that if fires directly affected elk we would detect a larger change in home range size and earlier migration for those animals with more area burned than for those with less. Change in home range size ($P = 0.65$, $n = 18$, power = 0.12; Fig. 2a) and migration timing ($P = 0.59$, $n = 16$, power = 0.13; Fig. 2b), however, were not related to amount of home range burned.

Table 1. Fire effects on movement and mortality.

Sex-Age	1988-89 Age	% Summer Home Range Burned	% Winter Home Range Burned	Moved?	Died?
Cow Be	Unk	57	4	N	N
Cow Di	Unk	31	18	Y	N
Dow Do	Unk	47	10	N	N
Cow Ka	Est 15	0	13	Y - before dying	Y
Cow Ru	Est 14	60	27	Y - before dying	Y
Cow Se	Est 8	0	40	Y	Y
Cow Sh	Est 8	31	30	Y - before dying	Y
% of Cows		Avg=32	Avg=20	71%	57%
Subadult Ad	3	56	59	Y	N
Subadult Ba	3	40	78	Y	N
Subadult Is	4	8	39	N	N
Subadult Ma	2	57	0	Y (to Gardiner)	N
Subadult Ne	3	9	59	Y	Y
Subadult Sa	5	57	36	Y (to Gardiner)	N
% of Subadult		Avg=38	Avg=45	83%	17%
Adult Bb	>6	31	0	N (in Gardiner)	N
Adult Ap	8	35	42	N	Y
Adult Ea	8	55	44	N	Y
Adult Fr	8	23	40	N	Y
Adult Ho	9	8	32	Y - before dying	Y
Adult Wa	7	53	82	Y	Y
Adult Zc	8	1	56	N	Y
% of Adult		Avg=29	Avg=42	29%	86%

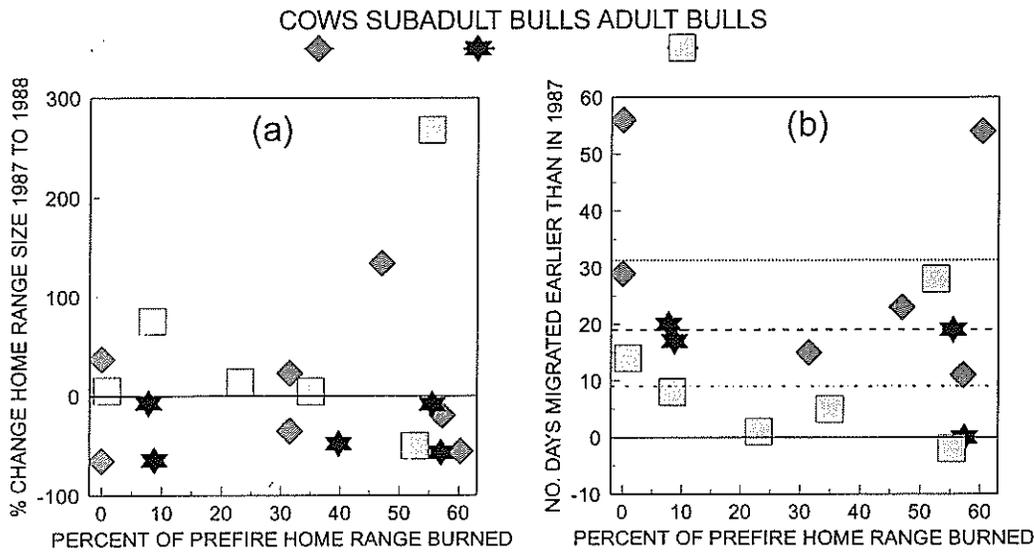


Figure 2. Short-term effects of fires on (a) percent change in summer home range size between 1987 and 1988 related to percent of prefire home range that burned and (b) number of days earlier in 1988 elk returned to the winter range compared to 1987 (early migration is positive, later is negative) related to the percent of the prefire home range that burned. Dotted and dashed horizontal lines in b represent means by sex-age classes.

The collared elk arrived on the northern winter range in 1987 an average of 16 days before snow began to accumulate on their respective summer ranges (range -12 [after snow fell] to 77 days before, $n = 18$, $sd = 23.1$). In 1988 this average was 29 days before snow began to accumulate (range -5 to 81, $n = 19$, $sd = 22.9$). In both years migration occurred significantly earlier than snowfall ($P < 0.01$ both years, $n = 18$ and 19; days before snow accumulation significantly greater than 0).

Because there was no difference in migration date between elk with $\leq 10\%$ of their home range burned ($n = 6$) and those with $> 50\%$ burned ($n = 7$), the earlier migrations were probably due to the severe drought of 1988 and not the fires. Morgantini and Hudson (1989) suggested that elk migrated from winter to summer range to access nutritious forage, though migrations from summer to winter range were induced by snow accumulation (Morgantini 1988). Fryxell and Sinclair (1988) felt that migrations were used to access high-quality food and/or reduce the risk of predation. High-elevation summer ranges usually accumulate enough snow to impede elk movements and deeply bury food, thus forcing elk to migrate. The collared elk in this study migrated before snowfall in 1987 and 1988, so cues other than snow were important in initiating movements from summer to winter range. Our findings of elk migrating prior to snowfall is in marked contrast to what has generally been reported. Garrott et al. (1987) found that mule deer migrated from summer to winter range before snowfall; they suggested that the cue to migration was photoperiod. Their deer migrated to winter range adjacent to irrigated, fertilized crops that were still green. In Garrott et al.'s (1987)

study, deer benefitted by migrating early to access higher quality forage on the winter range that had not senesced.

Grass production on Yellowstone's northern winter range was lower in 1988 than in 1987 due to the drought (Singer et al. 1989, D. Mattson, Pers. Comm., IGBST, Bozeman, MT), although Coughenour (1991) showed comparable or increased graminoid production between years at some winter range sites. The primary effect of the 1988 summer drought upon plant growth was early desiccation of forbs and grasses; plant phenology was hastened by two to three weeks compared to 1987. Collared elk began extensively feeding in forested areas two to three weeks earlier in 1988 than in 1987, a shift in habitat use we saw in 1987 after vegetation in open meadows cured. Edge et al. (1987) reported a shift in habitat use toward more forested stands as summer progressed that they suspected was related to plant phenology.

We cannot say precisely why elk migrated earlier in 1988, other than to speculate that it was due to early desiccation of vegetation caused by the drought, and would have occurred regardless of the fires. Woods (1991) found that over a three-year period marked elk in Banff National Park, Canada, migrated within 17 days of their migration date the previous year. Unfortunately other studies of Yellowstone elk have not given precise dates of migrations or expected variation in migration date. Skinner (1925) and Houston (1982), however, stated that Yellowstone elk fall migrations are initiated by snowfall, and as such, migration date would vary around the timing of snowfall. The points we make are that some

elk in Yellowstone migrate before snowfall and that in 1988 migrations occurred earlier than what is probably typical for Yellowstone elk. We suspect that elk migrated back to the winter range to find higher-quality forage in the form of perennial bunchgrasses, rather than feed on cured forbs on summer range.

Lovaas (1970) reported variation in hunter harvest of elk due to variation in timing of migration related to snowfall. Our data suggested that drought may also affect timing of elk migration. We suspect that variation in timing of migration resulting from drought-stressed summer ranges would alter elk accessibility and vulnerability to hunters. Early drought-induced migrations may affect hunter success and result in variable hunter harvest among years.

We observed the effects of fires on the movements of some individual elk. Three collared subadult bulls summering near each other (Indian Cr. to Roaring Mtn.) fled the advance of the North Fork fire that moved 14 km in one day (September 9). They had 56%, 57%, and 57% of their prefire home range burned. One bull moved 9 km from where he was located prior to the fire front passing in an attempt to flee. The fire caught up with and passed him. He then remained in the burned area outside his prefire home range for 12 days before moving back to it. Another bull moved at least 7 km from his prefire home range to escape the fires, rutted there, and then went back to his prefire home range after the rut and fed on regrowth in a burned meadow. The third bull moved more than 8 km from his prefire home range toward Mammoth and Gardiner, but did not return.

Although none of the radio-collared elk died, Singer et al. (1989) documented 246 fire-related elk mortalities resulting from the 1988 wildfires. Mortality occurred when fire fronts were more than 2 km wide and advances of 6 to 21 km per day. Most of the Yellowstone fires burned in mosaic patterns that provided escape patches from slow-moving fires and forage patches for post-fire use. Elk were often seen feeding near flames during the fires (Singer and Schullery 1989, Schullery 1989 and our observations). One radio-collared cow elk was observed feeding 75 m from active flames on 7 August, and five collared elk were observed using small unburned patches within extensive burns soon after the fire fronts had passed. These observations were similar to those of Gasaway and Dubois (1985) of moose using unburned "islands" inside a burn perimeter. The results showed no statistically detectable influence of the fires on the collared elk movements while they were on summer range. We conclude that few summer range movements resulted directly from the fires, and that when unusual movements occurred, they were mostly temporary. This is in agreement with the conclusions of Gasaway and Dubois (1985), Blanchard and Knight (1990) and Purcell et al. (1980). Our results indicated that short-term effects such as displacement and fire-caused mortality were minor

even in the large-scale Yellowstone fires and should not be important considerations governing decisions in land management prescriptions.

Winter 1988-1989

Winter 1988-1989 was the first winter after the fires. Fires burned 0% to 82% of individual ranges and did not differ among sex-age classes ($P = 0.11$, $n = 20$, power = 0.44), although cow ranges burned less than bull ranges (Table 1).

Twelve elk moved out of the home range area they occupied the previous two winters. Five cows moved (71%), 5 subadult bulls moved (83%), and two adult bulls moved (29%). Two subadult bulls moved to Gardiner, and 1 adult bull wintered in Gardiner, where they were supplementally fed hay. The two adult bulls moved less than 3 km from their home range and later died. The low proportion of adult bulls moving out of their home range indicated strong site fidelity despite having substantial portions of their range burned. Subadult bulls were more flexible in their response, with most moving toward areas that were less burned.

Mortality rates were highest for adult bulls, less for cows, and least for subadult bulls (Table 1). Stepwise logistic regression indicated that the probability of dying was related to animal age and proportion of winter home range burned; sex-age class, burning of summer home range, and whether they moved or not did not enter into the model. We had no index to animal condition prior to winter, but it was probably lower than the previous two years due to drought effects on plants. We suspect that poorer pre-winter condition also contributed to mortality of older-aged elk.

Winter diets during 1988-1989 differed significantly from the previous two winters ($P < 0.01$, $n = 49$). Postfire winter diets included less grasses and more trees than previous years (Figure 3). Postfire cow diets contained more grasses than bull diets ($P = 0.03$, $n = 26$). Because cow diets in 1988-1989 included more trees but a smaller proportion of their home range was burned than for bulls, dietary changes probably reflected both the effects of fire and weather on forage availability. We often observed elk feeding on charred lodgepole bark, bark and twigs of fallen aspen, and needles and twigs from fallen conifers (Douglas-fir, spruce, lodgepole pine). We speculate that elk fed on charred conifer bark primarily because it was the most abundant, available food source, but also because the charring volatilized phenolics which would typically make the conifer bark unpalatable to elk (Jakubas et al. 1994).

Postfire diet quality was poorer than in previous winters, being comprised of more indigestible fiber and lignin (Figure 4) reflecting the increase of trees in the diet. Neutral detergent fiber, acid detergent fiber, and lignin differed between pre and postfire periods ($P < 0.01$,

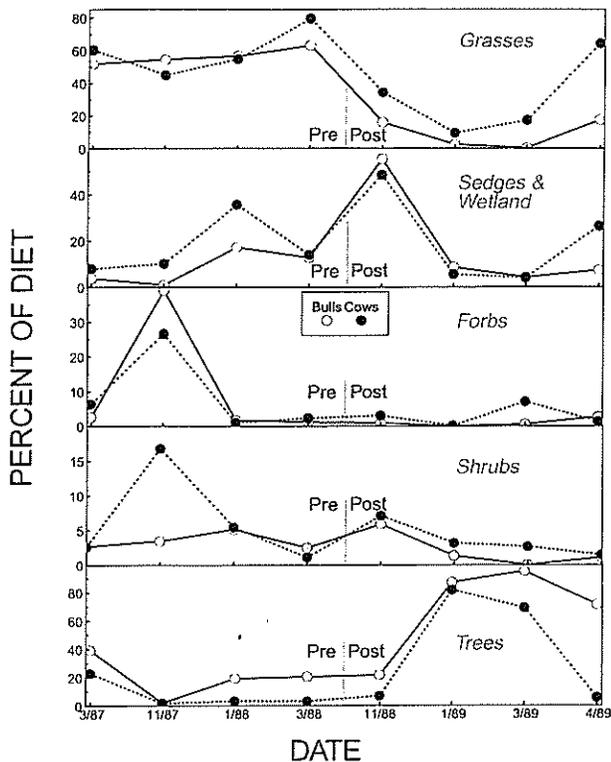


Figure 3. Bull and cow elk winter diet composition by forage classes determined from microhistological analysis of fecal samples.

$n = 63$), but not between the sexes ($P = 0.84$, $P = 0.40$, $P = 0.82$ respectively, $n = 63$, power = 0.04-0.13). Protein was similar pre (7.13%, $sd = 0.8143$, $n = 25$) and postfire (7.01%, $sd = 0.6085$, $n = 39$; $P = 0.54$, power = 0.09), but high fecal nitrogen postfire may not have indicated a comparable diet. The abundance of protein-binding tannins in the trees of postfire diets may have elevated fecal nitrogen levels (Mould and Robbins 1981, Robbins et al. 1987). We speculate that available dietary protein in postfire diets was much lower than the 7% indicated by the fecal analyses.

Animal activity was significantly lower during the winter 1988-1989 than the previous two years for all sex-age classes ($P < 0.01$, $n = 789$). Reductions in bull activity were greater than that observed for cow activity (Figure 5). The reduced activity was apparently influenced by temperatures in February averaging 6°C colder than previous winters (Figure 5). Animals reduce activity during winter to conserve energy (Moen 1976), but too little activity does not allow much time to feed. Activity may have been affected by animal condition - elk that were monitored prior to death showed a gradual, but continuous decline until death in amount of time spent active.

Summer 1989

In the summer of 1989 seven of the eight surviving elk used home ranges that contained burned areas (Table 2). Elk appeared to use burned habitats in proportion to their availability ($C^2 = 11.05$, $P = 0.09$, $n = 7$ elk, power = 0.88).

Conclusion

Our study suggested that elk responses to environmental disturbances were a complex function of animal age and sex, individual behavior, drought effects on forage phenology, quality, and abundance, and weather patterns. Elk were faced with formidable conditions during the winter 1988-1989 from the combined effects of drought on winter range forage abundance and quality, fires on winter range reducing forage supplies, high animal numbers competing for limited resources, and a winter of moderate severity. Reduced forage and early plant senescence during summer prevented some elk from accumulating enough fat reserves to survive the coming winter. Subadult bulls may not rut as hard as older bulls and thus may enter the winter in better

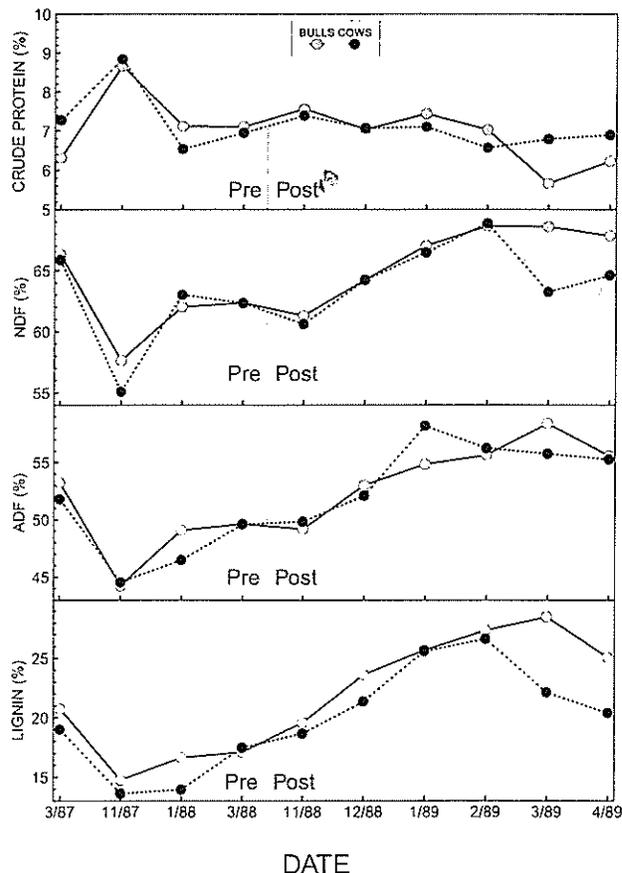


Figure 4. Bull and cow elk winter diet quality indexed by chemical analysis of fecal samples.

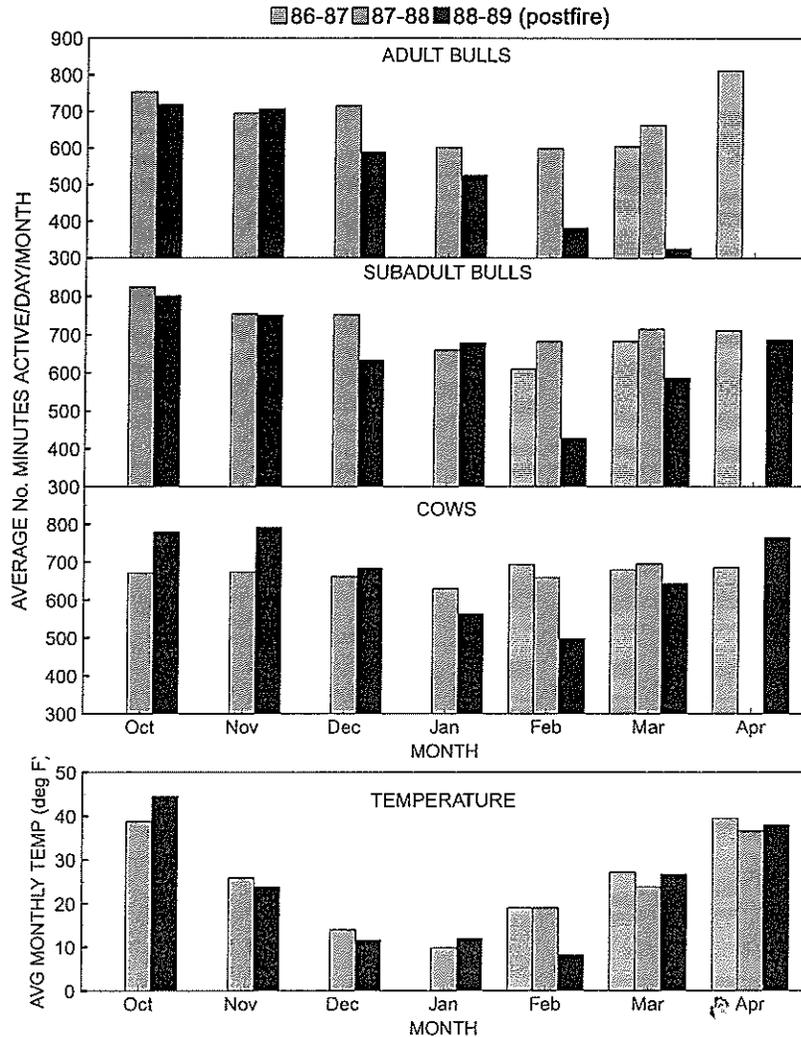


Figure 5. Winter activity patterns (average number of minutes active per individual monitored) by sex-age class and month (October to April), and average temperature for the same period.

Table 2. Elk use of burned areas during summer 1989.

Sex-Age	% 1989 Summer Home Range Burned "Available":	% 1989 Summer Locations in Burned Area "Use"	Use/Available
Cow Be	68	62	0.92
Cow Di	32	25	0.78
Cow Do	47	69	1.47
Subadult Ad	67	48	0.72
Subadult Ba	0	0	N/A
Subadult Is	20	33	0.82
Subadult Ma	61	50	0.82
Adult Sa	65	61	0.94

condition and have higher survival (Flook 1970). Subadult bulls are also more flexible in home range use permitting them to explore alternative areas when food becomes scarce.

Fire effects were confounded by summer drought effects in 1988 and prevent us from conclusively showing the effect of either environmental factor alone. Extensive summer drought and fires, however, will probably result

in earlier movement by elk back to winter range, poorer pre-winter body condition, lower summer and winter nutrition, and increased winter mortality.

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Yellowstone Elk Population Responses to Fire — A Comparison of Landscape Carrying Capacity and Spatial-Dynamic Ecosystem Modeling Approaches

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Abstract. We used two modeling approaches to examine 1988 fires effects on elk population dynamics, in the winter following the fire, the first three post-fire years and over the long-term. A nutritionally based landscape carrying capacity model (LCCM) indicated that the fires would have little impact in the first winter or the following few years. Over the longer term, the model indicated that the winter range might eventually support 15% more elk and the summer range might support 60% more elk, however both responses would decay over a period of two to three decades as forest canopies regenerate. Winter range was more limiting than summer range. A spatial-dynamic model (SAVANNA) was parameterized to demonstrate the capabilities of ecosystem modeling. The LCCM and ecosystem models provided similar results in the short term - there were negligible fire effects on simulated elk populations in the first few years. Using a historical weather sequence, the ecosystem model predicted an initial drop in elk population size after the fire of 5-10%, followed by recovery after five years, reaching 10-15% higher levels 15-25 years post fire. Confidences in long-term LCCM and ecosystem model predictions were limited by information about long-term herbaceous plant responses to fires of different severities, particularly in sagebrush and forest understories. More information is also needed about the effects of snow and available biomass on winter elk foraging. Spatially explicit ecosystem modeling appeared to provide a more comprehensive and realistic approach to analyses of elk-vegetation-fire interactions compared to nutritionally-based or population-based modeling approaches, but further work is needed to bring it to its potential predictive capacity.

Keywords: Elk; Modeling; Population dynamics.

Introduction

The northern Yellowstone elk herd is hypothesized to be food-limited, particularly during the winter when snow

forces the herd to concentrate onto low-elevation winter ranges (Cole 1976, Barmore 1980, Houston 1982, Boyce and Merrill 1991, Coughenour 1994, Coughenour and Singer 1995). Fire potentially alters the degree of food limitation of the elk herd, through its manifold impacts on vegetation and other ecosystem processes. Therefore, the processes and the extent of food limitation must be quantified to assess fire impacts on the population.

The immediate effect of fire is a loss of forage. Thus during the first winter after the fires there was concern that the elk would be severely stressed by the loss of forage in the fires. Although winter feeding was suggested, this was immediately dismissed as inappropriate (Christiansen et al. 1989). Elk moved onto winter ranges 4-6 weeks early in 1988, and more elk migrated out of the park than in prior winters (Singer et al. 1989). The herd declined by about 40% over the winter of 1988/89, however about 37% of the decrease was due to an especially large offtake by hunters (Singer et al. 1989). Other factors could have contributed to the die-off. The drought of 1987-1988 could have reduced winter forage supplies. Deep snows could have reduced foraging area (Farnes 1996) and forage intake rates. Finally, the relatively large herd size could have heightened competition for available forage. A complete assessment must consequently disentangle the effects of snow, fire, and drought in terms of their impacts on forage intake and subsequent mortality.

Over the longer term, fires could improve elk habitats, and thus herd sizes. (Boyce and Merrill 1991). The primary effect of fire, of course, is to convert forests with closed canopies to earlier successional stages dominated by herbaceous plants. There is abundant evidence that there is less forage biomass under closed forest canopies (Basile and Jensen 1971, Collins and Austin 1978, Irwin and Peek 1983, Crouch 1986, Scotter 1980). In Glacier National Park, for example, fires created more favorable habitats comprised of young conifer stands and mosaics of shrub and conifer communities (Martinka 1974). At a

larger scale, elk populations declined in much of the Rocky Mountain region over the last 50-70 years due to fire suppression (Scotter 1980). Elk herds expanded in Idaho after the 1910 fires, when burned forests were converted to shrub and brushfields with more abundant browse (Leege 1968). But, as forests regenerated, elk numbers decreased.

The northern Yellowstone elk herd (Houston 1982) is currently comprised of about 20,000 animals that winter in the low-lying valleys of the upper Lamar and Yellowstone Rivers. Most of the winter range is contained in the northern portion of Yellowstone National Park (71%), while the remainder lies just outside of the northern park boundary. Lodgepole and other pine and spruce-fir forests cover 25% of the winter range, Douglas fir covers 20% and the remaining 45% is open grassland and sagebrush grassland. Approximately 283 km² or 20% of the 1,400 km² winter range burned in 1988. This included about 137 km² or 20% of the sagebrush/grasslands and meadows and 146 km² or 23% of the forested areas.

The impacts of forest fires on elk forage supply are confounded by elevation. Most of the higher portions of the winter range are forested, while most of the lower portions are non-forested. As snows are deeper at higher elevations, the benefits of forest burning on forage supply may be significantly offset by the low availability, especially during severe winters when snow greatly reduces the size of the winter range and elk foraging efficiency.

About 30% of the ~5,100 km² summer range of the northern herd (as delimited by Houston [1982]) burned. However, only 124 km² or 15% of the 830 km² of meadows and sagebrush/grasslands burned in comparison to 1,500 km² or 35% of the forests. The degree of summer range limitation of herd size in Yellowstone has not been evaluated, so it is difficult to predict the consequences of summer range fires. While conditions for foraging are obviously worse during winter, summer foraging determines stored energy (fat) reserves which are important for winter survival. Thus summer ranges could be more limiting than winter ranges if they are relatively small or unproductive.

The objective of this research was to assess the potential effects of the 1988 fires on the "carrying capacity" of winter and summer elk ranges over the short and long-term. The primary approach to this problem is to link a dynamic carrying capacity model with a geographic information system to calculate total energy and nitrogen transfer to the elk herd (Coughenour 1994). We also evaluate the potential for using a more complex, spatially explicit ecosystem model. We point out limitations in current knowledge, and suggest research that would lead to improved understanding of elk-vegetation-fire interactions.

Methods

Comparison of Methods to Estimate Carrying Capacity

Carrying capacity (K) can be derived in several different ways (Caughley 1979, McNab 1985, Coughenour and Singer 1991). (1) "Management" K could be defined as the maximum number of animals to maintain a certain vegetation composition, or other management objective. (2) "Ecological" K can be defined as the size of the animal population when it is at equilibrium with its food supply (Caughley 1979). Equilibrium population size can be derived from empirical relationships between population growth rate and population size (eg. Houston 1982). Boyce (1990) and Boyce and Merrill (1991) relaxed the equilibrium assumption by effectively making K a function of variable weather. (3) "Nutritionally-based" K is the number of animals that can be supported with the available food supply, and can be estimated by dividing forage production (kg) by animal forage requirement (kg/animal) (eg. Hobbs et al. 1982). The area available for foraging varies with snow cover, and the amount of forage per available area varies with precipitation. Consequently, northern elk winter range K varies among years in response to precipitation and the severity of the winter (Coughenour 1994). Nutritionally-based K does not predict how populations will respond to variable K. However, survival rates have been computed by dynamically simulating mean animal energetic status, and applying a statistical relationship between mean energy status and the population survival rate (Hobbs 1989, Coughenour 1994). (4) An "ecosystem modeling" approach to K links nutritional and population approaches. In principle, this was the approach embodied by applying simple predator-prey models to herbivore-plant systems (Caughley 1976), but increased realism is achieved by modeling plant growth responses to weather, landscape variation, and herbivory; herbivore spatial distribution and forage intake rate responses to forage and snow cover; herbivore energetic status, and; consequent ungulate population responses.

In this analysis, we use a spatial-dynamic implementation of a nutritionally-based carrying capacity model (Coughenour 1994), and then demonstrate the potentials of a spatial-dynamic ecosystem modeling approach to K.

Landscape Carrying Capacity Model

Overview

The effects of the 1988 fires on short and long term population dynamics were assessed with a landscape carrying capacity model (Figure 1). This model provides a nutritionally-based estimate of the number of animals that can meet their energy and nitrogen requirements on either the winter or the summer range given the abun-

Landscape Carrying Capacity Model

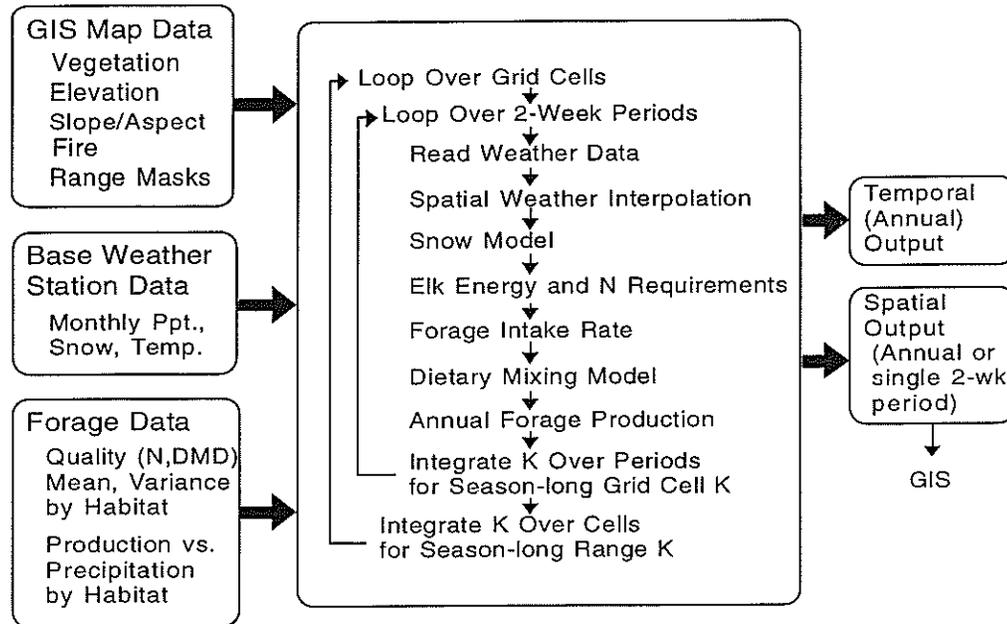


Figure 1. The landscape carrying capacity model.

dance, distribution and quality of the forage. Winter carrying capacity is strongly affected by snow depth and distribution.

Weather and Snow

Precipitation and snowfall were estimated from monthly data collected at five base weather stations (Mammoth, Gardiner, Tower, Cooke City, Lake). Station data are spatially interpolated to derive estimates for each grid-cell. Estimates are corrected for elevation using monthly regressions of precipitation on elevation (Coughenour 1992). Snow is added to the snowpack and it melts at a rate proportional to temperature. Snow model output consists of monthly maps of snow depth on the winter or summer range. Snow depth maps showed characteristic patterns of deeper and longer-lasting snows at higher elevations and in more severe winters.

Elk Ranges

The maximum extent of the winter range of the northern herd was delimited by entering locations of elk group sightings during aerial winter censuses into the GIS. The outermost locations of the sightings were connected to form a polygon of 1,400 km², which is considerably larger than the 1,000 km² winter range size estimated earlier (Houston 1982). Within the maximum extent, the actual winter range extent varies among two-week periods and years in the model in response to simulated snow cover. The model effectively removes burned areas from the range extent where forage is completely lost to fire. The summer range extent was roughly the area proposed by Houston (1982, Figure 4.2),

which encompasses about 4,900 km². Calculations were performed for each of the 5,605 25-ha grid-cells on the winter range or 19,178 25-ha grid-cells on the summer range.

Forage Production

Total forage production is calculated on an annual basis for each habitat, based upon water-year precipitation. Snow depth, elk energy requirements and forage intake rates are calculated for two-week periods over the winter or summer season. Spatial variation in forage supply and weather are calculated from digitally mapped data residing in a geographic information system (GIS). The Yellowstone N.P. GIS data base includes the habitat and vegetation cover maps of Despain (1990), topography, geology, roads, streams, annual precipitation, 1988 fires, and other data encoded as maps of 50m x 50m grid cells. For modeling purposes these data were converted to 500m x 500m grid cells. The habitat map was simplified into 11 functional types: (1) dry Douglas fir, (2) moist Douglas fir, (3) wet forests, (4) predominately lodgepole-pine forests with *Vaccinium* dominated understories, (5) lodgepole forests with other types of understories, (6) xeric, (7) dry and (8) mesic sagebrush/grassland, (9) sedge meadow, (10) hairgrass meadow, and (11) the dry valley grasslands near Gardiner.

Forage production responses to water year precipitation in sagebrush/grasslands were estimated from a linear regression model ($r^2=0.32$, $p<0.0001$, $n=25$) developed from data collected over 18 years between 1935-1950 and 1986-1989 in many different studies (Houston 1982, Coughenour 1991, Frank and McNaughton 1992). Mean

production on upper winter range sites was 67 g/m². Regression model predictions were adjusted for other habitat types using empirical scalars, since there were insufficient data to derive precipitation regressions for each. Douglas fir understories are about 65% as productive as sagebrush/grasslands (Houston 1982, Norland and Singer 1994, Singer, Coughenour et al. unpubl. ms.). Lodgepole pine forest understories are about 30% as productive as dry meadows (Basile 1975, Collins and Austin 1978). Hairgrass and sedge meadows produce about 2.5x and 4.5x times more production than sagebrush/grasslands, respectively (Houston 1982, Frank and McNaughton 1992, Mueggler and Stewart 1980). Forage responses to fire are explained below.

Responses of Forage to Fire

A digital map of the 1988 fires was read into the model to delimit burned and unburned areas. Fire impacts on forage were applied to burned grid-cells.

The immediate effect of the fire was a loss of forage in the winter of 1988/89. Forage biomass in burned grid-cells was set to zero that winter. Subsequent short-term responses to the fire were mostly based on studies conducted between 1989-1991 (F. Singer and J. Norland, unpubl. data, Singer, Coughenour et al. unpubl. ms., Singer and Harter 1995). In the summer of 1989, there was 77% as much forage on burned as on unburned sagebrush/grasslands, while in 1990 burned forage production was 90% of unburned. We hypothesized complete recovery by summer of 1991, in accordance with findings of Antos et al. (1983) and Hobbs and Spowart (1984). In Douglas fir understory there was 43% as much forage on burned as on unburned sites in 1989 (mean of lightly and moderately burned sites) and 70% as much on burned sites as on unburned sites in 1990 (Singer, Coughenour et al. unpubl. ms.). In the lodgepole pine understory there was 29% as much forage on burned as on unburned sites in 1990, and 70% as much in 1991. On a mesic summer range meadow, forage mass on a burned site was 112% of that on an unburned site in 1991. We hypothesized that burned and unburned productivities would be equal in the third post-fire year in all habitats.

We based our hypotheses of longer term responses on observations from similar systems elsewhere. Long-term responses result initially from an increase in basal cover, number of plants, and sizes of perennial plants over years. Later, it is influenced by the reestablishment of tree canopies. Thus, it is related to vegetal succession. We estimated that forage production would increase by 20% on burned sagebrush grasslands after a decade based on forage productivities of habitats with and without sagebrush (Mueggler and Stewart 1980). Forage production will then decrease to prefire levels after 25 years of sagebrush regrowth. Although Crouch (1986) found that understory production in thinned lodgepole stands equaled

or surpassed that in unthinned stands in year two and had doubled in year five in stands thinned to 17% tree cover, we modeled a gradual increase to a maximal three-fold stimulation of understory production in burned subalpine forest by year 11, and a decrease to pre-fire levels by year 25 (Basile 1975). In Douglas fir burned understory, we gradually increased forage production to 154% of that in unburned understories in year 11.

Changes in forage quality were based on sampling during summers of 1989-90 and winters of 1990/91 and 1991/92 (Singer, Coughenour et al. unpubl. ms.). Within winter feeding craters, dry matter digestibility (DMD) was lower in burned than unburned Douglas fir, but was unaffected in sagebrush/grassland. There were no fire effects on protein. Fire had few impacts on winter forage quality outside of feeding craters in 1990/91 - protein was slightly lower on burned than unburned sedge meadows, DMD was lower in burned than unburned lodgepole pine, moist Douglas fir understory and xeric sagebrush/grassland. In feeding craters, protein was higher in burned sagebrush/grassland and Douglas fir, while DMD was higher under burned Douglas fir. Fall forage qualities were higher in burned winter range grasses in 1989 and 1990. In summer, protein and DMD concentrations were higher in burned than unburned lodgepole pine understories in 1989 and 1990. On a summer range moist meadow, protein was elevated in 1989 but DMD was unaffected. Generalized short-term fire impacts were developed for each habitat based on these data. We assumed there were no fire impacts on forage qualities in unforested habitats after three years (e.g. Hobbs and Spowart 1984). Normal frequency distributions of forage N and DMD were generated for the dietary mixing model from observed means and variances.

Elk Energetics and Foraging

Elk energy requirements are derived from equations for thermoregulatory costs (Parker and Robbins 1985), travel costs as a function of snow depth (Parker et al. 1984), and gestation (Hobbs 1989, Robbins 1983), after Hobbs (1989). The equations were parameterized for elk from values published in the literature. Costs are calculated in terms of kcal per animal per minute, and these are multiplied by time spent in different activities. Seasonal activity budgets were based on data of Craighead et al. (1972). Although activity patterns vary in response to weather and location, the seasonal activity data captures much of the variation and a detailed behavior model was beyond our objectives.

Energy reserves are depleted during the winter and replenished during the summer. For winter model runs, energy reserves are subtracted from demands. For summer runs, energy reserves must be added to total demands. Maximum fat reserves of 16% and 11% of body weight were assumed for cows and bulls based on data

from deer and elk (Torbit et al. 1988, Schwartz et al. 1988, Cassier and Able 1990). Fat reserves were assumed to be normally distributed in the population with a coefficient of variation of 0.21, and individual animals were assumed to die when 67% of their reserves are depleted (Torbit et al. 1985, Hobbs 1989). Based on this distribution, a mean depletion of 26% of total reserves would result in about an 10% overwinter mortality rate. This would be a reasonable long-term mean annual mortality rate for adult elk (Houston 1982, Coughenour and Singer 1995). For example, mean mortality rates of cows aged 1-20 is 0.072, and for bulls aged 1-14 it is 0.21 (Houston 1982, Tables 5.8,5.9). If bull:cow ratio is 25, the mean adult mortality rate is 0.1.

Calculated energy requirements ranged between 42 and 52 kcal/kg/d on the entire winter range, with a mean of 43 kcal/kg/d. On snow depths that are more likely to be used by the elk, energy requirements were only 40-42 kcal/kg/d. Total requirements for the mean 254 kg animal in winter ranged between 10,414 and 10,922 kcal/d over winter. During summer, requirements were only 38-39 kcal/kg/d, including the energy needed to replenish reserves.

Nitrogen requirements are calculated after Hobbs et al. (1982). Metabolic fecal nitrogen requirements are proportional to forage intake rate. Endogenous urinary nitrogen requirements are scaled to metabolic body weight.

The effect of forage quality on elk carrying capacity is calculated using the dietary mixing model of Hobbs and Swift (1985). Forage energy contents (%DMD) and protein contents are assumed to be normally distributed based on observed means and standard deviations in different habitats and seasons (Singer, Coughenour et al. unpubl. ms.). The mixing algorithm progressively adds forage quality classes to the diet beginning with the highest quality items until the quality of the mix just satisfies requirement. The quality of the mix must increase as forage intake rate declines, thus reducing the fraction of plant tissues that can meet elk requirements.

Forage intake rate was allowed to vary in response to forage density and snow depth. Hobbs (1982) used a fixed intake rate, which was appropriate since that model was static. Coughenour (1994) used a fixed intake rate in the dynamic model, but estimates of K were inflated. Modeled intake rate increases asymptotically with forage biomass in a Type-II functional response, parameterized with data of Collins and Austin (1978), Wickstrom et al. (1984), and Hudson and Watkins (1986). Available forage is reduced by increasing snow depth according to a function suggested by Cassier and Ables (1990).

Carrying Capacity

Each season, carrying capacity is estimated from the mean animal days per ha (*Andha*) that can be supported

in each grid-cell (*nc*) in each two-week period (*np*) during the season, which is

$$Andha_{nc,np} = \text{Min} \left[\frac{Tfore}{Frate_{day}}, \frac{TforN}{Frate_{day}} \right] \times 10^4$$

where *Tfore* and *TforN* are total g/m² of forage that meet energy and nitrogen requirements respectively, at a daily forage intake rate of *Frate_{day}* g/d/animal and where 10⁴ is m²/ha.

The number of elk that can be supported that year is

$$\text{Elk} = \frac{Andha_{mn} \times Ha}{Days_{mn}}$$

where *Andha_{mn}* is mean animal-days per ha supportable over all grid-cells and all two-week periods, *Ha* is total ha on the seasonal range, and *Days_{mn}* is number of days in the season.

The number of elk that could be supported on winter or summer ranges was calculated for each year 1968-2012. Observed weather data were used over the period 1968-1991. After 1991, weather years were chosen at random from the 1968-1992 data set. Six runs of the model were conducted on winter and summer range using different random weather sequences 1992-2012; three with fires in 1988 and three without fires in 1988.

Spatial-Dynamic Ecosystem Modeling

An ecosystem model was used to make provisional predictions of elk population responses to forage supply and the 1988 fires. The SAVANNA model (Coughenour 1992, 1993) simulates ecosystem processes that influence plant-ungulate interactions (Figure 2). Ecosystem dynamics are simulated on a weekly basis over 5-100 year time spans. Grid-cells on the landscape are simulated in parallel, so organisms, as well as water or other materials can move or be spatially redistributed during a model run. Spatial (GIS) data are converted to model inputs at the beginning of a simulation. Spatial model output are passed to a GIS for display and analyses. A preliminary parameterization of the SAVANNA model was developed for the total annual range of the northern Yellowstone elk herd. The annual range was divided into 1,650 2 km x 2 km grid-cells. Coniferous trees, open herbaceous plants, understory herbaceous plants, and shrubs were simulated.

Weather data are converted to dynamic maps using topographically corrected spatial interpolation. The water balance on each grid-cell is simulated: including precipitation, runoff, infiltration, evapotranspiration, snow accumulation and snowmelt. Available soil moisture affects plant growth rate, along with temperature, light and

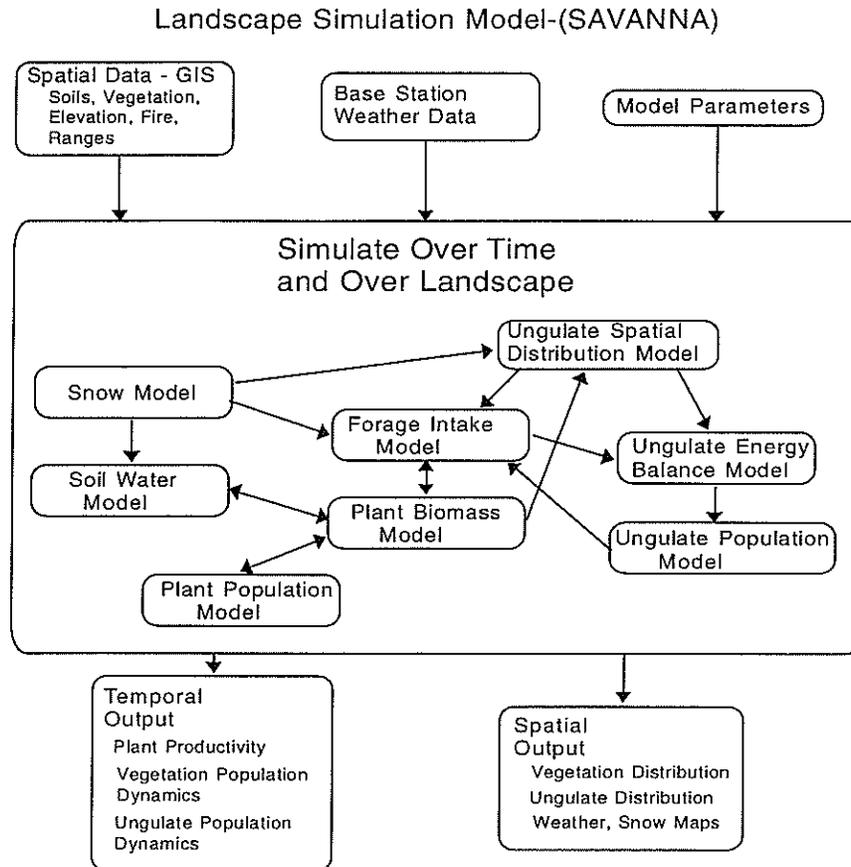


Figure 2. The SAVANNA spatial-dynamic ecosystem model.

herbivory. Plant growth is partitioned above and belowground. When aboveground plant tissues senesce, they are transferred to litter and become unavailable to herbivores. Nitrogen is taken up by roots and distributed in the plant. Leaf N concentration declines with advancing phenology.

A tree population model represents establishment, transfer among size classes, and mortality. Tree number and size dynamics determine tree cover on the landscape. Trees affect herbaceous understories through competition for light and water. Competition between trees and grasses only occurs on those portions of grid-cells where trees are rooted.

Elk are distributed over the simulated landscape in response to forage, snow, topography and tree cover on a monthly basis. Forage intake in each grid-cell depends upon forage biomass in the functional response, as well as snow depth. The energy balance of the mean animal in the population is simulated as the difference between energy intake and energy expenditures. Resultant mean body weight is converted to an index of animal condition, which then affects reproduction and survival. Elk population dynamics are simulated with a simple age/sex class model. This scheme provides an explicit and mechanistic

linkage from spatially and temporally variable forage abundance to elk population responses. Resultant elk herbivory affects plant growth and vegetation dynamics.

The 1988 fires map was read into the model and fire impacts were simulated for each plant functional group in each fire intensity class. Parameterized fire responses included fractions of aboveground tissues lost and fractions of plants that died in each fire severity class. Subsequent plant growth after the fire was affected by changes in tree cover, which increased light and water in former understory. Decreased shrub cover also provided more opportunities for herbaceous plant growth. Trees reestablished through seedlings, with subsequent increases in tree size and stand thinning.

Results

Landscape Carrying Capacity Modeling

Simulated forage biomass varied with annual precipitation between 37 and 81 g/m² on the winter range (66±8 g/m²) and 37-73 g/m² on the summer range (55±8 g/m²). Forage was less abundant on the summer range due to

greater forest cover. Burning decreased sagebrush/grassland production during the first two post-fire years and decreased forage production in simulated forest understories for the first three post-fire years. Subsequently, forage biomass was stimulated by burning -maximally in the 11th post-fire year. Sedge meadow production was not affected in the first year. It was stimulated in the next two years, and there were no fire effects after that. Forage biomass returned to unburned levels by the 25th post-fire year in all habitats. The fires enhanced total forage on the winter range by about 30% in the 11th post-fire year (1999), and by over 20% between 1994-2001.

Only a fraction of the total forage biomass could meet elk energy or nitrogen requirements, given the forage quality distribution on the range and the forage intake rate of the elk. Energy was always more limiting than nitrogen in that the supply of forage with sufficiently high energy content was smaller than the supply of forage with sufficiently high N content ($I_{fore} < I_{forN}$).

Model calculations indicated that the fires had little effect on winter or summer range carrying capacities in the year of the fire (Figure 3a). In the first three post-fire years winter range K was essentially unaffected, while the fires decreased summer range K by 4-8% (Figure 3b). In the first winter after the fire (1988/89), the model indicated that drought reduced total forage biomass to 37 g/m², or 56% of the long-term mean. The 1988 fires reduced total forage biomass on the winter range by another 20%. However, the fraction of total forage that could meet elk energy requirements with only 10% mortality that winter was very low - about 10%. This was a consequence of two factors. The functional response predicted a low forage intake rate that winter in response to low forage biomass densities and heavy snows reduced forage intake rates further. Given the resultant low forage intake rates, high forage energy contents were needed for elk to meet their energetic requirements. After accounting for these stresses, the fires only reduced the supply of adequate quality forage by an additional 12%.

The model indicated that the 1988 fires had little effect on winter range carrying capacity in post-fire winters 1989/90-1991/92 (Figure 3a). However the 1988 fires gradually increased carrying capacity until the 11th post-fire year, when the total stimulation was 16%. Fires depressed summer range K by 8% during the first two summers after the fires (Figure 3b). An increase in summer range K of over 62% was predicted by the 11th year post-fire. Winter and summer range K's decreased to unburned levels by the 25th year post-fire.

Estimates of winter and summer range K's made with the current version of the LCCM were considerably lower than those made with an earlier version (Coughenour 1994). Lower estimates were due to two changes in model assumptions. First, forage intake rate in the earlier version was set at a fixed value, as elsewhere (Hobbs et al. 1982, Hobbs and Swift 1985). In the current version, intake rate

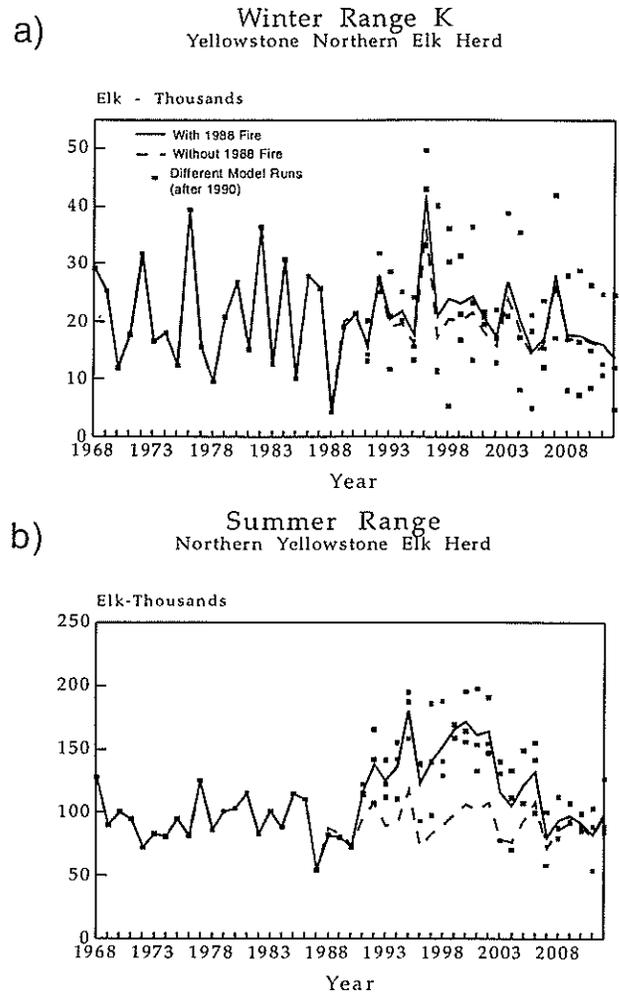


Figure 3. Carrying capacity model output for (a) winter range and (b) summer range; number of elk that can meet energy requirements while maintaining an adult mortality rate of 10%. Three burned and three unburned simulations were conducted in which weather years were randomly selected from 1968-1991 weather data during 1992-2011. Lines during 1968-1991 represent the means of three stochastic simulations.

is affected by forage biomass, so low production habitats, like lodgepole pine, support fewer elk the current model. Second, available forage biomass on any land area declines gradually from 25 cm to 50 cm of snow in the current model, while a simple threshold of 40 cm depth was used to exclude land area earlier. The decreased forage biomass then enters into the functional response.

Populations would be more likely to reflect winter rather than summer range responses to the fires, since winter range appears to be more limiting. Summer range K's would appear to be about 4 times greater than winter range K's on average. Energy-limited forage comprised about 60% of total forage. Conservatively, if the 60% was limited to a few species or the most productive plant tissues, then perhaps 50% of the 60% offtake would be sustainable. The summer range is shared with about 5,000 elk from three other herds, and perhaps 2,000-2,500

bison. Offtake from other herbivores like small mammals is unknown. Assuming an allowable use factor of 50% of the forage, the summer range may sustain about 50,000 elk. After subtracting at least 9,000-10,000 elk equivalents from other herds, this reduces the number to nearly 40,000 for the northern herd, which is still 1.6x mean winter range K. Furthermore, winter range K is much more variable than summer range K, due to the variability of winter weather. Periodic severe winters are highly limiting "bottlenecks" for the population.

Ecosystem Modeling

The level of verification achieved for most aspects of model behavior was judged sufficient for the model to be used for demonstration purposes here. Further parameterization would be required to use the model as predictive tool. The preliminary parameterization produced reasonable simulations of herb, shrub and tree biomass and population dynamics values fell within observed ranges, and the model responded realistically to weather, herbivory and fire.

The model successfully simulated population dynamics 1968-1991 (Figure 4a). The gradual increase after cessation of artificial herd reductions in 1968 was adequately simulated, indicating that long-term population recovery rate was correctly represented. The population ceased its growth with a die-off in winter 1975/76. The die-off was caused by reduced winter range area and negative effects of snow on forage intake rate. The simulated population grew again in 1977-78, followed by another winter die-off in 1978/79. The pattern was repeated a third time, ending in a die-off in winter 1981/82. During 1974-84, the population fluctuated around 15,000, which is the carrying capacity that was estimated using population data from 1968-1978 (Houston 1982, Boyce and Merrill 1991). However, the population gradually recovered from the three die-offs after 1980, growing to a transient high of over 25,000. The large die-off in winter of 1988/89 was correctly simulated. The magnitude of the predicted die-off corresponded with the sightability-corrected estimates of 22,000 elk in January and 13,000 elk in April 1989 (Singer, Coughenour et al. unpubl. ms.).

There was essentially no difference between with-fire and without-fire simulations with respect to elk population dynamics through 1991 (Figure 4b). Immediately after the fire in fall-winter 1988, the model simulated a 17% drop in forage biomass. During January-April there was a substantial transfer of standing dead forage to litter. Forage was below normal due to drought, and this was exacerbated by the transfer to litter. Deep snow conditions further contributed to reduced intake. Snow concentrated elk onto low elevations where there was intense competition for available forage. Reduced forage intake

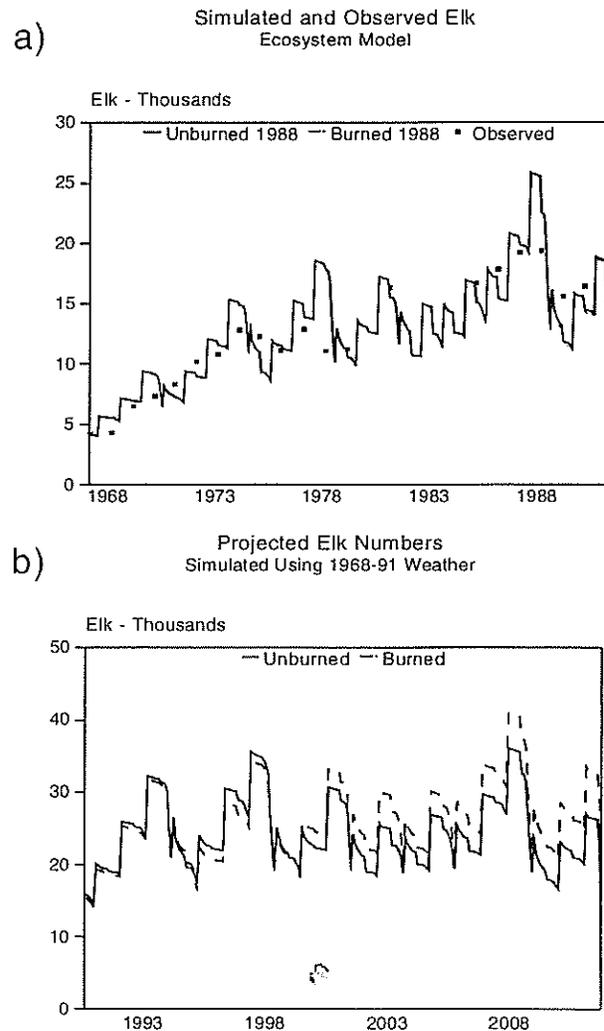


Figure 4. (a) Ecosystem model prediction of elk population dynamics 1968-1991, with and without fires in 1988. Observed data are calculated elk population sizes in early October, prior to annual hunts. (b) Ecosystem model predictions of elk population dynamics for 1992-2011 using 1972-1991 weather data (preliminary parameterization).

caused rapid weight loss, which resulted in a high rate of mortality.

The dynamics of the northern Yellowstone elk herd were simulated over the following 21 years, with and without fires in 1988 (Figure 4b) using 1972-1992 weather data. Many of the same dynamics occurred in the 1992-2011 and 1968-1992 simulations, which was a result of using the same weather sequence. The model simulated slightly depressed herd sizes in the first decade after the fire. It was not until then that elk herd size in the burned scenario surpassed that in the unburned scenario. The herd remained about 10% higher in the burned scenario for the duration of the simulation. Herd size fluctuated, but the long-term trend was a leveling off at a mean of

about 25,000 animals. If this were to be taken as the effective carrying capacity, it would be concordant with both the nutrition- and population-oriented definitions of the term.

Discussion

Landscape carrying capacity (LCCM) and ecosystem modeling results both indicated that the winter 1988/89 die-off was mainly a result of the combined effects of drought and deep snow. Loss of forage due to burning 20% of the winter range probably increased elk mortality by less than 5%. Much of the burned winter range was situated at disproportionately high elevations. Deeper snows at higher elevations drove elk down to less fire-impacted portions of the landscape. The effects of drought on elk were larger than the effects on plants. While drought reduced forage mass to 56% of the long-term mean, forage intake rate was reduced more, due to the non-linear shape of the foraging functional response. Heavy snows further reduced effective forage biomass density.

Another experiment with the LCCM indicated that the 1988/89 snow alone would have caused a 50% drop in K without fire, and a 48% drop with fire (Singer, Coughenour et al. unpubl. ms.). Drought alone reduced K's to 32-34% of the values with no drought or severe winter weather. Drought and severe winter weather together resulted in K's that were 16-18% as high as K with neither factor. Fire alone reduced K's to 80-84% of the values with no fire. Since K was reduced so greatly by drought and winter weather, the added effect of fire was negligible.

Although drought and fire are correlated, it was coincidental that deep and hardened snow and drought occurred during the same year. The result was a uncommonly large die-off, probably similar in magnitude to the one observed in the winter of 1919/20, which was also preceded by drought (Houston 1982). However, the ecosystem model suggested that the herd will return to pre-fire levels within 6-7 years. After that, the herd was predicted to fluctuate between 20,000-35,000 elk.

The LCCM and the ecosystem models both suggested that the 1988 fires would have little impact on the herd in the first three post-fire years. This was mainly due to the rapid recovery of herbaceous vegetation on non-forested habitats on the winter range (Singer, Coughenour et al. unpubl. ms., Singer and Harter 1994). Antos et al. (1983) documented a similar rapid recovery after fire. Late summer fires generally cause much less plant mortality than early season fires (Wright and Klemmedson 1965, Owensby and Anderson 1967). While forage was slightly depressed on burned sagebrush/grasslands in the first two years, less than 20% of these habitats burned. The depression was greater in burned forests, but these

habitats have little forage value. Greater fractions of the summer range burned, but summer range appears to be much less limiting to the elk herd.

After three years, both models predicted small increases in herd size. The magnitude and dynamics of these responses were strongly influenced by modeled vegetation responses to the fires, particularly forest understory regrowth, and the rate of forest canopy regeneration. Although the carrying capacity model represented a three-fold increase in forage production in burned lodgepole pine, winter K increased by only 5-10% (Figure 3a). Burned lodgepole pine comprised only about 10% of the winter range, and the most of the burned area was situated in areas of deeper snow. Furthermore, forage biomass was very low to begin with. Thus, the net effect of the fires was small. The increase in summer range K was much larger because burned forest comprised a much larger fraction of the summer range, and there were no confounding effects of elevation or snow.

The models differed in their predictions of the rate of return to pre-fire conditions. The carrying capacity model represented a peak response in 11 years, based on observations of Basile (1975). The ecosystem model response had not peaked after 25 years. For the first 50 years following fire, lodgepole pine forests are expected to remain relatively open and sunny, which will elevate herbaceous productivity (Romme and Despain 1989). Canopy closure is expected between 50-150 years post-fire. However, some forests could become permanent meadows where conditions are marginal for tree growth (Stahelin 1943, Knight and Wallace 1989).

Long-term predictions of elk population responses to fire were clearly limited by a lack of vegetation fire response data. The effects of fire on sagebrush/grasslands depends on herbaceous responses to sagebrush removal and sagebrush regeneration rate, yet neither is well understood. Forest understory production has received very little study apart from a few studies that have been conducted in patch-cut and clear-cut lodgepole pine forests in Montana (Basile and Jensen 1971) and Colorado (Crouch 1986). Long-term responses of herbaceous plants to forest canopy burning seem to be very poorly known. Thus, further understanding of the long-term responses of elk populations to the 1988 fires will require long-term studies of forage production on burned and unburned habitats, particularly forests and sagebrush stands.

Plant responses to fire are highly variable with burn intensity. Ideally, a fire severity map could be used to predict these variations. Unfortunately, we were not aware of any data which demonstrated differences in herbaceous plant responses in different fire severity classes. Thus, it would be useful in future studies to collect these data 1-3 years post fire. It would still be worthwhile to document responses to different fire severities 10 years post fire.

Predictions of elk population responses to fire were also limited by information about elk forage intake processes. Both models were quite sensitive to forage intake rate responses to forage biomass and snow depth during winter. There have been few, if any, studies of elk foraging during winter, especially of snow impacts on forage intake rate.

The combined approach of landscape carrying capacity and spatially explicit ecosystem modeling provided quantitative and explanatory predictions, and identified important knowledge gaps. The ecosystem modeling approach unified the nutritional and population approaches to carrying capacity: linkages between forage abundance, forage intake, energy balance, and population response were explicit. Feedback effects of herbivory on plants were modeled, but these were not given much attention here as they were somewhat peripheral to our objectives. It was clear that spatial heterogeneity must be considered in any analysis, particularly the dynamic distributions of vegetation, snow and elk. Further efforts are required, but it is clear that a spatially explicit systems approach is needed to determine plausible outcomes of the many processes and feedbacks involved in plant-fire-herbivore interactions.

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Comparative Ecosystem Properties in Summer and Winter Ungulate Ranges Following the 1988 Fires in Yellowstone National Park

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Abstract. Fire and large mammalian herbivores are important components of most grassland ecosystems. Ungulates often consume more forage in burned areas because the forage quality is usually improved following fire. One goal of this study was to determine whether the fires of 1988 influenced consumption patterns by ungulates. Another goal of this study was to measure the impacts that fire and grazing may have on net aboveground production. N and P availability in plants and soil and belowground root biomass measurements were made to help explain the potential patterns. Since ungulates also deposit N through their urine, a small urea fertilization experiment was conducted to determine whether consumption and production patterns might be influenced by urine patches. Summer and winter range study sites that burned in 1988 were chosen for comparison. At the winter range site, net aboveground production, consumption by herbivores, graminoid N concentration, % soil moisture, initial extractable soil N and net P mineralization were higher in burned areas early in the 1991 growing season when grazing was most intense. Ecosystem properties at the summer range site could not be correlated to fire or ungulate activity. It is hypothesized that a positive feedback loop involving intense fire, grazing and nutrient input from ungulates may partially explain the production and consumption patterns measured on the burned sites. Temporary sagebrush removal by fire, higher forage quality, and more productive forage patches likely influence ungulate utilization of burned areas as well. The results of this study suggest that fire and large mammalian herbivore interactions could have significant effects on ecosystem properties for up to three years following fire.

Keywords: Fire; Net Aboveground Production; Nitrogen; Ungulates; Yellowstone National Park

Introduction

Fire and large mammalian herbivores are important components in many grassland ecosystems. Fire and large mammalian herbivores commonly interact (Daubenmire 1968) because herbivores often preferentially forage on more nutritious regrowth that follows fire (Hobbs and Spowart 1984). Since both fire and large herbivore activity can stimulate ecosystem processes, their interaction could be synergistic. For example, grazing temporarily improves light, and soil temperature conditions that favor soil moisture/nutrient mineralization (McNaughton 1979, Knapp and Seastedt 1986). Intermediate grazing intensities positively affect graminoid production (McNaughton 1979, Detling 1988, Holland et al. 1992). Dung and urine deposition from ungulates also can increase the fertility of grassland patches (Day and Detling 1990). Fires also improve soil conditions that favor higher rates of nutrient mineralization and lead to improved plant growth (Raison 1979). By grazing and depositing nutrients to burned areas, large mammalian herbivores could enhance nutrient cycling rates and increase net aboveground production beyond unburned areas.

It is well known that fire and large mammalian herbivores can influence grassland ecosystem properties (Archer and Smeins 1991, Collins and Wallace 1990, McNaughton et al. 1988, Raison 1979). However, few studies have explicitly addressed how fire and large mammalian herbivore interact to influence ecosystem properties (but see Hobbs et al 1991). This is particularly true for sagebrush steppe grassland communities, which dominate a large portion of the western United States grasslands (West 1991).

During the 1988 summer, approximately 45% (400,000 ha) of Yellowstone National Park was burned (Christensen et al. 1989). Although the majority of fires occurred in forested areas, grassland areas also burned. The Yellowstone grasslands support populations of elk (*Cervus*

elaphus) n=22,500, bison (*Bison bison*) n=2500, mule deer (*Odocoileus hemionus*) n=2500, pronghorn antelope (*Antilocapra americana*) n=400-500 (Singer et al. 1989). The focus of this study was to: 1) determine whether large mammalian herbivores consume more forage previously burned areas, 2) determine whether fire and grazing affect aboveground production and 3) attempt to explain the consumption and production patterns by measuring N and P cycling and belowground root biomass in the Yellowstone grasslands.

Study Area

Yellowstone National Park (8995 km²) is located primarily in the northwestern portion of Wyoming, USA. The Park ranges in elevation from 1500 to 3300m and is dominated by conifer forests (79%) and, to a lesser extent, grasslands, including sagebrush steppe (Houston 1973). The Yellowstone climate is characterized by long cold winters and short cool summers. The majority of precipitation falls as snow and the growing season precipitation is usually low (~15cm).

Two study locations were chosen that represent summer and winter range for ungulates. The winter range site was located in the northern portion of Yellowstone National Park adjacent to Hellroaring Creek. This site is a large, southerly exposed, inclining plateau at an elevation of ~2000m. The winter site is primarily range for elk, typically from late fall to May. The summer range site was located in the central portion of Yellowstone in Hayden Valley. This site is composed of small undulating hillocks and swales at an elevation of ~2500m. The summer site is range used mostly by Bison typically from May to October. In general, mean annual temperature and precipitation for winter and summer ranges approximately are 3.8° C and 349mm and 0.6° C and 536mm, respectively (Frank 1990). The two study sites were dominated by cool season grasses: *Festuca idahoensis* and *Agropyron spicatum* and *caninum*, *Danthonia unispicata*, *Poa pratensis*, and *Stipa occidentalis*. Sagebrush, *Artemisia tridentata* (winter range) and *Artemisia cana* (summer range), were the dominant woody plants. The soils are derived from glacial till and are of primarily volcanic origin. The soils can be classified as Typic Cryoborolls, sandy loam and Typic Cryochrepts, silt loam, for the winter and summer ranges, respectively.

The burned portion of the winter range was a backfire that was ignited to stop an approaching fire in late summer 1988. The summer range fire occurred naturally and thus was a front burning fire. At each site one study plot was located in a burned and an unburned area. The plots were matched to minimize any intrinsic differences between them, e.g. topographic aspect, vegetation cover and species composition, soil texture and disturbance.

Methods

Net Aboveground Production and Consumption

Measurements for this study were taken during the 1990 winter and 1991 growing season. Net aboveground production and consumption by large mammalian herbivores was measured using moveable exclosures (1.5m x 1.5m). Four exclosures were randomly located at each plot, and moved monthly following snowmelt. The monthly interval minimizes the possibility of measuring regrowth of grazed vegetation while providing sufficient time to detect production increases of protected vegetation. Standing graminoid biomass was clipped inside and outside the exclosures within two 25 cm x 25 cm quadrants. Quadrant location was randomly stratified to avoid sampling in bare areas or disparate plant communities. Clipped graminoid biomass was sorted into live and dead components, and their mean dry weights compared inside and outside exclosures. The following derived variables then were calculated (McNaughton 1985): 1) Net aboveground production (\underline{aPn}) = sum of positive Δpg Where (pg) is the standing crop inside temporary exclosures. 2) Consumption by herbivores (\underline{H}) = $\underline{aPn} - gPn$ Where (gPn) is the net aboveground production outside of temporary exclosures. 3) Grazing intensity $\underline{G} = (1 - (g/ug))$ Where g = biomass inside exclosures and ug = biomass outside exclosures.

Plant Elements

The green graminoid biomass from randomly selected quadrants (n = 10/plot) used in production and consumption estimates were analyzed for nutrient content. Each bulk forage sample was sorted to live and dead components, washed with double distilled water, dried and ground with a Wiley mill. Green graminoid tissues were analyzed for nitrogen using a Carlo ERBA Autoanalyzer and for P, using a Inductively Coupled Argon Plasma Spectrophotometer (following McNaughton 1988).

Soil

Soil was collected in August 1991 to measure total nutrient concentrations. At each plot, soil was sampled from one randomly located 25x25 cm quadrant and separated at the 0-5 and 5-15 cm (5-10 cm at Winter Range) depths. Rocky soil below 10 and 15 cm at the winter and summer range, respectively, limited deeper soil extraction. Soils were removed from sagebrush interspaces only. The mineral soil was analyzed for N and P as described for plant elements above. pH and soil texture analysis were performed using standard methods and soil moisture was measured gravimetrically after drying for 48 hrs at 65° from soil mineralization cores (see

below). Roots (> 2mm diameter) were separated from the soil mineralization cores (initial cores only), washed with double distilled water, dried, and weighed. Larger roots, most likely from sagebrush, were avoided to better distinguish potential seasonal changes and plot differences for the dominant herbaceous vegetation. Furthermore, since soil cores were primarily taken from within bunchgrass interspaces, total belowground biomass should be considered underestimated. We did not measure changes in belowground biomass over the winter nor did we discriminate between live and dead roots.

Nutrient availability was measured over the winter of 1990/1991 (32 wk., September-May), and during the first, second and third months (4 wk.) following snowmelt, (May/June) 1991, (June/July) 1991, (July/August) 1991, respectively. Within each plot, nutrient availability was measured using an in situ method (Raison et al. 1979). At the beginning of each sampling period, three PVC tubes (3.8 cm x 15cm) were randomly inserted flush with the ground within sagebrush interspaces. Five tubes were used over the winter sampling period. PVC tubes were left uncapped and roots were not removed from within the cores. At the same time, a soil core was taken adjacent to each PVC tube, separated at the 0-5 cm and 5-10 or 5-15cm depths and extracted with 1N KCL for nitrate and ammonium (Siegel 1980) and Mehlich solution (Mehlich 1984) for P and other soil nutrients, respectively. Samples were kept refrigerated until extraction. Net mineralization/immobilization was considered the extractable nutrient concentration difference in the adjacent soil core (initial) from extractable nutrient concentration within the PVC tube at the end of the sampling interval (final). Therefore, a positive value at the end of a sampling period was considered the nutrient mineralized while a negative value was considered net immobilization by the soil biota.

Artificial Urine Patch Experiment

Artificial ungulate urine was applied to the summer range burned and unburned plots. Urea (54 g N/m²) diluted with three liters of distilled water was applied to four randomly located patches within sagebrush plants. Urea was applied to the ground within PVC rings (506 cm²) to eliminate run off. Net N mineralization within the ring area then was estimated over two months as described above.

Statistical Analysis

Net aboveground production and consumption were analyzed with a two factor ANOVA using plot and site. Since ungulates were present at the winter range site for only the first two months of the growing season, plant elements were initially compared for this time period using a three factor ANOVA with plot (burned/un-

burned), fence (ungrazed/grazed), and site (winter/summer) as main effects. Additionally, each site was analyzed separately for the entire growing season with a two factor ANOVA using plot and fence as main effects. Percent N data was arc sine transformed to attain normal distributions about the means. Soil data was subjected to two factor ANOVA using plots (burned vs unburned), and sites (summer vs winter range) for each of the respective sampling periods. Differences between factor levels were accessed using LSD range tests ($p < .05$) since it provides a good balance between giving adequate power and protection against Type I error rates (Olson 1987).

Results

Net Aboveground Productivity and Consumption

Net aboveground production (aPn) was not statistically different between sites ($F_{1,13} = .48, p = .48$) (Table 1). Net aboveground production was significantly higher at the winter range burned plot relative to the unburned plot ($F = 5.7, p = .031$), but there was no difference due to burning at the summer range. The aPn values were in the range reported by Frank and McNaughton (1992). Large mammalian herbivores did not consume more forage at one site compared with the other ($p = .93$). Within the winter range, mammalian herbivores consumed more forage in the burned plot compared to the unburned plot ($F = 7.86, p = .014$). At the summer range, mammals consumed forage independently of whether it was burned. At the start of the growing season, there was more standing dead biomass at the winter range burned plot compared to the unburned plot, but there was no difference at the summer range study site (Table 1). Grazing intensity (G) was greater at the winter range compared to the summer range ($F = 6.6, p = .02$). This was particularly evident in the winter range site (Table 1). At the winter range, grazing intensity was similar between burned and unburned plots the first month following snowmelt and standing dead biomass was significantly greater on the burned plot, therefore production in burned areas may have been significantly higher in 1990.

Table 1. Net aboveground production (aPn), consumption by herbivores (H), standing dead litter (DEAD) and grazing intensity (G). (1) and (2) are the months following snowmelt that the data was collected. Data are mean values with (1 S.E.).

	Winter Range		Summer Range	
	Burn	Unburn	Burn	Unburn
aPn (g/m ² /yr)	166 (14)	96 (26)	129 (23)	107 (15)
H (g/m ² /yr)	65 (17)	8 (5)	52 (18)	25 (15)
DEAD (1) (g/m ²)	73 (11)	15 (3)	60 (10)	64 (8)
G (1) (%)	.62(.05)	.63(.08)	.31(.10)	.56(.06)
G (2) (%)	.38(.08)	.12(.08)	.34(.11)	.23(.11)

Large mammalian herbivores consumed more forage where net aboveground production was greater ($r^2 = .79$, $y = -16.6(x)^{4.05}$, $p < .0001$, $n = 17$) (Figure 1). There appears to be a threshold of herbivory below which little or no consumption occurs of 100 g/m²/yr net aboveground production. Frank and McNaughton (1992) reported a similar results, and it may be a common phenomenon in the Yellowstone grasslands.

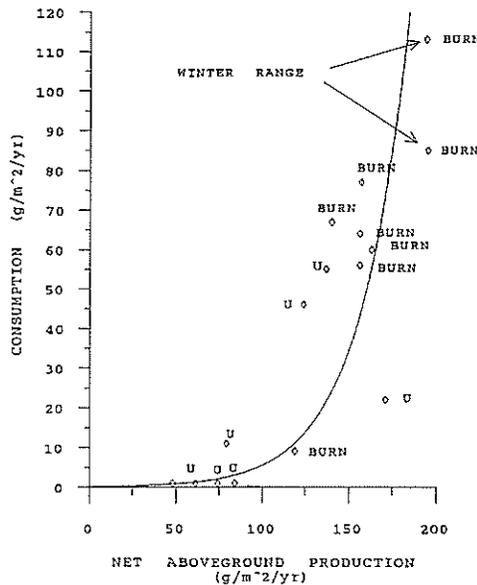


Figure 1. Regression of consumption by herbivores on net aboveground production for summer and winter range sites. Burn=burned plot and U-unburned plot. Data points refer to respective mean values measured at individual exclosures.

Plant Elements

Nitrogen and phosphorus concentrations in live graminoids decreased throughout the growing season (Figure 2). Graminoid N and P levels were not significantly different between sites ($F_{1,77} = .177$, $p = .68$). However, at the winter range study site, nitrogen was significantly greater in burned plot compared to the unburned plot the first month following snowmelt ($F_{1,19} = 5.29$, $p = .03$) (Figure 2a). Mean P levels in the summer range burned plot were greater (3666 mg/kg) compared to unburned areas (2896 mg/kg) ($F_{1,46} = 6.4$, $p = .01$) and may reflect the higher soil P concentrations found at this plot (Table 2). There were no differences in N graminoid levels inside and outside exclosures, but P levels tended to be greater in the presence of grazers the second month following snowmelt at the winter range ($F_{1,18} = 3.26$, $p = .09$). Lastly, plant N and P levels were well correlated ($r^2 = .79$).

Soils

Total soil N and P soil concentrations were generally higher in the surface soil layers compared to subsurface layers (Table 2). N and P levels in surface soils also were similar between burned and unburned plots although this pattern was not evident in the subsurface soils. The amount of organic N at the summer range burned site was high relative to the unburned plot. Although surface soil P was considerably higher at the summer range burned site compared to the unburned plot, there was little

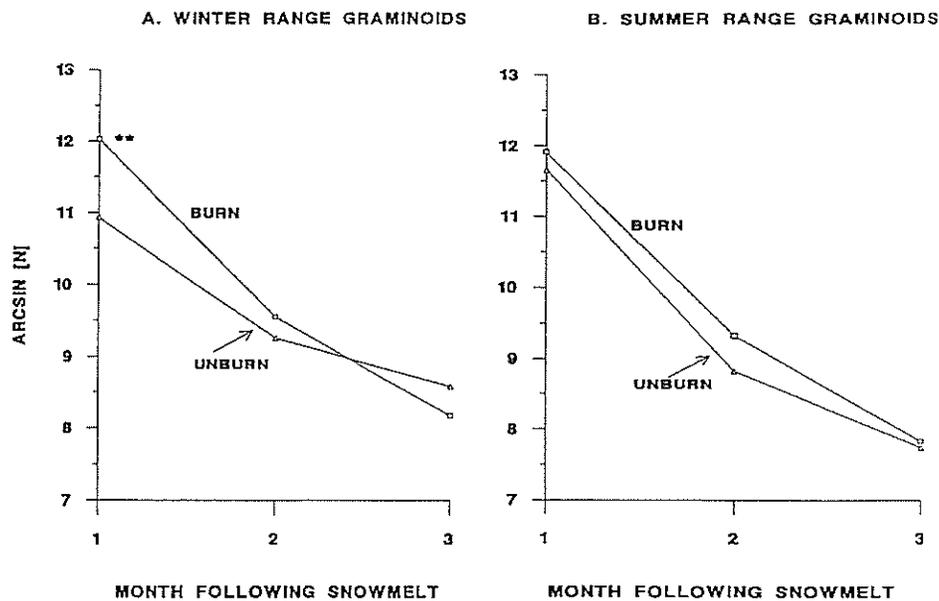


Figure 2. Graminoid N levels through the 1991 growing season for summer (A) and winter (B) ranges. Values are arc sine transformed means taken at the beginning of each month following snowmelt. Values are for green graminoids only.

Table 2. Mean net mineralization rates, root biomass, total soil nutrient pools and soil properties from burned and unburned plots. NH_4 = net ammonification, NO_3 = net nitrification, P = net phosphorus mineralization.
* Soil depths are 5 = 0-5 cm, 15 = 5-15 cm. soils at winter range site could only be sampled to 10 cm. Different letters following respective means indicate significant depth differences (LSD, $p = .05$).

	Winter Range			Summer Range	
	Depth*	Burn	Unburn	Burn	Unburn
NH_4	5	.50 a	3.27 a	8.01 a	9.24 a
mg/kg	15	-.60 a	-.38 a	-.01 b	.16 b
NO_3	5	22.01 a	19.55 a	16.56 a	13.10 a
mg/kg	15	10.95 b	9.65 b	8.15 b	3.75 b
P	5	20.40 a	3.89 a	7.78 a	6.83 a
mg/kg	15	20.58 a	-.61 a	16.47 a	5.92 a
ROOT BIOMASS	5	108 a	136 a	224 a	235
g/m^2	15	46 b	45 b	70 b	63 b
N TOTAL	5	.75	.72	.92	.41
%	15	.55	.48	.31	.31
P TOTAL	5	819	890	675	
mg/kg	15	648	803	611	525
pH	5	6.41	6.32	5.66	5.61
	15	6.16	6.35	5.01	5.31
% Sand	5	49	51	50	38
	15	52	51	47	36
% Silt	5	48	42	44	50
	15	41	42	45	52
% Clay	5	3	7	6	12
	15	7	7	8	12

difference at the winter range. Soil pH was higher at both burned plots and, except for the winter range unburned plot, higher in surface soils compared to subsurface soils (Table 2). Except for the summer range unburned plot, % sand, silt and clay were similar between sites and plots (Table 2).

Soil moisture was greater on burned plots ($F_{1,20} = 14.4$, $p = .001$) but not significantly different between sites (Figure 3a,b). At the winter range site, soil moisture was significantly greater in the burned plot the first month following snowmelt, but mean values were almost identical the last two months when the ungulates had moved off the site (Figure 3a).

The first month after snowmelt initial extractable N ($\text{NH}_4 + \text{NO}_3$) levels were significantly greater in burned plots at the winter range site ($F_{1,20} = 4.20$, $p = .05$) (Figure 3c). Initial extractable N also was significantly higher in burned plots the second month following snowmelt ($p < .05$), but there were no site differences at the start of this month. Net ammonification showed no distinct trends although it was greater in the summer range (Table 2). Very little net ammonification occurred in the subsurface depths relative to surface soils. Net nitrification was higher than ammonification and was approximately 50%

higher in the 0-5 cm depth compared to the subsurface depths (Table 2). Over winter net nitrification was significantly greater in the winter range ($F_{1,42} = 18.61$, $p < .0001$) and greater in burned plots (14.5 ppm) compared to unburned plots (9.08 ppm) ($p = .077$). Nitrification levels were high in the subsurface soils in late summer and this may be suggestive of potential nitrate leaching.

Approximately 70% of net mineralization occurred in the 0- 5cm depth, and 92% of net mineralization was dominated by nitrification. Net N mineralization was not significantly different between burned and unburned areas. Net N mineralization, however, was significantly higher during the winter at the winter range compared to the summer range ($p < .05$) (Figure 4a).

At both sites phosphorus mineralization was significantly higher on burned plots during the winter ($F_{1,42} = 7.60$, $p = .008$) (Figure 4b). This significant main effect was due to higher mineralization in the winter range burned plot (46.78 ppm) compared to the unburned plot (-.35 ppm). Initial extractable P was significantly greater at the summer range site compared to the winter range ($p < .05$).

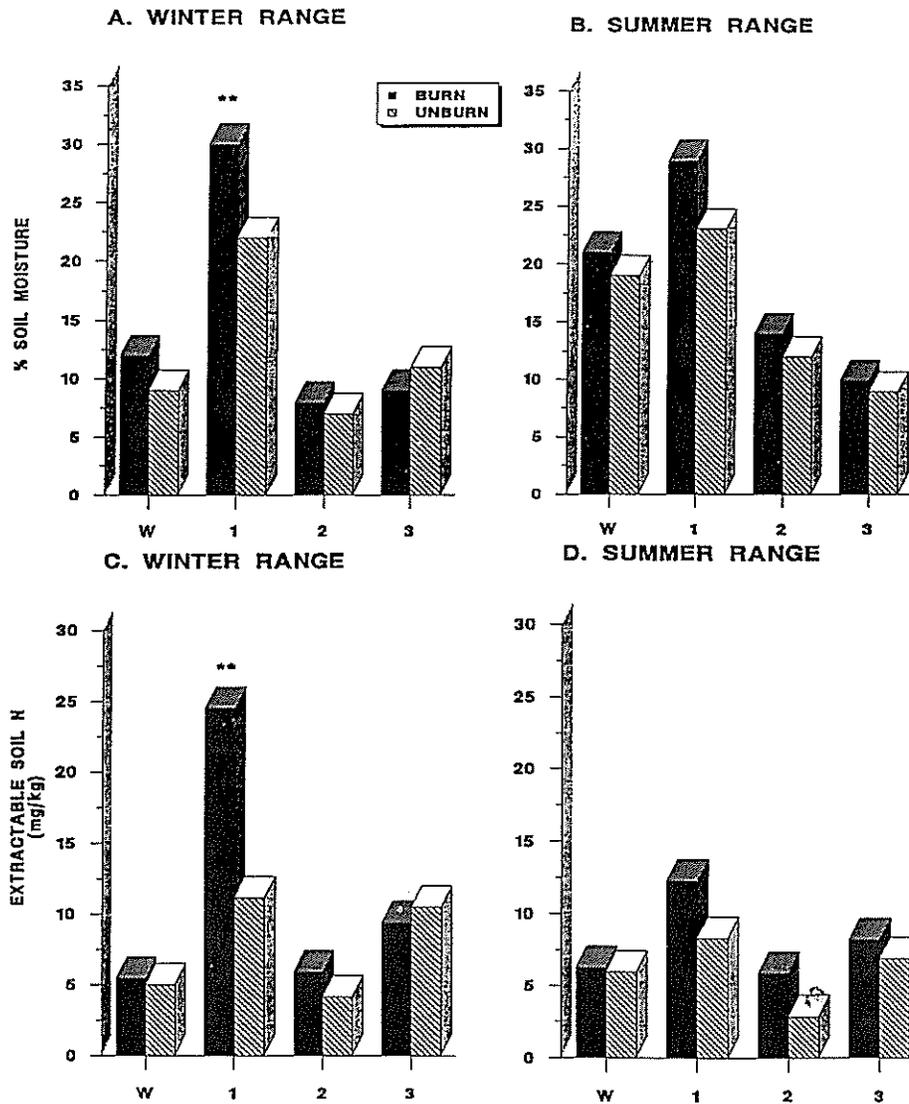


Figure 3. Mean percent soil moisture (A) and (B) and initial extractable soil N levels (C) and (D) measured at the beginning of each sampling period. x-axis symbols are W = winter and 1,2,3 are first, second and third months following snowmelt, respectively. ** indicates a significant difference between burned and unburned plots (LSD, $p < .05$).

Belowground Root Biomass

Belowground root biomass (roots < 2mm diameter) was greater at the summer range ($F_{1,86} = 6.82$, $p = .01$) and in the 0-5 cm soil depths ($F = 19.1$, $p < .00001$) (Table 2). Belowground biomass did not differ between plots. At the winter range site, belowground biomass remained constant during the growing season. Belowground, but it was greater in late summer at the summer range ($F_{1,20} = 6.99$, $p = .015$) (Figure 4c). The belowground biomass values were lower than reported elsewhere for similar Yellowstone plant communities (Coughenour 1991) likely due to the exclusion of larger roots and because soils core were taken primarily from between bunchgrass

interspaces. Belowground biomass and mineralization rates were not correlated.

Artificial Urine Patch Experiment

Net N mineralization was highly stimulated by application of artificial ungulate urine (Figure 5). Net ammonification was similar between burned and unburned plots, but the higher amount of net nitrification at the burned plot resulted in a significantly higher amount of net N mineralized ($p = .014$). Although highly variable, mean P mineralization was lower in simulated urine patches (-16.06 mg/kg) compared to non-treated patches (4.26 mg/kg) over the same time period.

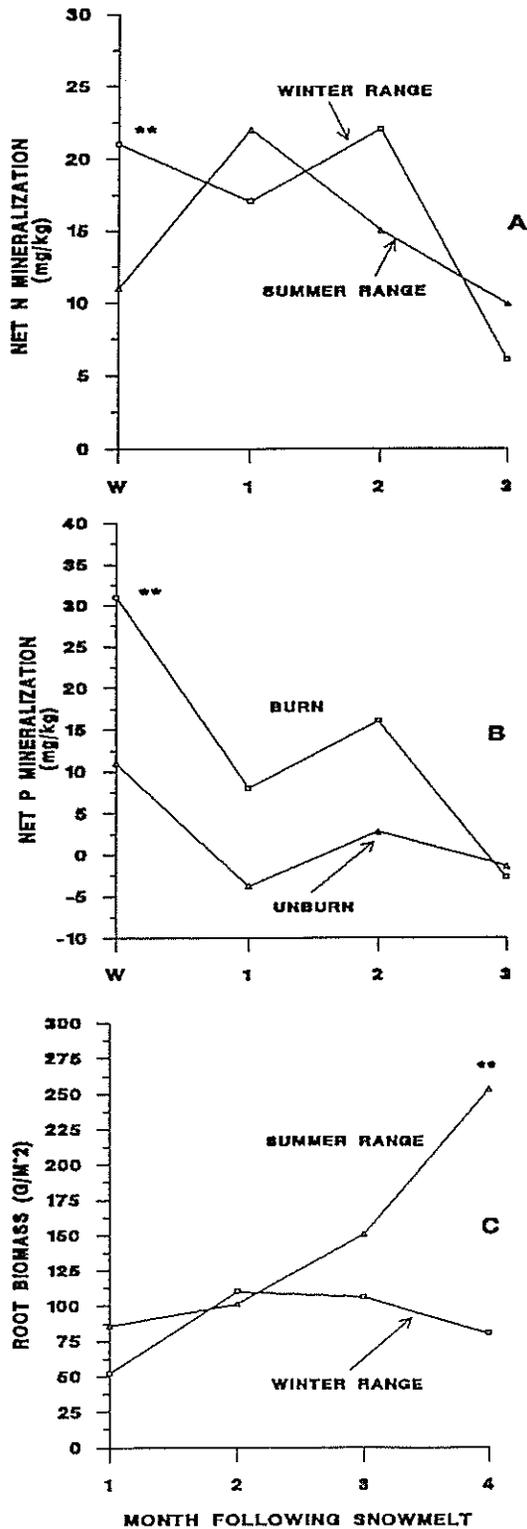


Figure 4. Mean net N mineralization (A), mean net P mineralization (B) and mean root biomass (C). (B) are values from burned and unburned plots for both sites. ** indicates a significant difference between plot or site variables for the respective time period measured (LSD, $p < .05$). x-axis values are as in Figure 3.

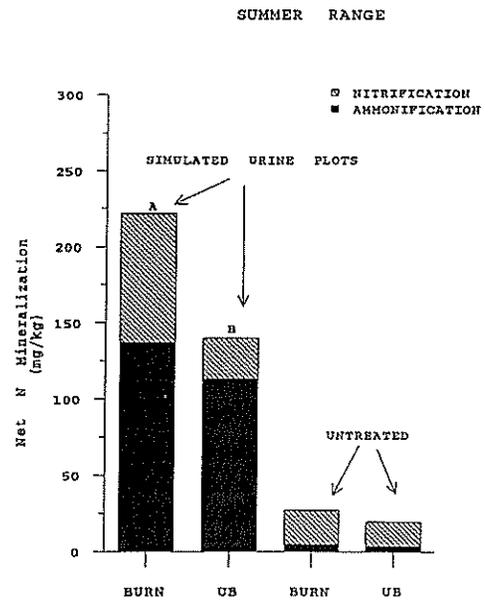


Figure 5. Mean net N mineralization for simulated urine patch pilot experiment. Different letters above bars are significant plot differences (LSD, $p < .05$). Untreated sample means averaged for a two month period are shown for comparison. Burn = burned plot and UB refers to unburned plot.

Discussion

The ecosystem properties measured at the winter range differed from the summer range site. At the winter range site, net aboveground production, consumption by herbivores, % soil moisture, graminoid N concentration, initial extractable soil N and net P mineralization were higher in burned areas early in the growing season. The summer range site had few plot differences that could be related to fire or large mammalian herbivore activity. It is hypothesized that the measured differences at winter range site resulted mainly from burning effects. The effects of ungulates, however, cannot be ruled out.

Fire and ungulate grazing have been found to affect the net aboveground productivity of grasslands. McNaughton (1979, 1984) and Knapp and Seastedt (1986) provide evidence that net production is actually adversely affected in the absence of fire and/or grazing. In Yellowstone National Park, Frank and McNaughton (1992) have found strong positive relationships between grazing and production in different grassland communities. In sagebrush grasslands, some research has found that production was reduced or remained the same following fire (Reddmann 1978 and Mueggler and Blaisdell 1958) while others (Hanson 1929 and Blaisdell 1953) found that fire could stimulate production as much as 300%. Such mixed results suggest the stimulatory nature of grazing and fire effects on net production must be understood in

the context multiple ecological factors (e.g. McNaughton 1983).

It is generally accepted that climate, specifically precipitation, drives many ecosystem variables in semi-arid ecosystems (Noy Meir 1973, Sala et al. 1992). Positive correlations between soil moisture and nutrient mineralization (Burke 1989, Schimel and Parton 1986) and net aboveground production (Mohammad et al 1982, Gay and Dwyer 1965, Rauzi 1964, Smoliak 1956) are common in grasslands similar to those measured in this study. Since soil moisture was significantly higher on the winter range burned plot early in the growing season and this could partially explain the higher production values found there.

The differences in soil moisture were likely due to the greater standing dead biomass in the burned plot. The greater amount of standing dead biomass may have reduced evaporative losses from the soil and trapped more snow during the winter. The soil water relations may have also been affected by the removal of sagebrush roots by the fire, upward soil water movement, and dew deposition (Schimel and Parton 1986).

The higher soil moisture at the winter range burned plot is also likely related to the higher extractable soil N levels. N mineralization and soil moisture are related in arid and semi-arid systems (West 1991) and the greater soil moisture may have created a brief N mineralization pulse. The high initial extractable N levels are good evidence that short-term mineralization pulses could influence net primary production patterns.

N and P soil mineralization exhibited different patterns at the two sites. The higher over-winter N mineralization at the winter range could be reflective of frequent freezing and thawing events (DeLuca et al. 1992) and wetting and drying events (Schimel and Parton 1986). Compared to the high elevation summer range snowpack cover was generally lower and more spatially variable at the winter range site mainly because of the southern exposure and prevailing wind patterns (B. Tracy, personal observation). These factors may cause more freeze/thaw and wet/dry cycles to occur at the winter range site there compared to the summer range site. P mineralization also tended to be higher at the winter range, particularly over the winter, and this could be important because P availability is related to N mineralization, nitrification, fixation, and absorption in arid and semi-arid systems (Cole and Heil 1981). Higher P mineralization rates could have contributed to the higher N accumulation in the grasses and the greater production found at the winter range burned plot. The higher winter N and P mineralization rates may be common to winter ranges in Yellowstone and may help sustain production levels early in the spring when grazing intensity is high.

Generally, the N mineralization patterns measured were similar to those found by Burke (1989), Schimel and Parton (1986) and Charley and West (1977) for western

United States semi-arid grassland ecosystems. Mineralization levels, however, were highly variable between plots, and this may partially explain the lack of significant plot differences. Such variation could be related to ungulate urine patches, which have been found to significantly alter the heterogeneity semi-arid grasslands (Jaramillo and Detling 1992). The high net N mineralization stimulation found in the urea pilot experiment indicates that urine patches may be important in increasing soil N heterogeneity. Furthermore, horizontal soil organic matter distribution (Hook et al. 1991), differential snow accumulation (Bowman 1992) and small mammal disturbance (Andersen 1987) may also contribute to the observed heterogeneity. It is also possible that mineralization differences are simply difficult to detect three years following fire (e.g., Hobbs and Spowart 1984).

It has been hypothesized that high winter N and P mineralization rates could be common to Yellowstone winter ranges; alternatively, it is possible that there may be characteristic patterns of belowground biomass that are found at summer ranges. At the summer range site, belowground biomass tended to increase late in the season while remaining relatively constant at the winter range. The late season grazing that is typical of Yellowstone summer ranges could have caused increases in belowground biomass if the grasses responded to the grazing by increased energy allocation to root growth. Similarly, Caldwell et al. (1981) and Richards (1984) have found that *Agropyron spicatum* will continue to increase belowground biomass well into the summer following defoliation. Photosynthesis and/or carbon stored in the remaining grass culms therefore could be important in influencing root growth patterns into the late summer. Belowground biomass increases in response to late season grazing could help maintain net aboveground production levels the following season when the ungulates return to the summer range.

Preferential use of burned areas by ungulates is common in many grassland ecosystems (Daubenmire 1968). The preferential use can result from several interactive factors including: higher nutrient quality of burned regrowth (Willms et al. 1981, Hobbs and Swift 1985), less standing dead biomass (Willms et al. 1980) and increased foraging efficiency due to changes in the plant community structure (Daubenmire 1968). Grazer avoidance of greater standing dead biomass does not adequately explain the winter range grazing patterns since standing dead biomass was initially higher on the burned plot when the ungulates were grazing this area. If preferential use of burned areas occurred it most likely was caused by higher forage quality and changes in the plant community structure.

The higher N graminoid levels at the winter range burned plot were likely the result of N-rich soil patches, which could have resulted from several factors. The presence of ungulate urine patches is one explanation for

the high N graminoid levels (Day and Detling 1990). In Yellowstone, Coughenhour (1991) found that plant N levels were stimulated by grazing but in the context of higher N recycling rates associated with urine deposition. Urea from ungulate urine also could be directly assimilated in to the foliage (Bowman and Paul 1990) and this may be an important factor that increases graminoid N levels in large herbivore dominated systems. Although plant N levels were not measured in the artificial urine pilot experiment, additional work at the winter range site has found graminoid N content in artificial urine patches was significantly higher (3.32%) compared to untreated controls (2.23%) ($p < .05$). A higher concentration of urine patches in burned areas could influence grazing patterns since Day and Detling (1990) have found that wild ungulates will preferentially graze N-rich urine patches.

Contrarily, Hobbs et al. (1991) suggest that the structure of the grazing landscape influenced ungulate foraging more than forage quality improvements that resulted from fire. This could be relevant to Yellowstone since the temporary removal of sagebrush by fire dramatically changed the grazing landscape. At the winter range, the removal of sagebrush made the grazing landscape more uniform compared to the unburned plot, this uniformity could have influenced ungulate foraging. Additionally, foraging efficiency was probably higher at the winter range burned plot since ungulates could consume more forage without expending as much energy walking amongst the sagebrush. Positive reinforcement of such behavioral cues may be further strengthened by consumption of more nutritious burned regrowth (Woolfolk et al. 1975, Svecar 1989). In contrast, the fire at the summer range did not completely remove sagebrush plants from the landscape and therefore grazing patterns may not have been similarly affected.

We hypothesized that the production and consumption patterns found in 1991 may be the result of a positive feedback loop involving intense fire and ungulate activity (Figure 6). At the winter range site, fire temporarily removed sagebrush from the plant community and possibly stimulated nutrient mineralization the following spring, 1989, a year of near normal precipitation (Frank 1990). The resultant higher quality forage and improved grazing landscape may have caused ungulates to spend more time on burned areas, not only grazing but resting as well (B.Tracy, personal observation). Localized dung and urine deposition was likely greater in burned areas for this reason. Aboveground production was probably increased and when the ungulates moved off the winter range in the spring, high amounts of standing dead biomass accumulated. As a result, soil water conditions improved and the high N and P winter mineralization rates provided a large belowground nutrient pool for plant growth the following spring. Lack of sagebrush, and small-scale forage nutrient improvements, possibly caused by urine patches or high soil water availability, again influenced ungulate grazing patterns. These nutrient-rich patches also may have been more productive and subsequently regrazed during the spring green-up. Given adequate precipitation, fire and grazing effects then might have combined to increase production and consumption rates in the winter range burned area over unburned areas. The fire at the summer range may not have been as intense likely due to the late season grazing that removed a large amount of standing dead biomass. It is possible then that this hypothetical positive feedback loop was not initiated at the summer range, and that ecosystem properties were not strongly influenced by the 1988 fires.

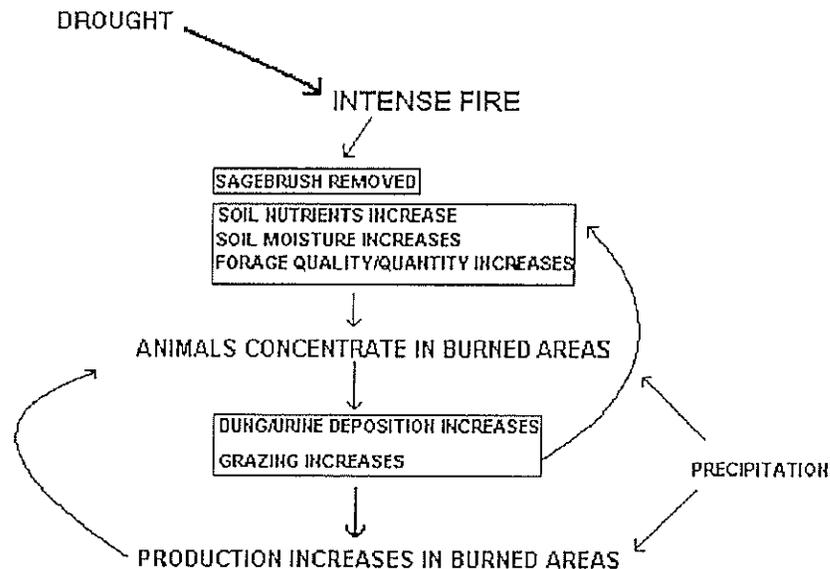


Figure 6. Diagram of a hypothetical positive feedback loop that may explain patterns of net aboveground production and consumption in burned areas.

Acknowledgments. J. Terenzi, E. Moloney, and M. Lutz assisted with field and laboratory work. Margaret McNaughton assisted with sample processing. John Pastor and Jim Coleman provided beneficial reviews of this manuscript. John Varley and the staff at the Division of Research in Yellowstone helped facilitate this project. This work is funded by a University of Wyoming-National Park Service Research Center grant CA 1268-1-9010.

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Winter Range Plant Production and Elk Use Following Prescribed Burning

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Abstract. We documented changes in plant production, elk (*Cervus elaphus*) forage value (the product of plant production and elk dietary preference) and elk use of four sagebrush-dominated sites (*Artemisia* spp.) subjected to prescribed burning on a south-central Montana elk winter range from 1988-93. All sites showed increased graminoid and forb production and decreased shrub production in ≥ 1 of ≤ 5 years following burning. Forage values on burned sites peaked in the first year after burning, but remained above pre-burn levels ≤ 9 years after burning. Elk use increased 144-680% on all sites, peaking from 1-4 years following burning, and remained above pre-burn use levels for ≥ 9 years after burning. Increased forage values on sites after burning reflected greater production of plants with higher food preferences for elk. Because such increases were concurrent with increasing elk use on these sites, this suggested that burning and elk grazing may have been interactive in increasing production of preferred forage species. A generalized plant production-ungulate interaction model is suggested and a schedule for optimizing benefits of burning on similar winter ranges is proposed.

Keywords: *Cervus elaphus*, elk, fire, Montana, plants, prescribed burning

Introduction

Fire and grazing are interdependent processes (Hobbs et al. 1991), both of which profoundly affect plant community structure and function (Wright and Bailey 1982, McNaughton 1984, McNaughton et al. 1988). The Greater Yellowstone Ecosystem in general, and Yellowstone National Park in particular exhibit spectacular influences and effects of both processes (Singer et al. 1989). Burning and grazing change the amount, composition, and nutritional quality of vegetation. On western range lands, prescribed burning increases forb and graminoid production on sagebrush-dominated shrublands.

Elk, which are grazing ungulates, benefit from fire because they are able to make better use of the resulting increases in forb and grass production, and are better able to digest the higher nutritional quality plants which regenerate on burned sites (Boyd 1978, Hobbs et al. 1979, Hobbs et al. 1981, Hobbs et al. 1983, Baker and Hansen 1985). In turn, heavy grazing by ungulates reduces or suppresses further burning on such sites by limiting fuel accumulation (Hobbs et al. 1991). The fact that vegetation on burned areas is often greater in amount and higher in nutritional value than similar vegetation from unburned areas (Asherin 1976; Hobbs and Swift 1985, Van Dyke et al. 1991) is of particular significance on winter ranges, which are typically inadequate in both amount and quality of forage for animal maintenance (Torbit et al. 1985). Ungulates store energy in reserve throughout the summer and catabolize this energy in winter when forage quantity and quality fall below maintenance requirements. Prescribed burning on elk winter range can improve the production and nutritional levels of plants and, therefore, result in improved animal condition and increased survivorship.

The functional and numerical responses of elk changes in plant populations caused by burning have been documented in a number of studies (Rounds 1981, Rowland et al. 1983, Jourdonnaise and Bedunah 1990, Van Dyke et al. 1991). However, few field studies have concurrently monitored both quantitative and qualitative responses of plants following burning with changes in elk use of burned sites.

Our objectives were to (1) quantify changes in amount and nutritional quality of vegetation following burning and (2) to quantify changes in elk use of burned areas. We sought to provide a quantitative measurement of these responses to better assess possible impacts and uses of prescribed burning upon vegetation and elk populations, and to better understand the interactive effects of fire and grazing.

Study Area and Methods

Burns were conducted on USFS lands of the Beartooth District of the Custer National Forest in 3 areas: (1) the North Line Creek Basin (NLCB), (2) Mill Draw (MD), and (3) Gold Creek (GC). Detailed descriptions of topography, climate, vegetation and locations of burns have been previously described by Van Dyke et al. (1991).

Winter game surveys from 1975-93 and relocations of radio-collared elk from 1 March 1988 to 16 December 1991 (Skubinna and Van Dyke 1991) confirmed that NLCB, MD and GC received use by elk of the Line Creek population in fall, winter and spring. The NLCB also received winter use by the Bennett Creek elk population, a herd which summers in north-central Wyoming. Heaviest use in the NLCB and MD occurred from mid-December through Mid-April. Heaviest use of GC occurred in November and December, and then in March, April, and May, with little use in January or February. No livestock grazing has been permitted on any of the areas since the early 1970's.

Controlled burns of similar size and intensity were conducted in the NLCB in October 1984 and March 1988 (approximately 40 ha and 30 ha, respectively) on separate sites in the basin by USFS personnel. In April 1989 a 50 ha area was burned in MD. In March 1990 a 60 ha burn was conducted in GC.

Vegetation and elk pellet density sampling methodologies have been described previously (Van Dyke et al. 1991). A wildfire burned the MD control plots (previously unburned) in 1991, making it impossible to make use of them in this or subsequent years. In 1993, 3 control macroplots were reestablished in MD in a part of the drainage not affected by the 1991 wildfire. Permanent control macroplots could not be established in GC because topography and logistics of the prescribed burned required the entire area to be burned. On this site vegetation was sampled prior to burning and pre-burn vegetation was treated as the control. Increased allocations of funding and manpower in 1993 permitted increasing the number of macroplots in each burn from 5 to 10, and permitted intensive vegetation sampling in 5. In the NLCB, 4 additional control plots also were established and intensively sampled.

Forage values were computed for all species in each treatment as the product of species' forage preference rating for elk times its dry weight biomass on the site (U.S. Forest Service 1988). Preference ratings were adjusted to reflect preferences of local populations using actual food habits data determined from fall, winter and spring pellet samples of Line Creek and Bennett Creek elk (Van Dyke et al. 1991).

Plant sample sizes varied by year according to budget allocations and are given in tables. The Analytical Chemistry Laboratory of Montana State University, Bozeman determined total moisture and protein content

of plant samples through procedures described by the Association of Official Analytical Chemists (AOAC 1965). Percent total moisture values were then used to determine the percentage dry weight in each sample, and, from these estimates, to determine average dry weight production in kg/ha.

Statistical Analysis

Differences in elk use at different sites and in different years were compared through an Analysis of Variance using General Linear Models (GLM) procedures for unbalanced designs (Mendenhall 1968, SAS Institute Inc. 1989: 891-996). The model treated elk use as the response variable and evaluated the significance of year, site and years after burning as main effects. Specific differences evaluated were (1) differences between site-specific burns and their associated controls in a given year and (2) differences in the same treatment type in different years. Where significant overall differences were detected, differences between individual means were evaluated using Tukey's test of multiple means. Because there was no control in MD in 1991 and 1992, elk use of burns in those years was compared to average elk use on MD control sites in 1989, 1990, and 1993 using Dunnett's two-tailed t-test (Dunnett 1955). Because a concurrent control was not present at the GC site, elk use in each year following the burn was compared to elk use immediately prior to the burn (1989) through the same test. Differences in plant production and plant protein levels at different sites and in different years were evaluated similarly. Rarely, low budget allocations, unforeseen circumstances in the field, or low amounts of plant biomass in a particular plant category required estimates of plant production or protein levels based on single estimates from control plots. In such cases the control estimate was compared to a 95% CI of the same variable from the corresponding burned plot. Control estimates not within the 95% CI were considered different.

Results

Plant Response

Patterns of plant replacement and succession followed similar patterns on all sites (Figure 1). Overall, graminoid coverage tended to reach maximum levels of 60-70% 7-8 years after burning. Forbs reached up to 60% coverage immediately after burning, but then progressively declined. Shrubs were completely eliminated following burning, but began to be reestablished 1-2 years afterward and to show significant increase in coverage 6-7 years after burning. Plant volume after prescribed fire was lower in all years through 9 years after burning (Figure

2). Total plant production on burned sites did not normally exceed control levels, but graminoid production was higher on burns at all sites in most years (Table 1). Despite differences in spring and summer weather in different years, total and categorical plant production did not differ in different years on the same site.

Protein levels in all plant categories were higher following burning, on all sites and higher than site-specific controls in most years (Table 2). Shrubs retained elevated protein levels ≤ 6 years after burning, forbs and graminoids ≤ 4 years. Highest absolute levels of protein occurred in graminoids in the same year after burning, in forbs in the same or following year, and in shrubs 2 years after burning.

The GLM evaluating plant production revealed that site, year and plant type had significant effects on total production ($P < 0.03$, all cases), and the number of years after burning also approached significance in its effects ($P = 0.07$). Production on the MD burn averaged higher than either burn in NLCB, and forbs always contributed less to total plant production than shrubs or graminoids ($P < 0.05$). The GLM evaluating plant protein levels found all factors (site, year, years after burning and plant type) to have a significant effect on protein response ($P < 0.01$, all cases).

When production was evaluated using separate GLM's for each plant category, years after burning was a significant factor in graminoid production ($P < 0.01$) and a marginally significant factor in forb production ($P = 0.06$), though it was not significant to shrub production ($P = 0.12$).

Forage values in fall, winter, and spring peaked one year after burning (Figure 3), and declined through the fourth year after burning. In the fifth year, following peak elk densities on the NLCB sites, forage values rose

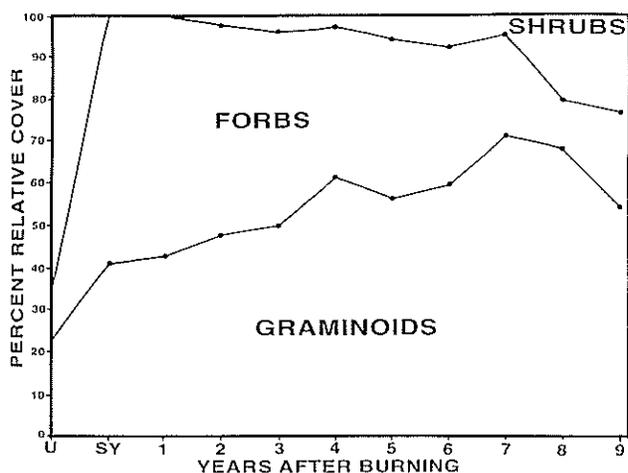


Figure 1. Percent relative cover on bunchgrass-sagebrush sites on Line Creek elk winter range through 9 years after burning, south-central Montana, 1984-93. U = unburned sites. SY = same year as burn (plants sampled after burning). Estimates represent means of ≥ 30 samples.

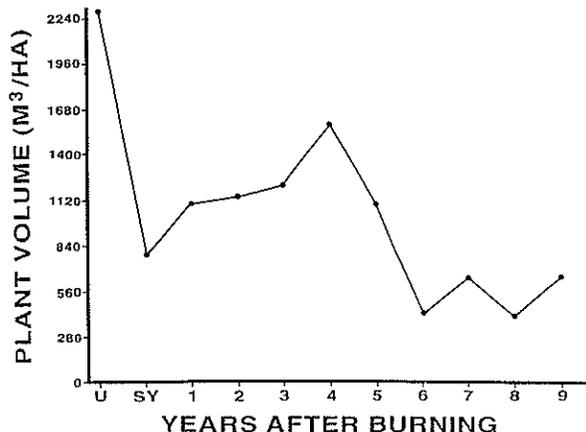


Figure 2. Plant volume (m^3/ha) on bunchgrass sagebrush sites on Line Creek elk winter range through 9 years after burning, south-central Montana, 1984-93. U = unburned sites. SY = same year as burn (plants sampled after burning). Estimates represent means of ≥ 30 samples.

significantly, and remained at relatively high levels through seven years after burning.

Animal Response

Elk use increased on all sites after burning and remained higher than control levels ≤ 9 years after burning (Figure 4, Table 3). Increases were usually significant by one to two years after burning. The length of increased use was inversely related to number of elk using the area and length of seasonal occupancy on the site (Figures 5-8). Gold Creek, which experienced the lowest numbers of elk for the shortest amount of time annually, was the site in which elk use most quickly returned to preburn levels. North Line Creek, which received the heaviest elk use for the longest winter periods, still retained higher elk use on burned sites up to nine years after burning. Elk use on control sites was not different at the end of the study (1993) than initially, indicating that increased pellet densities on burns reflected increased use by elk and were not due to an overall increase in the elk population.

Discussion

Prescribed burning achieved three important results: (1) removal of sagebrush, (2) increased production of forbs and graminoids and (3) increased plant protein levels. All of these effects tend to be beneficial for range management in general and elk in particular, and were accompanied by significant increases in elk use of burned sites. The primary effect of burning on plant production was not an increase in total site production, but a shift away from shrubs toward graminoids and forbs, plant categories containing species more palatable for elk.

Table 1. Plant production (kg/ha, dry weight) by category on burned and unburned (control) plots on the Line Creek elk winter range in south-central Montana, 1988-92. SE/N in parentheses. NS = Not sampled.

Site	Plant Category	Year				
		1988	1989	1990	1991	1992
North Line Creek 1988 Burn	Graminoids	511.7 ^a (5.2/2)	668.6 (289.0/3)	746.8 (132.6/4)	917.0 (448.6/5)	1377.4 ^b (377.0/5)
	Shrubs	112.6 (25.5/2)	198.4 ^b (89.4/3)	218.6 (48.2/2)	160.3 ^b (61.5/2)	NS
	Forbs	613.0 (241.1/2)	196.1 (87.0/3)	467.4 (276.4/3)	307.7 ^b (41.9/4)	417.6 (343.5/5)
	Total Production	1237.3 (220.9/2)	1063.1 (235.8/3)	1206.6 (264.3/4)	1379.5 (536.2/4)	1795.0 (589.8/5)
North Line Creek 1984 Burn	Graminoids	1060.0 ^a (65.8/3)	725.9 (228.7/3)	1059.7 ^b (346.0/6)	929.1 (104.8/5)	824.9 (370.4/5)
	Shrubs	102.3 (96.1/3)	313.1 (254.3/2)	166.7 ^b (113.9/3)	403.7 ^b (232.4/3)	NS
	Forbs	317.5 ^a (62.5/3)	180.3 (113.3/2)	79.6 (0.0/1)	232.7 (135.6/2)	260.4 (165.3/5)
	Total Production	1479.8 ^a (209.5/3)	1155.3 (84.8/2)	1156.6 (323.3/6)	1264.4 (100.3/5)	1085.3 (499.3/5)
North Line Creek Control	Graminoids	155.0 (0.0/1)	287.5 (121.6/3)	537.0 (368.2/5)	542.5 (216.2/5)	583.6 (251.9/4)
	Shrubs	218.4 (0.0/1)	774.3 (187.5/2)	926.0 (435.3/5)	970.3 (313.6/5)	1068.4 (506.8/4)
	Forbs	49.3 (0.0/1)	31.5 (0.0/1)	56.1 (0.0/1)	107.0 (0.0/1)	68.8 (0.0/1)
	Total Production	422.7 (0.0/1)	1007.5 (179.3/2)	1474.2 (421.8/5)	1534.2 (315.2/5)	1669.2 (684.5/4)
Mill Draw 1989 Burn	Graminoids	NS	557.5 (211.3/3)	1551.1 ^b (318.2/6)	966.9 ^c (205.8/5)	1748.1 ^c (367.5/5)
	Shrubs	NS	0.0 ^b (0.0/3)	0.0 ^b (0.0/6)	0.0 ^c (0.0/5)	0.0 ^c (0.0/5)
	Forbs	NS	194.9 (105.8/2)	439.0 (208.1/5)	447.4 ^c (68.6/5)	229.4 (87.2/5)
	Total Production	NS	687.5 (202.9/3)	1916.9 ^b (323.0/6)	1414.3 (222.6/5)	1977.5 ^c (322.7/5)
Mill Draw Control	Graminoids	NS	334.5 (151.2/3)	454.7 (203.6/4)	NS	NS
	Shrubs	NS	663.6 (0.0/1)	748.4 (188.7/5)	NS	NS
	Forbs	NS	90.4 (0.0/1)	109.8 (12.7/2)	NS	NS
	Total Production	NS	1088.5 (151.2/3)	1249.8 (315.4/4)	NS	NS
Gold Creek 1990 Burn	Graminoids	NS	223.6 (89.6/5)	448.6 (97.6/5)	741.3 ^d (365.6/5)	708.7 ^d (450.1/5)
	Shrubs	NS	1234.1 (396.3/6)	0.0 ^d (0.0/5)	0.0 ^d (0.0/5)	0.0 ^d (0.0/5)
	Forbs	NS	30.0 (0.0/1)	585.6 ^a (365.7/5)	1076.0 ^a (231.0/5)	537.0 ^a (265.6/5)
	Total Production	NS	1559.9 (435.0/5)	1034.2 (407.1/5)	1817.3 (500.4/5)	1245.6 (282.6/5)

^a 95% CI does not include control mean.

^b Different from site control level in same year. $P < .05$.

^c Different from Mill Draw average, 1989-90. $P < 0.05$.

^d Different from pre-burn production in Gold Creek in same plant category. $P < 0.05$.

Burning of sagebrush enhances forage quality by increasing availability of mineral N for plants regenerating after burns (Hobbs et al. 1991). This enhancement in forage quality was reflected in increased protein levels in plants following burning, particularly in graminoids, which cycle nutrients faster than other plant types. However, protein levels also declined fastest in graminoids, the plant category elk used most, and peak elk use did not coincide with peak plant protein levels on the most heavily used sites in North Line Creek. This suggested

that the primary benefit and attraction of burns for larger numbers of elk was not directly related to nutritional quality. Elk use of the North Line Creek burn sites did not rise significantly above control levels until 2 years after burning, and did not peak until 4 years after burning, when graminoid protein levels had already declined to pre-burn levels. Nevertheless elk continued to use these burns at significantly higher levels than control sites through 9 years after burning. This suggested that: (1) use of burns was influenced by learned behavior and

Table 2. Plant protein levels (% dry weight) by plant category on burned and unburned (control) plots on the Line Creek elk winter range in south-central Montana, 1988-92. SE/N in parentheses. NS = not sampled.

Site	Plant Category	Year				
		1988	1989	1990	1991	1992
North Line Creek 1988 Burn	Graminoids	8.6 ^a (0.2/2)	6.7 (0.6/3)	7.9 ^b (0.7/4)	5.4 (0.4/5)	6.6 ^b (0.2/5)
	Forbs	9.4 ^a (0.2/2)	10.8 ^a (0.3/3)	8.8 (0.8/3)	6.9 (0.6/4)	9.8 (1.1/5)
	Shrubs	9.8 ^a (0.0/2)	10.4 (1.1/3)	11.1 ^b (0.6/2)	8.9 (0.1/2)	NS
North Line Creek 1984 Burn	Graminoids	6.6 (0.7/3)	5.6 (0.3/3)	6.3 (0.8/6)	5.3 (0.5/5)	5.3 (0.5/5)
	Forbs	7.2 ^a (0.8/3)	8.2 (0.5/3)	8.3 (0.0/1)	5.4 (2.4/2)	8.3 ^a (1.2/5)
	Shrubs	8.9 (1.7/3)	9.0 (0.8/2)	11.1 ^b (0.6/3)	7.9 (0.5/3)	NS
North Line Creek Control	Graminoids	5.7 (0.0/1)	6.4 (0.5/3)	5.9 (0.6/5)	5.5 (0.4/5)	4.8 (0.4/4)
	Forbs	3.6 (0.0/1)	7.5 (0.0/1)	7.1 (0.0/1)	7.5 (0.0/1)	10.4 (0.0/1)
	Shrubs	8.1 (0.0/1)	8.3 (0.1/2)	8.0 (0.4/5)	8.4 (0.9/5)	7.3 (0.2/4)
Mill Draw 1989 Burn	Graminoids	NS	10.0 ^b (0.7/3)	8.1 ^b (1.5/6)	6.1 (0.1/5)	6.1 (1.1/5)
	Forbs	NS	10.4 (0.9/2)	9.9 (0.7/5)	7.5 (0.8/5)	10.6 ^c (1.3/5)
	Shrubs	NS	NS	NS	NS	NS
Mill Draw Control	Graminoids	NS	5.7 (0.3/3)	5.1 (0.4/4)	NS	NS
	Forbs	NS	7.5 (0.0/1)	8.9 (0.9/2)	NS	NS
	Shrubs	NS	7.5 (0.0/1)	6.9 (0.4/5)	NS	NS
Gold Creek 1990 Burn	Graminoids	NS	4.3 (0.4/5)	12.2 ^d (1.1/5)	4.4 (0.2/5)	5.1 (0.9/5)
	Forbs	NS	7.8 (0.0/1)	11.9 ^d (1.6/5)	6.2 (0.9/5)	8.8 (1.2/5)
	Shrubs	NS	5.7 (0.3/6)	NS	NS	NS

^a 95% CI does not include control mean.

^b Different from control, same site, year, and category. $P < 0.05$.

^c Different from Mill Draw Control average (1989-90), same plant category. $P < 0.05$.

^d Different from pre-burn levels in Gold Creek, 1989, same plant category. $P < 0.05$.

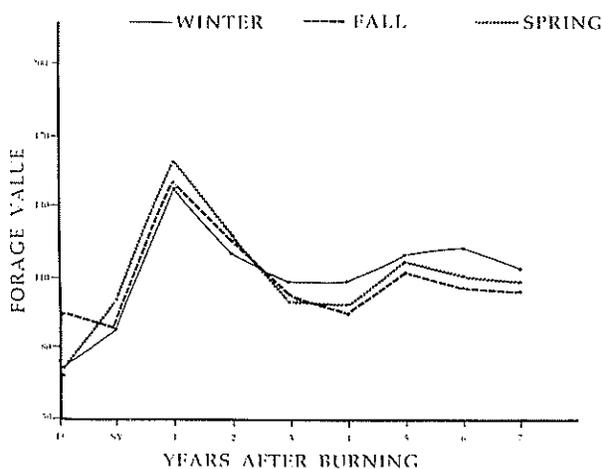


Figure 3. Seasonal forage values (plant production X elk food preference rating) of plant communities on bunchgrass-sagebrush sites on Line Creek elk winter range through 7 years after burning, south-central Montana, 1984-91. U = unburned sites. SY = same year as burn (plants sampled after burning). Estimates represent means of ≥ 30 samples.

However, protein levels also declined fastest in graminoids, the plant category elk used most, and peak elk use did not coincide with peak plant protein levels on the most heavily used sites in North Line Creek. This suggested that the primary benefit and attraction of burns for larger numbers of elk was not directly related to nutritional quality. Elk use of the North Line Creek burn sites did not rise significantly above control levels until 2 years after burning, and did not peak until 4 years after burning, when graminoid protein levels had already declined to pre-burn levels. Nevertheless elk continued to use these burns at significantly higher levels than control sites through 9 years after burning. This suggested that: (1) use of burns was influenced by learned behavior and tradition as much as by plant nutritional quality and (2) that elk may regard quantitative benefits of sites (i. e. increased graminoid abundance) sufficiently attractive to maintain such traditions even when qualitative benefits (higher protein levels) have disappeared.

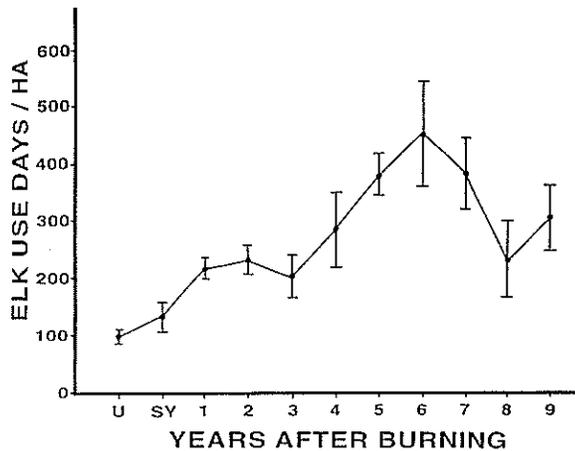


Figure 4. Means and 95% C.I. of elk use days/ha on bunchgrass-sagebrush sites on Line Creek elk winter range through 9 years after burning, south-central Montana, 1984-93. U = unburned sites. SY = same year as burn. Estimates represent means of ≥ 30 samples.

tropical grasslands (McNaughton 1976), the per capita availability of food to elk on the Mill Draw and Gold Creek sites would be relatively high, favoring selection for high nutrition. The 2-3 fold increase in elk numbers on the North Line Creek sites would favor selection for maximizing forage biomass and forage intake rates. Thus, even older burns with low nutrient quality would still convey advantages to elk in a system of low overall productivity as long as specific productivity of graminoids remained high.

Elk are highly selective foragers, and also may have compensated for declining average plant nutritional levels on the North Line Creek burns by increasing forage selectivity. This possibility is supported by the fact that dietary protein levels in this population were higher than

average plant protein levels in both winter and summer (Van Dyke et al. 1991, Van Dyke et al. 1995, respectively). Hobbs and Spowart (1984:554) noted that elevations in dietary protein levels in bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) on burned sites occurred mainly from changes in diet selection rather than from improvements in diet quality. Similar findings have led other investigators to warn that attempts to estimate diet quality from average forage quality may significantly underestimate the former (Hobbs and Spowart 1984).

Management Implications

Grazing and burning are interactive processes. Graz-

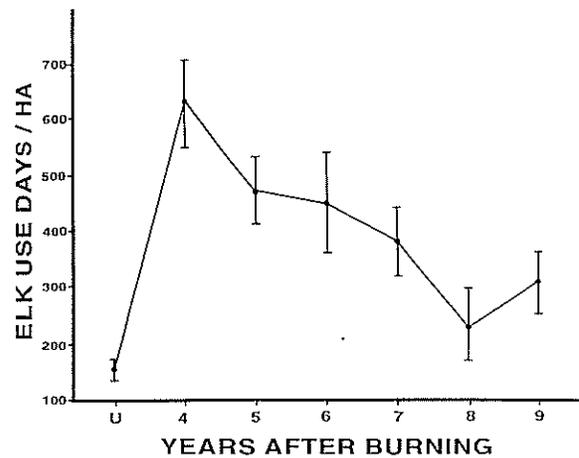


Figure 5. Means and 95% C.I. of elk use days/ha on North Line Creek Basin burn (1984) and associated unburned (U) sites, south-central Montana, 1988-93. Estimates represent means of ≥ 30 samples.

Table 3. Elk use (days/ha) on burned and unburned (control) plots on the Line Creek elk winter range in south-central Montana, 1988-93. SE/N in parentheses. NS = not sampled.

Site	Year					
	1988	1989	1990	1991	1992	1993
North Line Creek 1988 Burn	254.3 (49.8/30)	294.8 (52.1/30)	331.3 (47.5/30)	389.2 (64.8/30)	185.0 (38.8/30)	283.2 (54.4/30)
North Line Creek 1984 Burn	628.1 (79.9/30)	474.0 (60.8/30)	452.8 (93.2/30)	383.4 (64.8/30)	213.9 (67.1/30)	304.4 (57.9/30)
North Line Creek Control	221.6 (85.1/6) ^a	211.9 ^a (87.0/6)	57.8 ^b (73.1/6)	250.5 (101.6/6)	96.3 (130.1/6)	67.4 ^b (52.8/30)
Mill Draw 1989 Burn	NS	115.6 (32.4/30)	210.0 (48.8/30)	281.3 ^c (53.8/30)	158.0 (51.5/30)	38.5 (17.4/30)
Mill Draw Control	NS	188.8 ^b (107.3/30)	119.5 ^b (85.9/30)	NS	NS	54.6 (64.2/18)
Gold Creek 1990 Burn	NS	23.2 (12.7/30)	0.0 (0.0/30)	138.9 ^d (34.7/30)	81.0 ^d (26.1/30)	63.7 (16.2/30)

^a Different from 1984 burn, same year. $P < 0.05$.
^b Different from burn(s) in same area, same year. $P < 0.05$.
^c Different from average Mill Draw control use, 1989-93. $P < 0.05$.
^d Different from Gold Creek pre-burn (1989) use. $P < 0.05$.

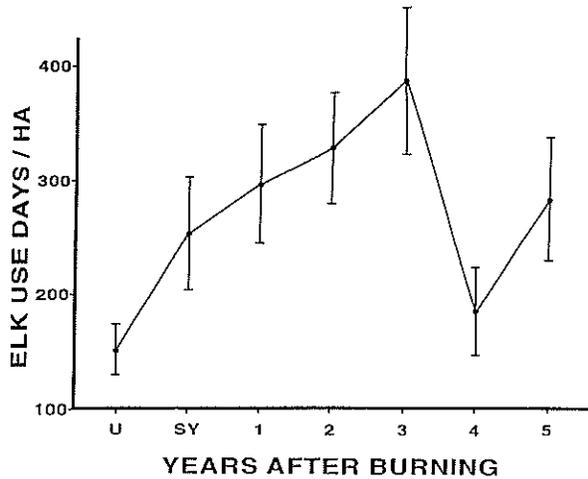


Figure 6. Means and 95% C.I. of elk use days/ha on North Line Creek Basin burn (1988) and associated unburned (U) sites, south-central Montana, 1988-93. SY = same year as burn. Estimates represent means of ≥ 30 samples.

(Van Dyke et al. 1991, Van Dyke et al. 1995, respectively). Hobbs and Spowart (1984:554) noted that elevations in dietary protein levels in bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) on burned sites occurred mainly from changes in diet selection rather than from improvements in diet quality. Similar findings have led other investigators to warn that attempts to estimate diet quality from average forage quality may significantly underestimate the former (Hobbs and Spowart 1984).

Management Implications

Grazing and burning are interactive processes. Grazing conserves N in the ecosystem that would otherwise be lost through combustion in burning, and grazing tends

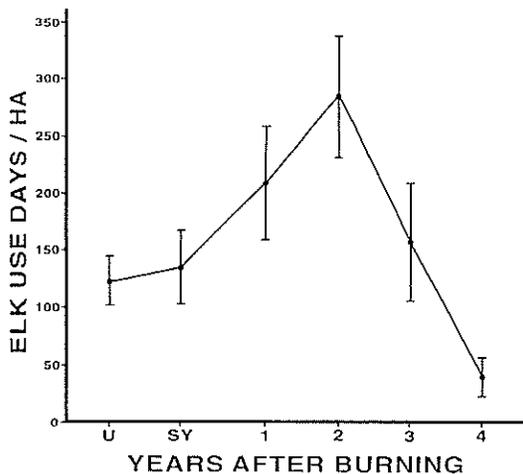


Figure 7. Means and 95% C.I. of elk use days/ha on Mill Draw burn (1989) and associated unburned (U) sites, south-central Montana, 1989-93. SY = same year as burn. Estimates represent means of ≥ 30 samples.

to prevent the accumulation of biomass that may be necessary for burning to recur (Hobbs et al. 1991). This was evident on our study sites where the most heavily grazed sites (NLCB) tended to be those in which sagebrush was slowest to become reestablished. This principle should be noted because an ideal burning schedule which optimizes graminoid protein levels may be impossible to achieve if there is insufficient biomass in heavily grazed areas to carry subsequent fires. Longer burning rotations may be necessary to optimize actual elk use in larger herds, because time is required for use traditions to become established. Longer rotations also may be necessary to permit elk use to decline sufficiently to permit biomass buildup and shrub reestablishment to allow reburning of heavily used sites.

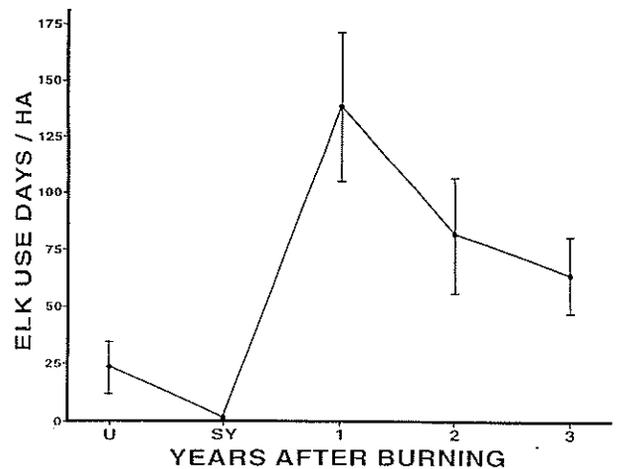


Figure 8. Means and 95% C.I. of elk use days/ha on Gold Greek burn (1990) and associated unburned (U) sites, south-central Montana, 1990-93. SY = same year as burn. Estimates represent means of ≥ 30 samples.

As Torbit et al. (1985:84) noted, "It is probable that winter ranges will always be incapable of meeting nutritional requirements." Forage quality and digestibility decline throughout winter, and declines are greatest in graminoids, which make up the bulk of winter diets of elk in this population. Because prescribed burning of sagebrush communities increases both amount and quality of graminoids, its applications on winter ranges would be of benefit to elk. When managing for relatively small (<150 individuals) herd units, burns should be repeated at ≤ 3 year intervals, because elk use will follow changes in graminoid protein levels on the burned site. For larger (≥ 150 individuals) herd units, burning intervals of up to 9 years may still provide benefit for elk, because larger elk groups may respond primarily to graminoid quantity rather than graminoid quality, and will continue to use burns at rates greater than unburned sites even after graminoid protein levels have declined.

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The Aldo Starker Leopold Memorial Lecture If I Were Superintendent . . .

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"There are several good reasons for preserving adequate samples of all ecosystems..." "[including] the scientific, 'baseline' value of retaining combinations of soils, plants, and animals that formed the fertile ground we now exploit with such abandon."

A. Starker Leopold (1985)

I believe that all of us wish that our research will ultimately help to shape management. Even the most basic ecological research provides insight into how the system works that ultimately should give perspective on how one might manage the ecosystem. It is my objective in this essay to speculate on how we might use research results reported at this conference to manage the Greater Yellowstone Ecosystem (GYE) better. To capture Superintendent Bob Barbee's attention, I will do this in the context of imagining that I were superintendent of Yellowstone National Park.

Research results presented at this conference upset our fundamental premises of how the Yellowstone ecosystem functions. In fact, I am chagrined to think that if we had implemented policy based upon our understanding of the system five years ago, such policy would have missed the mark. This carries two important messages: (1) we must carry on in our attempt to understand this complex ecosystem, and (2) management approaches must be flexible to assimilate new information. Although there is a substantial amount new emerging at this conference, I will highlight a few presentations that to my mind really change our understanding of the role of fire in the GYE.

Five years ago, we believed that the fire regime on the Yellowstone plateau had for many centuries been driven primarily by landscape-scale fires that occurred every two or three hundred years. Based upon dendrochronological studies (Romme and Despain 1989), we knew that the last major fires in the system were in the mid-1700's, and the last major fire before that appeared to be some 200-300 years earlier. Such a pattern of fire history seemed to make sense because high-elevation forests are not highly productive and it takes a long time to accumulate enough fuels to carry a fire. It also seemed reasonable that weather conditions as occurred during the summer of 1988 were rare enough that major fire events would be infrequent. As superintendent I would have

garnered comfort from such data because there was less reason to worry about another major wildfire for a couple hundred years. Although the political backlash from the fires of 1988 may have stifled our ability to manage fires, we would have some 300 years to wait for a more enlightened administration that would recognize the wisdom in letting natural fires burn.

But now Millspaugh and Whitlock (unpublished data) have informed us that we had it all wrong. Although it is true that over the past 500 years the interval between fires was long, Millspaugh and Whitlock's data show that before that time fires were more frequent, perhaps every 100-150 years. And with the shorter interfire period, fires were likely smaller in scale as well. So it would be wrong to lock ourselves into a mindset that fires are necessarily rare events in Yellowstone. We probably also will need to reevaluate our premises about the scale of fires that occur naturally on Yellowstone's landscape.

In 1988, ecologists recognized that there is nothing unique about fire in the Greater Yellowstone Ecosystem—fires occur almost every year. But what was unique about the 1988 fires was their massive scale. The fundamental question is whether there are important ecological consequences associated with fires of such magnitude. Or would ecologists be just as happy with smaller fires that might be more controllable? Does the scale of burns have ecological consequences that would alter the way the Yellowstone ecosystem functions? Turner (unpublished data) addresses this issue in more detail, but my reading is that we would be hard pressed to point to differences between large and small fires that would substantially alter ecological processes in Yellowstone over the long term. Granted, the landscape might look different under a smaller-scale fire regimen, in part due to patterns of revegetation by lodgepole pine (*Pinus contorta*). And some geophysical processes might be altered. But otherwise, our search for big picture, big-scale effects has been unrewarding thus far.

Next, I was stunned to learn that since the 1988 fires, aspen (*Populus tremuloides*) has not been able to escape ungulate browsing (Kay and Wagner 1994, Renkin and Despain 1994) as was postulated previously (Despain et al. 1986). We know that fire stimulates suckering and releases aspen clones from apical dominance, allowing more rapid growth (DeByle and Winokur 1985). But small fires resulted in heavy browsing because ungulates were attracted to these areas (Bartos and Mueggler 1981). So the hypothesis was that all we needed was a large fire to allow aspen to escape ungulates. But alas, the ungulates still hammer aspen and the immediate future for many aspen stands looks bleak if they are not released from browsing. It appears that a complex interaction among ungulate populations, climate, and fire governs dynamics of aspen in the GYE.

Many of us were surprised to learn of the magnitude of perturbation to stream structure and biological communities observed postfire in areas subjected to heavy burns, e.g., in Cache Creek and tributaries. Minshall et al. (unpublished data) postulate that it will take decades or centuries before the prefire conditions will be restored in these streams. Likewise, Meyer et al. (unpublished data) found major geomorphological changes attributable to the 1988 fires. So again we have a shaken foundation, and we must abandon beliefs that we will see rapid recovery from the fires of 1988.

If I were superintendent I would be frustrated by how rapidly our understanding of the GYE seems to change. Such is the nature of science: we are in the business of building hypotheses and rejecting them. Much of ecology still entails descriptive work, and relatively few examples exist in community ecology where we have enough experimental research to make powerful inferences. Ecologists are struggling to build a body of information that constitutes reliable knowledge (Romesburg 1981). Yet, management decisions will be made, irrespective of the frailty of our understanding. We cannot wait for ecologists to complete all of the necessary experiments that would be required to have a solid ecological basis for making sound management decisions.

How can one expect to manage under such uncertainty? If I were superintendent I would be very uncomfortable about implementing management programs to force the ecosystem towards some target—some management goal based upon someone's vision of how the ecosystem ought to look. From what we have seen, any such target appears almost certain to change. In particular, I would be leery of scientists who believe that they understand Yellowstone well enough to shape direction for management of the Park. It is almost incomprehensible to me that ecologists could actually establish "quantitative and measurable standards of ecosystem structure and function" (Bonnicksen 1989, Wagner and Kay 1993:268).

Paradigms for Conservation

This all gives pause to reflect on the ultimate purpose of Yellowstone. Congress gave us loose guidelines but clearly our priorities for conservation have changed through time, especially in recent years (Grumbine 1992). A number of paradigms for conservation have been championed for Yellowstone, and it proves to be a useful exercise to examine alternative approaches for management in Yellowstone in view of the great uncertainty about how this ecosystem functions.

I will consider 4 alternatives for ecosystem management:

1. "Adam Smith's Vision": Restoring private property rights to the landscape (Baden and Leal 1990).
2. "Starker's Vignette": Active management to attain a prescribed goal (Leopold et al. 1963).
3. "Biodiversity Bandwagon": Giving top priority to the preservation of biological diversity (Diamond 1992).
4. "Ecological-Process Management": Viewing parks as ecological baseline preserves (sensu Sinclair 1983).

Adam Smith's Vision

Baden and Leal (1990) saw problems—in part based upon economic criteria. People see waste if trees are allowed to rot or if an elk herd is insufficiently harvested. It is difficult for some to imagine why we might leave Yellowstone's oil in the ground. To rectify what these authors believe to be deficiencies in government management, they propose transferring Yellowstone to private concerns in the expectation that competitive capitalism will work better than government. But I find it difficult to imagine how an area the size of Yellowstone could be protected through a scheme involving the purchase of public lands and conservation easements by environmental organizations (Olson 1990). Particularly troublesome would be protection of migratory ungulate populations.

I will cavalierly dismiss Baden and Leal's (1990) "New Resource Economics" approach if for no other reason than the American public will not tolerate oil and gas mining or hunting in Yellowstone. There are few landscapes remaining in North America that have escaped the heavy hand of human use, and there are many of us that expect places like Yellowstone to be spared such fate. "Perhaps it is correct that Aldo Leopold has not yet displaced Adam Smith, but he certainly had a better land ethic" (Boyce 1990:60).

Starker's Vignette

Aldo Starker Leopold chaired a committee advisory to the Secretary of the Interior on wildlife management in the national parks (Leopold et al. 1963). One of the often-cited quotes from their report was that national parks should preserve "a vignette of original America." The idea is that management programs should attempt to restore and maintain areas to look as they did when European humans first visited. The Leopold report was criticized shortly after its publication for not recognizing that ecological processes are dynamic (Frome 1992). Yet, a complete reading of the Leopold report suggests that such criticism was misplaced. For example, Leopold et al. (1963) explicitly recognized that "most biotic communities are in a constant state of change due to natural or man-caused processes of ecological succession." Their notion of a vignette was clearly on a large scale, taking into account ecological processes such as fire and predation.

Starker Leopold's committee, however, clearly had in mind that manipulations were needed to achieve "a vignette of original America." Specifically, they thought that it was necessary to control ungulate populations and to set fires to restore processes altered by humans.

Cole (1971) challenged the premise that ungulate populations needed to be controlled in Yellowstone; he argued instead that plant-herbivore interactions would limit elk (*Cervus elaphus*) populations. Cole's natural regulation hypothesis appeared coincident with Errington's (1971) *Of Predation and Life* published during an era of wildlife biology when predators had been overly persecuted and rationales were developing to protect several predators from extirpation. Perspectives have changed somewhat and it is now widely recognized that predators, wolves (*Canis lupus*) in particular, can be major forces in population regulation (Seip 1992). Predictions for Yellowstone National Park are that wolves will reduce elk numbers by 15-25% (Boyce 1992). Yet ungulates in Yellowstone are migratory; in the Serengeti migration has resulted in wildebeest (*Connochaetes taurinus*) populations possibly being regulated more by forage than by predators (Fryxell et al. 1988). We cannot accurately predict the efficacy of wolves as predators on Yellowstone's migratory ungulates and thus forecasting the consequences of wolf recovery is speculative.

Native Americans also might have been a factor reducing ungulate populations before European settlement (Kay 1990). Likewise, Native Americans may have set fires in Yellowstone. We know that North Americans killed wildlife in the park, and there is evidence that they set fires in other places. But there is no evidence of the large-scale killing that would be necessary to reduce ungulate populations nor do we have any evidence that Native Americans set fires in Yellowstone.

Existing technology does not allow us to reconstruct the extent of predation by wolves or Native Americans (Schullery and Whittlesey 1992). Even if our management objective included restoration of the role of Native Americans by culling ungulates, we have no way to estimate the number of animals that should be killed. Such intervention by culling herds would be arbitrary, and would seem particularly unwise now after 25 years when the elk population appears to be converging on carrying capacity. By implementing a cull now we would lose much in terms of our understanding of ungulate plant-herbivore dynamics, and we would gain nothing beyond protecting northern range vegetation from "damage" caused by ungulate browsing (Kay 1990). Rather than "damage" I submit that plant-herbivore interactions indeed alter vegetation structure and composition, but as scientists we are in no position to classify such effects as "damage."

We know well that we can manipulate ungulate populations through harvest (Beasom and Roberson 1985), but we do not understand ungulate-vegetation interactions well enough to anticipate the dynamics in the absence of such control. To restore the ecosystem, wolves need to be there. But it is not clear that we have the knowledge to replace wolves as predators. Likewise, we do not have the knowledge to be able to restore the influence from North Americans using primitive tools, e.g., spears and bows and arrows, to kill wild ungulates in the park — humans who migrated into the park seasonally and occupied the park at unknown densities. It is naive to think that we could restore the complex ecological effects of Native Americans in the Yellowstone ecosystem.

Strong feelings are often expressed by wildlife managers and range managers that elk must be culled in Yellowstone park. I have attempted to understand why this is such a contentious issue and I have discussed the matter with a number of individuals from each discipline. It appears to me that different issues are at stake. Range managers believe that by allowing ungulate populations to reach such high levels in Yellowstone, the federal government has imposed a double standard, because such heavy range use by domestic livestock would not be tolerated on federal lands outside the park. Dodd (1993) went so far as to suggest that Yellowstone now provides a baseline by which livestock use on public lands outside the park may be evaluated! I agree that such a baseline will be very useful indeed for understanding the role of grazing, but I doubt this will determine the level of livestock use that Americans will tolerate on other federal lands. Various agencies of the federal government indeed have different mandates, and not all lands should be managed using the same criteria.

Some wildlife biologists, on the other hand, fear that sport hunting may be threatened. By demonstrating that

hunting is not necessary in Yellowstone, some wildlife biologists believe that the National Park Service is undermining a fundamental justification for sport hunting (Pengelly 1963). This view is offered by Kay (1990): "if natural regulation is correct, ungulates do not have to be hunted or preyed upon to prevent them from damaging their environments. ...This would remove a major ecological rationale for sport hunting and wolf reintroduction." Based upon Kay's (1993) objections to wolf recovery, we must conclude that his mission is one of justifying sport hunting. Incidentally, from Kay's (1990) thesis I cannot discern how one establishes that ungulates are "damaging" their environments. Attempts to perpetuate hunting in national parks have proven to be socially unacceptable (Wood 1984), and not ecologically "necessary." Ecological relationships may be altered as a consequence of reducing ungulate populations by hunting, but this does not demonstrate the ecological necessity of hunting.

The bottom line, however, is that we cannot reconstruct exactly how the GYE looked in 1850, and we cannot restore Native Americans to the scene. Likewise we cannot control climate which can have a major influence on ecosystem structure and dynamics. So a vignette of original Yellowstone is regrettably an unrealistic target.

Biodiversity Bandwagon

It has become fashionable, indeed mandatory, that biological diversity be considered in federal agency resource management plans; there are many who believe that biodiversity ought to be guiding national park management. This is partly due to cogent arguments championed by Myers (1979) and Wilson and Peter (1988) that humans stand to lose a great deal with the loss of genetic diversity. From a homocentric perspective, our future might be compromised by the loss of genetic information contained within the earth's biota — genetic information that may have medicinal or industrial uses, or that may provide genetic resistance for domestic organisms. These arguments have triggered considerable interest in conservation, particularly in preserving tropical rain forests—host to an amazingly high proportion of the earth's species.

But should biodiversity preservation be the priority for management of all national parks? Is preservation of biotic diversity the only conservation goal worthy of consideration? If preservation of biological diversity were our objective in conservation, the GYE would be one of the last places on earth where we would focus our attention since it is an area of remarkably low species richness. Indeed, if Yellowstone's ancient caldera were to erupt again tomorrow, we would lose remarkably few species—at most a few specialized taxa associated with thermal areas, e.g., Ross' bentgrass (Dorn 1989, Boyce

1991). Few of our national parks were established because of their biotic resources—most were designated because of their scenic or recreational values.

Ecological-Process Management

Sinclair (1983) argued that national parks ought to be managed as ecological baselines so that we can evaluate the consequences of human influences on managed landscapes. Indeed, it is exactly this idea that underlies the park service notion of "natural regulation" although much semantic debate over natural regulation has occurred. As it is currently used, natural regulation constitutes ecological-process management whereby management actions will be focused on actions that minimize or reverse the influence of humans on natural ecological processes operating in the ecosystem. Presumed tests of natural regulation proposed by Houston (1976) were incorrect (Boyce 1991). Natural regulation has become a management approach rather than a hypothesis or experiment.

Humans have influenced every ecological system on earth; it is impossible to escape such global influences as increased carbon dioxide in the atmosphere. But as Mary Meagher (pers. comm.) has suggested, "Although humans have changed some parameter values, the ecological processes are still the same."

Of course this management paradigm embraces biodiversity preservation as well, because it is fundamental to managing for ecological processes that one must "save all the parts" (Leopold 1949, Barker 1993). Invoking ecological-process management in the GYE does not risk loss of any threatened or endangered species (despite ominous projections and predictions by several generations of observers that Yellowstone will somehow self destruct [e.g., Wagner and Kay 1993:269]). To my mind, ecological-process management should be the direction for the GYE.

Pregnant Consequences

One might argue that ecological-process management is the current direction driving Yellowstone's management, and that I am simply touting the "party line." Although there are, indeed, some people within the National Park Service who believe that ecological-process management is the wisest approach, the approach certainly is not accepted universally by NPS personnel. Furthermore, there appear to be a number of shortcomings in the way in which resource management in the GYE is taking place that could be rectified. I will list a few.

Wolf Recovery

Restoring wolves to the GYE is clearly a flagship program for ecosystem management. We cannot infer

with confidence the consequences of wolf recovery (Boyce 1992), but we know they were here through the 1920s, and in other regions wolves have been shown to be important components of the ecosystem (Mech 1991). One of the values of biodiversity is redundancy in the system so that if a species is lost, ecosystem function is not lost but falls back to another species (Keddy et al. 1993). But as top-level carnivores, wolves have no ecological equivalents in the system that can replace predation on bison (*Bison bison*), elk, and moose. Granted, bears (*Ursus arctos*), lions (*Felis concolor*), and coyotes (*Canis latrans*) kill many elk calves in Yellowstone each spring, but this is quite different from the expected role that wolves will play in the ungulate community (Cook 1993). With the lack of an effective surrogate for wolf predation, it is particularly important that wolves be restored. The integrity of the GYE has been compromised by the elimination of wolves from the system (Karr 1993).

Wildfires

Fire management policy for Yellowstone has remained remarkably intact despite the political uproar during the summer of 1988. And so it should. Results of this conference will not change ecologists' perspective—fire is an integral part of forest ecosystems in the Rocky Mountains. We should encourage the National Park Service to keep Smokey the Bear out of Yellowstone National Park!

Eliminating Exotic Species

Fly anglers will encounter great discomfort grouping brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), and lake trout (*S. namaycush*) in the same category as spotted knapweed (*Centaurea meculosa*). But they are all exotic species that clearly do not belong in a park managed for natural ecological processes. We know that foraging by fishes can drastically alter the structure and abundance of freshwater fauna and flora (Drenner and McComas 1980, Bradford et al. 1993). Indeed, the National Park Service has a clear policy against exotic species in national parks (Dennis 1980). Yet, Yellowstone manages exotic trout for sustained harvest! This is simply inconsistent.

Regrettably, in many instances we must simply succumb to exotics, and accept them as new integral components of the ecosystem. This is especially true for several species of exotic plants that have become naturalized in North America. Yellowstone does little to battle most exotic plant species that occur in the park, and for good reason. The park has virtually no chance of eliminating well-established species, such as timothy (*Phleum pratense*) or dandelions (*Taraxacum* spp.), from the park. Likewise it is impractical to consider eliminating brown trout from the Madison River.

Winter Use

Winter recreation on snowmobiles is in conflict with ecological-process management in Yellowstone National Park. Bison have learned to use the hard-packed snowmobile trails to move to new foraging areas, thereby greatly increasing the winter carrying capacity of bison in the park (Meagher 1993). Because of the enormous popularity of winter recreational use in the park, terminating it probably will not be acceptable to the public. But much could be done to restrict winter use. For example, it seems feasible to require a permit for winter visitors using snow track vehicles just as float trips down the Grand Canyon are regulated. And if I were superintendent, I would work to restrict winter visitation as much as possible by delaying the initial opening and initiation of trail grooming, and by closing the park to snowmobiles as early as would be tolerated. Surely if the National Park Service could justify closing the dumps to bears because viewing areas at the dumps seemed inconsistent with the park's mission (Despain et al. 1986), it could also justify curtailing the winter incursion of snowmobiles for the same reason.

Transcending Park Boundaries

Defining ecosystem boundaries is an arbitrary business. There are no rules defining the boundaries of an ecosystem; rather, they depend upon the ecological process of interest (Patten 1991). Because elk migrate outside Yellowstone National Park every winter, some people have argued that Yellowstone does not constitute a complete ecosystem (Houston 1982, Chase 1986). Indeed, if we are to manage elk within Yellowstone in a manner consistent with ecological-process management, it would help to be able to expand park boundaries to include these elk wintering areas. The federal government missed an opportunity to secure the Royal Teton Ranch north of Gardiner, Montana a few years ago, and current management of the property by the Church Universal and Triumphant seems inconsistent with regional land-use plans. Yet most lands in the GYE are already in federal ownership and implementing ecosystem management is more a matter of convincing various government agencies to agree on directions for management. An ardent effort in this direction was initiated about five years ago with the preparation of a draft *Visions for the Future* document prepared by the inter-agency Greater Yellowstone Coordinating Committee. Local business and development interests mustered enough political excitement that the *Visions* document effort was eviscerated. The visionary draft document was replaced by A Framework for Management that does nothing to facilitate coordination between the National Park Service and the U.S. Forest Service as originally intended. The vision process needs to be reinstated and completed this time.

Hunting in Grand Teton National Park

After breaking down some of the interagency boundaries, and having restored wolves to the GYE, there is an excellent opportunity to resolve the long-standing issue of winter feeding at the National Elk Refuge (NER) and hunting of elk in Grand Teton National Park (Murie 1951, Wood 1984, Boyce 1989). Winter provisioning of hay for elk at the NER began early in this century due to conflicts between cattle and elk for ranchers' hay stacks. But the U.S. Fish and Wildlife Service, which manages the NER, currently justifies its winter feeding program as providing forage to replace that on lands now occupied by the town of Jackson and adjacent livestock operations. In view of the great importance of elk to the area, I find the Fish and Wildlife Service justification for feeding to be compelling, but inconsistencies exist in the actual management of the feeding program. Rather than providing feed comparable to that produced on lands where elk have been displaced, the NER is run rather like a cattle feeding operation where enough feed is provided so that the average elk does not lose weight during winter (Boyce 1989). Because no restriction on winter feeding exists, the normal over-winter mortality has been essentially eliminated, thereby requiring that elk be hunted in Grand Teton National Park to ensure sufficient mortality through hunter harvest so that the population is kept within reasonable bounds. Such hunting within a national park also is inconsistent with the general policy of the National Park Service.

With wolves to help redistribute elk throughout the herd unit, and with only the amount of feed provisioned that would be produced naturally in the area occupied by the town of Jackson, Wyoming, the need to continue the hunt in Grand Teton National Park will be obviated. Local opposition to such change is likely to be strong, as indicated by previous instances when the public did not think that enough feed was provided for elk (Boyce 1989). By initiating a NER management plan that considers limited feeding as an alternative, educating the public, and encouraging public input into such a plan, the U.S. Fish and Wildlife Service might eventually win public support for a program to reduce winter feeding.

Science and Management

Science and resource management should not be divorced. One of the most effective ways to improve natural resource management programs is through an iteration of science and management, i.e., adaptive management or "learning by doing" (Walters 1986). It has always concerned me that rangers and resource managers in the National Park Service often have negative attitudes regarding research and science, which is especially surprising because most of them have professional training in a natural resource science. If I were superintendent I would reward rangers who implement monitoring programs evaluating the efficacy of their management pro-

grams. Likewise, I would reward scientists whose research most effectively influences management in a way that complements (rather than circumvents) the government's research-grade evaluation process. And I would work extremely hard to ensure close alliance with the Interior Department's new research agency, the National Biological Survey.

It is sometimes claimed that ecological-process management entails no management at all (Chase 1986, Kay 1990). This is simply false and is normally claimed only in the context of Yellowstone's failure to control ungulates. Accusations of non-management are incongruous given the effort to restore wolves, to eliminate mortality sinks for grizzly bears (*Ursus arctos*), to close Fishing Bridge, and to curtail harvests of cutthroat trout (*Oncorhynchus clarki*) (see Boyce 1991). And it took management conviction almost beyond belief for Robert Barbee to stand up to the intense political and media pressure criticizing his position on fire management during the summer of 1988!

Much of the motivation for this essay comes from a recent paper by Wagner and Kay (1993) championing Starker's vignette. Obviously I do not accept their views, and I hope that my arguments are convincing. The GYE is inexorably on a course toward ecological-process management; federal agencies in the GYE are breaking new ground. I believe this to be a sagacious course of management, and because of it, Yellowstone will maintain its status as a global paradigm for conservation.

"To anyone concerned about the conservation of nature the very name Yellowstone is like a battle cry. This is where it all started; Yellowstone was the first wilderness set aside for a national park, and it remains an inspiration and the confirmation that dreams can be made to come true."

*H.R.H. Prince Phillip
(from Sutton and Sutton 1972)*

Acknowledgments. John Varley invited me, Dennis Knight suggested the title, and Paul Schullery made me write this. Thanks to Alan Haney, Mary Meagher, Evie Merrill, Neil Payne, Frank Rahel, Paul Schullery, and John Varley for critiques and discussion.

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Poster Session

Interpretation of the National Fire Danger Rating System for Yellowstone National Park

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Abstract. The National Fire Danger Rating System (NFDRS) produces indices that are used to assess fire danger for large areas. Index values can be part of a comprehensive set of criteria to be used in deciding whether to allow natural ignitions to burn as prescribed fires. An analysis of the relationship between NFDRS indices and historical fire business aids interpretation of fire danger. Percentiles and logistic regression were used to relate NFDRS indices for the Mammoth, Wyoming, weather station to historical fire occurrence and size for Yellowstone National Park. Based on this analysis, Energy Release Component appears to be a good indicator of fire business.

Keywords: Wildfire; Forest fire; Weather; Fire danger rating; Yellowstone National Park.

Introduction

The decision to declare a new ignition a wildfire or a prescribed fire is a difficult one. Designation must be timely, and the decision embodies a high degree of uncertainty and potential risk. The National Fire Danger Rating System (NFDRS) can provide information to be used in the prescribed natural fire decisionmaking process, but is only one of many factors that must be considered (Andrews and Bradshaw, in press). Other information to be considered includes factors such as potential threat to life and property, available suppression resources and funds, existence of defensible boundaries given potential fire behavior, and the probability that the fire will reach administrative boundaries. NFDRS can provide information on fire potential as it relates to state of the fuel, based on current and previous weather. Relationship of indices to historical fires provides a basis for defining critical levels of fire danger beyond just percentile levels of the index. The fire season can be tracked by plotting and comparing indices to critical levels, to past seasons, and to historical averages and

maximums. In addition, potential fire danger can be calculated into the future for several weeks based on various weather scenarios.

The Fire Management Policy Review Team that was formed after the 1988 fire season recommended that NFDRS indices be considered as part of a comprehensive set of criteria to be used in deciding whether or not to allow natural ignitions to burn as prescribed fires (USDA, USDI 1989). In a list of issues needing further analysis, the task force noted the need for validation of the relationship between NFDRS indices and actual fire occurrence, severity, and size. In this paper we discuss methods for examining the relationship between fire danger rating and fire business. We present examples from an analysis for Yellowstone National Park, showing differences in the performances of indices as a reflection of the fire season.

NFDRS is a rating of fire potential for a general area rather than fire behavior information for a specific location. It reflects general weather patterns based on afternoon weather observations at fixed stations (Deeming et al. 1977). Fire danger rating cannot be used to predict the behavior of a specific fire. Other tools such as the BEHAVE fire behavior prediction system (Andrews 1986) or fire growth simulation (Finney 1994; Andrews and Bevins, in press) should be used for site-specific fire behavior.

Site-specific fire behavior predictions relate to things that can be observed, measured, or quantified—rate of spread, flame length, or fire perimeter. Fire danger rating, on the other hand, is related to something more nebulous—fire potential for large areas. The question is how to assess how well an index reflects changing fire potential through the fire season. We use 'fire business' as a quantification of the fire season. As fire danger increases, we expect an increase in fire activity—more reportable fires and more large fires. Historical fire occurrence and size, being readily available data, are used as indicators of fire business. Discovery date and final

In keeping with the philosophy of NFDRS being fire danger for large areas, we use fire data for all of Yellowstone National Park. For this analysis we used only the weather station at Mammoth, Wyoming to calculate indices. Our data base included weather and fire data for 1965 through 1992: 4,369 days and 639 fires. We define a fire day to be a day on which a fire was discovered, a large fire day as a day on which a fire of final size over 10 acres was discovered, and a multiple fire day to be a day on which five or more fires were discovered. There were 531 fire days, 42 large fire days, and 11 multiple fire days. The classification is done three times. For example, a large fire day is also classified as a fire day.

Figure 1 is a diagram of the 1978 National Fire Danger Rating System, showing information used in calculating each index. Note that wind is used to calculate Spread Component (SC) but not Energy Release Component (ERC), and that SC calculations are weighted toward the fine fuels while ERC calculations are weighted toward the heavier fuels. Therefore, ERC reflects seasonal drying and wetting trends if it is based on a fuel model that includes 100-hour and 1,000-hour timelag fuel. ERC based on fuel models without the 100-h and 1,000-h categories has no "memory" of past weather, being based only on each day's weather observations, with only live fuel moisture being carried over from the previous day. Burning Index (BI) is a mathematical combination of SC and ERC. Keetch-Byram Drought

Index (KBDI) has also been suggested as an indicator of seasonal drying (Burgan 1988) and is available as a fire danger index. Precipitation amount over 0.2 inch and maximum temperature are the only weather values used in calculating KBDI; fuel type is not a consideration.

Figure 2 shows seasonal plots for the 1987 and 1988 fire seasons for SC, BI, ERC, and KBDI. SC, BI, and ERC are based on fuel model G, which includes all fuel size classes: 1-h, 10-h, 100-h, 1,000-h, and live. The weather used in the calculations is from the Mammoth station; the fires for the whole Park are indicated on the plots. Dashed lines indicate the maximum and average values for 1965 through 1992.

The 1987 and 1988 fire seasons were quite different. In 1987 there were 34 fires and 973 acres; only 1 fire was over 10 acres. The year 1988 set new standards for "worst case" with 60 fires and 861,531 acres. Notice that a seasonal trend is not apparent for SC and BI, while the difference between seasons is clear from the ERC and KBDI plots. KBDI increases steadily throughout the 1988 season due to lack of significant precipitation. ERC dropped off in the fall due to high night-time humidity and precipitation less than 0.2 inch. This decrease in ERC corresponds to a decrease in fire business. Throughout the season, fire business was concentrated at high levels of ERC, while fires occurred throughout the full range of KBDI values.

The fire characteristics chart (Andrews and Rothemel 1982) provides a way to display SC, ERC, and BI as a

U.S. NFDRS System Structure

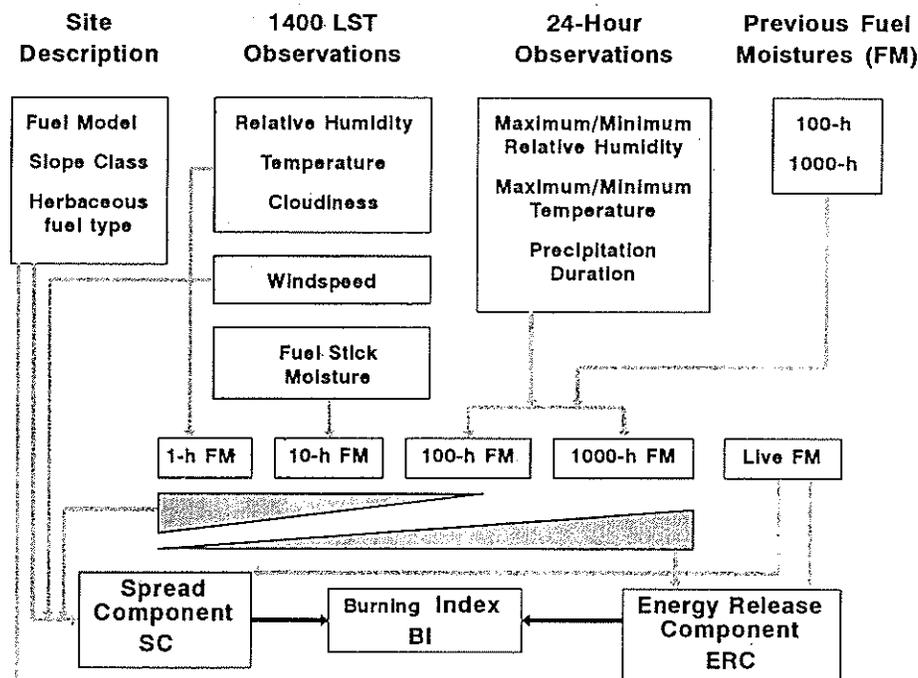


Figure 1. Structure of NFDRS showing the relationship among site description, weather observations, intermediate fuel moisture calculations, and final indices.

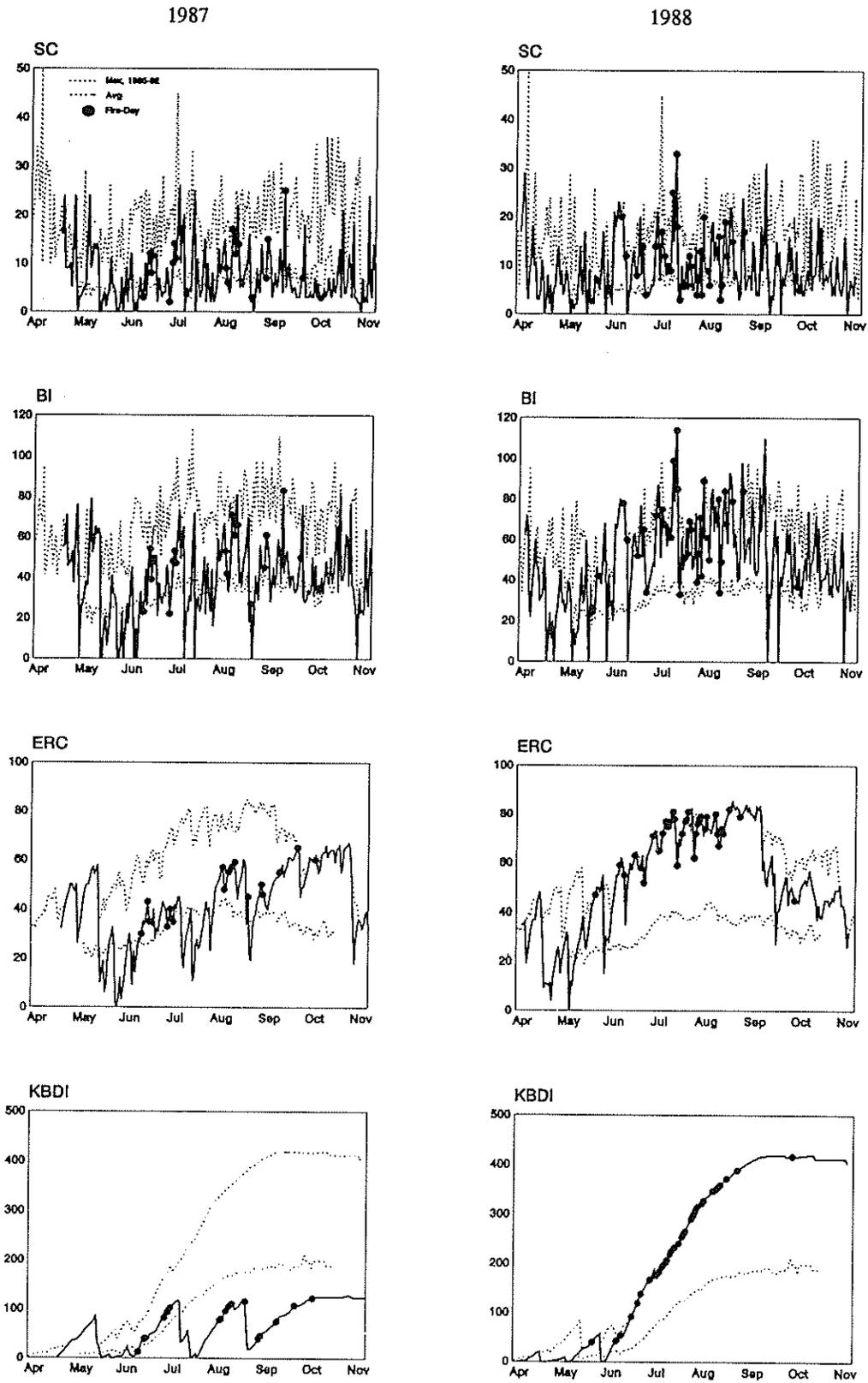


Figure 2. Plots of the 1987 and 1988 fire seasons for SC, ERC, BI, and KBDI.

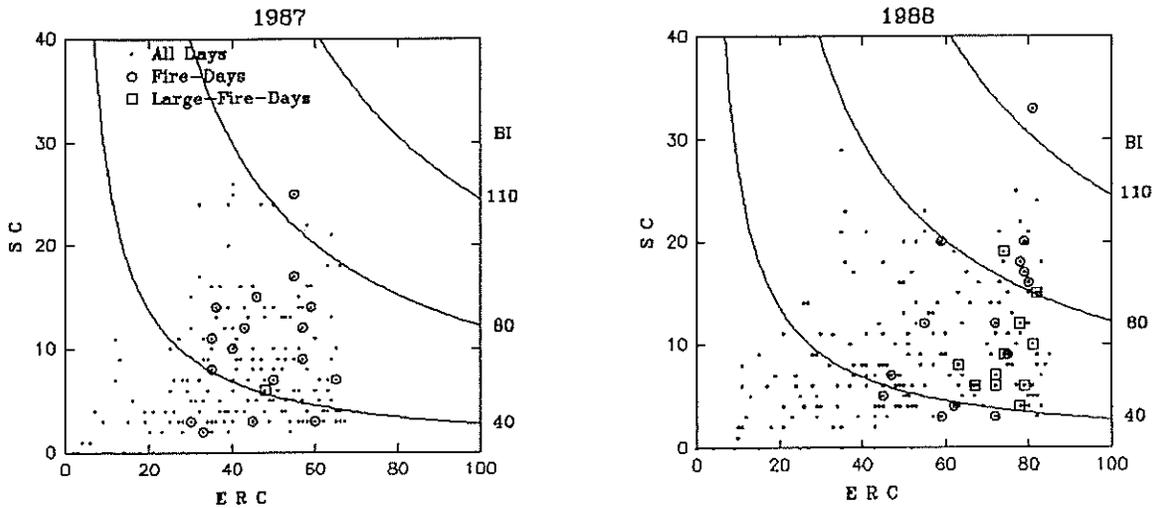


Figure 3. Fire characteristics charts showing SC, ERC, and BI for all days, fire days, and large fire days for 1987 and 1988.

single point. Figure 3 shows the comparison between 1987 and 1988. The indices are plotted for all days through the burning season with an indication of fire days and large fire days. Note that higher fire occurrence and larger size are associated with high values of ERC and BI.

A common way of looking at historical fire danger is by means of percentiles for all days in the historical data base (Main et al. 1982). This method can be extended to examine the relationship between fire business and fire danger rating by developing percentiles for fire days, large fire days, and multiple fire days as well as for all days. Figure 4 shows the percentile curves for Energy Release Component for fuel model G and for the Keetch-Byram Drought Index. If there were no relationship between fire business and fire danger, then the four curves on each graph would be similar. The shift in the curves indicates that more fire business is occurring on higher fire danger days. Table 1 shows data for five

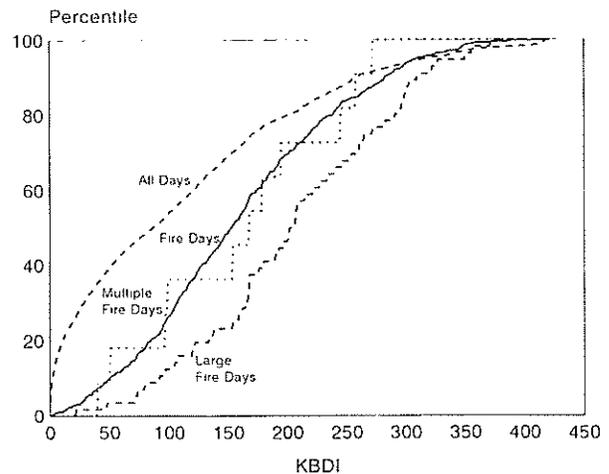
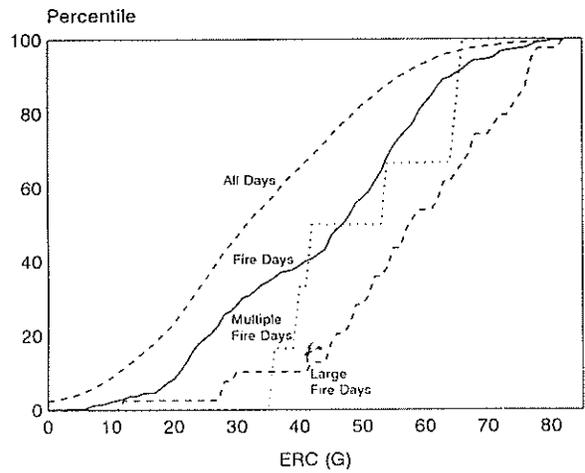


Table 1. Number and percentage of days in each index class.

INDEX	All days		Fire days		Large fire days		Multiple fire days	
	#	%	#	%	#	%	#	%
ERC								
0 - 18	872	20	29	5	1	2	0	0
19 - 35	1593	37	142	27	2	5	1	9
36 - 50	1137	26	134	25	7	17	5	46
51 - 65	619	14	174	33	12	28	2	18
> 65	148	3	52	10	20	48	3	27
Total	4369	100	531	100	42	100	11	100
KBDI								
0 - 25	1230	28	17	3	1	2	0	0
26 - 75	826	19	71	13	3	7	2	18
76 - 150	969	22	175	33	6	14	2	18
151 - 250	839	19	184	35	17	40	5	46
> 250	505	12	84	16	15	36	2	18
Total	4369	100	531	100	42	100	11	100

Figure 4. Percentile curves for all days, fire days, large fire days, and multiple fire days for ERC (fuel model G) and for KBDI for the Mammoth weather station and fires for all of Yellowstone National Park for 1965 through 1992.

levels of ERC and of KBDI. Bar charts of the data are given in Figure 5. Although only 17% of the days had an ERC over 50, 43% of the fire days and 76% of the large fire days occurred when ERC was over 50. And note that only one of the 11 multiple fire days occurred when ERC was less than 36.

Another way to relate fire danger to fire history is to use logistic regression (Loftsgaarden and Andrews 1992),

which is designed to handle binary data (0 or 1). Each day is classified in three ways: as a fire day (1) or not (0); as a large fire day or not; and as a multiple fire day or not. Figure 6 shows the resulting curves for probability of a fire day, large fire day, and multiple fire day as a function of ERC (fuel model G) and as a function of KBDI. Table 2 gives selected probability values from the curves in Figure 6. The probability of a fire day is 5%

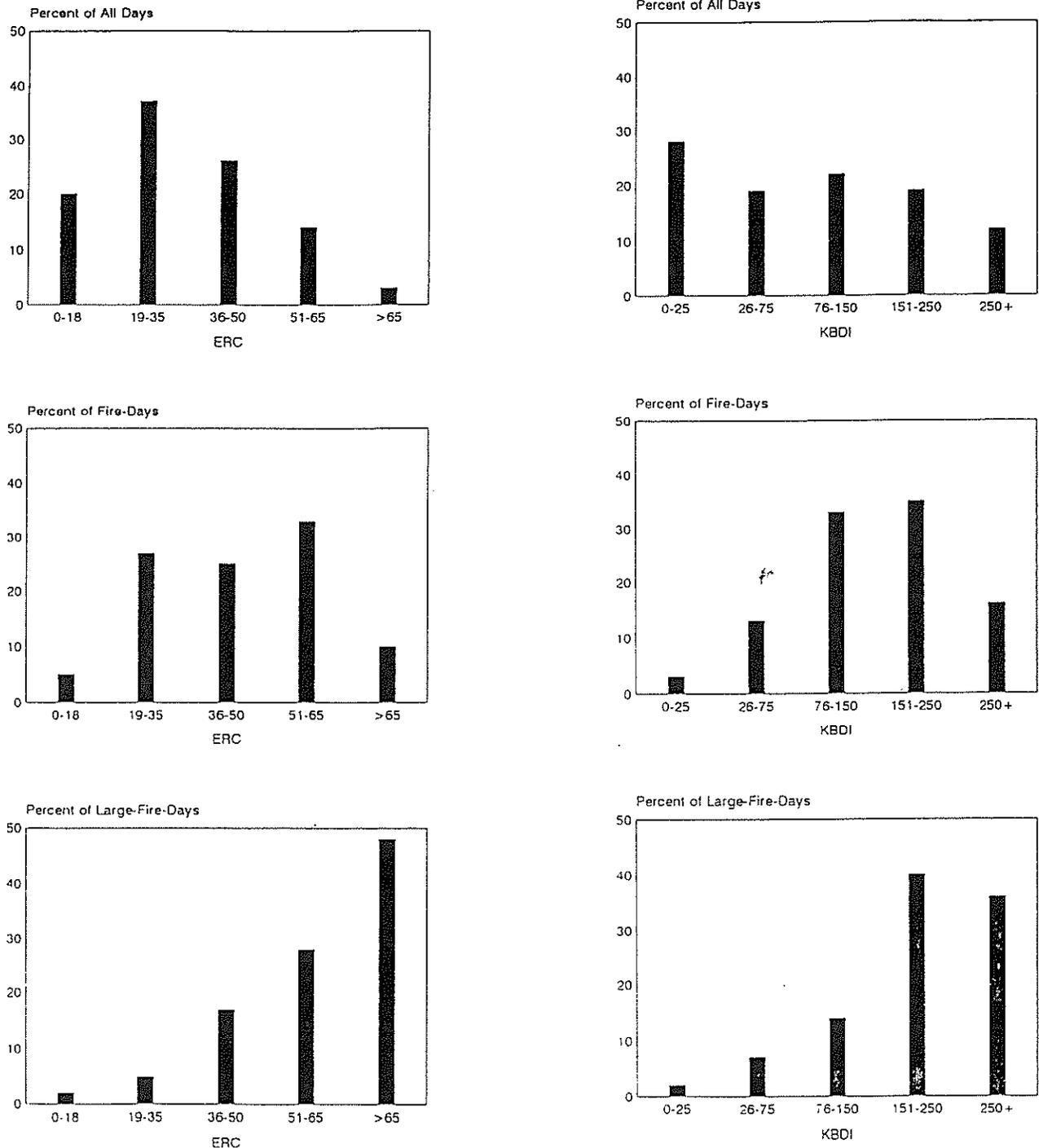


Figure 5. Bar charts for percentage of all days, fire days, and large fire days for the data in Table 1.

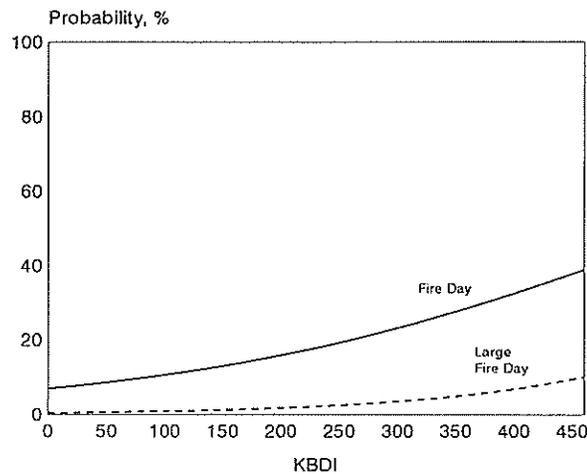
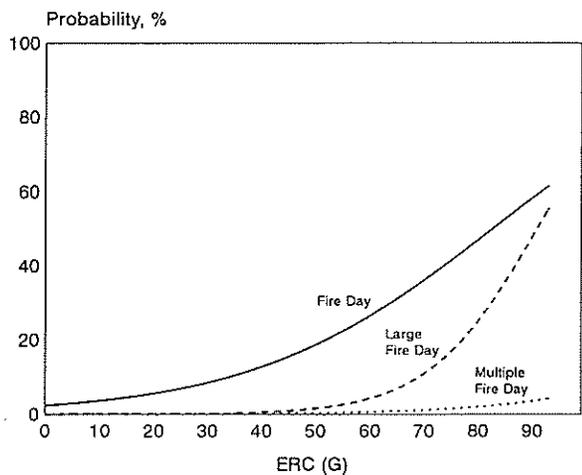


Figure 6. Probability of fire days, large fire days, and multiple fire days from logistic regression based on the same data as were used for the percentiles in Figure 4.

Table 2. Probability from logistic regression for selected index values.

INDEX	Fire day probability, %	Large fire day probability, %	Multiple fire day probability, %
ERC			
18	5	0	0
35	10	0	0
50	20	1	0
65	30	8	1
KBDI			
25	8	1	0
75	10	1	0
150	13	1	0
250	20	3	0

when ERC is 18 and 20% for ERC of 50. Probability of a large fire day increases from 1% to 8% as ERC goes from 50 to 65.

Although NFDRS cannot predict the behavior of individual fires, it can be used as an indicator of fire danger for a large area and can be used as a factor in prescribed natural fire decisionmaking. This analysis indicates that Energy Release Component, fuel model G, is a good indicator of fire danger for Yellowstone National Park.

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Physical and Chemical Responses of Streams in Yellowstone National Park Following the 1988 Wildfires

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Abstract. Wildfire can profoundly influence the physical and chemical characteristics of streams over time. The present study examined five years of temporal change in physical and chemical properties of 21 stream sites differentially affected by the 1988 wildfires. The percent catchment burned among sites ranged from 0% to over 90%. The degree of physical change was assessed using summed Coefficients of Variation (CV's) based on ten important measures of aquatic habitats. The degree of habitat change, as indicated by greater CV's, was positively correlated to the % catchment burned. Chemical changes over time also were examined for measures of nitrogen (NH_4 , NO_3), phosphate (OPO_4), alkalinity, and hardness. Few temporal changes were observed in the chemical measures except for nitrogen. Nitrate levels were elevated in most streams of burned catchments suggesting a loss of nitrogen from the catchment even after five years. In contrast, little increase in nitrate was observed in burned Fairy (75% burned) and Iron Springs (40% burned) Creeks suggesting a strong interplay between catchment geology/morphology and stream response to fire. These data show that streams are influenced directly by catchment fire, and that recovery trajectories among streams vary depending on the degree of catchment disturbance.

Keywords: Streams; Wildfire; Water chemistry; Habitat; Disturbance

Introduction

The wildfires of 1988 influenced 32 percent of the stream systems in Yellowstone National Park, affecting 20 separate river basins (Minshall and Brock 1992). Streams affected ranged in size from 1st order up to 4th order. Typically, streams larger than 5th order have shown little affect from large scale wildfire (Minshall et al. 1989) being mitigated by relatively large basin size and amount of stream flow. The present study focussed

on 21 stream sites 1st through 4th order in size with catchments differentially burned by the 1988 wildfires.

Most studies to date report similar short-term physical changes in streams resulting from their catchments being burned. These studies have suggested increases in overland flow and sediment inputs (surface erosion) because of vegetation loss on surrounding sideslopes (Tiedemann et al. 1979, Minshall et al. 1989, Minshall and Brock 1992). This loss in terrestrial vegetation translates into enhanced stream discharge, peak flows, the timing of flow events, and consequently enhanced scouring of stream channels (Minshall et al. 1989, Minshall and Brock 1992).

The chemical response of streams to wildfire has been variable. In general, nitrogen concentrations have increased during (Spencer and Hauer 1991) and following wildfire (see references in Tiedemann et al. 1979, Minshall and Robinson 1993). Little change in phosphorus concentrations have been observed in streams following wildfire, although a few studies have shown slight increases in phosphorus levels (Tiedemann et al. 1979). Further, it is anticipated that cation concentrations should increase immediately following fire resulting from ash inputs (Tiedemann et al. 1979), but any chemical changes should dissipate in less than three years as riparian vegetation recovers (Minshall et al. 1989). The present study encompassed five years of water chemistry and physical data following wildfire, and thus should add important insights towards short-term and intermediate-term chemical and physical responses of streams following wildfire. Our objective was to examine changes in water chemistry and physical conditions among study sites in relation to differences in burn characteristics.

Methods

The study examined physical and chemical changes in 21 sites ranging in size from 1st through 4th order.

Streams were surveyed in early October 1988 (immediately following the fires) and mid-August 1989, 1990, 1991, and 1992 during baseflow. Figure 1 displays the general locations for the study streams, and Minshall and Robinson (1993) provide the exact site coordinates. Streams ranged in percent catchment burned from 0% (Rose Creek) to 92% (EF Blacktail Deer Creek)(Table 1).

Physical characteristics used to determine habitat changes among years included the range in annual stream temperature, bankfull width, mean embeddedness, mean bottom water velocity, mean water depth, mean substrate size, median substrate size, width:depth ratios, channel area change, and channel area ratios (present year divided by previous year) between years (Minshall and Robinson 1993). The average amount of channel area change, channel area ratios, bankfull widths, and width:depth ratios were determined from five permanent cross-sectional transects located at each site. Transects were placed about 50 m apart along the stream at each site and profiles recorded each year. The first transect at a site was located randomly, and transects primarily were associated with riffle/run habitats. Mean embeddedness, water depth, bottom velocity, and substrate size were recorded at 100 random points each year located in a 200-m reach of each stream being bounded within the first and last transect.

Temporal change for each habitat measure was estimated using Coefficients of Variation (CV) based on yearly means (i.e., $N=5$ for CV) (Robinson et al. 1994). These ten habitat CV's were summed for an overall indication of habitat change among years for each site and regressed against the percent (%) catchment burned. In addition, these summed habitat CV's were used to arbitrarily group sites as showing low, medium, or high amounts of habitat change over the five years of study (Table 1). Summed CV values were less than 2.00 for streams showing little change (five streams), between 2.00 and 3.00 for streams of medium change (seven streams), and greater than 3.00 for streams showing a high amount of physical change (nine streams).

Water chemistry was monitored either on site (e.g., specific conductance and pH) or collected and analyzed in the laboratory using standard methods (APHA 1989). Samples returned to the laboratory were analyzed for total hardness, alkalinity, ortho-phosphorus, ammonia, and nitrate. Temporal changes in these chemical parameters were represented graphically with sites separated by degree of habitat change as described above. It was expected that streams showing greater physical change would also show greater temporal change in chemical properties, especially in nitrogen concentrations.

Results and Discussion

Physical Changes

Summed habitat CV's ranged from 1.41 (unburned Rose Creek) to 4.05 (80% burned 2nd order Fairy Creek) (Table 1). Higher summed CV's were indicative of greater habitat change during the study period. Some variables appeared to be more sensitive to the effects of fire than others. For example, burned sites exhibited major changes in channel morphology that were not evident for streams draining unburned catchments (Figure 2). Streams of burned catchments showed channel widening and deepening resulting from enhanced flows during spring runoff and periodic summer and autumn rainstorms (Minshall and Robinson 1993). There was a significant positive regression of the summed habitat CV's against % catchment burned ($r^2=0.67$) suggesting the measured physical changes were a result of the wildfires.

Water Chemical Changes

Essentially no temporal change was observed in total hardness in all streams regardless of the % catchment burned or degree of physical change (Figure 3). Total hardness values were always less than 100 mg/L, with most streams showing values of less than 60 mg/L. This lack of change also was seen for values of alkalinity, specific conductance, and pH (Minshall and Robinson 1993).

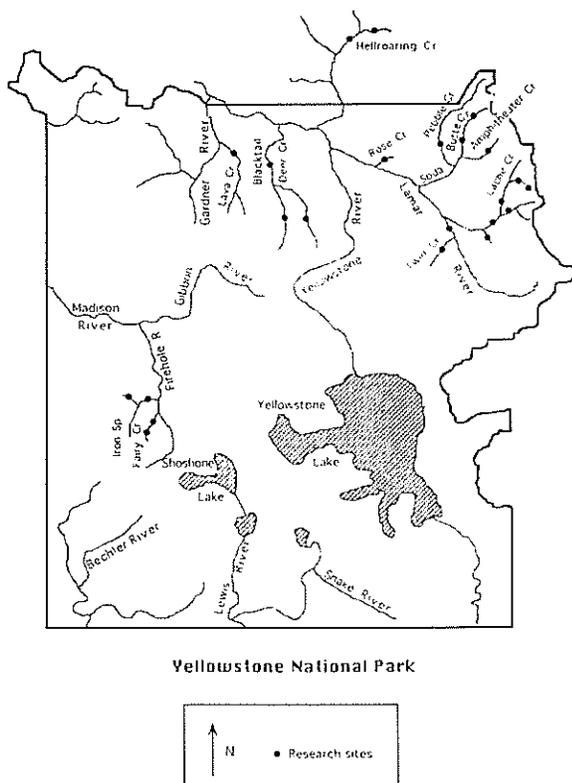


Figure 1. Map of study site locations.

Ortho-phosphate concentrations have remained relatively low for all streams, although some streams showing medium and high amounts of physical change displayed slight increases in ortho-phosphorus levels in 1989 (Figure 4). Concentrations of ortho-phosphorus were always below 0.2 mg/L suggesting this nutrient is most likely limiting in these streams and may not display substantial increases in base-level concentrations over time as a result of wildfire.

Nitrate was the only nitrogen constituent to show obvious concentration increases in streams of burned catchments following the wildfires (Figure 5). Nitrate levels typically increased 3-4X in streams showing medium and high amounts of physical change, suggesting a substantial loss in nitrogen from burned catchments. However, streams of burned catchments having little physical change displayed no increase in instream nitrate levels. In addition, there was a positive regression in the

Table 1. Mean values and CV's among years for important habitat characteristics for the study sites.

Stream	Order	Percent Burned		Annual Temperature Range	Channel Area Change	Ratio Channel Area	Width: Depth Ratio	Bankfull Channel Width	Embeddedness	Bottom Velocity	Water Depth	Substrate Size (mean)	Substrate Size (median)	Summed CV's
Blacktail Deer, EF	1	92	mean CV	18.00 0.09	0.59 0.47	1.06 0.11	52.33 0.70	665.00 0.67	0.38 0.41	0.26 0.30	13.18 0.12	10.78 0.42	5.02 0.32	3.61
Blacktail Deer, WF	1	90	mean CV	19.00 0.10	0.65 0.21	1.07 0.09	33.70 0.18	550.40 0.07	0.46 0.31	0.16 0.25	16.78 0.16	15.02 0.14	7.85 0.29	1.79
Upper Cache	1	64	mean CV	16.33 0.08	1.14 0.62	1.01 0.03	141.95 0.64	704.80 0.49	0.37 0.32	0.12 0.38	5.72 0.34	7.24 0.27	3.63 0.49	3.66
Fairy	1	76	mean CV	19.25 0.02	0.25 0.49	1.16 0.19	13.46 0.59	307.40 0.54	0.59 0.26	0.30 0.40	23.72 0.11	0.95 0.19	0.34 1.00	3.81
Twin	1	68	mean CV	15.00 0.09	1.32 0.54	1.07 0.04	49.12 0.30	643.80 0.30	0.38 0.33	0.18 0.62	13.34 0.17	19.20 0.13	12.36 0.22	2.75
Lower Cache	2	47	mean CV	17.50 0.03	0.99 0.61	1.05 0.04	70.42 0.28	832.00 0.56	0.36 0.09	0.26 0.24	11.12 0.35	14.18 0.24	6.12 0.07	2.52
Upper Cache	2	71	mean CV	20.33 0.20	2.54 0.69	1.04 0.03	83.86 0.59	764.80 0.56	0.37 0.19	0.19 0.29	9.36 0.07	8.44 0.15	5.65 0.50	3.27
Fairy	2	81	mean CV	24.50 0.06	0.31 0.37	1.00 0.07	30.26 0.57	395.60 0.07	0.37 0.43	0.18 0.45	18.06 0.49	4.98 0.72	0.38 0.82	4.05
Iron Springs	2	5	mean CV	8.25 0.20	0.99 0.81	1.06 0.21	17.85 0.41	237.40 0.20	0.82 0.28	0.22 0.29	14.62 0.31	2.68 0.87	2.90 0.24	3.81
Blacktail Deer, Main	2	88	mean CV	16.00 0.08	0.85 0.90	1.11 0.16	45.21 0.26	710.80 0.49	0.34 0.43	0.33 0.27	15.26 0.24	11.10 0.40	11.93 0.11	3.32
Amphitheater	2	2	mean CV	12.75 0.13	0.97 0.45	1.04 0.07	82.19 0.21	1115.80 0.23	0.36 0.13	0.30 0.06	13.78 0.17	16.80 0.12	10.03 0.27	1.83
Rose	2	0	mean CV	12.00 0.10	0.36 0.38	1.01 0.02	40.68 0.09	416.20 0.04	0.31 0.15	0.21 0.24	10.32 0.10	12.66 0.13	8.15 0.15	1.41
Pebble	3	17	mean CV	19.33 0.10	0.59 0.32	1.01 0.03	60.89 0.15	1101.00 0.02	0.41 0.21	0.34 0.22	18.30 0.14	19.48 0.20	11.95 0.32	1.71
Cache	3	68	mean CV	20.50 0.09	8.50 0.77	1.04 0.10	242.62 0.23	4606.80 0.12	0.32 0.21	0.30 0.94	19.40 0.11	14.02 0.26	10.14 0.37	3.21
Hellroaring	3	59	mean CV	18.50 0.14	0.97 0.33	1.03 0.04	73.75 0.14	1234.20 0.13	0.29 0.20	0.28 0.40	16.90 0.14	16.50 0.20	10.55 0.28	2.00
Iron Springs	3	39	mean CV	9.50 0.16	0.60 0.30	1.07 0.17	21.80 0.27	587.00 0.30	0.37 0.22	0.37 0.52	26.78 0.08	6.94 0.47	3.40 0.21	2.70
South Cache	3	39	mean CV	20.50 0.22	1.57 0.54	1.04 0.07	106.73 0.21	1707.00 0.17	0.31 0.11	0.26 0.31	16.18 0.09	16.16 0.25	10.25 0.27	2.24
Lava	3	47	mean CV	19.00 0.09	1.51 0.85	1.07 0.18	32.40 0.09	768.00 0.02	0.34 0.17	0.40 0.41	23.92 0.08	23.52 0.72	14.07 0.60	3.21
Cache	4	59	mean CV	19.33 0.13	1.03 0.48	1.00 0.03	120.33 0.30	2052.00 0.03	0.43 0.26	0.25 0.22	18.20 0.21	16.68 0.10	11.49 0.28	2.05
Hellroaring	4	46	mean CV	19.00 0.13	2.18 0.42	1.00 0.05	133.62 0.20	2614.40 0.06	0.25 0.40	0.26 0.34	20.20 0.15	12.60 0.11	9.75 0.15	2.03
Lamar	4	50	mean CV	20.25 0.07	1.83 0.49	1.01 0.01	84.98 0.08	2872.80 0.03	0.44 0.19	0.24 0.37	33.92 0.07	20.94 0.13	18.35 0.30	1.75

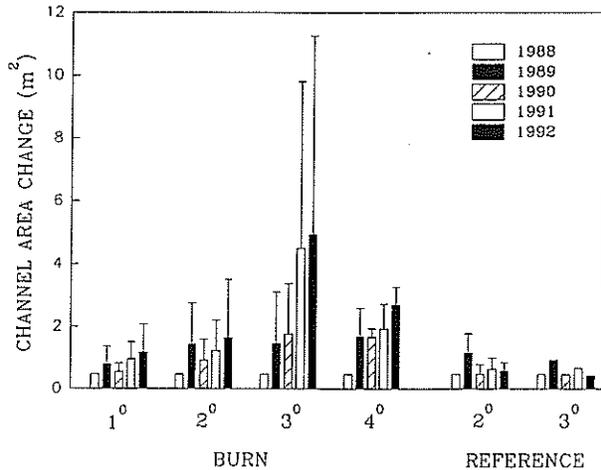


Figure 2. Amount of channel area change (in m²) over time in burned and unburned streams grouped by stream order. Bars represent means +1 SD. N=5 for 1st, 2nd, and 3rd order burn streams, 3 for 4th order burn streams, 2 for 2nd order unburned streams, and 1 for 3rd order unburned streams.

range of nitrate concentration in each stream against the % catchment burned with catchments showing little physical change removed from the analysis (Figure 6). These data suggest that nitrogen losses were greater from burned catchments experiencing a high amount of physical change than catchments with a similar percent of their catchment burned but showing little change in stream

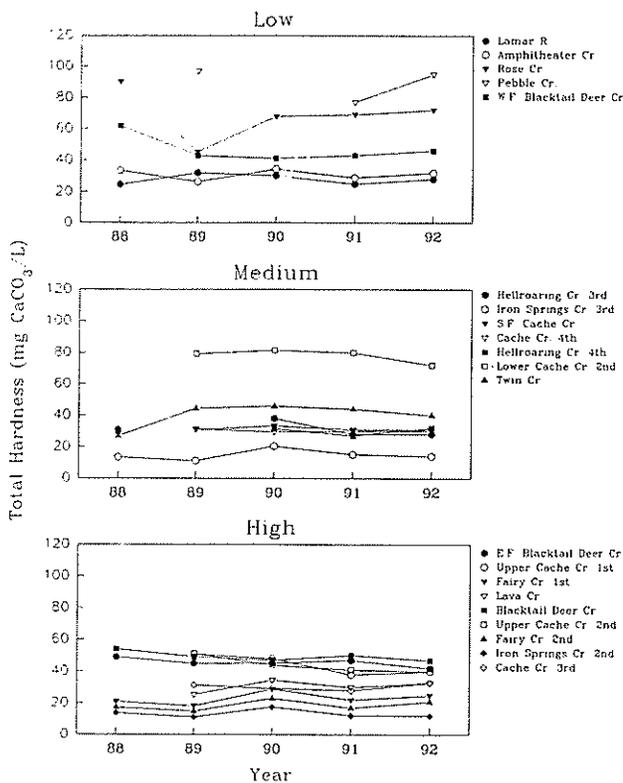


Figure 3. Temporal changes in total hardness concentrations (mg/L CaCO₃) for each study stream with sites grouped in respect to degree of physical change based on summed habitat CV's.

physical properties. The probability of increased lateral nutrient inputs is greater in heavily burned catchments than in less extensively burned catchments because of increased overland flow moving burned debris into streams (Minshall and Brock 1992). Whether this increase in nitrate concentration in burned streams is biologically important has yet to be determined.

In summary, these data suggest substantial physical changes occurred in streams impacted by the 1988 wildfires. Streams in more extensively burned catchments displayed greater changes in physical properties than

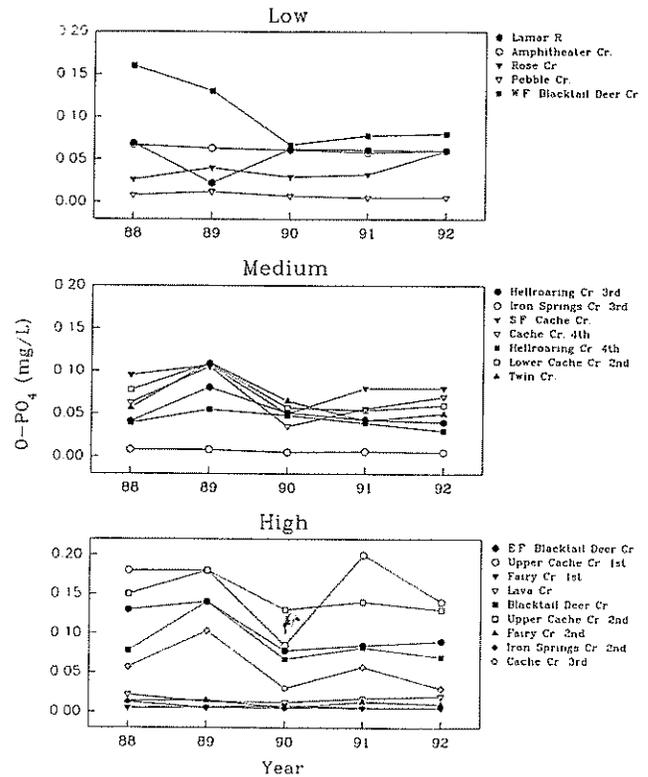


Figure 4. Temporal changes in ortho-phosphorus levels (mg/L) for each study stream with sites grouped in respect to degree of physical change based on summed habitat CV's.

streams of less extensively or unburned catchments. Major changes were observed in channel morphology with channels being eroded (e.g., to bedrock in some cases) and moved laterally (e.g., greater than 30-m in Cache 3rd order). Many streams in burned catchments also experienced additional physical changes in 1992, four years after wildfire (Minshall and Robinson 1993).

In addition, streams of burned catchments exhibited increases in nitrate levels in the years following the wildfires suggesting a substantial loss of nitrogen from these catchments. Little change was observed for other chemical constituents such as phosphorus and cation concentrations. However, Spencer and Hauer (1991) found elevated instream phosphorus levels during a firestorm which they attributed to high levels of ash and

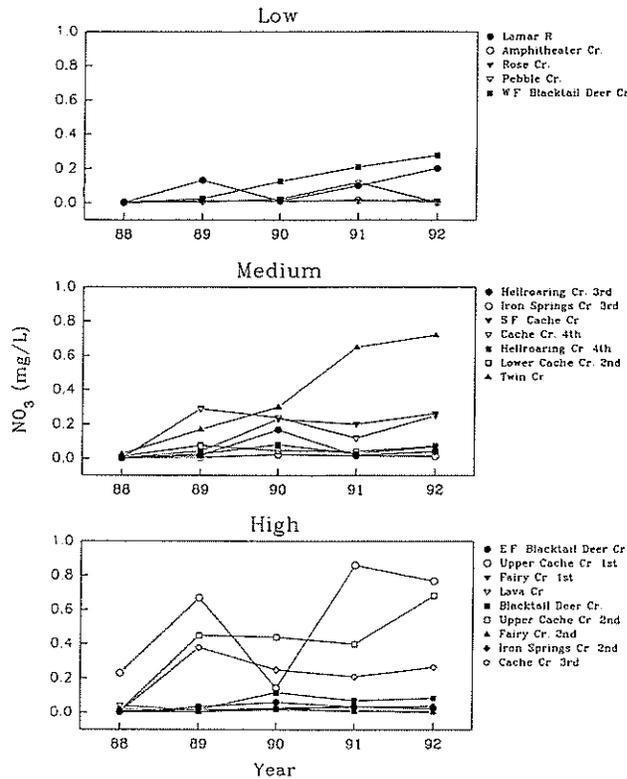


Figure 5. Temporal changes in nitrate levels (mg/L) for each study stream with sites grouped in respect to degree of physical change based on summed habitat CV's.

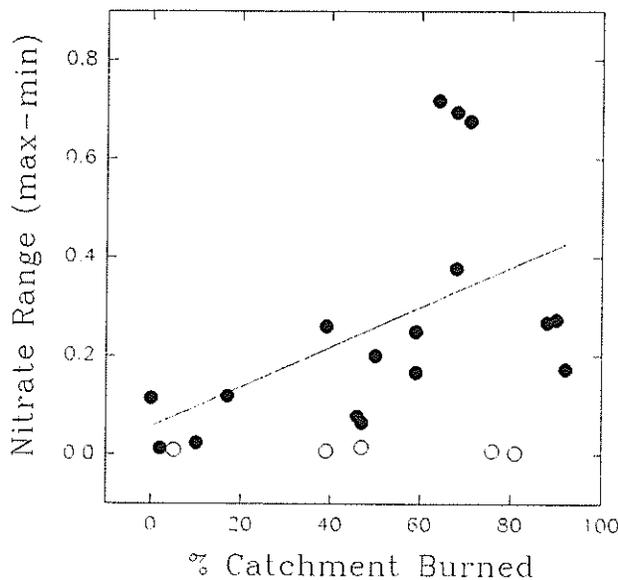


Figure 6. Regression scatterplot of nitrate range (maximum-minimum) for the five years of study for each study stream against the percent catchment burned. Closed circles represent sites showing medium and high amounts of physical change; open circles represent sites showing low amounts of physical change based on summed habitat CV's.

burned debris entering the stream. Some of our more disturbed streams did show slight increases in phosphorus levels the first year following the wildfires suggesting lateral inputs of burned debris from which phosphorus may leach or direct inputs from overland runoff. These data suggest that streams are influenced directly by catchment fire, and that recovery trajectories among streams vary depending on the degree of catchment disturbance following fire.

Acknowledgments. Numerous individuals have assisted in the collections, processing, and analysis of the diatom samples and physical data over the study period, especially G. T. Boltz, D. G. Carty, P. D. Dey, D. L. Mahony, M. J. McIntyre, J. M. Minshall, G. C. Mladenka, D. C. Moser, C. A. Nelson, B. E. Olenick, S. E. Relyea, and R. L. Vannote. T. V. Royer reviewed an earlier draft of the manuscript. We thank R. E. Gresswell and R. D. Jones of the U.S. Fish and Wildlife Service and J. D. Varley of the National Park Service for their efforts to facilitate our work in Yellowstone National Park. Funding for the project was provided by the National Park Service, National Science Foundation and Idaho State University.

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Effects of the Yellowstone Fires of 1988 on Elk Habitats

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Abstract. The short term effects of the 1988 Yellowstone fires were predicted to change several elk habitats and elk behaviors. This paper presents investigations on those predictions. Forage biomass did not increase on the winter range habitats of burned sagebrush or Douglas fir forest as predicted, but decreased where moderate soil heating (heating to a depth of 5cm) was extensive. Forage protein and digestibility were higher from fall and spring forages and from forages found in elk snow feeding craters as predicted. Snow depths did not increase as measured in elk snow feeding craters in sagebrush and Douglas fir forest habitats as predicted due to the mosaic pattern and partial canopy burn characteristics of the fires. Elk diet diversity after the fires on the winter range did not increase as predicted. Elk habitat use did not increase on summer range meadow-forest mosaic habitat two years after the fires nor did winter range habitat use increase on sagebrush and Douglas fir forest habitats several years after the fires as predicted. Burned willow protein and digestibility increased as did leaf sizes and shoot length as predicted, but production increased only at half the sample sites, less than what was predicted. Ungulate use of burned willows increased after the fires such that willow stature had not increased, creating a lack of willow response to fires. The short term effect of the fires had an unpredictable effect on elk and elk habitats revealing that the patterns and mechanisms of fire effects had yet to be fully established in all situations in Yellowstone.

Introduction

The large Yellowstone fires of 1988 provided an unexcelled opportunity to document the effects of fire on elk (*Cervus elaphus*), since a number of studies on elk and their habitats had been conducted just prior to and continuing after the fires. The Yellowstone fires of 1988 burned about one-third of the winter range and about one-half of the summer range of the 3rd largest elk herd in

North America. Partly as a result of the continuing controversy over the management of the elk population, elk were rated one of the highest priority species to study following the 1988 fires.

The purpose of our investigation was to sample the short term effects of the fires of 1988 on elk habitat use, elk forage biomass, elk forage quality, and snow characteristics in key elk winter habitats. We also studied the effects of the fires on willow biomass production, forage quality, willow morphology and rates of use by elk to document whether or not fires enhanced willow status.

We investigated the following hypotheses:

1. Elk will concentrate on burned areas due to a variety of changes brought on by the fires such as: increases in plant diversity and landscape diversity (Christensen et al. 1988) and earlier and longer lasting periods of green forage (Peet et al. 1975, Hobbs and Spowart 1984).
2. Elk diets will increase in diversity due to changing palatability of burned forages (Leege 1969, Asherin 1976).
3. Production of bunchgrass forages, following some initial declines, will increase dramatically over pre-burn levels, as will tissue nutrient concentrations (Merrill et al. 1982, Christensen et al. 1988, Boyce and Merrill 1989).
4. Burned forests and sagebrush habitats will have greater snow depths due to the loss of tree canopy interception of snow.
5. Burning will cause willows to have enhanced forage quality, higher production, and increased stature.

Methods

Elk Summer Habitat Use

Summer habitat use by elk was estimated through the use of elk pellet groups. Three sites in the meadow-forest mosaic were chosen on the summer range of the Northern Range elk herd (Houston 1982) where burned and unburned areas were in close proximity (Figure 1). The burned areas include a mix of mosaic and canopy burned areas. Spatial analysis (Palmer 1988, Robertson 1987) on a pilot study done in the summer of 1989 on burned and unburned areas found that pellet densities were spatially dependant at several scales. At small scales, less than 20m pellet groups were found spatially dependant which is probably related to the fact that pellets form a clumped distribution (White and Eberhardt 1980). Because of the clumped nature of the pellet groups, long transects approximately 250m and 1.25m wide were selected to ensure that a sample included several clumps along with areas between clumps. At larger scales, dependance was also found which was thought to be related to the pattern where elk pellet densities were highest in the meadows and declined at distances further into the forest. In order to establish if the pattern of elk pellet group densities changed due to burning, ten belt transects were randomly placed in meadows, in the forest less than 100 m from a meadow edge, and in the forest more than 100 m from

any meadow edge in both burned and unburned areas in the three sites. Counts of elk pellet groups were done only in August 1990. The counts were of all pellet groups for the current summer. Pellets from the previous summer were easily distinguished from the current summer's pellets.

Diet Diversity

Elk fecal pellet samples were composited from at least 10 separate pellet groups at each sampling site throughout the winter at various locations on the northern range in the winters of 1985-86, 1986-87, 1989-90, and 1990-91. Composition of wintering elk diets on the northern range before and after the fires was determined through microhistological analysis of fecal pellets at Washington State University. Diversity for each diet was calculated with Shannon's index (Ludwig and Reynolds 1988). Diversity before and after the fires was tested with the Mann-Whitney U test (Wilkinson 1990).

Fall Forage Biomass

Four sites each were chosen in Douglas fir habitats and sagebrush habitats in the fall of 1989 and 1990 where forage biomass was estimated (Figure 1). At each site a burned and unburned area was chosen for sampling which had similar characteristics. In the Douglas fir burned sites, the samples were further stratified as to moderate soil heated areas where soils were heated to a depth of 5cm, and light soil heated areas where only surface materials were charred. In each burned and unburned area a 60m transect was randomly placed along which 15 0.5m² plots were systematically placed. In each of the 15 plots biomass under 40 cm was estimated using the canopy intercept method (Frank and McNaughton 1990) which is a nondestructive method of biomass estimation having been extensively used in Yellowstone. Biomass in 1990 was classified as to dead or green. Shrub biomass was made up only of current years growth. Data were analyzed in a blocked ANOVA fashion with multiple comparisons done using the Tukey-Kramer method (Wilkinson 1990).

Forage Quality on the Northern Range

Forage quality as indexed by the percentage of protein and amount of in vitro dry matter digestibility was estimated for fall, winter and spring forages. In the fall of both 1989 and 1990, 12 random samples of *Agropyron spicatum* and *Festuca idahoensis* were collected in each of three sites in burned and unburned sagebrush habitats within several days of each other (Figure 1). The same design was used on *Poa* spp. in burned and unburned Douglas fir forest habitat. During the winters of 1989-90

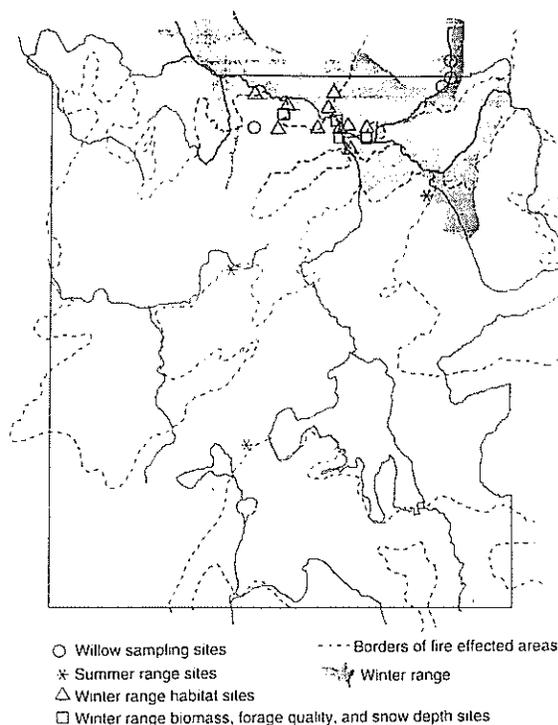


Figure 1. Map of Yellowstone National Park with locations of sample sites.

and 1990-91, 12 forage samples were collected from randomly selected elk snow feeding craters at three sites each in burned and unburned sagebrush and Douglas fir forest habitats within several days of each other. In the spring of 1990 and 1991 graminoid forage samples were hand collected from randomly selected elk feeding sites. Out of the 12 samples collected, eight had both protein and dry matter digestibility determined with the remaining 4 having dry matter digestibility determined. Crude protein (Assoc. Off. Anal. Chem. 1970) and in vitro dry matter digestibility (Tilley and Terry 1963) were analyzed at the Nutritional Analysis Lab, Colorado State University. Data were analyzed in blocked ANOVA fashion.

Snow Characteristics of the Northern Range

Snow depth and density were measured for the winters of 1989-90 and 1990-91 at four sites within both burned and unburned sagebrush and Douglas fir habitats (Figure 1). At each site, 10 elk snow feeding craters were randomly selected. Snow depth and density at the elk snow feeding craters were measured with a standard Soil Conservation Service snow sampler. An additional site in a canopy burned Douglas fir habitat was selected to compare with the other burned sites. The winters were stratified into two periods early, December to the middle of February, and late, middle of February to yearly April. Depth and density were analyzed in a blocked ANOVA fashion.

Elk Winter Habitat Use

Elk habitat use on the northern range during the winter was indexed through the measurement of elk feeding craters in snow. Two habitats, sagebrush and Douglas fir forests, were chosen because they constitute the largest amount of habitat on the northern range and are used extensively by elk. Ten sites each were selected in sagebrush and Douglas fir forest habitats where burned and unburned areas were in close proximity (Figure 1). In each burned and unburned area a belt transect measuring 0.3 to 1km long and 4m wide was randomly placed. All individual feeding craters were counted within the transect. Transects were surveyed in December and January for the early winter period and in February and March for the late winter period during the winters of 1989-90 and 1990-91. Data were analyzed in a randomized block fashion using multipermutation statistics (Biondini et al. 1988).

Willow Responses to Fire

Three willow communities sampled in July of 1988 before the fires were burned by the Hellroaring Fire in

August of 1988 (Figure 1). These sites were sampled post burn and that data compared to the pre burn data. Another site was sampled post burn along Blacktail Deer Creek where the creek served as a firebreak. Willows on the west side of the creek were burned by the North Fork fire on 9 September 1988, but willows immediately across the creek escaped the fire. Site condition and aspect were similar for comparisons. Willow at two of the sites were classified as tall, 121+cm (Upper Slough Creek), willows at Blacktail Deer Creek were classified as intermediate, 81-120 cm, while willows at Middle Slough were classified as suppressed (<80cm) using the analysis of Singer et al. (1994).

Willow biomass pre-burn and in burned and unburned sites following the fires was estimated from measurements taken in 15 random circular plots of 9.3 m² each in each treatment. Within each plot, the height of the tallest leader, widest shrub crown diameter, perpendicular shrub diameter, and species of each willow clump were measured. On every fourth individual shrub of each species, the number of rooted stems, number of shoots per stem, length, height, and basal diameter of current annual growth were measured. Aboveground biomass was estimated from a random subsample of twig weights against twig length and basal green twig diameter at the base of the current annual growth following MacCracken and Viereck (1990). Log-log predictor regressions were calculated for each species and each year. Squared Multiple R values were high ($r^2=0.78-0.97$) and the plots of the residuals were normal. Percent shoot use each winter was sampled by counting browsed and unbrowsed shoots on 30-50 marked clumps at each site.

Willow clump height, shoot lengths, and shoot weights of 10 randomly selected shoots per plant were recorded in 1989 at the Blacktail site, one year following the fires. Leaf surface areas were measured using a leaf area meter (Beerling and Fry 1990) on eight shoots randomly collected from 10 burned and unburned willows at the Blacktail Deer Creek site. Moisture stress of burned and unburned willows was sampled during July of 1989 using a Scholander pressure bomb (PMS Instrument Co., Corvallis, OR). Water stress was measured predawn (0300-0600 hr) in order to reduce fluctuations in readings due to varying day time temperatures and cloud cover. The distal 12 cm of two shoots from each of 10 clumps was cut, and the water pressure measured immediately. Forage quality of shoots was sampled from the same sets of shoots collected for weights. All shoots were gathered from the primary browse zone. Shoots were oven dried for 48 hours at 50-60C. Crude protein (Assoc. Off. Anal. Chem. 1970) and in vitro dry matter digestibility (Tilley and Terry 1963) were analyzed at the Nutritional Analysis Lab, Colorado State University.

Results

Elk Summer Habitat Use

Elk activity, as indexed by density of pellet groups, was compared to burned and unburned meadow-forest mosaic habitat on the summer range. Comparisons were made between burned and unburned meadows, forest edge, and forest interior. Elk activity did not vary between any of the comparisons over the three sites on the summer range (Figure 2).

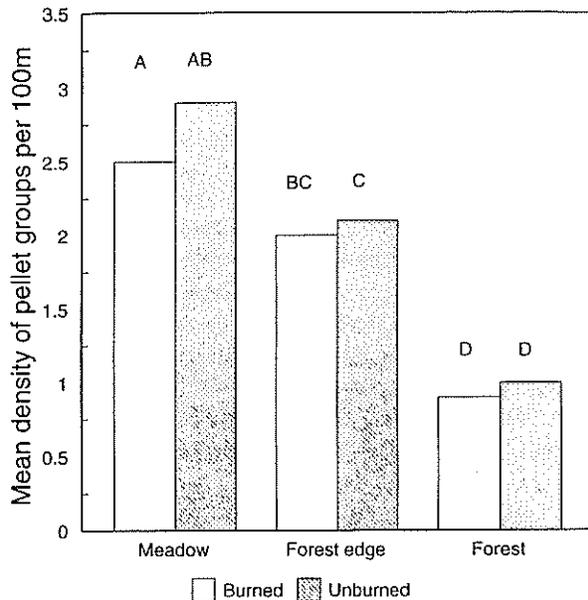


Figure 2. Mean density of pellets groups per 100m of transect. Means denoted with the same letter are not significantly different at $p > 0.05$.

Diet Diversity

Diet diversity of wintering elk on the northern range was compared before and after the fire. Diversity before the fires was 2.4 (SE 0.06, $n=15$) and after 2.3 (SE 0.06, $n=32$). No difference was found between diversity before and after the fires.

Fall Forage Biomass

Sagebrush fall forage total and graminoid biomass was significantly lower on burned areas in 1989 and 1990 while forbs had a significantly higher biomass (Figure 3). Green biomass did not differ in 1990 while there was significantly more dead biomass. Douglas fir fall forage biomass did not significantly differ between the light soil heated areas and the unburned areas, whereas the moderately soil heated areas had significantly lower biomass

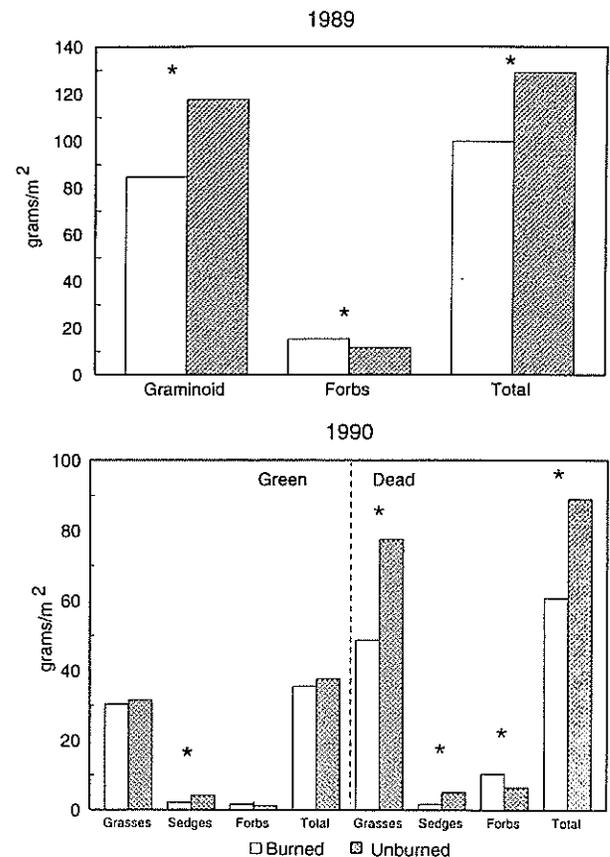


Figure 3. Comparison of fall biomass in burned and unburned sagebrush grasslands. Comparisons denoted with a * are significantly different $p < 0.05$.

(Figure 4). In 1990, forb biomass in the moderate and light soil heated areas was significantly higher.

Forage Quality on the Northern Range

Burned fall forage protein was significantly higher in the selected grasses the second year after the fires with two of the three species being significantly higher the first year (Table 1). Burned fall digestibility was significantly higher the first year after the fires with only one species significantly different two years after the fires. Winter forage protein from elk snow feeding craters was significantly higher the second year after the fires in both habitats with the same response as the fall protein levels of *Festuca idahoensis* (Table 2). Burned winter forage digestibility was significantly higher only the second year after the fires in the sagebrush habitat. Burned spring forage protein was significantly higher two years after the fires and was still significantly higher three years after the fires (Table 3). Burned spring forage digestibility was only significantly higher in the sagebrush habitat two years after the fires.

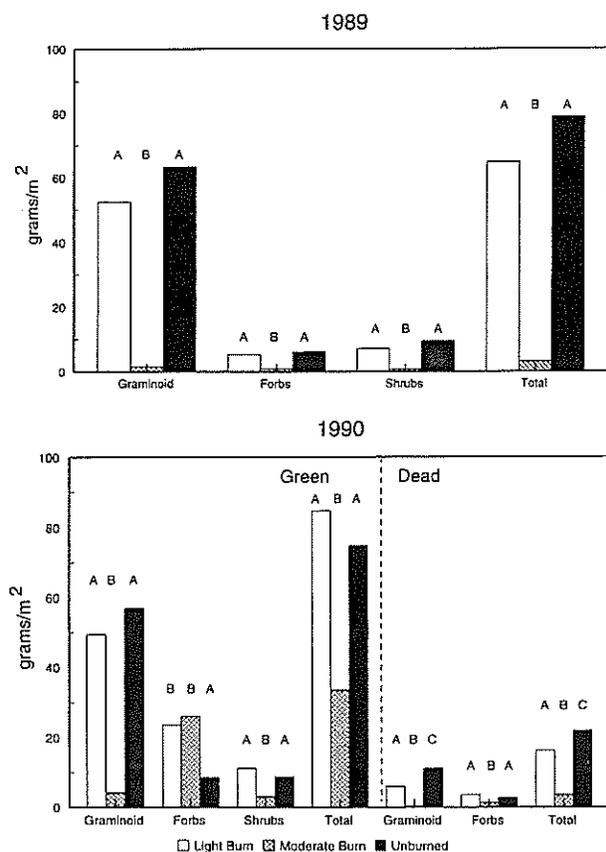


Figure 4. Comparison of fall understory biomass in lightly burned, moderately burned, and unburned Douglas fir forest. Means denoted with the same letter are not significantly different at $p > 0.05$.

Table 1. Mean percentage of protein and dry matter digestibility (DMD) of winter forages collected in feeding craters in burned and unburned sagebrush grasslands and Douglas fir forests during the winters of 1989-90 and 1990-91 (SD in parenthesis). Burned to unburned comparisons not followed by the same letter were found to be significantly different at $P < 0.05$.

Habitat	%Protein		%DMD	
	Burned	Unburned	Burned	Unburned
Winter 1989-90				
Sagebrush	4.7 (1.8)A	4.9 (1.1)A	51.1 (5.9)A	51.4 (5.5)A
Douglas fir	4.6 (1.5)A	4.6 (1.3)A	47.9 (6.7)A	51.8 (6.4)B
Winter 1990-91				
Sagebrush	5.3 (1.4)A	4.4 (1)B	47 (3.2)A	44.4 (3.6)B
Douglas fir	6.2 (2.2)A	5.1 (1.2)B	45.8 (4.2)A	45.1 (4.2)A

Snow Relations on the Northern Range

Snow depths at elk feeding craters did not differ between burned and unburned habitats at any time after the fires (Figure 5). At the additional canopy burned Douglas fir habitat site snow depths were significantly higher three of the four periods ($p < 0.05$) compared to the

Table 2. Mean percentage of protein and dry matter digestibility (DMD) of three grasses collected in the fall of 1989 and 1990 (SD in parenthesis). Burned to unburned comparisons not followed by the same letter were found to be significantly different at $P < 0.05$.

Forages	%Protein		%DMD	
	Burned	Unburned	Burned	Unburned
Fall 1989				
<i>Agropyron spicatum</i>	6.4 (1.9)A	4.2 (0.7)B	57.2 (6.4)A	50 (5.4)B
<i>Festuca idahoensis</i>	10.7 (1.8)A	11 (7.7)B	67.3 (5.8)A	63.6 (4.6)B
<i>Poa spp.</i>	17.2 (2.2)A	8.7 (2.3)B	78.9 (3)A	67.9 (6.2)B
Fall 1990				
<i>Agropyron spicatum</i>	4.6 (0.7)A	3.9 (1.2)B	45.9 (3.9)A	45.1 (5.6)A
<i>Festuca idahoensis</i>	7.4 (2)A	5.9 (1.1)B	56.9 (7)A	54.3 (6.5)B
<i>Poa spp.</i>	7.7 (2.9)A	6.4 (1.8)B	56.9 (6.8)A	54.5 (7.7)A

other burned Douglas fir habitat sites. Snow density was significantly higher for burned habitats three of eight periods (Figure 6).

Elk Winter Habitat Use

Elk crater densities did not differ between burned and unburned areas either during early or late winter sampling periods in the sagebrush and Douglas fir forest habitats ($p > 0.05$).

Willow Responses to Fire

Percent willow leader use by elk increased dramatically following the fires on the burned willow clumps (Figure 7). Higher rates of herbivory were apparently related to higher protein levels and generally higher

Table 3. Percent protein and percent dry matter digestibility (DMD) of spring forages collected in 1990 and 1991 in burned and unburned sagebrush grasslands and Douglas fir forests on the Northern Range (SD in parenthesis). Burned to unburned comparisons not followed by the same letter were found to be significantly different at $P < 0.05$.

Habitat	%Protein		%DMD	
	Burned	Unburned	Burned	Unburned
1990				
Sagebrush	26.6 (3.4)A	18.7 (2.3)B	76.6 (3.3)A	72.8 (3.4)B
Douglas fir	28.1 (3)A	25.3 (3.1)B	77.3 (4.1)A	75.7 (3)A
1991				
Sagebrush	24.4 (3.2)A	22.5 (2.5)B	75.2 (3.7)A	73.2 (3.1)A
Douglas fir	27.1 (4.3)A	25.1 (4.8)A	78.7 (3.3)A	78 (4.4)A

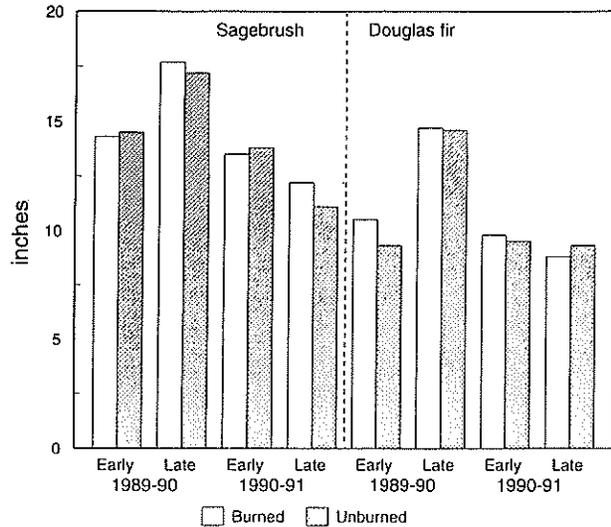


Figure 5. Comparison of mean snow depths of burned and unburned sagebrush grasslands and Douglas fir forests. Comparisons denoted with a * are significantly different $p < 0.05$.

digestibility of burned willows (Table 4). Wolf and Geyer willows had significantly higher protein concentrations for all three willows height classes. Digestibility increased in burned suppressed willows, but decreased in burned tall willows; the average increase in digestibility was 6.2% for suppressed willows of all three species.

Burning produced a variable effect on willow production. Burned stands produced 44% more aboveground biomass at one site, 24% more at a second site, but six and 97% less biomass at the other sites (Table 5). In particular, burned sections of Upper Slough-3 site produced almost no biomass after the fires. The fire at this site burned into the duff, and burned nearly all of the root

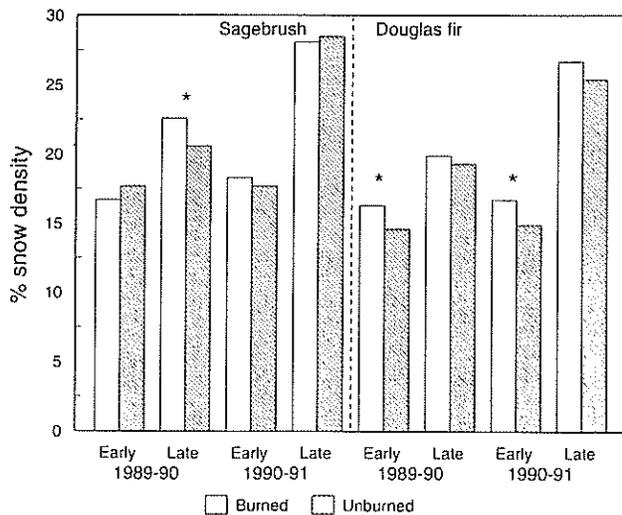


Figure 6. Comparison of mean percent snow density of burned and unburned sagebrush grasslands and Douglas fir forests. Comparisons denoted with a * are significantly different $p < 0.05$.

systems of the willows. Wherever we observed extensive soil heating at other sites on the Northern range, willow recovery was also minimal.

A cooler, surface grass fire (light soil heating) swept through the Blacktail Deer Creek study site, where willows were stimulated by the fires. Shoots from burned willows averaged 39-75% longer, leaf surface areas were 91-105% greater, and shoot weights were 160-200% greater (Table 6). Burned willows were consistently shorter than nearby unburned willows (Table 6), apparently because ungulates were rapidly removing the new tissues. Apparently a result of the greatly increased aboveground tissues and leaf sizes, burned willows exhibited greater water stress than unburned willows of the same species (ANOVA, $F = 7.54$, $p < 0.007$). The effect of location on water stress was also significant ($F = 25.74$, $p < 0.001$).

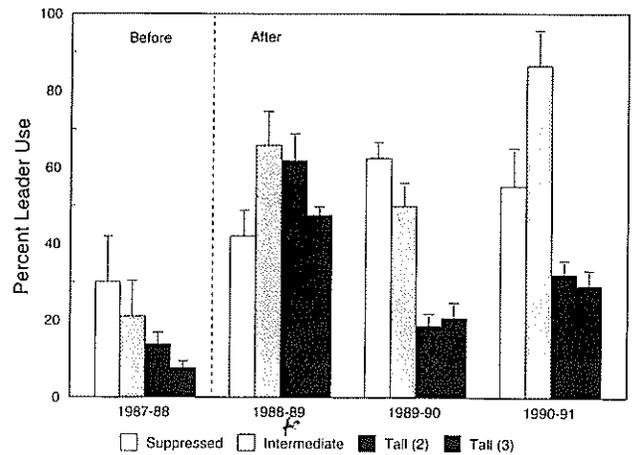


Figure 7. Percent of total number of willow leaders browsed each winter in the four height communities. All four communities were burned during the fires of 1988.

Table 4. Nutritional constituents (% protein and % dry matter digestibility (DMD)) of common willow species in three height classes in 1989. Burn comparisons denoted with * are significantly different $p < 0.05$. Standard error in parentheses.

Community Species	% Protein		% DMD	
	Unburned	Burned	Unburned	Burned
Suppressed				
Booth	8.86 (0.84)	9.35 (0.96)	48.96 (3.83)	56.27 (1.01)*
Wolf	7.63 (0.33)	13.65 (1.27)*	48.6 (1.17)	51.64 (1.16)*
Geyer	8.66 (2.15)	13.56 (1.54)	44.38 (2.42)	52.66 (1.14)*
Intermediate				
Booth	9.61 (0.54)	10.96 (1.23)	52.04 (0.32)	48.46 (2)
Wolf	7.63 (0.34)	13.65 (1.27)*	48.6 (1.17)	51.64 (1.16)
Geyer	6.77 (1.31)	7.99 (0.56)	38.35 (0.9)	42.14 (0.56)
Tall				
Booth	9.56 (0.42)	10.34 (0.43)	53.64 (1.75)	49.83 (3.26)*
Wolf	10.05 (1.18)	9.71 (1.01)	52.05 (4.04)	45.67 (1.27)
Geyer	8.96 (1.11)	9.53 (0.4)*	58.07 (4.42)	51.5 (2.11)*

Table 5. Willow biomass (g/m²) before and after the fires of 1988. Burn comparisons denoted by * are significantly different p<0.05. Standard error in parentheses.

	Before		After		
	1988	1989	1989	1990	1990
Willow Community	Unburned	Unburned	Burned	Unburned	Burned
Intermediate	NA	301 (87)	540 (137)*	97 (28)	174 (29)*
Suppressed	41 (5)	27 (89)	42 (7)*	16 (3)	11 (3)
Tall (2)	193 (31)	405 (53)	370 (93)	24 (5)	23 (9)
Tall (3)	473 (29)	32 (94)	0*	91 (15)	3 (1)*

Discussion

Elk summer habitat use

Little or no change in the pellet group pattern for the summer range forest meadow complex two years after the fires suggested elk use behavior had not changed. Relying on pellet groups as an index of elk behavior or habitat use is debated (Collins and Urness 1984, Leopold et al. 1984) with studies showing lack of correspondence of elk densities with certain behaviors and use of habitats (Collins and Urness 1981) while large scale studies have found correlation with use patterns and pellet densities (Loft and Kie 1988, Edge and Marcum 1989). The study design used here resembled those studies done at larger scales which had better correlation with habitat use. So we feel that our interpretation of no change in elk behavior is supported. In addition, there is a logic that if an elk behavior is associated with fecal deposition then a change in that behavior should result in a change in the pellet group pattern. For a behavior to change without an associated change in pellet group pattern would mean that the behavior had changed its relationship with fecal

Table 6. Willow shoot size, leaf surface areas, and heights of burned and unburned Booth and Geyer willow at the intermediate community site for 1989. Burn comparisons denoted by * are significantly different p<0.05. Standard error in parentheses.

	Booth Willow		Geyer Willow	
	Unburned	Burned	Unburned	Burned
Height of Willow Plants (cm)	124.7 (4.2)	61.6 (8.7)*	142.3 (10.7)	93.8 (7.2)*
Shoot Length (cm)	40.3 (2.5)	55.9 (2.6)*	36.1 (3.7)	63.1 (2.3)*
Shoot Weight (g)	2.2 (0.2)	4.5 (0.4)*	2.1 (0.2)	3.4 (0.2)*
Leaf Surface Area/ Shoot (cm ²)	103 (9)	197 (17)*	75 (5)	154 (8)*

deposition in a burned area and not in an unburned area or visa versa or the behavior is not at all associated with fecal deposition. We feel that these behaviors are not likely and so the result of no change is better supported.

The finding of no change in elk behavior or habitat use patterns contrasts with findings by others which found preference of burned habitats by elk (Leege 1969, Davis 1977, Roppe and Hein 1978, Collins et al. 1978). Other studies have found no preferences (Skovlin et al. 1983) as well. Evidently elk do respond differently to fire effects and in the Yellowstone situation there was no change in short term behavior on the summer range. The design of the study looked at patch and habitat use so there could be changes occurring at small scale plant level behaviors or at larger scales of landscape selection. Finally, changes in summer habitat use may occur later than two years after fires because factors such as succession have yet to take place.

Diet Diversity

Contrary to the hypothesized effect of fire on elk diets there was no change in diversity. One reason for this could be that the samples taken after the fires came from locations where the combination of burned to unburned habitats varied. Most elk appeared to feed from a combination of burned and adjacent unburned sites. The hypothesis of an increase in diversity was based on the suggestion that fire causes elk to utilize previously unpalatable forages (Leege 1969, Asherin 1976). Shrubs are the forage which are suspected to change in palatability, and there was no noticeable increase in shrub use after the fires. As time progresses palatability may increase as changes occur in the plant communities and succession takes place, if so diversity may yet change.

The microhistological technique used for diet identification has been questioned as to its accuracy (Alipayo et al. 1992), but a recent review by Alipayo et al. (1992) found that the technique is accurate. Shrubs and perennial plants were accurately represented in diets of several ungulates. Winter forages available to Northern Range elk consist of perennial plants and shrubs, annual plants except for robust ones are not present during the winter.

Fall Forage Biomass

Only the light burned Douglas fir forest area acted as predicted with an increase in forb biomass by the second year after the fires. The moderate burned Douglas fir forest and sagebrush habitats had declines in biomass with some recovery by the second year after the fires. The action of soil heating may explain why both the moderate burned Douglas fir forest and sagebrush habitat, which had extensive areas of moderate soil heating, had significantly lower biomass. Moderate soil heating would kill seeds and many plants even those with parts below

ground normally protected from fire (Despain et al. 1989, Knight and Wallace 1989, Bartos et al. 1994). Light soil heating kills very few seeds and plants. Moderate soil heating then reduces the number of plants available to potential biomass. Eventually the effect of the soil heating will lessen and plant numbers should increase to where biomass will equal or even surpass biomass in the unburned areas (Leege 1969, Peek et al. 1979, Merrill et al. 1982, Brown and DeByle 1989, Bartos et al. 1994, Cook et al. 1994).

Forage Quality on the Northern Range

Forage quality as measured by crude protein and digestibility generally increased on all burned areas during all seasons. The magnitude of the response was highest the first year after the fires with a lower increase the second year. This observation is in agreement with other studies (Peek et al. 1979, Hobbs and Spowart 1984, Wood 1988, DeByle et al. 1989). Quality of winter elk forages found in the elk snow craters, however, was still higher on burned sites as compared to unburned sites two years after the fires. The higher quality may be the result of elk selecting sites which had higher quality (Rowland et al. 1983, Hobbs and Spowart 1984, Seip and Bunnell 1985, Canon et al. 1987).

Snow Relations on the Northern Range

The lack of difference in snow depth between burned and unburned sagebrush habitats was not surprising since the canopy of sagebrush may have insignificant influence on snow dynamics. However, the lack of difference in the Douglas fir forest snow depth was unexpected since the fires did reduce the canopy coverage of the trees. Normally coniferous trees intercept much of the snow not allowing it to reach the ground. Fires burn off needles and branches allowing snow then to reach the ground. Sites chosen for sampling did not have complete canopy burns but only partial and mosaic canopy burns which leave many trees with their needles and branches intact. With partial and mosaic burns there is less reduction in canopy coverage and the canopy coverage is more variable in space causing higher diversity of snow dynamics. The higher diversity of snow dynamics in the partial and mosaic burns creates a situation where elk have a diverse selection of snow depths and elk in this study selected for crater snow depths closer to the unburned area. Thus there was no real effect of the fires on elk crater snow depths and snow depths in burned Douglas fir forests probably do not restrict elk use or cause greater energy expenditure (Parker et al. 1984). The one site sampled where a complete canopy burn occurred did have higher snow depths compared to the other burned sites, which followed what has been found in other studies (Schaefer and Pruitt 1991, P. Farnes personal communication).

Snow density differed three of eight periods with higher density in the burned areas. At this time, the influence of snow density on elk is not well understood (Parker et al. 1984, Bunnell et al. 1990). Most likely density does not have that great effect on elk behavior and the differences found here are probably not great enough to influence elk.

Elk winter habitat use

The lack of any difference in winter habitat use the second and third winter after the fire does not follow the hypothesized effect of more use by elk of burned habitats. The hypothesis is based in part on the response of elk to the change in landscape diversity brought about by fires (Christensen et al. 1988). The results of this study did not look at the landscape level changes in elk use but only at patch level changes. Thus this study could find no change in patch use while a change in landscape could be taking place. At the patch level there were changes due to fire effects such as increased forage quality and highly variable forage biomass. Elk however, did not respond to the patch level changes by changing their use of patches. The lack of response was not predicted because others have found elk to respond to fires (Leege 1968, Davis 1977, Roppe and Hein 1978, Collins et al. 1978). Possible factors which could account for the lack of response are: (1) patch level changes did occur due to fire, but these changes were not large enough to trigger changes in elk habitat use patterns, (2) mature elk are tied into home ranges and learned responses and on a short term basis were not able to change home ranges or learned responses, and (3) factors such as succession have not yet taken place. Elk habitat use may still respond to the fires in the future as succession and turnover in elk individuals takes place.

Willow Responses

Protein and digestibility concentrations were dramatically increased in willows by the fires of 1988. Fire changes conditions so that increased resources such as nitrogen, light, and moisture are available to plants. Burned birches in Alaska possessed higher protein and higher potassium concentrations than did unburned birches (MacCracken and Viereck 1990). Protein content also increased in four species of woody browse, but the increase was directly related to the intensity of the fire (DeWitt and Derby 1955). Nutrient concentrations increased due to burning in the previously unpalatable ninebark (*Physocarpus malvaceus*) to such an extent that the species was preferred by elk following burning (Leege 1969, Asherin 1976).

Our observation of increase in willow biomass production at less than half of our study plots is noteworthy. Two or three fold increases in production are more

Two or three fold increases in production are more typically reported following burning of willows (Wolff 1978, MacCracken and Viereck 1990). Burning typically allows willows to rapidly grow beyond reach of fall browsing ungulates as reported for moose in Alaska (Wolff 1978). However, on our study sites, ungulate herbivory increased on burned willows, apparently because of a large increase in nutritive concentrations and possibly palatability, to such an extent that all burned willows were shorter three years post-fire than were unburned willows. Nearly all of the willow plants in other stands died or their growth was greatly suppressed by the fires. No positive stature responses by willows to the fires of 1988 were observed. We propose three explanations for the general lack of willow response: (1) willows are herbivore stressed by excessively high numbers of elk, (2) willows are water stressed due to climatic changes and lower water tables (Singer et al. 1994), or (3) a willow has become such a rare diet component for elk, and since burned willows were significantly more nutritious, herbivory by even lowered densities of elk were sufficient to keep burned willows in a reduced stature.

Summary

The short term effects of the 1988 fires produced several changes in elk habitats and behavior but these changes did not all follow what had been hypothesized or reported in the literature. Forage biomass did not increase on the burned areas as predicted but actually decreased where moderate soil heating was extensive. Snow depths did not increase in the burned area as predicted but that was due to partial and mosaic characteristics of the fire. Elk diet diversity did not increase as predicted after the fires. Forage protein and digestibility in burned habitats did increase after the fires as predicted, and also decreased several years after the fires as predicted. Willows did have increased production, shoot lengths and leaf sizes as predicted, but subsequent winter herbivory by elk and other ungulates right after the fires have resulted in no change in the stature of the willow communities. The actual winter elk habitat use on the burned areas did not increase as predicted in comparison to the unburned areas. There were no changes in elk behavior patterns on the burned summer range compared to the unburned summer range which had been predicted to change.

In Yellowstone the short term effects of the 1988 fires had unpredicted effects on elk and elk habitats. Such unpredictability reveals that fire effects have yet to be established in all situations and mechanisms behind the effects have not been determined for dependable prediction. Establishing what short term changes the 1988 fire effects have on elk population and elk ecology cannot be

effectively assessed. Other factors such as the effect of the size and spatial arrangement of the fires along with factors such as the climate and population dynamics need to be further assessed (Turner et al. 1994).

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The Ecological Implications of Fire in Greater Yellowstone: A Summary

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During and after the 1988 fires, there were many predictions on how greater Yellowstone area (GYA) ecosystems would be affected. Some were based on research that had been done previously; others stemmed more from anecdotal evidence or untested hypotheses. Five years later, 225 scientists and managers from six federal agencies, six state agencies, and 24 colleges and universities gathered in Mammoth to compare the results of their research. Like the fires themselves, the meeting was historic. As Superintendent Bob Barbee observed, "The opportunity to learn did not go to waste." Numerous reports are now being written that will affect management and research in the future. Some of the highlights are presented in this summary.

Vegetation Change

The paleoecologists at the conference described fire frequency and vegetation changes as far back as 10,000 years ago. At that time, Engelmann spruce was beginning to invade the tundra vegetation that had predominated over GYA landscapes since the retreat of the glaciers. A spruce-dominated woodland apparently persisted for many centuries. However, with continued warming and drying, forests of lodgepole pine and Douglas-fir became more common throughout the area. About 5,000 years ago a cooling trend began, and predictably, Engelmann spruce and subalpine fir became more abundant. Douglas-fir now persists only at the lowest elevations.

Prior to 1988, ecologists had learned that fires in stands of Douglas-fir occurred on average every 20-50 years, depending on location, and that stands dominated by lodgepole pine, Engelmann spruce, and subalpine fir burned every 200-300 years. All available evidence now suggests that, prior to 1988, the most extensive fires occurred 285 years previously, in about 1703. Lake-bottom sediments, with layers of charcoal, indicate that the length of time between fires was shorter about 8,000

years ago when the climate was drier. Even then, however, the GYA must have been a "non-equilibrium landscape" characterized by large-scale fires that burned large areas. Notably, such fires burn unevenly. Data presented at the conference indicates that 75 percent of the land area that was subjected to crown fire in 1988 is within 200 m of a less severely burned or unburned patch (50 percent was within 50 m).

Succession following the 1988 fires has been highly variable from one area to another. Lodgepole pine was a very successful pioneer species, as predicted, but the density of new seedlings in burned areas varies greatly (from nearly zero to over 100 seedlings per square meter!). Lodgepole pine seedling density is correlated with heat severity, the prefire abundance of serotinous cones, elevation, seed-bed characteristics, and postfire climatic conditions. Intense fires may burn most of the seeds contained within the serotinous cones, though the heat tolerance of the seeds appears to be considerable.

Generally, lodgepole pine seedlings were most dense where serotiny was high in the forest that burned; within any serotiny class, seedlings were more dense near the edges of burned areas where burn intensity was moderate. Engelmann spruce, subalpine fir, whitebark pine, and aspen can be early invaders along with the lodgepole pine in some areas. Regardless of species composition, new even-aged stands are developing. Tree age can vary greatly in these "even-aged stands," with the broadest range of ages occurring where, for whatever reason, the initial density of tree seedlings and other plants was sparse. Nevertheless, more than 75 percent of lodgepole pine seedlings present today in burned areas were established within the first two years after the fires.

One of the most surprising results of the 1988 fires has been a dramatic increase in the number of aspen seedlings. Abundant seed apparently was dispersed into the burned areas and soil moisture conditions apparently were favorable, probably because of the relatively moist year that followed the fires combined with less soil drying

due to lower rates of transpiration. Aspen also are capable of root sprouting following fires. Higher densities of sprouts did occur in some burns, but notably, not in others. In all cases, the aspen continues to be heavily browsed by elk, causing some stands to persist only as shrubs.

It remains to be seen if new aspen clones will develop because of the fires. Data presented at the conference suggest that most tree-sized aspen on the northern winter range in Yellowstone National Park developed between 1870 and 1890, a period when both elk and beaver populations might have been low because of intensive hunting and trapping. The cause of aspen and willow decline continues to be a controversial issue, with most of the evidence pointing to heavy browsing by elk. Elk browsing also may limit the establishment of new trees in burned Douglas-fir woodlands, but the magnitude of this effect has not been determined.

Animal Populations

The effects of the 1988 fires on animals were as variable as the effects on plants. Generally, there was no observable adverse effect on the trumpeter swan, bald eagle, and peregrine falcon. The osprey, mountain bluebird, various species of woodpeckers, and the cavity-nesting Barrow's goldeneye and bufflehead appeared to benefit. The greatest diversity of bird species was observed where fires were of moderate intensity and resulted in a patchy mosaic of burned and unburned forest. Even woodpeckers were uncommon in large, severely burned forests. The Clark's nutcracker was observed caching whitebark pine seeds in burned areas.

Changes in insects and other terrestrial invertebrates depended on burn intensity. Predictably, significant declines in litter-dwelling species were noted when the forest floor burned. This was in contrast to reptiles and amphibians which typically burrow into the soil or which select moist habitats that would burn with less intensity. Some insects were favored by the fires, especially those that could invade fire-damaged but surviving trees.

Insect-caused mortality was higher after the fires on fire-damaged Douglas-fir, Engelmann spruce, and subalpine fir (due, respectively, to Douglas-fir beetles, spruce beetles, and wood borers). Some lodgepole pine mortality was caused by the pine engraver. The mountain pine beetle remains an important cause of lodgepole pine mortality in general in the west, but very little mortality in the GYA can be attributed to this beetle during the last five years.

The 1988 fires had a significant effect on some winter ranges. Burned forage, in combination with hunting pressure, low forage production during the dry summer, and a severe 1988-1989 winter, led to a 38-43 percent reduction in the northern Yellowstone elk herd. The

scarcity of food during the winter appeared to force some elk to feed on the bark of lodgepole pine. Though conifer bark normally is viewed as low quality food, the heat of the fires may have volatilized some of the resinous compounds, thereby making it more palatable. Moreover, because of the nutrient-rich phloem layer, tree bark can be quite nutritious. By 1993 the elk populations throughout the park had essentially recovered. Burned areas were used more for grazing than unburned areas (regardless of the pattern of burning). New willow sprouts became an important food in burned riparian habitats.

With regard to other large mammals, pronghorn antelope have become more abundant since 1988, possibly because of more nonforested habitat at lower elevations. Moose, in contrast, may have declined in abundance because of less winter cover. Bison mortality apparently was affected more by severe weather conditions than by the fires. Grizzly bears have less whitebark pine seeds available to them, but close observations indicate that roots and rodent caches are being used more often. At this time it appears that the grizzly and black bear populations have been affected very little if at all.

Aquatic Ecosystems

Popular hypotheses prior to 1988 were that large scale fires in the GYA would lead to the nutrient enrichment of aquatic ecosystems because of higher rates of nutrient leaching from watershed soils, and that fish productivity would increase because of the additional nutrients. Several studies found that the streamwater was enriched with nitrogen, and one study found some evidence for increased fish growth rates in rivers. However, after five years there was no evidence that the growth of cutthroat trout had changed appreciably in Yellowstone Lake. Investigators found great year-to-year variation in growth and suggested that fishing harvests and population year-class abundance probably had a more important effect than the fires.

High sediment loads were observed in the streams draining some burned watersheds, but usually only after heavy thunderstorms or during spring runoff. While some fish mortality was attributed to these episodes of erosion, no significant effects on fish populations could be detected. Changes in other aquatic organisms, such as diatoms and benthic invertebrates, were observed in small streams, but there were no obvious effects on the organisms of the larger rivers. Streamflow increased in some watersheds due to less transpiration from vegetation, but abnormal flooding did not always occur.

Overall, the magnitude of the effects of fire on aquatic ecosystems appears to be dependent on channel gradient, the steepness of valley slopes, the amount of surface runoff, the percentage of the watershed that burned, the proportion of the riparian vegetation that burned, and the

degree to which the upland and riparian vegetation has recovered. A wide range of these watershed conditions were available for study in the GYA.

What next?

The papers presented at the conference indicate once again that ecosystems are highly variable from place to place and from one year to the next. For example, lodgepole pine was an early invader in many areas, as predicted, but not everywhere. Also, erosion was accelerated in some areas, but the amount of soil loss and subsequent sediment deposition in streams varied greatly from place to place, and in most cases was within the normal variation observed before the fires.

Animal responses also were variable. This variability, occurring within a relatively small area (such as the Yellowstone landscape), provides excellent opportunities for scientists to improve their predictive abilities. Such high variability also suggests that caution should be used in making broad generalizations, whether for a national park, national forest, or an extensive mosaic of federal, state, and private lands. Nevertheless, predictions about fire behavior and the effects of fire can now be based on much more information than was available in 1988. This represents a significant scientific accomplishment.

There is still, however, much to be learned. Indeed, some of the spatial and temporal variability in the way ecosystems responded to the 1988 fires is puzzling. Explanations may be possible only with additional research on, for example, the effects of fire and other variables on microbial organisms in the soil, or trees other than lodgepole pine and aspen. Studies that focus on small scales, individual species, or specific ecosystem processes should be complemented with more holistic research at the scale of several watersheds or whole districts.

Scientists should also consider doing experiments with the young postfire ecosystems. For example, what would happen if dense stands of lodgepole pine saplings are killed by another fire (or some other mechanism) within 5-10 years after a stand-replacing fire in old-growth? If aspen are present, whether as root sprouts or young seedlings, the effect could be the rapid development of a new aspen grove where a pine stand might otherwise have occurred. Similarly, what would be the effect of reduced browsing on aspen and Douglas-fir adjacent to winter ranges? Additional fenced exclosures should be established to determine if (or where) the elk population is capable of preventing the reestablishment of the forests and savannas that were burned in 1988.

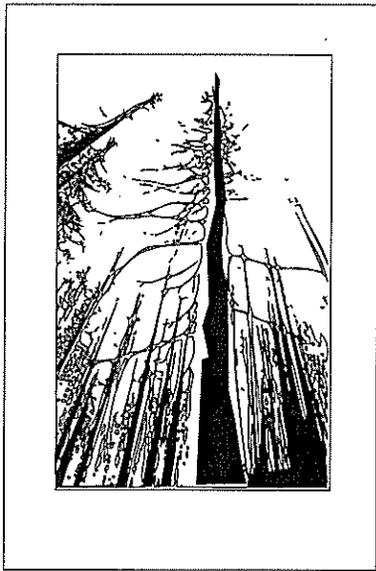
Other experiments could be done by fertilizing streams or lakes to simulate the effects of the fires, or by manipulating postfire riparian vegetation along portions of some streams. The knowledge gained thus far by

taking advantage of the 1988 fires could be augmented greatly with carefully designed, more controlled experiments. Some would be appropriate for Yellowstone or Grand Teton National Parks; others might be acceptable only on adjacent national forest lands. The best science, pursued in as many directions as possible, should be encouraged so that there is more information available for evaluating the "natural regulation policy" and other management paradigms.

The value of long-term data for determining the effects of disturbances became eminently clear during the conference. The nature of mature ecosystems depends to a large extent on the history of an area and what happens during the first few years after disturbances. Answers to numerous important questions would not have been possible without the long-term records of the U.S. Geological Survey, U.S. Fish and Wildlife Service, USDA Forest Service, Soil Conservation Service, and National Park Service. The magnitude of the 1988 fires, along with their value for understanding ecological phenomena beyond the boundaries of the GYA, mandate that long-term research and monitoring programs should be continued (including those initiated in 1989). Moreover, such data (including historic photographs) should be carefully archived and used more frequently.

The value of simulation modelling for understanding ecological interactions also was quite evident during the conference. Several models were described. Whether designed for large-scale questions and used in conjunction with satellite imagery and geographic information systems, or for small-scale questions pertaining to a specific process, the simulation approach to ecological research helps prevent scientists and managers from becoming too simplistic in the interpretation of their data.

A larger modelling effort is now called for, primarily because the value of an individual study is greatly enhanced when it is integrated with others. Simulation models also help in establishing research priorities. Developing defensible ecosystem models that are useful at the scale of landscapes is a significant challenge, but, with managers and scientists working together more closely than in the past, this goal should be possible. The payoffs will be substantial for education, new scientific methods, visitor satisfaction, the best possible stewardship for two of the world's favorite national parks, and improved ecosystem management throughout the region.



INTERNATIONAL ASSOCIATION OF WILDLAND FIRE
ISBN 1-887311-00-9