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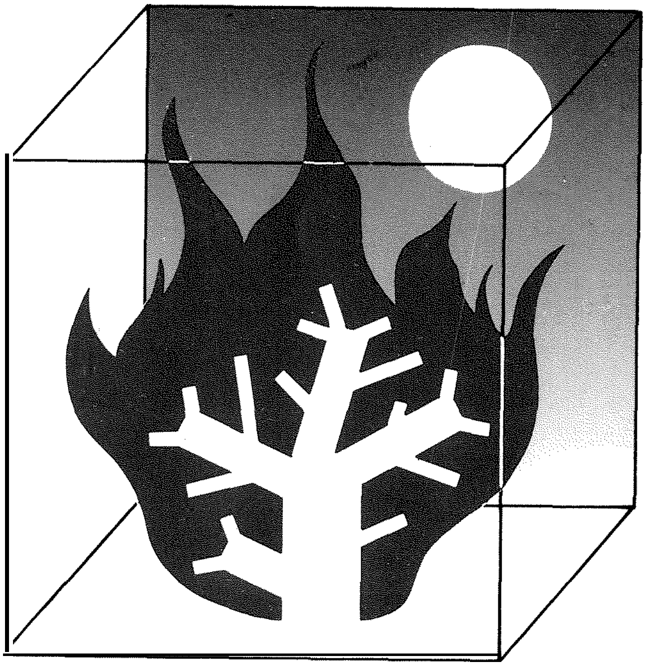
Fire and the Environment:

Ecological and Cultural Perspectives



Proceedings of an
International Symposium

Knoxville, Tennessee
March 20-24, 1990

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Forty-one papers based on oral presentations are included under four categories: Fire Ecology; Fire Management; Cultural; and Fire History. In addition, three papers are presented from a special session on the 1988 fires in the Greater Yellowstone Area and fourteen papers are presented from a poster session.

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Fire and the Environment: Ecological and Cultural Perspectives
Proceedings of an International Symposium

Editors
Stephen C. Nodvin and Thomas A. Waldrop

Knoxville, Tennessee
March 20-24, 1990

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PREFACE

Fire and the Environment: Ecological and Cultural Perspectives was an international symposium held on March 20-24, 1990, in Knoxville, TN. The meeting was attended by over 150 researchers, land managers, and wildlife managers. Forty-one papers based on oral presentations are included under four categories: Fire Ecology; Fire Management; Cultural; and Fire History. In addition, three papers are presented from a special session on the 1988 fires in the Greater Yellowstone Area and fourteen papers are presented from a poster session.

Papers and posters were selected by the program committee based on title summaries submitted prior to the meeting. The major objective of the editorial committee was to compile a proceedings covering a broad range of topics with papers representing new results, ongoing research, overviews of past research, and new ideas or hypotheses. Preference was given to papers covering cultural aspects of fire; such as public perception of fire, fire policy, wildland/urban interface, historical and prehistoric roles, fire and climate, use of fire toward management objectives, and effects of fire exclusion; and ecological effects of fire on climate, air quality, water quality, nutrient cycling, wildlife, fisheries, vegetation, and soils. After the meeting, papers were submitted to the editorial board for review. Each paper was given a blind review by two peers and one grammatical editor. Reviewer comments were incorporated by authors and submitted to the editorial board for approval. Some papers required additional revision but all papers were accepted. These proceedings have been prepared electronically from copy supplied by the authors. Authors are responsible for the content and accuracy of their papers as well as any stated opinions or conclusions.

The steering committee gratefully appreciates the efforts of authors and reviewers who contributed to a successful and informative program. Our appreciation is given to Brian Ostby and John Mullins, who arranged the poster session, and to Janet Paces, Ellen Williams, and Julie Smith, who served as assistants to the Program Chairman and proceedings editors. A special note of thanks is given to the moderators who provided additional insight to each topic and kept each Session on schedule. Moderators included William Boyer, Southern Forest Experiment Station; Bob James, USDA Forest Service, Region 8; Gary Schneider, The University of Tennessee; Eugene McGee, The University of Tennessee; Joe Abrell, USDI Park Service; Frank Woods, The University of Tennessee; Joe Clayton III, Tennessee Division of Forestry; Dale Wade, Southeastern Forest Experiment Station; David Van Lear, Clemson University; Larry Landers, Tall Timbers Research Station; Thomas Waldrop, Southeastern Forest Experiment Station; and Stephen Nodvin, USDI Park Service.

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VARIABLE FIRE REGIMES ON COMPLEX LANDSCAPES: ECOLOGICAL CONSEQUENCES, POLICY IMPLICATIONS, AND MANAGEMENT STRATEGIES

Norman L. Christensen, Jr.[1]

INTRODUCTION

Half a century ago, fire policy in most public and private agencies charged with the management of wilderness was neatly summarized in the so-called 10 A.M. Rule: If a fire starts, it should be extinguished by 10 the next morning. Our attitudes toward fire and other natural disturbances in wilderness landscapes have changed during recent decades. We now recognize that disturbances caused by fire, wind, insects, and pathogens play key roles in a variety of ecosystems processes. The folly of excluding or trying to exclude agents of disturbance from landscapes is now obvious to most wilderness managers.

Despite this knowledge, articulation of operational policies and management strategies for wilderness preserves has proven to be a daunting task. What are the proper fire regimes for our diverse wilderness ecosystems? How and why have the frequency and behavior of fire changed through time? How have human activities such as a century of fire exclusion, landscape fragmentation, and alteration of ignition patterns affected tire regimes? How can we reintroduce fire into landscapes so altered? How can wilderness tire managers accommodate nonwilderness values such as recreation, timber and watershed resources, and air quality? Finally, how do we know when we are managing fire correctly?

In this paper, I shall argue that questions such as these can only be answered in the context of a clear understanding of wilderness processes and overall wilderness management objectives. I shall assert that wilderness management should be based on the answers to three questions, and since we have generally answered two of these questions incorrectly presents us with our most difficult management challenges.

NATURAL DISTURBANCE AND MANAGEMENT POLICY

Wilderness management can be reduced to answering correctly three questions: 1. What should be preserved? 2. How should preserves be configured? 3. How should management be executed (Christensen 1988)?

What should we preserve?

The actual foci of preservation in particular wilderness ecosystems are often identified in nebulous, nonoperational terms or are not stated at all. The question must be answered in both philosophical and practical terms. We must first agree on the categories of items that will be the objects of preservation (i.e., genotypes, species, ecosystems, landscapes, etc.). Having made this decision, we must then determine which items within a category are worthy of preservation; that is, we must produce "shopping lists"--lists of rare and endangered species, or inventories of various ecosystem types, for example. The formulation of such lists is often the occasion for battles over the dedication of land to wilderness or nonwildemess management. In many regions, our ignorance of ecosystem variability prevents us from making such lists.

How should preserves be configured?

Patterns of natural disturbance have rarely, if ever, been a major consideration in the spatial configuration of wilderness preserves. However, if a wilderness preserve is to include the full range of patterns generated by natural disturbance, the frequency, area1 extent, and behavior of such disturbances must be considered. Ideally, a preserve should be sufficiently large to include not only the variety of post-disturbance age classes typical of a pristine wilderness landscape, but also the range of variation in disturbance severity. When disturbances occur on small spatial scales and at high frequency, small preserves will suffice. However, in environments in which large-scale fires are the norm (e.g., western coniferous forests and shrublands), few existing preserves are large enough. In addition, those who determine preserve boundaries should understand the effects of landscape features on the behavior of disturbances.

How should management be executed?

The details of procedures for managing natural disturbances depend on a variety of considerations. For unpredictable and uncontrollable disturbances such as the Mt. St. Helens eruption, management will focus on post disturbance intervention and will likely involve compromises between the wish to allow the affected area to recover as it would have in our absence and the potential consequences of the lack of intervention for areas outside the preserve (e.g., flooding, siltation, etc.). In the case of fire, where management intervention may alter the course of the disturbance, additional issues must be addressed. The manager must

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[1] Professor and Dean, School of the Environment, Duke University, Durham, NC 27706.

decide the extent of disturbance that is acceptable within the constraints of the design of the preserve. For example, assuming suppression is a real option, should a naturally ignited tire be allowed to become so large that containment is impossible or allowed to consume a major portion of the preserve? We know very little about the ecological consequences of artificially limiting the size of such disturbances. Are there wilderness processes that depend on the occurrence of tires of large spatial extent?

FIRE REGIMES AND ECOSYSTEM RESPONSE

Many of our views about the role of natural disturbance in general, and of wilderness fire in particular, reflect the evolution of ecological theories pertaining to succession, the recovery of ecosystems from disturbance. Clements' (1916) theory of succession portrayed wilderness as the touchstone of stability and order. Natural disturbances such as tire not only alter the structure of ecosystems, but render the landscape less habitable. Pioneer species that colonize such disturbed areas are usually organisms with high dispersal ability and considerable tolerance of harsh conditions; such organisms are rarely effective competitors under favorable growing conditions. Clements posited that these vagrant species become established and alter the environment of a disturbed site by stabilizing and enriching soil and by creating a microclimate that favors establishment of other species. Similarly, these new invaders alter their environment so as to favor yet another wave of immigrants. This succession of species continues until a community of organisms is established that maintains its environment in such a way as to perpetuate itself. This so-called climax ecosystem was considered to be the most stable assemblage of organisms that could exist on a given site within the constraints of regional climate.

Thus, ecosystems develop much like individual organisms from simple beginnings toward increasing complexity and stability. Ecologists of Clements' era recognized that individual organisms would necessarily die, but asserted that the regeneration of climax community species was associated with small-scale disturbances such as the deaths of individual trees.

Over spatial scales of interest to wilderness managers, the composition and structure of climax ecosystems was thought to remain constant over long periods of time. In Clements' (1935) words, "Under primitive conditions, the great climaxes of the globe must have remained essentially intact, since fires from natural causes were undoubtedly infrequent and localized." The quantity of data supporting this theory was quite small. However, we generally require little data to support theories that portray the world as we wish it to be. It was indeed appealing to view wilderness as inevitably converging on stability. The vision of a climax ecosystem as a "super organism" composed of species performing specific functions as if they were roles much like the organs and tissues of an individual organism was proof of the "balance of nature."

This model of ecosystem change provided clear guidelines for management of wilderness. The object of management (what should be climax ecosystems. The supposed structure of attributed to climax communities was often based on romantic accounts by early explorers and naturalists. The view that species comprising natural communities were regenerated by small disturbances implied that questions about preserve configuration could be answered by reference to economic and political factors. If the dominant species can reproduce in openings created by the demise of individual trees, then relatively small areas should be sufficient to perpetuate the entire community. Consequently, the boundaries of our major wilderness parks have very little in common with natural ecological barriers or divides. Finally, it was clear that the key to preserving wilderness areas ***(management execution.?)*** thus defined was the prevention of catastrophic disturbances. Only in this way could we nurture wilderness to its climax state.

Research over the past three decades has taught us that Clements' theory was at best too simple and at worst flat wrong. Long-term studies demonstrate that the process of ecosystem change is not nearly so predictable or simple as Clements imagined (See Christensen 1991 for a review).

Perhaps the most startling discovery was that many ecosystems become increasingly ***unstable*** during succession, particularly in areas where fire is an important factor. Early in the development of most forests there is an abundance of green, moist, and relatively non-flammable plant tissue. However, as communities develop, dead woody debris accumulates increasing the ability of such communities to carry a fire. Exclusion of fire from such systems may result in additional fuel accumulation, increased flammability, and higher fire intensity when fires eventually occur. We have learned that fire is an essential and inevitable agent of biomass decomposition in many forest ecosystems.

If succession following disturbance is not a linear, predictable process that terminates with the establishment of a stable climax community, perhaps we can view it as a deterministic and stable cycle, driven by internal feedbacks such as fuel accumulation and inevitable fires. In this view, ecosystems are dynamically stable, like a pendulum with a period determined by return times between disturbances.

Alas, wilderness landscapes are not so easily modeled. Disturbances are indeed regulated in part by internal feedbacks, but actual periods or return times are quite variable and heavily dependent on extrinsic factors such as variations in regional climate. Furthermore, variations in disturbance intensity result in highly variable trajectories of postdisturbance change. Thus, the pendulum may swing in a highly chaotic random fashion. Wilderness landscapes are best viewed as an ever-changing "patch mosaics," and the frequency distribution of patch types may vary as a consequence of short- and long-term changes in climate and other chance factors (See Pickett and White 1985).

The pattern of successional change from less to more habitable conditions proposed by Clements is often reversed in the case of postfire ecosystem succession. As forests develop following fire, mineral nutrients such as nitrogen and phosphorus become less available in the soil as they are taken up and stored in plant tissues. Thus, low fertility, organic debris in the forest floor, and shade cast by mature trees may severely limit opportunities for seedling establishment and growth of the young plants in late succession ecosystems. The ash raining onto burned soils is an effective fertilizer, and postfire microclimate often favors successful plant reproduction.

This pattern of environmental change in relation to tire has resulted in evolution of plant adaptations that concentrate reproductive effort in the period immediately following the fire. Such adaptations include underground buds that are protected from heat, production of seeds that germinate only when heated, cones or fruits that open only when heated, and production of flowers only following tire. The evolution of such adaptations has not simply made some ecosystems tolerant of fire; it has made them dependent on it. Burned areas quickly lose their bleak aspect and, by the end of a single growing season, are carpeted with new growth.

Describing the evolution of knowledge in another area, Samuel Clements quipped that "the researches of many commentators have shed considerable darkness on this subject, and should they continue we shall soon know nothing about it. " What once appeared to be a tidy linear process leading inevitably to stability on relatively small spatial scales is now seen as a dynamic, chaotic, and complex pattern of change in which the word "stable" may have little if any meaning.

POLICY, MANAGEMENT, AND RESEARCH IMPLICATIONS

Policy Considerations

Given the variability in fire history, tire behavior, fire effects, and fire responses, it is clear that fire policies must vary from preserve to preserve. Nevertheless, I suggest that successful policies will have three common characteristics: (1) clearly stated operational goals, (2) identification of potential constraints, and (3) recognition of the variability and complexity of the successional process.

It is not enough to acknowledge that fire is an important natural process in an ecosystem and then simply reintroduce fire to the ecosystem. We must formulate specific operational goals for fire management programs. We do not set aside wilderness preserves in order to bum them. Rather we should withhold, apply, regulate, and respond to fire in order to accomplish specific management goals. The specification of these goals is made more difficult by the complexity of change on many landscapes.

The difficulty of setting operational goals is illustrated by the problems that the National Fire Management Policy Review Team (Philpot 1988) encountered when it attempted to define the specific goals of the Fire Manager Programs in federal wilderness areas. The overall goal was relatively simple--i.e., "to restore fire to a more natural role." But this formula begs the question "What is natural?" The Review Team defined natural as "those dynamic processes in components which would likely exist today and go on functioning, if technological humankind had not altered them." Putting aside the implication that Native Americans lacked technology, this statement seems to suggest that if natural processes are simply allowed to operate, ecosystems will converge to some preferred state. Although the details are far from clear, we are beginning to appreciate that landscape change is more chaotic than convergent.

Specification of objectives requires a clear understanding of the specific elements for which a preserve was dedicated. These may include historical features, species preservation, or preservation of entire wilderness areas. With regard to specific objects or species populations, policy objectives will likely be clear. However, a great deal of confusion exists regarding what constitutes wilderness. Wilderness is usually defined in contrast to human-altered landscapes, where wilderness represents the lack of human intervention. Given this definition, the phrase "wilderness management" should be considered an oxymoron. However, the pervasiveness of human influence ranging from the dissection and fragmentation of landscapes to global climate change may create conditions in which the most potent form of human intervention may be restraint.

We cannot simply set aside a piece of real estate and expect that, in the absence of human intervention, "those dynamic processes and components" will go on functioning as if "technological humankind had not altered them." We have created a world that we are obliged to manage. Given this situation, we are obliged to formulate policy based on operational definitions of wilderness. In particular we need to be explicit about such goals as preservation of ecosystem processes, biodiversity, and heterogeneity.

It is essential that policymakers understand the potential constraints on management in wilderness preserves. Within the realm of the "natural," a wide variety of landscape configurations is possible. However, within the constraints of preserve design, not all these configurations are equally desirable. Million-acre fires may be natural phenomena on the Yellowstone Plateau, but the desirability of such fires in the context of the altered landscape can be determined only by evaluating the costs and benefits of events on this scale.

In many cases, policymakers are faced with competing or conflicting preserve objectives. For example, the Organic Act of 1916 that established the National Park Service extols managers to "conserve the scenery in natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations . . . ." It does not take a lawyer to detect the multitude of ambiguities and possible interpretations in this statement. For that matter, the 1963 Leopold Committee's assertion that the proper goal of national park conservation is the preservation of a "vignette of primitive America" is open to various interpretations. Some would view it as a mandate for the so-called "living museum" approach to park management, where the goal is to preserve "snapshots" of the past. Alternatively, the term vignette can be defined as a "moving picture" so as to include the process orientation of current Park Service policy.

The constraints on fire management posed by liability to other public and private resources are considerable. This is particularly true in wilderness preserves where goals include recreation or watershed management, and in situations where arbitrary borders separate wilderness from land dedicated to nonwilderness functions. The constraints on conservation of wilderness in an increasingly urbanized context are exemplified by issues such as air quality and smoke management. For example, burning in Sequoia National Park contributes to air quality problems in California's Central Valley. It may be natural that wilderness fires inject particulates into the atmosphere, but the emission of these particulates may be deemed unacceptable by air quality authorities who must consider that the atmosphere is already polluted with a host of anthropogenic emissions.

Fire policies must recognize the constraints set by preserve design. We have chosen to preserve relatively little of once vast expanses of wilderness, and the borders of most preserves bear precious little relation to the natural processes necessary for their preservation. The acceptability of tire events of particular intensities or spatial extent cannot be based solely on the naturalness of such events. Given the constraints of preserve design, many natural events may be deemed unacceptable or at least undesirable. This is particularly true where we can preserve only small fragments of formerly large landscapes. In these situations it is important to understand the ecological costs of not allowing large scale or high intensity events to occur.

Perhaps the most significant constraint on policy development is ignorance. Stewards of wilderness cannot claim, nor does the public have a right to expect, perfect knowledge. The only fair expectation is good faith. Policy makers and the public must understand the limits of our understanding.

When I was in my late teens, my grandmother took me to task for some transgression, the specifics of which now escape me. My excuse was that I was just trying to do what I thought was right. Grandma's reply? "Norman, you should not do what you <u>think</u> is right, you should do what <u>is</u> right!" I thought for a moment and said "Grandma, that's the dumbest thing I have ever heard."

The public's expectations are much like my grandma's. Managers must be ever cognizant of what I shall call Grandma's Law: "All we can ever do is what we <u>think</u> is right." However, what managers consider right has changed markedly as our understanding has developed over the past several decades. Thus, I propose a corollary to Grandma's Law: "Just because you think you are right does not guarantee that you are.

Fire policies must allow for the variability and complexity of the process and its context. We are learning that variability is an essential component of fire regimes and that policies should not necessarily seek to replicate mean values of intensity, return time, etc. Furthermore, policy options and goals will vary considerably across the spectrum of fire regimes. Because we can prescribe low intensity fires like those that occur in grasslands with high scientific precision, we expect similar precision in the application of tire in heavy forest fuels. However, our management options in these latter situations may be more akin to those for large scale disturbances such as hurricanes and volcanic eruptions.

Finally, policies must be developed against a backdrop of constant change. In his classic paper on succession, Henry Chandler Cowles (1901) characterized succession as "a variable converging on a variable. " Given the pervasiveness of human-caused environmental change, the notion of "natural" may be moot at best.

Management Considerations

Management involves the development of interventions to achieve specific policy objectives. Recognizing our considerable uncertainty and ignorance about the processes we must manage, management should be thought of as a direct application of the scientific method. Its success depends not only on a clear understanding of available options (hypotheses), but also on a monitoring system that provides direct feedback to managers regarding management consequences (experiments and tests).

Fire management options include complete suppression, planned-ignition prescriptions, natural emission prescriptions, "let bum" strategies, and a range of fire surrogates. Where complete fire suppression is necessary, guidelines for managing the effects of suppression are critical. Such effects include those of employing fire retardants, plow lines, and heavy equipment. Where fires cannot be allowed to burn, managers may need to consider surrogates for burning such as mechanical field manipulation and artificial cutting.

Planned emission prescriptions must differentiate between the means and the ends. Historically, most prescribed burning protocols have been developed in the context of silvicultural management in which the end goals are field reduction and discouragement of competitors (i.e., reduced diversity). Management goals in wilderness areas will likely be quite different and require different burning protocols. In developing bum plans it is important to distinguish between fires set to restore fuel conditions to some "natural" state and fires set to simulate a "natural" process.

Prescribed natural ignition programs allow fires ignited by natural causes to bum so long as they are within prescribed guidelines. In a sense, such fire management programs substitute knowledge for intervention. They assume that threshold levels of tire behavior can be established beyond which fires can and should be suppressed. These is serious question whether such fire programs are realistic and natural. For example, such plans may call for the suppression of ecologically important but intense fire events. Furthermore, given the extent of landscape fragmentation and alteration, it is unlikely that fire regimes developed in this manner will simulate the full range of natural processes.

Only in the largest wilderness areas will an unmodified "let bum" fire management plan be a viable alternative. Nevertheless, wildfires will occur and tire management plans must provide clear guidelines for specific postdisturbance interventions. These guidelines must include appropriate measures for erosion mitigation, reforestation, and wildlife management interventions. Those who formulate guidelines for postfire interventions should consider the benefits of the intervention and their environmental and monetary costs, and should consider the likelihood of their success.

Any reasonable management system must have a built-in program for evaluating management's success in accomplishing policy goals. Such a monitoring program should be viewed as a set of research hypotheses especially designed to test whether management is providing the desired effects on specific dependent variables such as fire diversity, decomposition and nutrient cycling, and landscape heterogeneity. Monitoring programs not only provide information that can be used to adjust to management protocols, but also serve to inform basic scientific research programs.

Research Needs

It is clear that there is much that we do not know regarding the role of fire in wilderness ecosystems. I feel three areas deserve special attention. (1) There is much to learn about the causes and consequences of variability in fire regimes. For example, the Yellowstone fires taught us that models of fire behavior are not easily transferred among ecosystems. Even within a landscape, interactions between climate and fuels may result in multiple patterns of fire behavior. The consequences of variation in fire behavior are also little known. Fire often results in a pulse of resource availability which, although ephemeral, may greatly influence patterns of species establishment. The variability in such pulses may have much to do with the biodiversity of landscapes throughout the fire cycle. (2) Although we know that variation in the spatial and temporal scale of fire events can greatly affect patterns of species response, the specifics of such patterns and their mechanisms are poorly understood. Implicit in much of wilderness tire management is the notion that many small events can be substituted for a single large event, but in most cases this assertion has not been tested. (3) Given the constraints on fire management programs, it is important to understand the ecological consequences of departures from "normal" tire regimes. Are there ecological costs associated with the exclusion of high intensity tires from certain parts of the landscape?

LITERATURE CITED

Christensen, N.W. 1988. Succession and natural disturbance: paradigms, problems, and preservation of natural ecosystems. In :Agee, J.K.; Johnson, D.R. eds., Ecosystem management for parks and wilderness. Seattle: University of Washington Press. 62-86.

Christensen, N.L. 1991. Wilderness and high intensity fire: how much is enough? Proceedings, Tall Timbers Fire Ecology Conference 17:9-24.

elements, F.E. 1916 Plant succession: an analysis of the development of vegetation. Carnegie Institute Publication 242. Washington, DC: Carnegie Institute.

elements, F.E. 1935. Ecology in the public service. Ecology 16: 342-363.

Cowles, H. C. 1901. The physiographic ecology of Chicago and vicinity: a study of the origin, development, and classification of plant societies. The Botanical Gazette 31: 73-108, 145-182.

Pickett, S.T.A.;White, P.S., eds. 1985. The ecology of natural disturbance and patch dynamics. New YorK: Academic Press.

FIRE ECOLOGY

EFFECTS OF FIRE EXCLUSION ON TALLGRASS PRAIRIE AND GALLERY FOREST COMMUNITIES IN EASTERN KANSAS

Marc D. Abrams and David J. Gibson[1]

Abstract-The purpose of this review is to synthesize a long-term body of research dealing with tire exclusion effects on tallgrass prairie and gallery forest communities on Konza Prairie in eastern Kansas. Upland and lowland prairie communities burned in spring at intervals ranging from l-l 1 years were consistently dominated (70-90 percent cover) by *Andropogon gerardii*. With this increasing interval between fires other dominant warm-season grasses, *A. scoparius* and *Sorghastrum nutans*, had decreased cover, whereas forbs and woody species had increased cover. Aboveground biomass was higher on an annually burned versus unburned lowland prairie, due to stimulated graminoid production. Sites unburned for 10 or more years were converting to woodlands dominated by *Juniperus*, *Ulmus*, *Gleditsia* and *Celtis*. Older gallery forests occurred in stream channels and ravines and were comprised of overstory *Quercus* and *Celtis* and understory *Celtis*, *Cercis* and *Ulmus*. The gallery forests on Konza Prairie dramatically increased from the time of European settlement (1850) to present; this has been attributed to decreased tire frequency and intensity in the region. With continued tire exclusion this century further succession in these forests has caused oak replacement by more shade tolerant species.

INTRODUCTION

Eastern Kansas receives approximately 33 inches (83.5 centimeters) of precipitation annually, which is enough to sustain forest vegetation on all but the most xeric sites. Historically, however, the region has been dominated by *Andropogon* - *Sorghastrum* - *Panicum* tallgrass prairie. When forest vegetation does occur it is usually restricted to thin bands along ravines and stream channels, called gallery forests. It is well recognized that frequent tire in the region limits woody vegetation expansion and helps to maintain tallgrass prairie (Abrams 1988c). Moreover, the composition, structure and productivity of tallgrass communities can vary dramatically with relatively small changes in tire frequency (Abrams and Hulbert 1987, Gibson 1988). Following European settlement in the mid-1800s, the number, extent and intensity of fire most likely decreased in eastern Kansas, resulting in changes in the ecological characteristics of prairie and gallery forests in the region (Bragg and Hulbert 1976; Abrams 1986). Similar changes in woody and prairie vegetation occurred in eastern Oklahoma after decades of fire suppression (Collins and Adams 1983).

Since the late 1970s the effects of fire and tire exclusion in tallgrass prairie and gallery forest communities have been studied on Konza Prairie in northeast Kansas. Studies conducted in one or both community types include fire effects on plant species composition, structure and productivity. The purpose of this review is to synthesize these studies with special reference to the effects of fire exclusion the grassland and forest communities on Konza Prairie.

KONZA PRAIRIE

Konza Prairie Research Natural Area is 3,487 hectares of tallgrass prairie habitat in Riley and Geary counties in the Flint Hills of northeast Kansas. The Flint Hills are along the western border of the tallgrass prairie province and because of the steep and rocky topography include the only extensive area of unplowed tallgrass prairie in North America. Gallery forests in the region are dominated by *Ouercus* spp. (oak) and *Celtis occidentalis* (hackberry) and range from about 10 to 300 meters wide in protected portions in the prairie interior.

Specific methods for prairie and gallery forest data collection and analysis can be found in papers by the authors cited hereinafter. Prairie composition and productivity studies were concentrated on 10-100 hectare watershed units, burned in mid- to late April at various intervals since 1972. Each watershed contains relatively broad, level upland (Florence cherty silt loam or cherty silty clay loam soils) and lower slope (Tully silty clay loam soils) sites. Florence soils are relatively thin, well-drained and have numerous chert fragments in the top soil, whereas Tully soils are deep, gently sloping and were formed from thick colluvial and alluvial deposits, with few rocks (Jantz and others 1975). Because the upland Florence soils store less water than Tully soils, plants present become water-stressed sooner during dry periods than plants on deep Tully soils (Abrams and others 1986).

The climate of the study area is continental, characterized by hot summers, cold winters, moderately strong surface winds and relatively low humidities (Brown and Bark 1971). The average length of the frost-free season is 180 days. Mean annual temperature was 12.8” C (range = -2.7 to 26.6“ C) and mean annual precipitation was 83.5 centimeters based on a 30 year record (1951-1980). Precipitation ranges from 2.1 to 13.4 centimeters per month with May and June being the wettest and December- February being the driest months.

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[1] Assistant Professor of Forest Ecology/Physiology, School of Forest Resources, The Pennsylvania State University; Assistant Professor of Plant Ecology, Department of Biology, University of West Florida.

Annual precipitation varies greatly and droughts occur frequently. In northeast Kansas, drought occurred during 38 percent of the months between 1931 and 1968 and of these 11 percent were rated severe or extreme (Brown and Bark 1971).

COMPOSITION OF PRAIRIE

Presettlement Conditions

Although accurate presettlement conditions are not known, it is generally accepted that the tallgrass prairie developed and spread in an environment that included tire at frequent intervals in the range of once every year to once every ten years (Kucera 1981; Axelrod 1985; Hulbert 1973). In the Kansas Flint Hills, frequently burned tallgrass prairie is dominated by big bluestem (Andropoeon gerardii) and other tall warm-season grasses (e.g., Andropogon scoparius, Sorehastrum nutans, and Panicum virgatum). These species along with a number of forbs, e.g. Solidago missouriensis and Vemonia baldwinii, occupy the majority of space in the community and are referred to as matrix species (Collins and Gibson 1990), whereas a large number of rarer interstitial species occupy the spaces, e.g. Ambrosia psilostachya, Artemisia ludoviciana.

Effect of Fire Exclusion on Species Composition

On Konza Prairie, studies of permanent plots carried out since 1981 (Abrams and Hulbert 1987, Gibson and Hulbert 1987; Gibson 1988) indicate that in the absence of grazing species richness increases with time since fire until approximately 8 years, after which richness declines again (Gibson and Hulbert 1987; Collins and Gibson 1990). This effect was only observed in the context of the long-term study and was not necessarily discernible on a yearly basis (table 1). Fire exclusion from the tallgrass prairie allows the build up of a soil seed bank (Abrams 1988a), which along with the more suitable microsite conditions and heterogeneous community structure (Collins and Gibson 1990) results in a more species-rich community.

Andropogon perardii is the dominant species (cover = 70-90 percent) on Konza Prairie irrespective of fire treatment or topography (table 1). Nevertheless, the cover of A. sconarius, S. nutans and other warn-season species decrease significantly with time since burning (table 1) (Abrams and Hulbert 1987; Gibson and Hulbert 1987). In contrast, Panicum virgatum showed no response to fire but had higher cover on the deeper, moister soil of lowland sites. Cover of

Table 1. C-nity and plant species cover data (x- percent + standard error) for three unburned and two annually burned upland (Florence cherty silt Loam) and lowland (Tully silt clay Loam) soils on Konza Prairie in northeastern Kansas in 1984. Values for each c-nity parameter or species followed by the same Letter are not significantly different; * • values < 0.05 percent. (After Abrams and Hulbert 1987)

Community data	Burned treatment	Lowland	Upland
Total species cover	burned	176.5 + 3.2a	179.0 + 4.9a
	unburned	184.0 + 6.4a	171.4 + 7.1a
Species richness	burned	16.3 + 1.0a	20.1 + 0.8b
	unburned	18.3 + 0.9a	21.2 + 0.7b
Species/treatment	burned	46.0 + 2.8a	54.0 + 0.7a
	unburned	57.0 + 2.8b	60.3 + 2.4b
Species data			
-Grasses-			
Andropogon gerardii	burned	83.5 + 5.1a	80.6 + 2.2a
	unburned	84.5 + 2.2a	79.6 + 2.5a
A. scoparius	burned	43.3 + 4.4a	24.0 + 4.9b
	unburned	5.4 + 1.4c	8.7 + 1.3c
Sorghastrum nutans	burned	21.5 + 3.0a	33.4 + 4.6b
	unburned	4.4 + 1.0c	3.8 + 0.9c
Panicum virgatum	burned	12.5 + 4.5a	5.6 + 2.1bc
	unburned	5.6 + 2.4ab	1.9 + 0.9c
Poa pratensis	burned	0.0 a	*a
	unburned	21.9 + 4.0b	24.9 + 4.8b
-Forbs and woody plants-			
Aster ericoides	burned	1.3 + 06a	0.5 + 0.3a
	unburned	8.7 + 2.0b	7.8 + 1.7b
Salvia azurea	burned	*a	14.1 + 5.0b
	unburned	*a	1.1 + 0.3c
Ambrosia psilostacha	burned	2.8 + 1.1a	2.5 + 1.1a
	unburned	10.2 + 2.3b	8.2 + 1.5b
Artemisia ludoviciana	burned	0.1 + *a	0.1 + *a
	unburned	12.6 + 2.9b	8.0 + 1.7b
Amorpha canescens	burned	4.4 + 1.9a	1.1 + 0.4b
	unburned	0.3 + 0.1b	1.6 + 0.5b

the dominant cool-season grass *Poa pratensis*, was not affected by topography but was greatly reduced by annual burning (table 1). The sensitivity to burning of this and other cool season species is due to the loss of terminal growth from spring burning (Abrams and Hulbert 1987). Warm-season species are still dormant during spring burning and do not show such sensitivity.

Cover of most forb and woody species increased with fire exclusion. *Salvia azurea* (= *S*. pitcherii) and *Amorpha canescens* are exceptions to this, with cover being significantly higher on annually burned upland and lowland soils, respectively (table 1). *Artemisia ludoviciana, Ambrosia psilostachva* and *Aster ericoides* are the dominant forbs on fire excluded sites. Overall, woody species and forb species cover increase with time since burning (Abrams and Hulbert 1987; Gibson and Hulbert 1987).

Multivariate analyses of species cover (Gibson and Hulbert 1987; Gibson 1988) have indicated that the species show an individualistic response to fire frequency and topographic position (fig. 1). This indicates that although it is clear that fire exclusion from the tallgrass prairie leads to an increase in the cover of many species, especially forbs (table 1), the rate of increase varies between species in a manner typical of secondary successions (e.g., Pickett 1982). In contrast to such typical models however, different species do not successively attain and then lose predominance. Rather, *A. gerardii* remains the dominant species throughout. s likely a reflection of the fact that given continued fire exclusion, grass dominated prairie is not the end-point of the successional pathway. Indeed, studies in Oklahoma indicate an eventual dominance of tallgrass prairie by woody vegetation after 3'2 years without tire (Collins and Adams 1983).

Sites that are burned every four years show cyclic fluctuations in community composition, although soil effects and landscape heterogeneity show a stronger relationship to the plant community (Gibson 1988). Ungrazed prairie maintained under such a frequent burning regime on Konza Prairie is considered to be perhaps as comparable to presettlement conditions as is possible under present day constraints. Exclusion of fire for three year periods under this regime is, however, sufficient time to allow for an invasion of woody species (Briggs and Gibson, unpublished data).

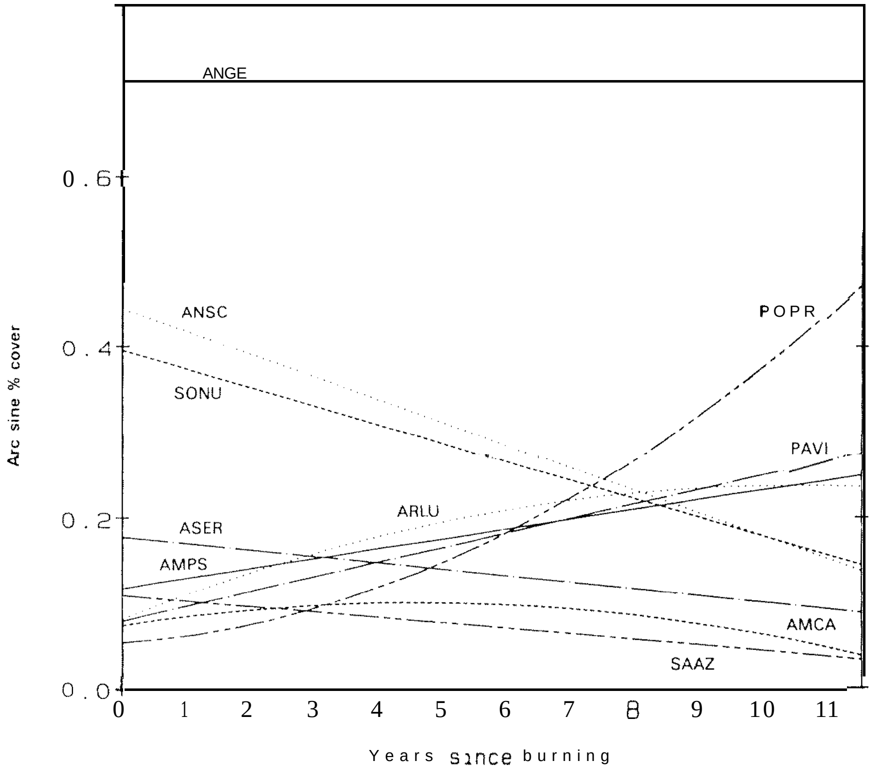


Fig. 1. Fitted 1st and 2nd degree polynomial regression lines of species distribution along a fire interval gradient identified by ordination analysis (Detrended Correspondence Analysis) (After Gibson and Hulbert 1987). ANGE = *Andropogon gerardii*; ANSC = *A. scoparius*; SONU = *Sorghastrum nutans*; PAVI = *Panicum virgatum*; POPR = *Poa pratensis*; SAAZ = *Salvia azurea*; AMPS = *Ambrosia psilostachva*; ARLU = *Artemisia ludoviciana*; AMCA = *Amorpha canescens*; ASER = *Aster ericoides*.

Prairie Productivity

Substantial differences in the seasonal (1984) production of aboveground biomass by graminoids and forbs were evident between an annually spring- burned and unburned watershed on lower slopes (fig. 2). Peak standing crop of aboveground production was significantly greater in the burned (430 + 26 grams per square meter) than unburned (368 + 31 grams per square meter) watershed. This difference between burned and unburned lowland prairie is consistent with the results of long-term studies of productivity on Konza Prairie (Abrams and others 1986; Briggs and others 1989). Peak live graminoid biomass was also greater in the burned (285 + 20 grams per square meter) than unburned (205 + 22 grams per square meter) site, whereas forb and woody plant biomass was typically two-three times greater in the unburned (maximum 94 + 15 grams per square meter) than the burned watershed (maximum 45 + 13 grams per square meter). Woody plants, the smallest component of the total, contributed little to total production. Both aboveground production and the live graminoid component showed a mid-season peak in late July-early August. In contrast, the biomass of forbs and woody plants showed little seasonal variation.

Invasion of Tree Species into Open Prairie

Woody species will rapidly invade open prairie in the absence of tire and grazing, given a sufficient time and local seed source (Gleason 1913; Weaver 1960; Grimm 1983; Bragg and Hulbert 1976). On Konza Prairie, the invasion of trees has been documented since 1971 by direct stem counts on over 500 hectares of open prairie. The principal tree species are triacanthos, Populus deltoides, Salix spp., Ulmus americana, and Celtis occidentalis (table 2). In frequently burned prairie, densities of 2-3 trees per hectare have been recorded, while in areas where tire has been excluded for 10 or more years densities range from 12 to 77 trees per hectare. Over a five year period, recruitment of all species into long-term unburned areas is 6-7 individuals per hectare (Briggs and

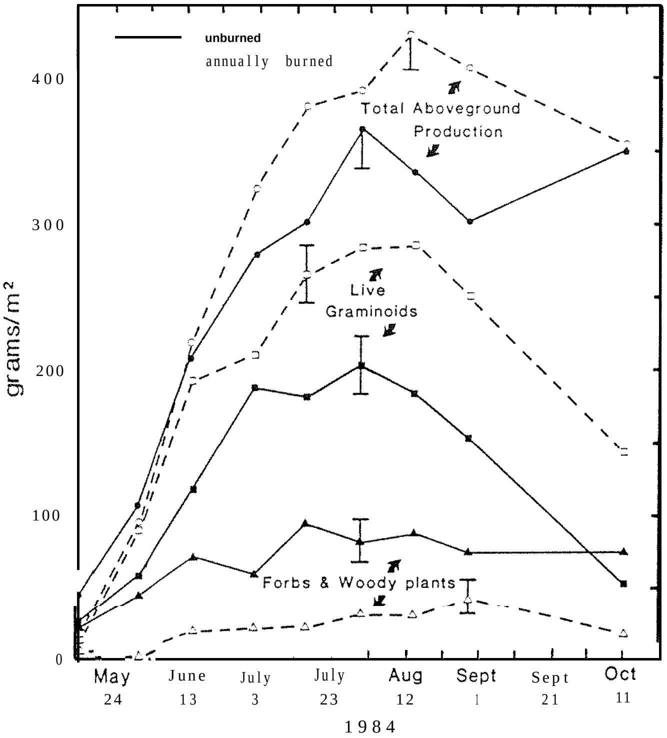


Fig. 2. The seasonal pattern of several components of aboveground biomass on a burned and unburned lowland soil during 1984 on Konza Prairie . Total aboveground production includes live graminoids, forbs, and woody plants, and current year's dead biomass. Vertical bar represents + standard error of the mean. (After Abrams and others 1986).

Table 2. Stem density, species number, diversity and dominant species (> 15 percent of total stem density) of tree species in the open prairie on annually burned and unburned (> 10 years) watersheds on Konza Prairie in 1986. Uatersheds N4D and N1B contain large areas of gallery forest along the stream channels.

Site and Burn Treatment	Tree Density (number per hectare)	Number of Species	Diversity (H')	Dominant Species (Density per hectare)
Annually Burned				
IA	2.5	6	1.23	Gleditsia triacanthos (1.5)
ID	2.9	4	0.94	Populus deltoides (0.5)
Unburned (10 years)				
UB	12.0	8	1.68	Salix sp. (4.1) Ulmus americana (2.8) G. triacanthos (0.7)
UC	29.6	9	1.28	G. triacanthos (12.6) P. deltoides (12.6)
N4D	54.7	18	1.50	U. americana (28.5) G. triacanthos (8.8)
NIB	76.9	13	1.20	U. americana (48.0) Celtis occidentalis (12.1)

Gibson, unpublished data). In areas of open prairie adjacent to stream channel gallery forests, Ulmus americana and Celtis occidentalis are the dominant invasive species. This is a reflection of their importance in the gallery forests (Abrams 1986). Other gallery forest dominants such as Quercus muehlenbergii, Q. macrocarna and Cercis candensis are only occasionally found in open prairie. The ability of these forest species to invade open prairie is related to their physiological ability to withstand the relatively more xeric open prairie habitat (Abrams 1988b). In areas further removed from the gallery forests, fire exclusion leads to an increase in the density of species that normally persist in frequently burned prairie albeit at low densities along the stream margins, i.e. Gleditsia triacanthos, Populus deltoides, and Salix spp. (table 2). These are short-lived, early successional species common in river floodplains and stream courses (Bellah and Hulbert 1974).

The spatial pattern of species invading open prairie from which fue has been excluded is a function of species dispersal vectors. Species such as Juniperus virginiana, which are bird dispersed, show a random pattern of distribution. In contrast, wind dispersed species such as Ulmus americana show an aggregated pattern. Juveniles of all species are clustered around adults, but at a greater distance for the bird dispersed species. At the landscape scale, invading tree species are (except J. virginiana) associated with the stream channels. Upstream of mature gallery forest, attenuated gallery forest, as seen on watersheds N4D and N1B (table 2) represents the first stages of gallery forest development in open prairie in the absence of tire.

GALLERY FOREST

Stand Classification and Ordination

Eighteen stands were method divided into four ecological groups along the polar ordination axis according to importance values of the three dominant species (fig. 3). Group 1 (stands 1,2,6,18) included Celtis occidentalis - Ouercus macrocarpa dominated stands, with Q. muehlenbergii and Ulmus as subdominants. Group 2 stands were dominated by Q. macrocarna (stands 3,9,10) or Q. macrocarna and Q. muehlenbergii (stands 4,7) with lesser amounts of Celtis and Ulmus. Quercus muehlenbergii and Q. macrocama were the dominants and Ulmus and Cercis canadensis the subdominants in group 3 (stands 5,8,11,12,14,16). Quercus muehlenbergii dominated stands in group 4 (stands 13,15,17), with Q. macrocarna, Cercis and Ulmus as subdominants. Stand positions along the polar ordination axis were highly correlated with increasing slope and decreasing silt, which may be interpreted as a moisture gradient from mesic (group 1) to xcric (group 4) (Abrams 1986).

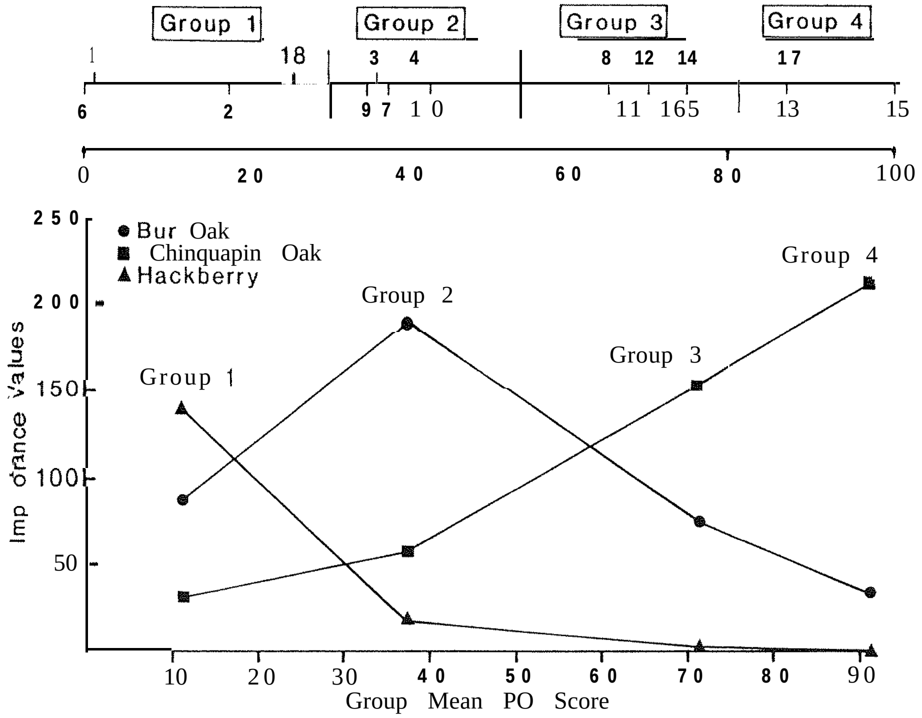


Fig. 3. Polar ordination analysis and the mean importance values for the dominant species in 18 gallery forest stands on Konza Prairie. The four stand types are identified.

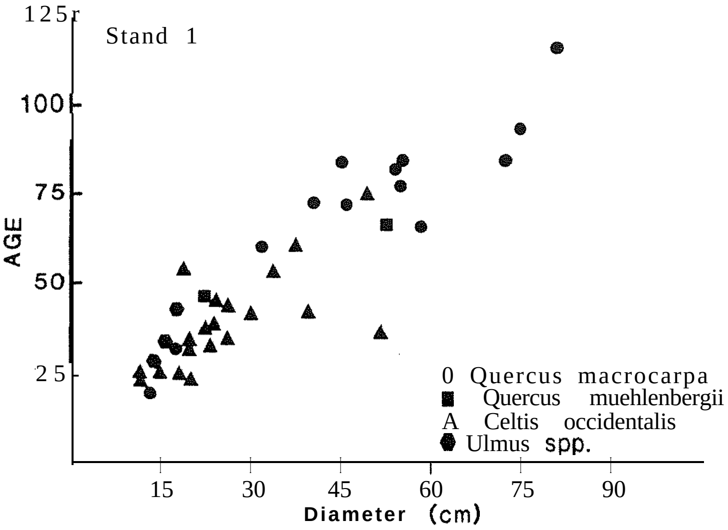


Fig. 4.
Age-diameter data
for gallery forest stand 1
on Konza Prairie.
(After Abrams 1986).

Age-diameter Data

Species age-diameter data from two representative gallery forest stands are shown in figures 4 and 5. Stand 1 (fig 4) is a Celtis - Q. macrocarpa oak stand in which Q. macrocarpa stems were the largest and oldest present; most Q. macrocarpa were over 40 centimeters diameter and 70 years old and formed an even-aged canopy. The size and age of Q macrocarpa was distinct from that of Celtis, which generally ranged from 10-40 centimeters diameter and 23-53 years old. In stand 8, a Q. muehlenbergii - Q. macrocarpa stand, oak species dominated the larger and older diameter and age classes, whereas Cercis, Ulmus and, to a lesser extent, Celtis dominated the smaller and younger classes (fig 5). A predominant age gap of 25-35 years separated these species groups.

HISTORICAL DEVELOPMENT OF GALLERY FORESTS ON KONZA PRAIRIE

Using data from the 1858 Original Land Office Survey of Konza Prairie and aerial photographs taken in 1939 and 1978, it was possible to determine changes in the extent of gallery forests during that 120-year period (fig. 6). In 1858 only two areas of continuous forest comprising about 5 hectares were noted. Occasionally, a few trees or scrubby timber and shrubs were recorded in other areas of Konza Prairie, especially along the stream channels and ravine bottoms, but in general this area was described as rolling prairie devoid of woody vegetation. The aerial photographs of Konza Prairie taken in 1939 and 1978 were in marked contrast to that described in 1858. During those periods a large expansion of the gallery forests to approximately 111 and 206 hectares occurred, respectively, with widespread invasion of shrublands and forests onto the prairie and development of shrublands into forests.

The distribution and overall ecology of the gallery forests on Konza Prairie has been greatly affected by anthropogenic factors. The limited extent of the gallery forests in 1858 was probably due to higher fire intensity and frequency prior to European settlement, which started about 1840 (cf. Penfound 1962). Following settlement, the number, extent and intensity of fire most likely decreased in the Flint Hills due to road construction, expansion of towns, agriculture, continuous cattle grazing, suppression of wildfire and recommendations against burning during the mid-1900s (Bragg and Hulbert 1976; Abrams 1985). Therefore, after settlement forests

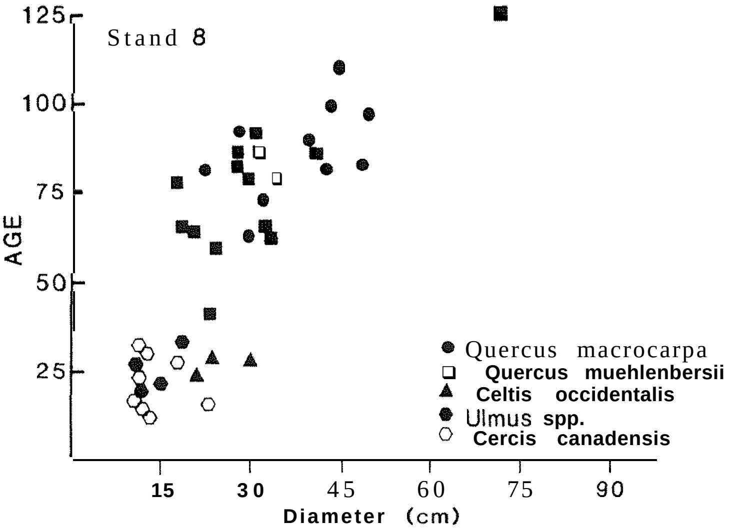


Fig. 5.
Age-diameter data
for gallery forest stand 8
on Konza Prairie.
(After Abrams 1986).

increased rapidly, which suggest that tire, rather than low precipitation, limited growth of woody vegetation in northeast Kansas (c.f Abrams 1988c).

It appears that a succession from shade intolerant Quercus species to the more tolerant Celtis and Cercis is taking place, despite these forests burning at intervals of about 11-20 years since the mid-1800s (Abrams 1985; Abrams 1986). Quercus macrocarpa and/or Q. muehlenbergii, which represented the largest and oldest species in each stand, showed very little recruitment into the tree size class for over half a century. In contrast, numerous Celtis, Ulmus and Cercis trees younger than 50 years old were present in these stands. On the mesic sites Celtis may be the future sole dominant. Already in group 1 stands (1,2,6,18) Celtis is the dominant despite it being younger and smaller than Q. macrocarpa. On the steeper, drier sites on Konza Prairie, where Celtis is rare, Cercis may replace Q. muehlenbergii. The small stature of Cercis does not rule it out as a potential replacement species here because the size of Q. muehlenbergii is limited on these harsh sites. Even though Ulmus is a dominant reproducer in nearly all stands, its potential as an overstory dominant is probably limited by the Dutch Elm Disease. This blight was discovered in Kansas in 1957 and has depleted many area forests of mature elms (Thompson and others 1978). The less advanced successional status of the xeric versus mesic forests on Konza Prairie suggests that the rate of succession in xeric forests is constrained by harsher environmental conditions and/or higher tire frequency.

CONCLUSIONS

Subtle and gross changes in fire frequency dramatically alter landscape patterns on Konza Prairie in the absence of grazing Annual burning treatment resulted in the greatest dominance for warm-season tallgrass species. Less frequently burned areas develop progressively less cover of several dominant grasses. However, cover of Andropogon gerardii, the dominant prairie grass, remained relatively unchanged in upland and lowland prairie burned at 1- to 11-year intervals. With increasing intervals between fire, total cover of forb and woody species increased. Lowland sites, especially along stream channels, unburned for 10 or more years show definite signs of conversion to forest dominated by Juniperus, Gleditsia, Ulmus and Celtis. Old established woodlands along stream channels and ravines had overstories dominated by Quercus and Celtis, with Celtis, Cercis and Ulmus in the understories. The distribution of these gallery forests since 1850 and successional changes resulting in oak replacement by more shade tolerant species are attributed to reduced tire frequency. Thus, our work on Konza Prairie provides further evidence that fire is a primary factor controlling community composition, productivity, structure and successional processes in tallgrass ecosystems, and that a frequent fire interval and possibly grazing and periodic drought are necessary maintain tallgrass prairie in a "pristine" condition.

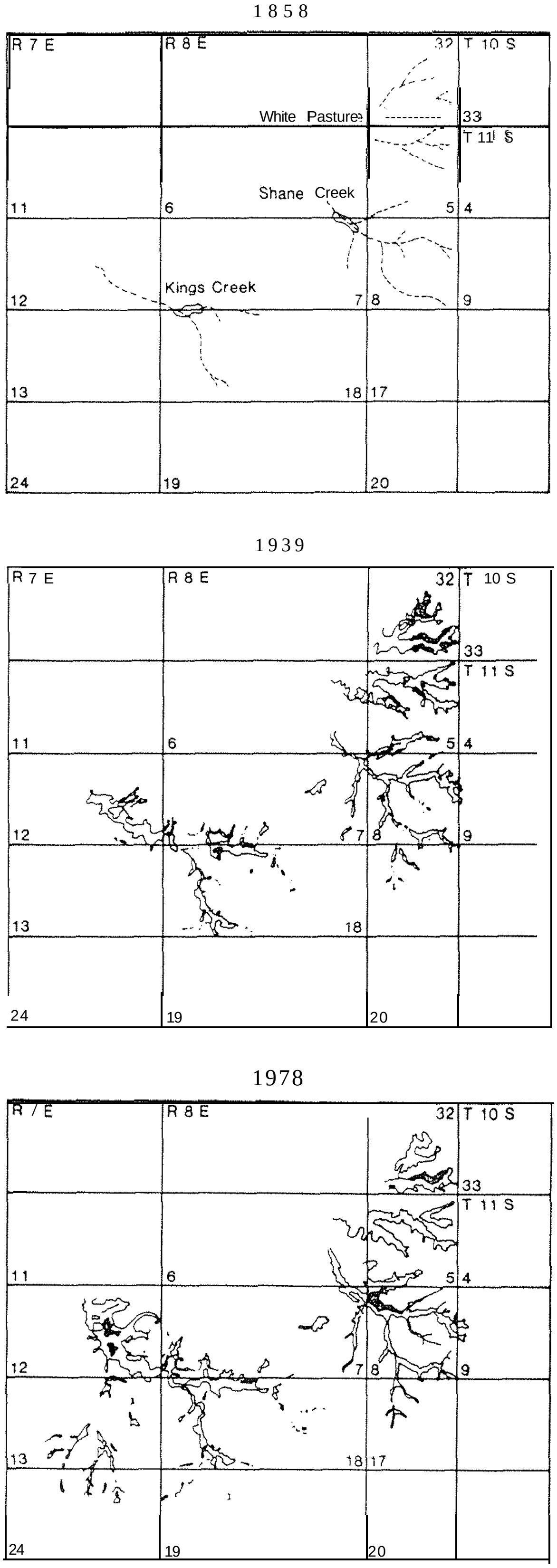


Fig. 6. Areal extent of gallery forests and shrublands (shaded) in 1858, 1939 and 1978 on Konza Prairie.

LITERATURE CITED

Abrams, M. D. 1985. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. Am. Midl. Nat. 114:188-191.

Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65:29-37.

Abrams, M. D. 1988a. Effects of burning regime on buried seed and canopy coverage in a Kansas tallgrass prairie. Southwest. Nat. 33:65-70.

Abrams, M. D. 1988b. Genetic variation in leaf morphology and plant and tissue water relations during drought in Cercis canadensis L. Forest Sci. 34:200-207.

Abrams, M. S. 1988c. Effects of prescribed tire on woody vegetation in a gallery forest understory in northeastern Kansas. Trans. Kansas Acad. Sci. 9:63-70.

Abrams, M.D., A.K. Knapp and L.C. Hulbert. 1986. A ten-year record of above ground biomass in a Kansas tallgrass prairie: Effects of fire and topographic position. Amer. J. Bot. 73:1509-1515.

Abrams, M.D. and L.C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. Am. Midl. Nat. 117:442-445.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51:163-201.

Bellah, R.G. and L.C. Hulbert. 1974. Forest succession on the Republican River floodplain in Clay County, Kansas. The Southwestern Naturalist 19:155-166.

Briggs, J.M., T.R. Seastedt and D.J. Gibson. 1989. Comparative analysis of temporal and spatial variability in above-ground production in a deciduous forest and prairie. Holartic Ecology 12:130-136.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29: 19-24.

Brown, M.J. and L.D. Bark. 1971. Drought in Kansas Kans. Agric. Exp. Stn. Bull. 547. 12p.

Collins, S.E. and D.E. Adams. 1983. Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass prairie. Vegetatio 51:181-190.

Collins, S.L. and D.J. Gibson. 1990. Effects of tire on community structure in tall and mixed-grass prairie. pp. 81-98. In: Effects of Fire in Tallgrass Prairie Ecosystems (S. L. Collins and L.L. Wallace, Eds.) Univ. Okla. Press, Norman.

Gibson, D.J. 1988. Regeneration and fluctuation of tallgrass prairie vegetation in response to burning frequency. Bull. Torrey Bot. Club 115:1-12.

Gibson, D.J. and L.L. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Gleason, H.A. 1913. The relation of forest distribution and prairie tires in the middle west. Toreya 13:173-181.

Great Plains Flora Association. 1986. Flora of the Great Plains. Univ. Press of Kansas, Lawrence. 1392 p.

Grimm, E.C. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U.S.A. New Phytol. 93:311- 350.

Hulbert, L.C. 1973. Management of Konza prairie to approximate pre-whiteman tire influences, pp. 14-19. In L. C. Hulbert (ed.), 3rd Midwest Prairie Conf. Proc., Kansas State University, Manhattan.

Jantz, D. R., R. F. Hamer, H. T. Rowland and D. A. Gier. 1975. Soil survey of Riley county and part of Geary county, Kansas, U. S. Dep. Agric. Soil Conserv. Serv. 71 p.

Kucera, C.L. 1981. Grasslands and tire, pp. 90-111. In H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan and W. A. Reiners (eds.), Fire regimes and ecosystem properties, USDA For. Serv. Gen. Tech. Rep. WO- 26.

Penfound, W.T. 1962. The savanna concept in Oklahoma. Ecology 43 :774- 775.

Pickett, S.T.A. 1982. Population patterns through twenty years of old field succession. Vegetatio 49:45-59.

Thompson, H.E., W.G. Willis and R.A. Keen. 1978. Controlling Dutch Elm Disease. Kansas State Univ. Agric. Exp. Sta. Bull. 626, 16 p.

Weaver, J.E. 1960. Flood plain vegetation of the central Missouri Valley and contacts of woodland with prairie. Ecol. Monogr. 30:37-64.

FIRE MANAGEMENT FOR MAXIMUM BIODIVERSITY OF CALIFORNIA CHAPARRAL

Jon E. Keeley'

Abstract-Two reproductive modes present in chaparral shrubs are affected very differently by fire. Some species, called "fire-recruiters," are dependent upon tire for seedling establishment. These species have contributed to the notion that the chaparral community is dependent upon tire for rejuvenation. In the absence of fire, chaparral is often described in pejorative terms which imply that long unburned conditions represent an unhealthy state. However, many shrub species, called "fire-persisters," do not establish seedlings after tire, rather they require long fire-free periods in order to establish seedlings. These species are vigorous resprouters, not only after tire, but throughout their lifespan. Older stands of chaparral are continually rejuvenated by recruitment of new resprouts and seedlings of these tire-resister species. It is suggested that the long-term stability and diversity of chaparral requires a mosaic of tire frequencies.

INTRODUCTION

California chaparral is considered a "tire-type" vegetation based on the fact that all species are resilient to the modem fire regime of fires every few decades (Kceley and Keeley 1988). Resilience of the vegetation is reflected in the relatively minor changes in community composition resulting from fire. Species present before fire return rapidly afterwards, either regenerating aboveground parts from basal resprouts or by seedling establishment.

In addition to being considered a fire-type vegetation, chaparral is also often described as a tire-dependent vegetation. This is based on both population and community level phenomenon. Certain species, Adenostoma fasciculatum (Rosaceae), Arctostaphylos spp. (Ericaceae) and Ceanothus spp. (Rhamnaceae) for instance, require fire for seedling establishment. Seeds are dispersed in a dormant state and accumulate in the soil until germination is triggered by fire, either from heat or a chemical leaching from charred wood (Keeley 1987). These species have specialized their reproductive biology to the extent that they are dependent upon fire for completion of their life cycle and may be referred to as "fire-recruiters". At the community level, fire-dependence is implied by the frequent suggestion that stands require fire for rejuvenation. Chaparral unburned for 60 years or more is often referred to as decadent, senescent, senile and trashy (Hanes 1977).

This fire-dependent paradigm of chaparral has guided fire management strategy in southern California, although it is perhaps generous to call the modem fire regime "a strategy," since most acreage in southern California bums by catastrophic wildfires. Nonetheless, federal, state and county agencies have prescribe bum programs for chaparral sites under their fire jurisdiction. Some areas that escape wildfires are burned under prescription at return intervals of approximately 15-25 years. Such a prescription follows logically from the commonly accepted dogma about the tire-dependence of chaparral. This, however, is not the whole story.

FIRE RESILIENCE VS. FIRE DEPENDENCE

While it is true that the chaparral community is highly resilient to fire, all species within the community are not fire-dependent. In fact, a large component of chaparral, while persisting in the face of recurrent fire, may actually decline after repeated tires. Included here are species such as Quercus dumosa (Fagaceae), Heteromeles arbutifolia Rosaceae), Prunus ilicifolia (Rosaceae), Cercocarpus betuloides (Rosaceae) and Rhamnus spp. (Rhamnaceae). These shrubs are resilient to fire by virtue of the fact that they are vigorous resprouters, yet they do not establish seedlings after fire. These species are "fire-persisters" but not "fire-recruiters." A management plan oriented towards long-term stability and maintenance of biodiversity needs to consider the conditions necessary for reproduction of these taxa.

The conditions under which these species recruit seedlings have not been well worked out. It is clear that these species do not establish seedlings after fire, and there are aspects of their seed germination physiology which account for this (Keeley 1987). On the other hand, studies of mature chaparral have consistently pointed out the lack of seedling reproduction under the closed canopy of this dense shrub vegetation (Sampson 1944; Horton and Kraebel 1955; Hanes 1971; Christensen and Muller 1975).

One clue to this mystery is an observation made in an early paper by Patric and Hanes (1964). These authors studied a stand of chaparral unburned for more than 60 years and noted seedlings of Quercus dumosa, Prunus ilicifolia, and Rhamnus crocea. Spurred in part by these early findings I have been investigating the fate of chaparral in the long absence of fire.

'Professor of Biology, Department of Biology, Occidental College, Los Angeles.

My focus has been on the demographic structure of stands free of fire for 100 years or more in some cases. This study has revealed large seedling populations in older stands of chaparral; from 1,000 to 40,000 seedlings per hectare for taxa such as Quercus, Rhamnus Prunus, Cercocarpus and Heteromeles (Keeley unpublished data). It is apparent that long fire-free conditions are required for seedling establishment by these fire-persister shrub species.

In summary, chaparral is dominated by shrubs that are resilient to tire. Some are fire-dependent taxa that recruit seedlings only in the first season after tire, and these are called fire-recruiters. Other shrubs, however, are not fire-dependent. They persist after fire but these tire-persisters require long fire-free conditions for seedling establishment (figure 1).

What is the best strategy for management of these systems. It appears that fire intervals on the order of every 20 years would potentially benefit fire-recruiters. Fire-persisters, while not obviously damaged by this fire return interval, over long periods of time will be threatened by the lack of opportunities for seedling establishment. I suggest the coexistence of these modes reflecs the natural stochastic fire regime. Under natural conditions, the eventuality of fire on any given site would have been nearly certain, however, the return interval over time would have been variable. Short return intervals would have provided opportunities for population expansion of fire-recruiters and long return intervals would have provided opportunities for population expansion of fire-persisters.

RESILIENCE TO LONG FIRE-FREE INTERVALS

Community stability is dependent on both tire-recruiters and fire-persisters being resilient to both short and long fire return intervals. The current tire regime of relatively short intervals of 20 years between fires does not pose an immediate threat to either group. I suggest that all chaparral shrubs are also resilient to long tire-free periods, although few chaparral sites remain unburned for more than a few decades.

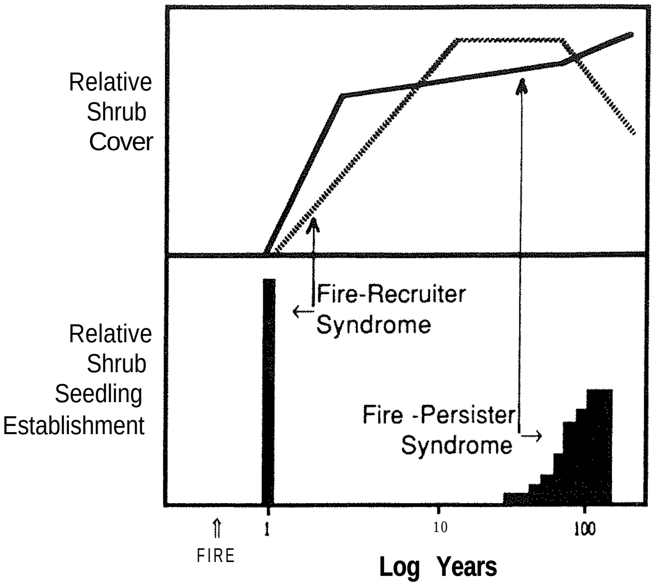


Figure 1.- Schematic illustration of the timing of seedling recruitment for chaparral shrubs described as fire-recruiters and as fire-persisters and longterm changes in relative shrub cover for fire-recruiters (dashed line) and fire persisters (solid line).

This notion would seem to be contrary to much of the dogma about the decadence, senescence and senility of chaparral stands older than 60 years. These terms, however, are seldom defined; a former student once suggested that a senile chaparral shrub was one which forgot to close its stomates, and this definition is about as good as any proposed in the literature. Most certainly these terms derive from observations that, due to natural thinning of shrubs (e.g., Schlesinger and Gill 1978), dead wood accumulates. However, something that is seldom appreciated is that dead stems are continually replaced by basal sprouting in all sprouting shrubs (figure 2). Consequently, the age structure of sprouting shrub populations are not even-aged and exhibit continuous recruitment and turnover of stems (figure 3). In other words, resprouting, in addition to functioning to rejuvenate shrubs after fire, functions to rejuvenate the canopy throughout the life of the stand.

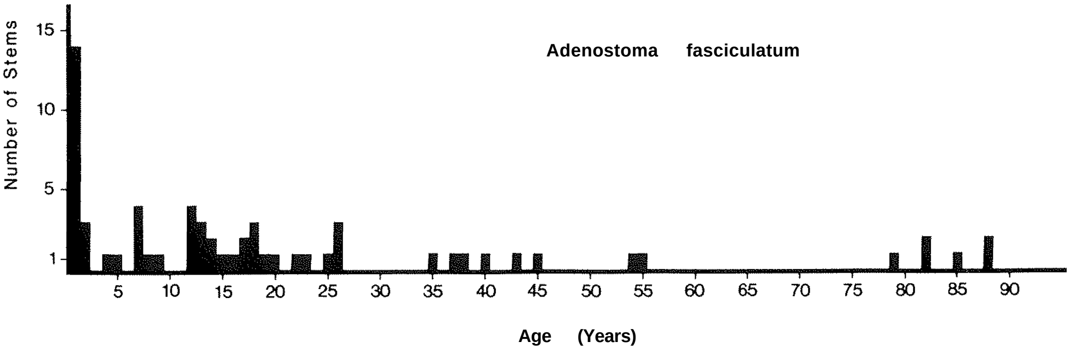


Figure 2.- Number of stems of different ages on a single resprouting shrub of Adenostoma fasciculatum in a stand of chaparral last burned 89 years ago (Keeley unpublished data).

How then did old stands of chaparral come to be described as senescent and unproductive? This idea is apparently derived from early studies which investigated browse production by different aged stands of chaparral (Biswell and others 1952; Hiehle 1964; Gibbens and Schultz 1963). These studies concluded that chaparral became very unproductive within several decades following fire. However, these studies were only concerned with production available of wildlife. Consequently they did not present valid measures of productivity, because production above 1.5 meters, which is unavailable for deer, was not included. Since most new growth in older stands occurs above 2 meters, it is not surprising that one would conclude that frequent fires were a necessity for maintaining productive chaparral communities. Since the concept of stand senescent seemed logically consistent with the fire-dependent nature of many chaparral species, this myth of low productivity in older stands of chaparral was not questioned by many chaparral ecologists and foresters. Modern studies, however, reveal that live biomass increases with age in chaparral (figure 4), and the terms decadence, senescence, and senility, while possibly true of some species, should not be used to describe chaparral communities.

In conclusion, chaparral is resilient to short and long fire-free intervals, and different fire-return intervals, favor different components of the vegetation. Longterm stability and biodiversity of chaparral communities may require a mosaic of fire regimes.

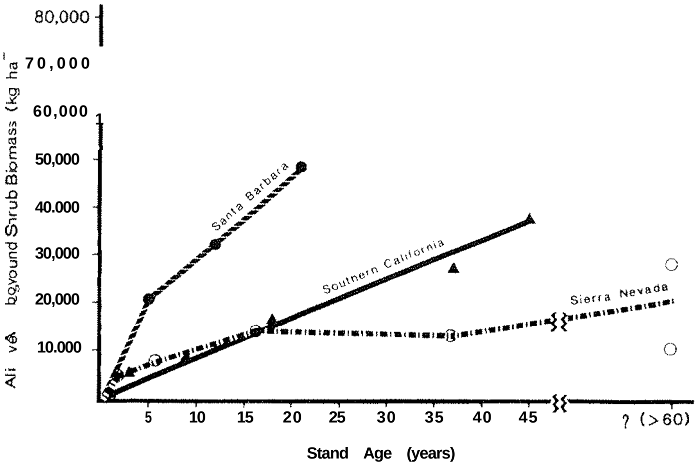
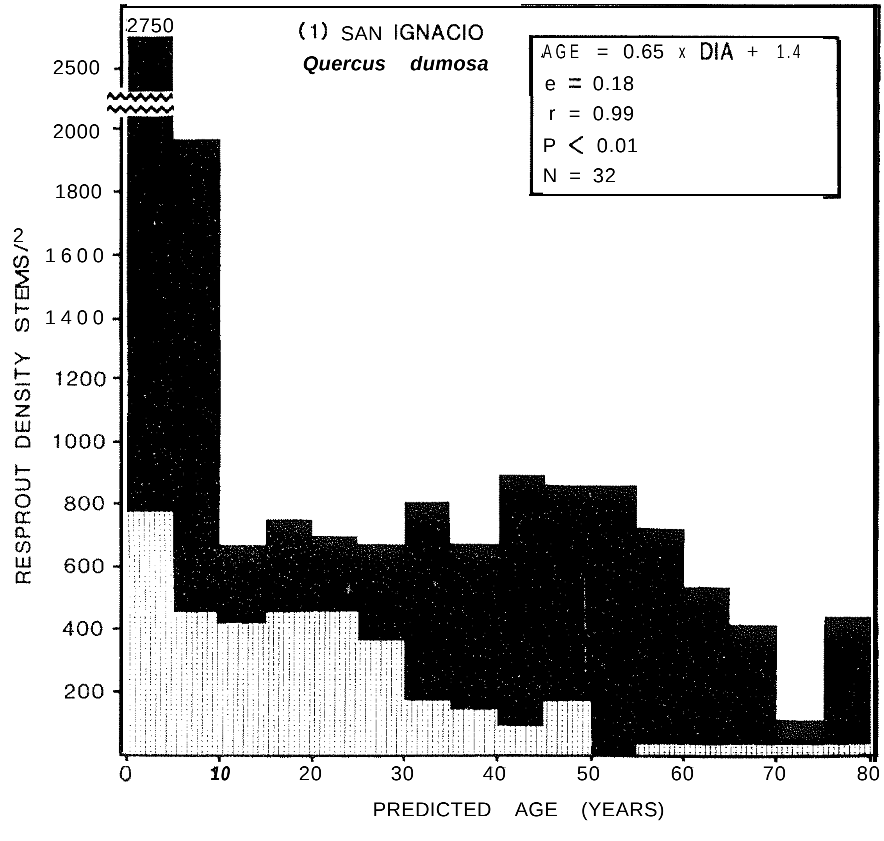


Figure 4.- Standing living biomass in chaparral stands as a function of age since last fire (from Keeley and Keeley 1988, with permission of Cambridge University Press, data from studies by Specht 1969, Conrad and DeBano 1974, Schlesinger & Gill 1980, Rundel and Parsons 1979, Stohlgren and others 1984, as cited in Keeley and Keeley 1988.)

Figure 3.- Predicted population age structure of Quercus dumosa stems sprouted from root crowns of mature shrubs in a stand of chaparral last burned 76 years ago (solid bars are living stems, vertical lines are dead stems). Stem diameters were measured in 36 4x4 m plots randomly placed in the stand. Age was predicted from the indicated regression line based on 32 stems aged by ring counts. In addition to the correlation coefficient, the estimate of relative error was calculated as the standard error divided by the mean value of y.



LITERATURE CITED

Biswell, H. H., R.D. Taber, D.W. Hedrick, and A.M. Schultz. 1952. Management of chamise brushlands for game in the north coast range of California. California Fish and Game 38:453-484.

Christensen, N. L. and C. H. Muller. 1975. Relative importance of factors controlling germination and seedling survival in Adenostoma chaparral. American Midland Naturalist 93:71-78.

Gibbens, R. P. and A.M. Schultz. 1963. Brush manipulation on a deer winter range. California Fish and Game 49:95-118.

Hanes, T.L. 1971. Succession after tire in the chaparral of southern California. Ecological Monographs 41:27-52.

Hanes, T. L. 1977. California chaparral, pp. 417-170. In: Barbour, M. G. and J. Major, eds. Terrestrial vegetation of California. John Wiley, New York.

Hiehle, J.L. 1964. Measurement of browse growth and utilization. California Fish and Game 50:148-151.

Horton, J.S. and C.J. Kraebel. 195.5. Development of vegetation after tire in the chamise chaparral of southern California. Ecology 36:244-262.

Kecley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68:434-443.

Keelcy, J. E. and S.C. Keeley. 1988. Chaparral, pp. 165-207. In: Barbour M.G. and W. D. Billings, eds. North American terrestrial vegetation. Cambridge University Press, New York.

Patric, J. H. and T. L. Hanes. 1964. Chaparral succession in a San Gabriel Mountain area of California. Ecology 45:353-360.

Sampson, A. W. 1944. Plant succession and burned chaparral lands in northern California. Agricultural Experiment Station, University of California, Berkeley, Bulletin 685.

Schlesinger, W.H. and D.S. Gill. 1978. Demographic studies of the chaparral shrub, Ceanothus megacarpus, in the Santa Ynez Mountains, California. Ecology 59:1256-1263.

FIRE AND OAK REGENERATION IN THE SOUTHERN APPALACHIANS

David H. Van Lear'

Abstract-Oak forests throughout the southern Appalachians have been historically maintained in a regime of frequent fire. Frequent tire over an indefinite time period favors oak establishment by reducing understory and midstory competition from tire-intolerant species and by creating preferred conditions for acorn caching by squirrels and bluejays. Fire also reduces populations of insects which prey on acorns and young oak seedlings. Once established in the understory, oaks have a tenacious ability to resprout when tops have been killed repeatedly by tire. The ability to continually resprout when numbers of other sprouting hardwoods have been reduced by fire allows oak to accumulate in the advance regeneration pool and dominate the next stand when suitable conditions prevail. Intense fires in logging debris also favor establishment and development of high quality oak-dominated stands. Tentative guidelines for the silvicultural use of tire to regenerate oak are discussed.

INTRODUCTION

The abundance of oak in the southern Appalachians and throughout eastern North America is related to past land use and extensive disturbance (Crowe 1988). Most of the river basins throughout the southern mountains were cut over and subsequently burned repeatedly around the turn of the century (Secretary of Agriculture's Report to Congress 1902). This type of disturbance regime evidently favored oak regeneration because oaks presently dominate mature mixed hardwood stands on mesic to xeric sites throughout the region.

Today oaks are often replaced by other species when mature stands are harvested, especially on better quality sites (Sander and others 1983). Failure to consistently regenerate oaks following harvest is widely recognized as a major problem in hardwood silviculture. Even though researchers generally agree that fire played a role in the establishment of oak-dominated stands at the turn of the century (Sander and others 1983; Crow 1988), no silvicultural guidelines exist for using tire to regenerate oak (Rouse 1986). The purpose of this paper will be to 1) describe the ecology of oak regeneration in regard to fire, and 2) present tentative guidelines for the silvicultural use of fire to regenerate oak.

It must be emphasized that these are <u>tentative</u> guidelines and must be tested prior to implementation as management recommendations.

THEECOLOGYOFOAKREGENERATION

Large seed crops are produced by oaks at 2- to lo-year intervals, although there is great variation among species (Sander and others 1983). In the southern Appalachians, acorn yields of greater than 1000 pounds per acre (fresh weight) occasionally occur which allow oak seedlings to become established. Deer and turkeys are major consumers of acorns, although Sciurids, especially chipmunks and flying squirrels, may consume more than half of the oak mast available to wildlife in the southern Appalachians (Johnson and others 1989).

In addition to wildlife predation of acorns, insects also consume large quantities of acorns. Annually about 50 percent of the acorn crop in Ohio is destroyed by the larvae of Curculio weevils, acorn moths, and gall wasps. Other insects attack germinating acorns and oak seedlings. However, recent studies indicate that prescribed burning may reduce populations of oak insect pests (Galford and others 1988). A reduction in insect predation would allow more acorns to be scattered and buried by jays and squirrels, thus enhancing the probability of successful germination, and also encourage subsequent seedling establishment.

Areas of thin litter are preferred by squirrels and blue jays for acorn burial, suggesting that recently burned areas provide conditions conducive to oak establishment (Galford and others 1988). An interesting and important ecological finding is that jays collect and disperse only sound nuts (Darley-Hill and Johnson 1981), which implies that if these acorns escape predation they will result in well-established first-year seedlings. Seedlings from freshly germinated acorns are unable to emerge through a heavy litter cover (Sander and others 1983). Germination and first-year survival are best when acorns are buried about l-inch deep in the mineral soil (Sander and others 1983).

Species in the oak-pine complex adapted during their evolutionary history to regimes of occasional and frequent fire by developing survival mechanisms which enabled them to withstand intense heat or to regenerate successfully following fire. Martin (1989) suggests that bark thickness may be the single attribute that best characterizes a species's adaptation to fire. While bark thickness is undoubtedly of great importance to the survival of mature trees in regimes of frequent fire, it

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'Professor, Department of Forest Resources, Clemson University, Clemson, SC.

is the ability to continually resprout following top-kill that enables most hardwood species, and especially oak, to regenerate under such conditions.

Although all hardwood species sprout in a regime of annual winter fire, sprouts remain relatively small and inconspicuous because of repeated top-kill by fire (Thor and Nichols 1974; Langdon 1981; Waldrop and others 1987). Annual summer fires eventually eliminate all hardwood sprouts. Biennial summer fires also gradually eliminate hardwood sprouts, but oak succumbs more slowly than other species (fig. 1). Oaks, in the absence of prolific root sprouters such as sweetgum, would gradually dominate the advance regeneration pool because of the tenacity of their sprouting (Carve11 and Tryon 1961; Waldrop and others 1987).

At the turn of the century, summer fires were quite common as farmers burned the land to facilitate grazing. They had learned from early settlers, who in turn had learned from their Indian predecessors, that growing season fires best maintained an open forest with a rich herbaceous layer (Komarek 1974). However, not all areas would bum every year, so hardwood sprouts would have survived in areas where fire occurred at irregular intervals. It is reasonable to assume that, because of their tenacious sprouting ability, oaks would have dominated the advance regeneration pool.

Periodic winter and summer bums at intervals of about 4-7 years allow a vigorous hardwood understory to develop (Langdon 1981; Waldrop and others 1987). However, stems generally remain small enough (< 2 in) to be top-killed by the next tire. Hardwood sprouting is more vigorous following periodic winter bums because of greater carbohydrate reserves (Hodgkins 1958). Thor and Nichols (1974) noted that even with periodic and annual winter burning, oak stems tend to increase at the expense of competing hardwoods. After two periodic winter bums and eight annual winter bums, oak stems comprised 61 and 67 percent of the total stems, compared to 51 percent oak stems on the unburned plots. Swan (1970) has similarly shown that surface fires increase the proportion of oak in a stand even if no seedling establishment occurs, i.e., by persistent sprouting.

A regime of frequent burning over long periods of time would create an open stand, whether burning occurs in pine or hardwood stands. In hardwood stands, long-term burning would tend to eliminate small understory stems outright and would gradually reduce the mid- and overstory canopy through mortality resulting from fire wounds. Increased light reaching the forest floor in these open stands would maintain the vigor of oak advance regeneration. Loftis (1990) demonstrated that elimination of the subcanopy by herbicides

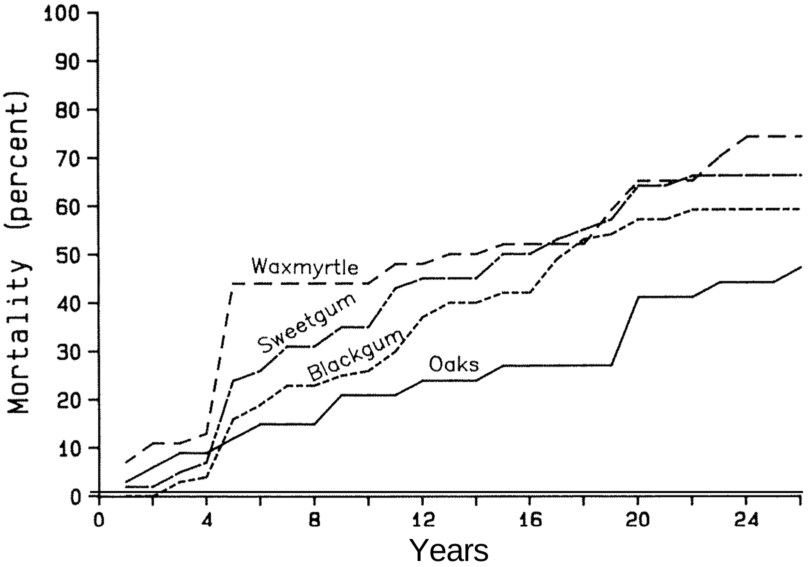

Figure I. Cumulative mortality of hardwood roots over 26 years of biennial prescribed burning (From Langdon 1981).

encouraged development of advance regeneration of red oak in mature mixed hardwood stands in the southern Appalachians. Long-term burning would have created stands similar to those created by injecting undcrstory hardwoods with herbicides.

Studies of effects of single fires on composition of mixed stands have produced varied results. McGee (1979) found that single spring and fall burns in small sapling-sized mixed hardwood stands in northern Alabama had little effect on species composition other than to increase relative dominance of red maple. However, a single intense wildfire in a young mixed hardwood stand in West Virginia shifted species composition to a predominately oak stand (Carve11 and Maxey 1969).

Broadcast burning of logging slash in the mountains of South Carolina and Georgia increased the number of oak sprouts and, more importantly, the number of top-killed oak stems (up to 6-in ground diameter) with basal sprouts (Augspurger and others 1987). Severe fires xerify forest sites by consuming much of the forest floor and perhaps even organic matter in the mineral soil, as well as by exposing the site to greater solar radiation through canopy reduction. Conversion of mesic sites to xeric conditions by intense tires or by a long regime of low intensity fires, along with their tenacious ability to resprout, could explain in large part the ability of oaks to dominate sites where more mesic species normally occur.

The absence of tire for long periods of time has allowed the composition and structure of the southern Appalachian forest to change to a condition where oak species can no longer dominate on better sites. Species that are intolerant of fire have become established and grown to a size where they, because of thicker bark associated with age, can resist fire damage. Such species as mockemut and pignut hickories, scarlet oak, red maple, and blackgum are examples of such species that arc often found on sites where fire has been long absent (Harmon 1984; Martin 1989). Suppression of fire has allowed mesic species, both trees and shrubs, to occupy drier sites where fire was once more frequent and oak more dominant. In particular, yellow poplar stands now often reach ridge tops and rhododendron has dramatically increased its area1 extent (Van Lear and Waldrop 1989; Martin 1989). Impenetrable thickets of ericaceous species such as mountain laurel and rhododendron now often dominate midstories and understories of hardwood stands in the Southern Appalachians and prevent desirable hardwood regeneration from becoming established (Beck 1988).

SILVICULTURAL USE OF FIRE IN OAK REGENERATION

There is no dispute among silviculturists that oak advance regeneration is necessary before a new oak-dominated stand can be regenerated (Clark and Watt 1971; Sander and others 1983; Loftis 1988; Lorimer 1989). However, while many acknowledge the role that fire may have played in creating the present mature oak stands, no silvicuttural guidelines have been developed for using fire to regenerate oak stands.

Based on the history of fire in the southern Appalachians and on documented ecological responses of oaks and associated species to fire discussed earlier, the following scenarios are presented as tentative guidctines for using fire in oak management. Further research will be necessary to test and fine tune these suggestions before they can be recommended as silvicultural practices.

To Promote Advance Regeneration

Little (1974) suggested, as did Van Lear and Waldrop (1989), that an extended period of repeated bums prior to harvest may be necessary to improve the status of oak in the advance regeneration pool, especially on better sites. The famous Santee Fire Plot study, although conducted in another physiographic region, showed that annual summer burns for 5 years in a pine stand in the Coastal Plain killed about 40 percent of oak root stocks compared to 55 to 90 percent of other woody competitors (Waldrop and others 1987). Biennial summer burning killed hardwood root stocks more slowly but the rate, of mortality for other woody species was still significantly greater than that of oak species. Annual winter burning, white not as effective as summer burning in altering species composition, still tends to xerify the site by consuming litter and reducing shading of top-killed understory species.

Thus, a regime of frequent understory bums, including both summer and winter bums, during a period of 5 to 20 years prior to harvest should promote oak seedling establishment and allow oak seedling-sprouts to dominate the advance regeneration pool (fig. 2). A relatively open stand with few midstory and understory trees would provide sufficient light for the oak advance regeneration to develop into stems of sufficient size to outgrow other species after the overstory is removed. Without frequent tire, all advance regeneration species would respond to the favorable light conditions in an open stand.

Pre-harvest burning reduces the forest floor, thereby encouraging burial of acorns by squirrels and bluejays. Burning theoretically reduces insect predation of acorns and young oak seedlings. The proposed burning regime should be a mix of summer and winter fires adjusted to maintain the vigor of the oak advance regeneration. There is no research

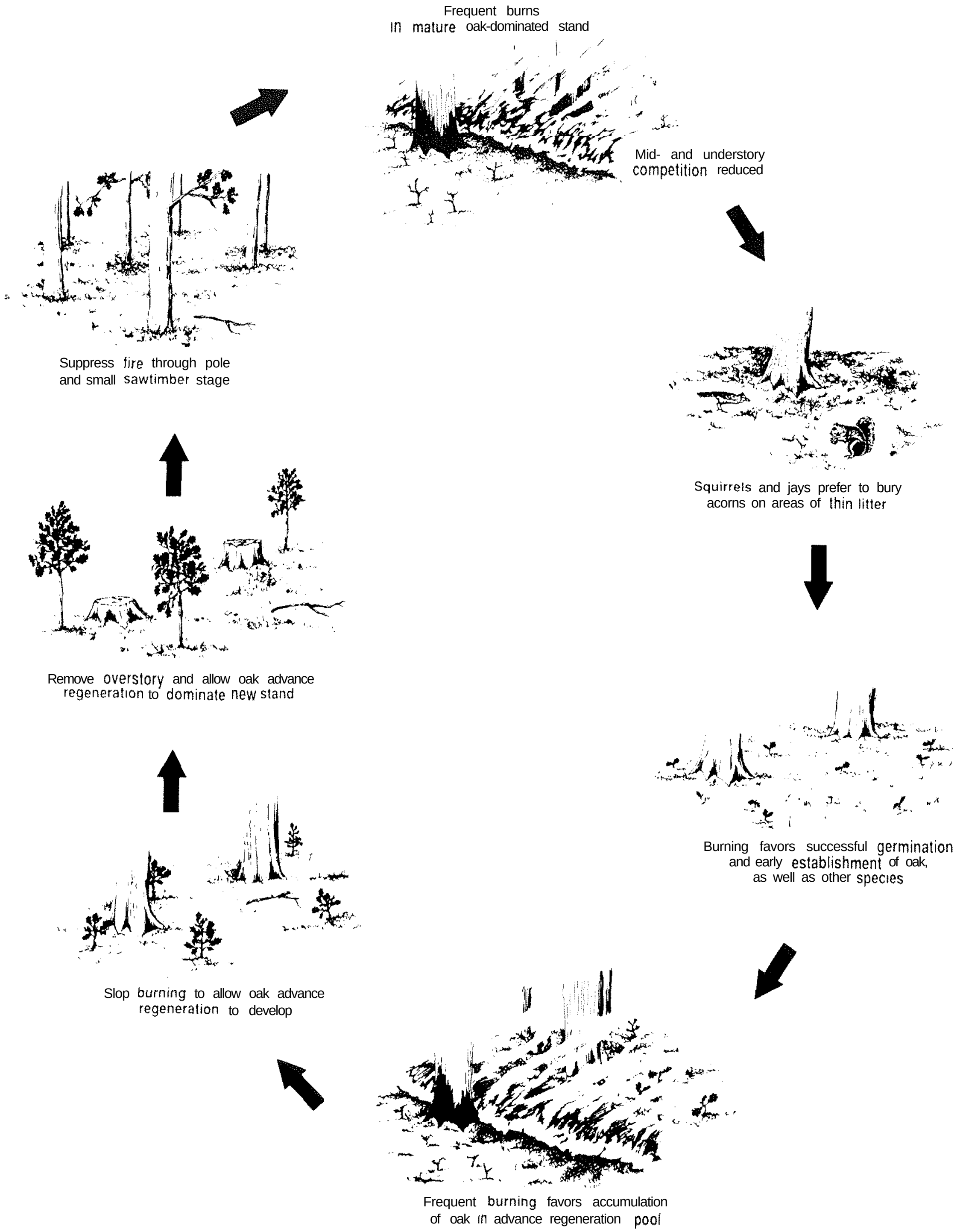

Figure 2. Tentative scenario of using prescribed fire to encourage advance regeneration of oak.

that currently documents what this mix of burns should be. Once an adequate number of oak seedling-sprouts are present and numbers of competing species have been sufficiently reduced, fire should be withheld to allow the oak advance regeneration to attain sufficient size to outgrow other species which germinate or sprout after the mature stand is cut. Sander and others (1983) recommends that 435 advance regeneration oak stems per acre over 4.5 ft tall be present before the overstory is removed.

Fire has been suppressed for so long in the southern Appalachians that it may be necessary to use herbicides to remove midstory trees that have grown too large to be killed by low-intensity fires. Loftis (1988, 1990) has convincingly shown that growth of advance regeneration of northern red oak can be enhanced by herbicidal removal of mid- and understory competitors. A combination of herbicide treatment and frequent fire may be required to secure oak regeneration and allow it to maintain its vigor in mixed hardwood forests which have not been burned for decades. Frequent understory burning will be necessary because singe burns benefit oak regeneration only slightly (Tcuke and Van Lear 1982).

Foresters have long recognized that wildfire during the growing season is a major cause of butt rot in hardwoods, but relatively little information is available concerning the relationship between prescribed fires of lower intensity and stem damage. Wendel and Smith (1986) found that a strip-head fire in the spring in an oak-hickory stand in West Virginia caused a decline in overstory vigor and resulted in death of many trees during the 5 years after burning. However, a low-intensity winter fire in a mixed hardwood stand in the southern Appalachians resulted in little or no cambium damage to large crop trees (Sanders and others 1987). Smaller trees did suffer stem damage, but in even-aged management these trees would be used for products not requiring stems of high quality. If not removed, these damaged trees would eventually succumb to disease and be lost from the stand. More research is needed to determine if and when low-intensity fires can be used without excessive damage to stems of large valuable crop trees in mature hardwood stands.

To Increase Quality and Numbers of Oak Stems after Clearcutting

The fell-and-burn technique for regenerating mixed pine-hardwood stands has been used successfully in the southern Appalachians and is fully described in Waldrop and others (1989). Basically, the technique involves felling residual trees left after commercial clearcutting when their crowns are almost fully leafed out. After curing for 1-3 months, the logging debris is broadcast burned with a high intensity fire conducted under conditions that produce little or no soil damage. Planting pine seedlings at low densities among the hardwood coppice produces a mixed pine-hardwood stand.

Broadcast burning following clearcutting of hardwood or mixed pine-hardwood stands promotes better quality oak sprouts by forcing them to develop from the groundline. Over 97 percent of all oak sprouts developing after broadcast burning of logging slash in the southern Appalachians were basal sprouts, versus 71 percent for unburned areas (Augspurger and others 1987). Suppressed buds higher on the stump are apparently destroyed by the intense heat of the fire. Sprouts from the base of the stump will not develop rot as readily as those from higher on the stump and can be grown on longer rotations for more valuable products.

Broadcast burning increases the number of oak sprouts, as well as the number of small oak stumps with at least one basal sprout. Small oak (< 6 in) stems in the understory of mature stands often are poorly formed and, unless killed back by fire or some other agent, will not develop into quality stems. However, when top-killed by the intense heat of broadcast burns, sprouts from these fire-killed stems are more likely to develop into sound timber trees than other types of oak regeneration (Roth and Hepting 1943).

Intense fires can sometimes result in the introduction of oak in the succeeding stand. Nowacki (1988) documented cases in northern Wisconsin where clearcutting of old-growth maple-hemlock stands and slash burning resulted in even-aged stands dominated by northern red oak. Lorimer (1989) suggested that these oak stands probably developed from acorns brought into the burned area by birds and animals. The author has made similar observations following an intense wildfire in the mountains of South Carolina.

SUMMARY AND CONCLUSIONS

There is no doubt that oaks in the southern Appalachians are being replaced by other species on better sites where oaks were once dominant. Oaks are definitely favored by some type of disturbance regime. Based on the history of this region and literature concerning responses of oak to fire, it appears that oak replacement is largely the result of a different fire regime from that which existed in the region in previous millennia. In the past, frequent fires allowed oak regeneration to accumulate and develop in the understory of open mature stands at the expense of shade-tolerant, fire-intolerant species. When the overstory of these stands was either completely or partially removed by various agents (wind, insects, wildfire, Indian clearing, harvesting, etc.), conditions were created which allowed advance-regeneration dominated by oak to develop into mature stands.

If oaks are to be maintained as a dominant overstory species on medium to good quality sites in the southern Appalachians, it seems that foresters will have to either restore fire to some semblance of its historical role as a major environmental factor or develop artificial methods that simulate the effects of fire. If research does not soon discover the secrets of maintaining oaks on these sites, foresters through their fire suppression efforts will have encouraged the demise of oak on these sites, much to the detriment of numerous ecosystem values.

LITERATURE CITED

Augspurger, M. K., D. H. Van Lear, S. K. Cox, and D. R. Phillips. 1987. Regeneration of hardwood coppice with and without prescribed fire. p. 82-92. In: Phillips, D. R (ed.). Proceedings Fourth Biennial Silvicultural Research Conference, Nov. 4-6, 1986, Atlanta, GA. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. SE-42. Asheville, NC.

Beck, Donald E. 1989. Regenerating cove hardwood stands. p. 156-166. In: Smith, H. Clay; Perkey, Arlyn W.; and Kidd, William E. (eds.). Guidelines for Regenerating Appalachian Hardwoods. May 24-26, 1988. Morgantown, WV. SAF Publications 88-03. West Virginia University Books, Office of Publications, Morgantown, WV.

Carvell, K. L. and W. R. Maxey. 1969. Wildfire adversely affects composition of cove hardwood stands. West Virginia Agricultural Experiment Station Bulletin 2(2):4-5.

Carvell, K. L. and E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. Forest Science 7:98-105.

Clark, F. Bryan **and** Richard Watt. 1971. Silvicultural methods for regenerating oaks. Oak Symposium Proceedings. August 16-20, Morgantown, WV. U.S. Department of Agriculture, Forest Service Northeastern Forest Experiment Station, Upper Darby, PA.

Crowe, T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)--a review. Forest Science 34: 19-40.

Darley-Hill and Johnson. 1981. Acorn disposal by the blue jay (*Cyanocitta cristata*). Oecologia 50:231-232.

Galford, Jimmy R., John W. Peacock, and Susan L. Wright. 1988. Insects and other pests affecting oak regeneration. In: Smith, H. Clay; Perkey, Arlyn W.; Kidd, William E. (eds.). Guidelines for Regenerating Appalachian Hardwood Stands. May 24-26, 1989. Morgantown, WV. SAF Publication 88-03. West Virginia University Books, Office of Publications, Morgantown, WV.

Harmon, Mark E. 1984. Survival of trees after low-intensity surface fires in Great Smokey Mountains National Park. Ecology 65(3):796-802.

Hodgkins, E. J. 1958. Effects of fire on undergrowth vegetation in upland southern pine forests. Ecology 39:36-46.

Johnson, A. Sydney, James M. Wentworth, and Philip E. Hale. 1989. Cumulative mast needs of forest wildlife. p. 18-23. In: McGee, C. E. (ed.). Southern Appalachian Mast Management Workshop Proceedings, August 14-16, 1989, Knoxville, TN.

Komarek, E. V. 1974. Appalachian mountains, mesophytic forest, and grasslands. p. 269-272. In: Kozlowski, T. T. and Ahlgren, C. E. (eds.). Fire and Ecosystems. Academic Press, New York.

Langdon, 0. G. 1981. Some effects of prescribed fue on understory vegetation in loblolly pine stands. In: Wood, G. W. (ed.). Prescribed tire and wildlife in Southern forests: proceedings of a symposium, April 6-8, 1981. Myrtle Beach, SC. Clemson Univ., Belle W. Baruch For. Sci. Inst., Georgetown, SC. p. 143-153.

Little, Silas. 1974. Effects of fire on temperate forests: Northeastern United States. In: Kozlowski, T. T. and Ahlgren, C. E. (eds.). Fire and Ecosystems. Academic Press, New York.

Loftis, David L. 1988. Regenerating oaks on high sites, an update. In: Smith, H. Clay; Pcrkey, Arlyn W.; and Kidd, William E., Jr. (eds.). Guidelines for Regenerating Appalachian Hardwood Stands. May 24-26, 1988, Morgantown, WV. SAF Publication 88-03. West Virginia University Books, Office of Publications, West Virginia. p. 199-209.

Loftis, L. David. 1990. A shelterwood method for regenerating red oak in the Southern Appalachians. Forest Science 36:917-929.

Lorimer, Craig G. 1989. The oak regeneration problem: New evidence on causes and possible solutions. University of Wisconsin, Dept. of Forestry, Forest Resource Analyses #8. 31 pp.

McGee, C. E. 1979. Fire and other factors related to oak regeneration. In: Holt, H. A. and Fischer, B. C. (eds.) Regenerating oaks in upland hardwood forests. John S. Wright Forestry Conference, Purdue University. Lafayette, IN. p. 75-81.

Martin, William H. 1989. The role and history of fire in the Daniel Boone National Forest. U.S. Forest Service, Daniel Boone National Forest, Winchester, KY.

Nowacki, G. J. 1988. Community and historical analysis of northern red oak along a moisture gradient in north-central Wisconsin. M.S. Thesis, University of Wisconsin Stevens Point.

Roth, E. R. and G. H. Hepting. 1943. Origin and development of oak stump sprouts as affecting their likelihood to decay. Jour. For. 41:27-36.

Rouse, C. 1986. Fire effects in northeastern forests: oak. United States Department of Agriculture, Forest Service General Technical Report NC-105. 7 p.

Sander, Ivan L., Charles E. McGee, Kenneth G. Day, and Ralph E. Willard. 1983. Oak-Hickory. In: Burns, Russell M. (comp.). Silvicultural systems for the major forest types of the United States. U.S. Department of Agriculture, Forest Service Agriculture Handbook No. 445. Washington, D.C. p. 116-120.

Sanders, D. L., D. H. Van Lear, and D. C. Guynn. 1987. Prescribed burning in mature pine-hardwood stands--effects on hardwoods and small mammals. In: Phillips, Douglas R. (comp.). Proceedings of the 4th biennial silvicultural research conference; 1986 Nov. 4-6; Atlanta, GA. Gen. Tech. Rep. SE-42. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, p. 93-96.

Secretary of Agriculture's Report to Congress. 1902. Forests, rivers, and mountains of the Southern Appalachian region. Government Printing Office. Washington, D.C.

Swan, F. R. 1970. Postfire response of four plant communities in southcentral New York state. Ecology 51:1074-1082.

Tcuke, M. J. and D. H. Van Lear. 1982. Prescribed burning and oak advance regeneration in the Southern Appalachians. Georgia For. Corn. Res. Pap. 30. 11 pp.

Thor, E. and G. M. Nichols. 1974. Some effects of fire on litter, soil, and hardwood regeneration. Proc. Tall Timbers Fire Ecology Conf. 13:317-329.

Van Lear, David H. and Thomas A. Waldrop. 1989. History, uses, and effects of fire in the Appalachians. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. SE-54. 20 p.

Waldrop, Thomas A., David H. Van Lear, F. Thomas Lloyd, and William R. Harms. 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. SE-45. 23 p.

Waldrop, Thomas A., F. Thomas Lloyd, and James A. Abercrombie, Jr. 1989. Fell and bum to regenerate mixed pine-hardwood stands: an overview of research on stand development. In: Waldrop, Thomas A. (ed.). Proceedings Pine-Hardwood Mixtures: A Symposium on Management and Ecology of the Type. April 18-19, 1989, Atlanta, GA. U.S. Department of Agriculture, Forest Service Gen. Tech. Rep. SE-58. p. 75-82.

Wendel, G. W. and H. Clay Smith. 1986. Effects of a prescribed tire in a Central Appalachian oak-hickory stand. U.S. Department of Agriculture, Forest Service Northeastern Forest Experiment Station NE-RP-594. 8 p.

RESPONSE TYPES TO PRESCRIBED FIRE IN OAK FOREST UNDERSTORY

H.R. DeSelm and E.E.C. Clebsch[1]

Abstract-We examined data collected on the understory of a prescribe-burned upland oak forest at the University of Tennessee Highland Rim Forestry Station from 1965 through 1989. Treatments were annual and periodic (once in five years) bums and no bum. Each was replicated three times.

Species number declined dramatically under the no-bum regime. Tree seedling establishment was inhibited and sprout size decreased in the annual and periodic bums--here the understory aspect is quite open. Tree sprout cover in the periodic burns followed the incidence of fire, it has lowest in the September following each winter burn. Graminoid cover, chiefly little bluestem (Schizachyrium scoparium), decreased to zero in the no-bum treatment. It was variable in other treatments but decreased irregularly from 1973-1975 to 1988. In 1989 it established a new high. Composite, legume and other forb cover declined to zero under the no-burn treatment. Composite cover in annual plots peaked in 1973-4 but decreased irregularly since; legume cover increased irregularly; other forb cover decreased irregularly in annual burn plots. Composite cover in periodic plots oscillated around tire years when cover was generally highest; legume cover peaked in four of the five fire years; other forb cover generally increased in the year following a fire. Twenty-two response-types occurred.

INTRODUCTION

Studies of the effects of fire on natural or man-fostered systems in central and southeastern United States are chiefly those in the grassland where these communities were long maintained as grazing land (Risser and others 1981) and in southeastern pineland which were also maintained as grazing and timberland (and for naval stores in the past) (Wahlenberg and others 1939). Summaries of the effects of fire on grasslands can be found in Risser and others (1981), Daubcnmire (1968a), Wright and Bailey (1982), Vogl (1974), and Collins and Wallace (1990). Summaries of the effects of tire on conifer forests especially southeastern forests are in chapters in Kozlowski and Ahlgren (1974), USDA Forest Service (1971), Wright and Bailey (1982), and Wood (1981). Older literature is summarized in Garren (1943), and Ahlgren and Ahlgren (1960). Use of fire in the central Deciduous Forest has been on the decline since abandonment of open range practices and intensification and specialization in land use (Vogl 1974, Chandler and others 1983). Fire use continues in hardwood and mixed forests as a wildlife management tool (Wood 1981), and to modify understory composition or size class structure (Wade and others 1989, Faulkner and others 1989). Studies on hardwood understory include Paulsell (1957) and DeSelm and others (1973, in press).

This paper is concerned with the consequences of 25 years of annual and periodic prescribed fires on the understory species in oak-dominated vegetation at Highland Rim Forest Experiment Station, Franklin County, Tennessee. The study contributes to an understanding of the maintenance of graminoid-forb understory and openings in the upland oak forests of this region and adds to our knowledge of response behavior of these species to fire.

For the period 19651970 the understory of the bum and control plots was examined (DeSelm and others 1973). In the six treatment years number of species sampled were 13, 23 and 35 taxa in control, periodic and annual bum plots, respectively. With increased burning, tree frequency and tree sprout cover decreased, grass and forb cover increased, and herbaceous vine and shrub cover became elevated on the periodic bums. Eighty-four percent of the species responded positively (by increased cover) to fire treatment by 1970. Tree, litter and soil changes were examined by Nichols (1971) and Thor and Nichols (1973).

THE STUDY AREA

The study area is at 36° 30'N : 86°W at the eastern edge of the Interior Low Plateau Province (the southeastern Highland Rim) in Middle Tennessee. The land surface here undulates and it has loess-derived soils in which a water-movement-inhibiting pan has developed in several series (Fenneman 1938, Fox and others 1958, Love and others 1959). Forest vegetation is of the upland oak swamp, post oak-blackjack, and southern red oak-scarlet oak types (DeSelm and others 1973). Conversion of this vegetation to agricultural land and to loblolly pine plantations is still occurring (Thor and Huffman 1969, USDA Soil Conservation Service 1971, Buckner and others 1986).

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[1] Department of Botany and Graduate Program in Ecology, The University of Tennessee, Knoxville.

Early surveyors report a few places with no forest, and such modern sites as the May Prairie have a physiognomic and floristic resemblance to midwestem prairie (DeSelm and others 1973). The origin and maintenance of grass vegetation and grass understory has in part stimulated this study.

American Indian use was followed by agriculture and livestock grazing between the late 1700s and early 1940s. Army maneuvers during World War II have been part of this site's history. The local farmers commonly burned off the woods in winter and a railroad line on the edge of the station also started fires annually (Faulkner 1968, Haywood 1823, DeSelm and others 1973).

METHODS

Data were collected on nine 1.8 acre experimental bum plots, 19651989 inclusive. Plots were split among annual, periodic (usually 5 years) and control. A 50-foot tape was stretched three feet above the ground between permanent stakes in each plot. At each one-foot mark a 0.19 inch diameter metal pin was lowered vertically to the ground and each "hit" on each vascular plant was recorded; those plants below three feet in height are herein called understory. Annual bums began in 1963; periodic bums were made in 1964, 1969, 1974, 1979, 1983 and 1988. Late winter bums were used to simulate the action of local land owners. Plant nomenclature follows Femald (1950).

Data reported here are cover (sum of hits per species x 2) along each SO-foot line. Cover values are averages of the three replications. No frequency or relativized data are reported. Years have been segregated into early 19651972, middle 1973-1981, and late 1982-1989 groups. Some taxa occur widely (the wides) across the series of years with somewhat variable-to-steady cover. In other taxa, the cover increases (the increasers), or the cover decreases (the decreasers), and in a few the cover increases (bulges) or decreases (sags) in the middle years. Taxa not present in the early years that appear later are termed "invaders." Taxa present in early or early and middle years but which arc not present in late years are termed "retreaters." Sporadics, which occur in early, middle, and late years, totaling 22 taxa, were not considered. Some terminology is from Vogl (1974).

RESULTS AND DISCUSSION

General

Taxa seen along the strips over the years totaled 141 species: 13 tree, 15 shrub, 2 woody vine, 21 graminoid, 22 legumes, 40 composite and 22 other forb taxa (counts excluded unknowns of various categories). This represented 52 percent of the 270 known vascular flora of the Station. Of these, 119 are included in this study. Two taxa occurred only in control plots: Gcntiana villosa and Liquidambar styraciflua (but in 0.01 acre plots, Liquidambar has been found in the periodic bum). Thus, all but one taxa was at least mildly fire tolerant. Although several State rare taxa occurred on the Forest (DeSelm 1990) only one occurred on the bum plots; Gymnopogon brevifolius is listed as a species of special concern (Somers and others 1989).

Forty-five taxa occurred in all three treatments, 39 taxa occurred in both burn treatments, 31 occurred in the annual bum only, and 12 occurred in the periodic bum only.

Total cover (sum of woody plant-graminoid-forb) in annual plots peaked in 1973--but by 1987 it decreased 43 percent after which it rose again. In the periodic plots total cover fell 46 percent between 1980 and 1987 after which it rose sharply. These 43 and 46 percent decreases in cover represented temporary increases in bare ground. Total cover in check plots decreased gradually until 1976 (the last year of herb cover), remained more or less steady through 1988, then increased in 1989 (Table 1).

Woody Plants

Cover by woody plants was irregular but more or less constant in annual plots over the year series. In periodic plots, woody plant cover increased irregularly. In check plots woody plant cover decreased through 1988; in 1989 it increased to the level approximating 1975 (Table 1).

Trees

Sum of cover of tree taxa on control plots apparently decreased until about 1979 after which it became variable. Some tree stems grew upward beyond the sampling line and were no longer recorded. Some young trees died under the developing canopy but others have spread onto the sampling line. Nyssa svlvatica, Quercus coccinea, Q. falcata Q. velutina and Vaccinium arboreum were recorded most to all years (Nyssa and Q. coccinea were decreasers). Quercus stellata, Q. marilandica and Carya tomentosa occurred in early or middle years. Liquidambar and Comus florida occurred in late or middle and late years. Acer rubrum appeared in 1969 and 1989, this apparently represented disappearance by height growth followed by recent sprouting. A summary of response types appears in Tables 2 and 3.

In annual bum plot strips, six taxa occurred widely (Carya, Nyssa, Q. coccinea, Q. stellata, Q. velutina and Sassafras albidum). Quercus coccinea and Q. velutina were deereasers, Q. stellata and Sassafras were increasers. Cornus florida, Q. falcata and Vaccinium arboreum occurred in early and/or middle years. Quercus lyrata was recorded in five middle and late years through 1983. The last several species, except perhaps Q. lyrata, were fire sensitive.

In periodic plots sum of cover of tree species and cover of several individual tree species was lower in fire years than between tires--they were burned back by the fires. Taxa with decreased cover on two to live tires were Carya. Nvssa, Q. coccinea, Q. falcata, Q. marilandica, Q. stellata, Q. velutina, and Vaccinium arboreum. Sassafras (present six years) and Q. lyrata (present two years) barely survived these tires. Acer rubrum was seen only recently (1982-1988). velutina and Vaccinium were increasers, Q. coccinea was a decreaser, and Q. falcata and Q. stellata increased in middle years (bulge species).

Shrubs

In the control plot strips, shrubs persisted various numbers of years under the developing canopy: Rhus glabra to 1965, Rubus (erect) to 1972, Ceanothus americana and Rhus copallina to 1974, Rubus (dewberry) to 1979, and Salix tristis to 1980. Vaccinium vacillans occurred each year, V. staminium appeared 1989. V. vacillans occurred in control oak-pine plots in southern New Jersey where its cover was reduced by 1950s drought (Stephenson 1965).

Certain shrubs in the annual burn plot strips occurred widely across the years (mostly many years): Ceanothus, Rhododendron nudiflorum, Rhus copallina, R. toxicodendron, Rubus (dewberry and erect), Salix tristis and Vaccinium vacillans. Increase in Rubus cover has been seen in central Wisconsin with tire (Reich and others 1990). Vaccinium vacillans and Rhus copallina increased in cover. In southern New Jersey V. vacillans's cover increased with burning frequency (Buell and Cantlon 1953). Rhododendron was a sag species. Ascvrum stragalum, Pyrus melanocarpa, Rhus glabra and Salix humilis persisted only one to three years (19651967). Ascvrum hypericoides and Vaccinium stamineum have been recorded since 1985 and 1988, respectively.

Shrub cover on periodic plot strips included the widely occurring Ceanothus, Rhus copallina, Rubus (dewberry and erect), Salix and Vaccinium vacillans. Among these, Ceanothus decreased in cover while Rubus erect, Salix tristis and Vaccinium vacillans increased in cover. Ascyrum hvpericoidcs and A. stragalum appeared in plot strips in 1983 and 1988 respectively. Rhus copallina cover peaked in fire years and dropped 50 percent or more in each of the following three to four years. Rosa Carolina and Rhus toxicodendron disappeared after 1967 and 1972, respectively. Rhus glabra behaved like Acer rubrum in the control plots, it occurred in both early and recent years, Rhus in 1965, 1983 and 1984.

Woody Vines

Woody vines were mainly Smilax glauca--only a few hits were made on Vitis aestivalis. In control plots, Vitis occurred 19651968 only. In these plots Smilax was a decreaser, early year covers averaged 5.8, later year covers averaged 1.5 percent. Canopy closure and deer browse affected coverage.

In the annual bum plot strips, Smilax cover decreased slightly. In the periodic bum plot strips cover varied from 2.0 to 20.6 per year. Compared to the previous year, cover increased one fire year, remained constant one fire year and decreased three fire years. In the year following fire, compared to the fire year, cover increased after one fire, and decreased after four fires.

Graminoids

Total graminoid cover in annual plots peaked in 1973, 1978 and 1989. In periodic plots it peaked in 1975, 1980 and 1989 (the year following a fire in each case). Graminoid cover decreased steadily in control plots (Table 1).

Little Bluestem--Schizachyrium scoparium

Control plot strips showed the disappearance of bluestem by 1977. Shade and tree litter are believed to be causes.

Cover of bluestem on annual bum plot strips increased irregularly to 1973, fell, peaked again in 1978, fell irregularly until 1988 and peaked again in 1989. Biomass of Schizachvrium also experienced multiple high and low value years in the 61 year record in Kansas (Gene Towne, personal communication). Although Andropogon gerardii cover increased with annual burning in Missouri, cover of Schizachvrium increased with alternate year fires (Kucera and Koelling 1964).

Periodic plot strip cover increased irregularly to 1975, decreased, increased again to 1980, decreased to 1988, then increased again in 1989. These variations do not match bum years. On two fire years, 1969 and 1988, cover decreased slightly from the year before, and it rose in 1974, 1979, 1983 from the year before. The positive effects of this treatment on the cover of this grass were certainly not dramatic. The high peaks of this grass in both treatments classed this taxon as a midphase bulge species. The 1989 peak may be part of a new trend.

Table 1. Total cover of graminoids, forbs, and woody plants by treatments and year.

	Annual			Periodic			Check		
Year	Gram.	Forbs	Woody	Gram.	Forbs	Woody	Gram.	Forbs	Woody
1965	32.6	54.4	24.6	35.3	27.5	37.6	57.4	16.8	43.6
1966	46.0	59.2	23.2	44.7	18.1	25.4	57.8	15.6	48.6
1967	54.2	43.7	21.0	32.6	2.6	23.4	37.4	9.6	43.0
1968	63.9	60.3	34.8	38.6	20.8	27.5	34.0	12.8	42.2
1969	58.7	43.4	23.2	33.6	37.9	28.1	14.0	6.4	28.6
1970	58.4	54.9	28.2	34.0	33.4	29.2	6.0	6.0	50.2
1971	63.2	49.8	18.0	39.3	18.2	41.4	8.6	9.4	31.2
1972	73.8	58.9	22.1	45.6	23.7	47.6	3.4	4.0	30.0
1973	99.6	68.5	24.3	52.0	16.2	42.1	3.4	4.0	26.0
1974	77.9	64.8	29.1	65.2	41.4	43.3	1.4	1.4	26.4
1975	69.6	53.2	32.5	85.0	40.6	63.6	0.0	0.6	21.8
1976	67.7	55.8	37.0	68.6	31.9	66.6	0.6		15.6
1977	51.3	36.7	16.4	28.9	25.2	61.3			14.4
1978	84.4	42.9	20.6	51.6	20.3	61.0			10.6
1979	70.3	45.2	23.3	60.7	70.6	43.9			7.4
1980	57.5	36.6	19.6	84.0	28.1	69.2			13.4
1981	63.1	43.6	24.3	62.4	29.2	68.1			13.6
1982	40.1	33.7	17.5	50.7	21.7	81.4			9.2
1983	51.7	40.2	27.1	54.7	37.0	62.0			12.4
1984	49.0	31.4	24.7	53.8	27.7	61.9			10.6
1985	45.0	39.5	27.0	44.8	20.1	53.8			14.6
1986	46.9	31.4	26.7	36.3	16.5	55.9			15.2
1987	57.0	26.8	19.3	30.6	15.6	52.2			9.8
1988	48.9	40.2	26.0	26.5	56.0	75.6			12.0
1989	94.7	42.6	24.0	104.3	39.9	89.7			20.6

Other Graminoids (Gramineae [Poaceae], Cyperaceae)

In control plots, other graminoids were represented by low cover of only seven taxa--no more than five present any one year. They persisted only through 1971.

Twenty-four other graminoids occurred in annual bum plots. Taxa present almost every year are Andropogon gerardii and Sorghastrum nutans with 6-10 percent cover per year. A few other graminoids occurred more or less widely: Andropogon gyrans, Carex sp., Eleocharis tenuis, and Panicum dichotomum and P. lanuginosum. Of all the above taxa, Andropogon gerardii and Sorghastrum were increasers, and the two Panicum species were decreasers. Aristida dichotoma disappeared after 1966, A. purpurea after 1972, Gymnopogon brevifolius after 1981, Panicum angustifolium after 1978, P. ravenellii after 1975, Scleria pauciflora after 1972, and Setaria geniculata after 1968. p o r a globularis occurred only in the middle years of the series. A few taxa appeared late in the series, Agrostis perennans in 1980, Digitaria ischaemum and Microstegium vimineum in 1989, Muhlenbergia tenuiflora in 1984, Panicum laxiflorum in 1977 and P. villosissimum in 1986. The Digitaria and Microstegium are widespread weeds.

Concurrent peaks and valleys of cover in the annual bums occurred in a few taxa some years, but the correspondence in peaks was not impressive and did not argue strongly for response to weather. Peaks and valleys were best expressed in the high cover species Andropogon perardii and Sorghastrum. These taxa also experienced rises and falls in biomass values on Kansas prairie (Gene Towne, personal communication). The sum of all other graminoid cover peaked in 1972, 1973, 1979, 1986, 1987,and 1989. Sorghastrum contributed greatly to all of these peaks. Andropogon gerardii contributed in 1979, 1987, and 1989.

Other graminoids in periodic hum plot strips numbered 19 species. A few taxa occurred 11 or more years, Andropogon gcrardii, Panicum commutatum, P. dichotomum, P. laxiflorum, P. microcarpon and Sorghastrum nutans. A. gcrardii was a bulge species, Sorghastrum was an increaser.

Two taxa were seen in the early or early and middle part of the series, Agrostis hvcmalis through 1976 and Muhlenbergia tenuifolia in 1965. A few taxa were seen only later, Aristida curtisii only in 1974, Panicum laxiflorum since 1976, P. sphaerocarpon in 1979, P. villosissimum since 1981, and Rhynchospora globularis in 1980.

The effects of the periodic fire on the total cover of all taxa in fire years was variable, some years cover increased, some years it decreases. However, the year following a fire, an increase in cover was achieved, the increase in cover was 1.1 to 9.7 times the cover the year before. Taxa with increased cover were the "fire follower" class of Lemon (1949). The effect is temporary; the second year after a fire, other graminoid cover total decreased.

Forbs

In 1965 and 1966 annual plot total forb cover exceeded woody plant and graminoid cover but after 1966 it decreased to a level intermediate between them. This suggested an early-in-the-treatment (early successional) forb dominant stage as was seen early in some southeastern seres (Quarterman 195'7, Oosting 1942). Annual bum forb cover peaked in 1973 but decreased irregularly to 1987--a 60 percent loss of cover. In periodic fire plots total forb cover peaked in 1969, 1974-5, 1979, 1983 and 1988 (each fire year). There was a decrease in total forb cover 1979-1987 of 79 percent of the 1979 value. Forb cover in control plots decreased irregularly through 1975 (Table 1).

Composites (Compositae, Asteraceae)

Sixteen composite taxa, including unknown categories, occurred in the control bum plots. Occurrences ranged from one to 10 taxa per year. All were eliminated by 1975.

Annual burn composites, expressed as total hits on all taxa, increased to a peak in 1973 and 1974 and decreased irregularly thereafter (but increased slightly in 1989). This decrease in cover was apparent to us and was a cause of comment. Recent plot photographs showed few composites in most late years compared to earlier years. Numbers of taxa in early years averaged 19.3, in late years 10.0. Taxa showing the above trend with peaks in 1973 or 1974, sometimes with additional peaks, were: Aster dumosus, A. hemisphericus, A. patens, A. undulatus, Corcopsis tripteris and Solidago odora. All but A. hemisphericus were bulge species.

Several taxa occurred only in the early years: Antennaria plantaginifolia through 1968, Hieracium gronovii through 1971, Scricocarpus linifolius in 1968. A few taxa persisted through the middle years: Helianthus angustifolius through 1978, H. silphioides through 1977, Solidago bicolor through 1977, S. erecta through 1981, and S. speciosa through 1974. Two taxa only occurred in the middle years: Helianthus strumosus and Senecio anonymus. Several taxa appeared only in late or middle and late years; these were Ambrosia artimisiifolia seen first in 1987, Erectitcs hieracifolia seen first in 1982, Eupatorium album seen first in 1975, E. aromaticum seen first in 1973, E. semiserratum seen in 1985, and Solidago canadcnsis seen first in 1973. The Ambrosia, Erectites, Eupatorium album, and Solidago canadcnsis were weedy taxa locally.

Helianthus hirsutus and Corcopsis major were decreasers--in the late years these taxa were present five of 16 possible times. H. mollis appeared to be on a two- to four-year low to high cover cycle. The reasons for this was unknown but its negative response to insect attack and wet weather were noted.

Total hits on composites increased and decreased with bums and between bums in the periodic plot strips. Composite cover generally peaked in fire years and decreased thereafter (although this did not happen during the wet year of 1989 after the 1988 fire).

A few taxa occurred only early in the total year sequence: Aster patens, Antennaria plantaginifolia, Gnaphalium obtusifolium, Solidago nemoralis and Vemonia flaccidifolia. A few other taxa occurred in early and middle or middle years: Aster hemisphericus, Eupatorium sessilifolium, Hieracium pronovii, Scnecio anonymus and Solidago speciosa. Some taxa occurred only in the middle and late or late years of the series: Aster simplex, Chrysopsis mariana, Erigeron canadensis, Solidago canadensis, and Solidago erecta. The Erigeron and S. canadcnsis were weeds locally. Chrysopsis spp. invaded burned longleaf pine stands (Heywood and Bumette 1934).

Sixteen other taxa occurred sparingly to frequently across the year-series. Solidago odora was a decreaser. A few year-frequent taxa peaked during fire years. They were Eupatorium aromaticum (five fires), Solidago odora (four fires), Helianthus silphioides and Aster dumosus (two fires), and Helianthus hirsutus, and Eupatorium rotundifolium (one fire each). On the other hand, Coreopsis major cover decreased in fire years (means were 0.52 percent cover in fire years versus 1.7 percent cover during non-tire years). Composite seedling rosettes (unknown Aster, composite, Eupatorium, Helianthus and Solidago) increased in cover the year after the fire years (four of five fires).

Legumes (Leguminosae, Fabaceae, Mimoseae, Caesalpinaceae)

Thirteen legume taxa occur in the control plots at the rate of one to six taxa per year. All were eliminated by 1970.

Twenty one named species, one hybrid and three unknown legume taxa occurred in the annual bum plot strips. Taxa which occurred only in the early years were Amphicarpa bracteata, Desmodium virginianurn and Psoralea psoralioides. Species which occurred in middle or early and middle years were Desmodium paniculatum, Lespedeza capitata and L. virginica. The hybrid L. intermedia x capitata occurred annually in the middle and late years.

Sixteen taxa occurred widely across the year-series; 10 taxa 13 or more years, six taxa occurred only 2-12 years. Of these wide taxa, Desmodium marilandicum, Lespedeza intermedia, L. repens, Stylosanthes biflora and Tephrosia virginiana were increasers. These were part of a general trend of increased legume cover with time; the cover increased 40.8 percent from the early to late year groups. Similar increases in legume importance were reported by Wahlenberg and others (1939). L. procumbens has a low-middle, and Schrankia microphvlla has a high middle year cover.

Sum-of-legume cover and certain species cover suggested cycles of 2-5 years intervals but dates of species peaks usually did not correspond. Response of legumes to periodic bums was various; a general response was that species drop out. The mean number of taxa in early years was 9.8; the mean number in the late years was 20 percent lower. Several legume taxa occurred in 12 or more years across the series. Included were three increasers Cassia nictitans, Clitoria mariana and Tenhrosia virginiana, Lesoedeza repens a decreaser, and L. intermedia a bulge species. Taxa present in early or early and middle years that disappeared later were: Amphicarpum bracteatum in 1969, Desmodium ciliare 1977, D. marilandicum 1976, D. viridiflorum 1967, Galactia volubilis 1981, Lespedeza hirta 1967, Psoralea nsoralioides 1968. Apparently only one species invaded, Cassia fasciculata; this has been present since 1975. Two taxa occurred only in the middle years, Desmodium obtusum and D. paniculatum.

Among wide taxa, peaks usually occurrcd in the periodic burn years. The two highest peaks (1979 and 1988) arc amplified by high cover of Cassia nictitans. Increase in frequency of C. nictitans with burning has been reported (Cushwa and others 1970). Four other taxa had high cover in three to four fire years compared to non-fire years: Clitoria mariana, Lespedeza repens, L. procumbens and Schrankia microphvlla. The cover of these taxa decreased in the years after each tire. Lesoedeza intermedia peaked in two tire years only. Cover of Lespedeza virginica and Tephrosia increased on three of live fires the year after the fire.

In periodic fire years the cover of Stvlosanthes biflora, which averaged 1.6, fell to zero--it was absent in fire years. It was another species influenced negatively by fire.

Other Forbs

In the control plots, other forb cover averaged low and lasted only until 1975.

In annual plot strips only Pvcnanthemum tenuifolium and unknown forb were present widely across the years. Seven taxa occurred only one year; eight taxa occurred 2-10 years.

Taxa occurring in the early or early and middle years in annual plots were Aureolaria virginica, Galium circaezans, Gerardia tenuiflora, Lobelia inflata, L. puberula, Scutellaria integrifolia, and Viola sagittata. Three taxa occurred only in middle of the sequence: Gerardia pectinata, Hypericum densiflorum, and Trichostema dichotoma. Late occurring taxa were Houstonia caerulea, Inomea pandurata, Lechea minor, and Rhexia mariana.

Over the annual bum year-series, the number of taxa declined slightly; the mean number of taxa in early versus late years was 4.8 versus 2.8, respectively. Similarly, the sum of all hits was 13.6 versus 5.0; this cover comparison was heavily influenced by an early-in-the-series peak by unknown forb cover in 1971, and peaks by Pycnanthemum tenuifolium in 1965 and 1968.

Periodic other forb bum plot data, as in the annual strips, contained few species and those that appeared did so for only a few years. One species, Hypericum densiflorum, disappeared--it was last seen in 1978. A few taxa occurred only in the middle of the year series: Acalypha virginica, Convolvulus sepium, Diodia virginica, Gerardia pectinata, Houstonia caerulea, Lechea minor and Lobelia puberula. The Diodia and Lobelia have been seen two years, the others one year. The only new taxon was Gerardia tenuifolia which appeared in 1983. Mean cover in fire years was 3.0; mean cover in non-fire years was 4.0; the difference suggested a depressing effect of tire on forbs. The year following the fire the mean cover was 5.8--the rise suggests a positive fertilization or release-from-competition effect. These effects can be seen in Potentilla simplex in which percent cover in fire years was low; in non-fire years it was intermediate; the year after a fire, cover was highest.

General Discussion

The methods used collected minimal annual data although they were favored by nearly exact position replication between years and places. The three-foot maximum height measurement over-emphasized disappearance of understory stems which grew taller than three feet. Early maturing species may not be seen, and late maturing species may have been over-represented in this constant-date sampling. The wet year of 1989 increased cover of some species groups markedly. Although time of year collection of data has always been a bias in ecological studies, in this summer-autumn flora bias is believed minimal. Animal activity may influence data; some Smilax was browsed and one Rhododendron was lost by burrowing. A peduncle-biting insect inhibited fruit set in Helianthus mollis.

Results expressed as percentage cover simply measured the degree of success achieved by the species in that environment (Daubenmire 1968b). A parallel expression is “number of years seen, " which represents the species response to comparatively stable soil conditions but changing climatic conditions **and** changing conditions of interspecific competition. Variable responses (variable occurrence, increase, decrease, invade, retreat) are typical behaviors of populations under stress (Grime 1979).

The mechanisms of response to fire, for the woody plants, were related to top death and subsequent growth of sprouts from suppressed or adventitious buds (Barbour and others 1987). Most herbs were hemicryptophytes with terminal bud which, if not injured by fire, provides post-bum growth potential (Daubenmire 1968b). Annual herbs (therophytes) comprise 11.2 percent of the flora of these plots--their occurrence is more or less equally divided between annual and periodic bum plots. They make up nearly one-fourth (23.5 percent) of invader occurrences in annual and periodic plots--a proportion twice that in the plot flora. They often invade burned grassland (Vogl 1974).

Species can be rated on their response to tire treatment. Only two taxa were exclusive to the control plots--this suggested that other taxa were at least tolerant of the stress of fires of this study and the long history of previous woods fires and accidental railroad tires. Of low tolerance were taxa which were early and early and middle retreaters, decreaser-retreaters, and the late and middle and late invaders. Widely occurring taxa make up the rest of the classes. Wide decreasers, wide sag species, and wide taxa with low cover in fire years were more tolerant than previous classes. The most tolerant were wides with peaks in tire years, certain wides with their own cycle of variable cover, those with middle year bulges, and wide increasers. Least tolerant taxa were called pyrophobes; most tolerant taxa here were called pyrophiles. But these terms are absolutes and express only the extremes of a group of classes of fire tolerance suggested above. In fact, these classes may be part of a gradient of responses to a large number of fire intensity/frequencies.

Burns

In both burn treatments, the canopy was open, and overstory trees were few. The 0.5-5.0 inch DBH class was essentially missing (DeSelm and others in press). In late years annual bum plots were grass-forb-woody plant dominated. In late years, periodic plots were woody plant-grass-forb dominated. Due to a flush of Cassia nictitans after the fire of 1988, the order was woody plants-forb-grass. In the wet year of 1989 the order was grass-woody plant-forb. In 1989 periodic plots had 44 percent more cover than annual bum plots. Total species number on periodic plots always increased in fire years and alter four fires, and decreased thereafter (see also Collins and Gibson 1990).

Individual species response to the two types of bum treatments were seldom identical; only 20 taxa (14 percent) had the same response to annual and periodic burning. The variety of responses suggested that the sprouting habit of trees and shrubs and the hemicryptophytic life form of most herbs here was not strictly fire adaptations, but were a fire response to adaptive mechanisms evolved under a complex of disturbances including fire, grazing, browsing, and/or drought.

The net response of legumes to fire was positive; there was an increase in cover in both annual and periodic treatments. The species number remained constant in annual bums (although it decreases slightly in periodic bums). A few legume taxa peaked dramatically in periodic fire years and two taxa peaked the year after a periodic fire. The legumes, plus Ceanothus (Bond, 1983), widely occurring in annual and periodic plots, and free-living N-fixers, replace at least **some** nitrogen volatilized in fires (Chandler and others 1983). Nitrogen losses are reported in soil in burned grassland (Collins and Wallace 1990).

After 27 years of treatment, eight taxa, all woody, occurred on the strips in control bum plots. This is similar to the 10 woody taxa after 20 years under loblolly pine in coastal South Carolina (Lewis and Harshberger 1976). Eleven herb taxa were present in the pine stand but there were none under oaks here. A more open canopy or physical factors associated with the litter or oak roots (McPherson and Thompson 1972) or allelopathic substances (Rice 1984) may be responsible for the contrasting numbers of taxon under these overstories. Slightly more woody taxa occurred in the oak plots here with fire (13 annual, 16 periodic taxa) than under pine (10 annual, 12 periodic taxa). Under oak 39 (annual) and 34 (periodic) herb taxa occurred; under pine 26 (annual) and 18 (periodic) herbs occurred. Although the species number is lower under pine, the percentage distribution of grass, composite and legume taxa is similar. The lower numbers of taxa in bum plots under pine versus oak may represent differential pre-plot-establishment land use history (as grazing intensity) or some factor as fertility or moisture holding capacity.

The plots described by Paulsell (1957) are floristically and physiognomically similar to our study plots. But his specific results, reported as species frequencies after seven years of treatment bear little similarity to ours.

Species Equilibrium

In the control plots, 42 taxa have retreated (including 10 woody taxa) and only three woody taxa have invaded for a net loss of 39 taxa. The overall loss rate was 1.1 taxa per year. Herbs persisted on control plots only until 1978--they disappeared at a rate of 1.6 taxa per year.

In the periodic burn plots there were 12 invader and 21 retreater taxa over the years for a net loss of nine species. In the annual burn plots there were 18 invaders and 33 retreaters for a net loss of 15 species. Eliminating species co-occurrence between annual and periodic plots there were 48 retreaters (nearly two per year) and 26 invading taxa for a net loss of 22 taxa (nearly one per year). These losses include three tree retreaters and one tree invader for a net loss of two tree taxa--hardly suggestive of succession toward forest stability. In all taxa, maximum disturbance (annual burn) has induced maximum species movements but with little likelihood of establishment of equilibrium vegetation (Grime 1979, Risser and others 1981).

In the periodic bums, live of 12 invaders appeared for the first time the year of one of the five periodic tires. That one species invading per (periodic) fire compares to the annual bums with 0.72 species per fire invading (18 invaders/25 fires).

Life Form/History

Much has been made of life history/life form as control of response to fire. In this flora very little is known of the details of life history response to stress. The form/family species classification used previously indicated a surge of Hemicryptophyte cover with increased fire as was expected (DeSelm and others 1973). Keeley (1981) has shown how life form/history determines response to tire. In this study many response types have been discussed. Only occasionally do they match with life form/family classes (Tables 2 and 3). The tree form, for example, occurred in 13 response types, shrubs occurred in 10, graminoids occurred in 12, legumes occurred in 15 and composites occurred in 13.

Equally, bum plot trees had 11 responses. Rhizome spreading shrubs had seven responses, other shrub six. Among herbs, annuals had nine responses and occurred only in bum plots. Chamaephytes (two species) had two responses in burn plots. Geophytes (five species) had three responses in bums and did not occur in check plots. Stolmferons herbs (three species) had five responses in fire plots. Climbing herbs (five species) had six responses in bum plots. Graminoids had 11 responses in tire plots, other forbs had 17 responses. Clearly much more needs to be known about the life history of these taxa to explain this level of variable response to tire. Such knowledge would aid those who seek to manage extensive wildland pastures of the southeastern United States (U.S.D.A. Forest Service 1981).

Table 2. Response types, treatment occurrence, numbers of taxa represented per type and life forms/families of taxa in burn and check plots.[1,2]

Response Type	Treatment[3] Occurrence	No. of Taxa in All Treatments	Life Forms, Families Among Taxa
UK	A, P, C	25	T, Sh, Gr, C, Le
UD	A, P, C	13	T, Sh, WV, Gr, C, Ot
UN	A, P, C	16	T, Sh, WV, Gr, C, Le, Ot
WA	P	8	T, C, Le, Ot
WAB	P	2	T
UAN	P	2	
UP	P	6	Sh, C, Le
WB	A, P	5	Gr, Le
WOB	A	5	C
wo	A	3	C, Le
WPN	P	3	Le
WPD	P	1	Le
WG	A	1	Le
ER	A, P, C	58	T, Sh, WV, Gr, C, Le, Ot
EMR	A, P, C	29	T, Sh, Gr, C, Le, Ot
EMDR	C	3	Sh, Gr
EDR	C	5	Gr
M	A, P	22	T, Gr, C, Le, Ot
MLI	A, P, C	10	T, Gr, C, Le
LI	A, P, C	23	T, Sh, Gr, C, Ot
WSK	A, P	32	T, Sh, Gr, C, Le, Ot
EL	A, P, C	5	T, Sh, WV, Le

[1] See text for species in response types.

[2] See table 3 for key to abbreviations.

[3] A • Annual, P • Periodic, C • Check plots.

Table 3. Key to response type abbreviations

A - Low in fire years of periodic burns
B - Bulge, curved year-trend, cover high in middle years
C - Composite
D - Decreaser, cover values decrease with years
E - Early years (1965-1972)
G - Sag, cover decreases in middle years
Gr - Graminoid
I - Invaders, taxa found on plots after initial inventory of 1965
K - Constant, cover varies Little between years, no trends
L - Late years (1982-1989)
Le - Legume
M - Middle years (1973-1981)
N - Increaser, cover values increase with years
0 - Own cycle, cover with apparent high-low periodicity
Ot - Other forb
P - Peak, cover peaks in periodic burn fire years
S - Scattered, taxa wide but only 1/3 - 2/3 of years represented
Sh - Shrub
T - Tree
W - Wide, occurs in two thirds of years scattered in early, middle, and late years
WV - Woody vine

CONCLUSIONS

General

Species in the same genus or family or life form group behaved both similarly in some cases and dissimilarly in other cases with respect to their long-term response to fire. It is impossible to generalize with any accuracy about any group. For example, in the genus Rhus in periodic plots, R. glabra appeared in early and late years, R. toxicodendron disappeared after 1972 and the cover of R. copallina, which was present throughout, peaked in tire years but was depressed between fires. In annual bums, R. glabra occurred only in early years, R. toxicodendron and R. copallina both occurred widely but the latter was an increaser. Other species in the same family or life form exhibit equally variable responses.

Cover of species on control plots changed as it did in treatment plots. The causes of change were not known in either case. Differences extant between bum (annual and periodic) and control plots were not necessarily due only to treatment effects on burned plots; there may have been equally large chronological developmental changes on control plots induced by or paralleled by canopy closure and litter accumulation.

In addition to widely occurring species--all species which exhibited little cover change, or which were increasers or decreasers--there were also other classes. Retreaters were present in early or early and middle years and disappeared thereafter. Invaders appeared in middle or middle and late years but were not present in early years. Sporadics, which occurred in early, middle and late years totaled 10 or fewer, have not been considered in this paper. Of the 22 response types seen among the 141 taxa, 10 types occurred in all three treatments, but a few others were specific to treatment or life-form-family categories. A gradient of response occurred among the species present. Those that responded most positively were called pyrophiles--those that responded least positively (but have been there long enough to see once) were termed pyrophobes. Most taxa occurred between these extremes.

Annual Burns

Some taxa seem to have oscillating cover even in the uniform treatment of annual bums. These wides may have responded to some internal growth cycle (as trees that fruit cyclically) (Fowells 1965). They may also have responded to annual weather changes (Fritts 1976). For example Towne and Owensby (1989) found annual Kansas prairie biomass correlated with precipitation. Or they may have responded to changes in competition from neighbors whose cover responded as above. Weather regimes seemed to be a likely source of year to year variation in species behavior. Its effects will be considered in a later paper.

A few taxa (as Schizachvrium) peaked in middle years, cover before and alter these peaks was generally lower. They were, in early years increasers, in later years decreasers. These may have been the oscilating cover type with their own cycle but with a very long time between peaks.

Taxa which occurred only in middle years may have been a low average cover example of the middle-years-peak species noted above. Or perhaps they should be considered invader-retreaters. They occurred in four form-family groups in all three treatments. With more extensive sampling, these might prove to be middle years peak species noted above. Wide, middle-year-sag species occurred as did those that occur only in early and late years.

Periodic Burns

Composite seedlings established in the year of periodic fires on those plots. Comparable cohorts of grass and legume seedlings were not seen. New taxa were also most likely to invade the periodic plots during bum years.

Six kinds of response types occurred in periodic burns only. Three of these had low cover in fire years, and high cover between tires; there were those with more or less constant cover between peaks and between valleys, those with a middle year-group bulge, and those which were increasers. Three other types have peak cover during fire years. There were those with constant or uniform peaks and valleys across the year-series, those which were increasers, and those which were decreasers.

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LITERATURE CITED

Ahlgren, I.F. and C.E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26: 483-533.

Barbour, M.G., S.H. Burk, and W.D. Pitts. 1987. Terrestrial plant ecology. Second Edition. Benjamin/Cummings Publ. Co., Menlo Park, CA.

Bond, G. 1983. Taxonomy and distribution of non-legume nitrogen-fixing systems. pp. 55-85. In: Gordon, J.C. and C.T. Wheeler (eds.), Biological nitrogen fixation in forest ecosystems: Foundations and applications. Martinus Nijhoff/Dr. W. Junk Publishers. The Hague, Netherlands.

Buckner, E., R. Evans, J. Mullins, and E. Thor. 1986. Converting “the barrens” from low-quality hardwoods to high-yielding loblolly pine plantations. pp. 50-52. In: D. R. Phillips (Compiler). Proceedings of the Fourth Biennial Southern Silvicultural Research Conference. Gen. Tech. Report SE-42.

Chandler, C., P. Cheney, P. Thomas, L. Trabaud and D. Williams. 1983. Fire in Forestry. Volume 1. John Wiley and Sons, New York.

Collins, S.L. and D.J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. pp. 81-98. In: S.L. Collins and L.L. Wallace (eds.) Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, Oklahoma.

Collins, S.L. and L.L. Wallace (eds.). 1990. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, Oklahoma.

Cushwa, C.T., M. Hopkins and B.S. McGinnes. 1970. Response of legumes to prescribed bums in loblolly pine stands of the South Carolina Piedmont. USDA Forest Service Research Note SE-140.

Daubenmire, R. 1968a. Ecology of fire in grasslands. Advances in Ecological Research 5: 209-266.

Daubenmire, R. 1968b. Plant Communities. A textbook of synecology. Harper and Row, New York.

DeSelm, H.R. 1990. Flora and vegetation of some barrens of the eastern Highland Rim of Tennessee. Castanea 55: 187-206.

DeSelm, H.R., E.E.C. Clebsch, and J.C. Rennie. In press. Effects of 27 years of prescribed tire on an oak forest and its soils in Middle Tennessee. Proceedings, Sixth Southern Silvicultural Research Conference, Memphis, TN, October 30-November 1, 1990.

DeSelm, H.R., E.E.C. Clebsch, G.M. Nichols and E. Thor. 1973. Response of herbs, shrubs and tree sprouts in prescribed-bum hardwoods in Tennessee. Proc. Annual Tall Timbers Fire Ecology Conference. No. 13: 331-344. Tallahassee, FL.

Faulkner, C.H. 1968. The old stone fort. The University of Tennessee Press, Knoxville.

Faulkner, J.L., E.E.C. Clebsch and W.L. Sanders. 1989 Use of prescribed burning for managing natural and historic resources in Chickamauga and Chattanooga National Military Park, USA. Environ. Manage. 13: 603-612.

Fenneman, N.E. 1938. Physiography of eastern United States. McGraw-Hill Book Co.. New York.

Femald, M.L. 19.50. Gray's Manual of Botany. 8th Edition. American Book Company, New York.

Fowells, H.A. (ed.). 1965. Silvics of forest trees of the United States. USDA Agriculture Handbook. No. 271

Fox, C.J., T.E. Beesley, R.G. Leighty, E. Lusk, A.B. Harmon, H.C. Smith, C. Methvin, R.L. Flowers, and L.E. Odom. 1958. Soil survey of Franklin County, Tennessee. USDA Survey Series 1949, No. 8.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Garren, K.H. 1943. Effects of tire on vegetation of southeastern United States. Bot. Rev. 9: 617-654.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Haywood, John. 1823. The civil and political history of the State of Tennessee. Printed for the author by Heiskell and Brown. Knoxville, Tennessee.

Heywood, F. and R.M. Barnette. 1934. The effect of frequent fire on chemical composition of forest soils in the longleaf pine region. Florida Agr. Expt. Sta. Bull. 265.

Keeley, J.E. 1981. Reproductive cycles and tire regimes. Pp. 231-277. In: H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan and W.A. Reiners (Tech. Coord.), Proceedings of the Conference Fire Regimes and Ecosystem Properties. USDA Forest Service General Technical Report No. 26.

Kozlowski, T.T. and C.E. Ahlgren (eds.). 1974. Fire and ecosystems. Academic Press, New York.

Kucera, CL. and M. Koelling. 1964. The influence of fire on composition of central Missouri prairie. Amer. Midl. Nat. 72: 142-147.

Lemon, P.C. 1949. Successional responses of herbs in the longleaf-slash pine forest after tire. Ecology 32: 135-145.

Lewis, C.E. and T.J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. Journal of Range Management 29: 13-18.

Love, T.R., L.D. Williams, W.H. Proffitt, I.B. Epley, J. Elder, and J.H. Winsor. 1959. Soil survey of Coffee County, Tennessee. United States Department of Agriculture, Soil Conservation Service Survey Series 1955, No. 5.

McPherson, J.K. and G.L. Thompson. 1972. Competitive and alletopathic suppression of understory by Oklahoma oak forest. Bull. Torrey Bot. Club 99: 293-300.

Nichols, G. 1971. Effects of annual and periodic tires in a hardwood forest on the Eastern Highland Rim. Thesis, M.S., University of Tennessee, Knoxville.

Ojima, D.S., W.J. Patton, D.S. Schimal and C.E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. pp. 118-132. In: S.L. Collins and L.L. Wallace (eds.), Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, Oklahoma.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Amer. Mid Nat. 28: 1-126.

Paulsell, L.K. 1957. Effects of burning on Ozark hardwood timberlands. Missouri Agriculture Experiment Station Res. Bull., No. 640.

Quarterman, E. 1957. Early plant succession on abandoned cropland in the Central Basin of Tennessee. Ecology 38: 300-309.

Reich, D.B., M.D. Abrams, D.S. Ellsworth, E.L. Kruger and T.J. Tabone. 1990. Fire effects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71: 2179-2190.

Rice, E.L. 1984. Allelopathy. Second Edition. Academic Press, Inc., New York.

Risser, P.G., E.C. Bimey, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Wiens. 1981. The true prairie ecosystem. Hutchinson Ross Publishing Company, Stroudsburg, PA.

Somers, P. and the Department of Conservation's Rare Plant Scientific Advisory Committee. 1989. Revised list of rare plants of Tennessee. Journal Tennessee Academy Science 64: 179-184.Stephenson, S.N. 1965. Vegetation change in the Pine Barrens of New Jersey. Bull. Torrey Bot. Club 92: 102-114.

Thor, E. and G.M. Nichols. 1973. Some effects of tires on litter, soil and hardwood regeneration. Proceedings of the Annual Tall Timbers Fire Ecology Conference 13: 317-329.

Thor, E. and P.J. Huffman. 1969. Direct seeding and planting of loblolly pine on the Highland Rim of Tennessee. Tree Planters Notes 20: 19-22.

Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37: 392-397.

USDA Soil Conservation Service. 1971. Tennessee soil and water conservation needs inventory. Soil Conservation Service, Nashville, TN.

USDA Forest Service. 1971. Prescribed burning symposium proceedings. Southeastern Forest Experiment Station, Asheville, NC.

USDA Forest Service. 1981. An assessment of the forest and range land situation in the United States. Forest Resource Report No. 22. Washington, D.C.

Vogl, R.J. 1974. Effects of tire on grasslands. pp. 139-194. In: T.T. Kozlowski and C.E. Ahlgren (eds.) Fire and ecosystems. Academic Press, New York.

Wade, D.D., D.R. Weise, and R. Shell. 1989. Some effects of periodic winter tire on plant communities on the Georgia Piedmont. pp. 603-611. In: J. H. Miller (compiler). Proceedings of the Fifth Biennial Southern Silvicultural Research Conference. General Technical Report, SO-74.

Wahlenberg, W.G., S.W. Greene and H.R. Reed. 1939. Effects of fire and cattle grazing on longleaf pine lands as studied at McNeill, Miss. USDA Tech. Bull. 683.

Wood, G.N. (ed.). 1981. Prescribed fire and wildlife in southern forests. Belle Baruch Forest Science Inst. Clemson University, Georgetown, SC.

Wright, H.A. and A.W. Bailey. 1982. Fire ecology. John Wiley and Sons, New York.

IMPLICATIONS FOR LONG-TERM PRAIRIE MANAGEMENT FROM SEASONAL BURNING OF LOESS HILL AND TALLGRASS PRAIRIES

Thomas B. Bragg[1]

Abstract-Data from prescribed bums of northwestern Iowa loess hills and eastern Nebraska tallgrass prairies were used to assess the effects of season of burning and implications for long-term management of grassland ecosystems. Overall forb cover declined most without burning (-22%). Compared to unburned areas, species number on both sites was higher (+5) with fall burning with the response most pronounced at the loess hills site. The response of species such as false sunflower (Heliopsis helianthoides) suggest that summer and fall burning may do most to encourage seedling germination and establishment. Other species, such as white aster (Aster ericoides) on the tallgrass site and gray goldenrod (Solidago nemoralis) at the loess hills site, increased in cover with summer or fall burning. Some species showed significant changes irrespective of treatment; in the tallgrass area, porcupine-grass (Stioa spat-tea) decreased and flowering spurge (Euphorbia corollata) increased.

The vegetative responses recorded suggest the likely importance of applying some summer and fall burning, in conjunction with the usual spring burning, to the long-term maintenance of diversity in the tallgrass, loess hills, and perhaps other, grassland ecosystems.

INTRODUCTION

The effects of tire in prairie ecosystems of the central North America have been extensively studied (for example, see Vogel 1974; Risser and others 1981; Wright and Bailey 1982). Generally, studies have determined that fire is a natural component of these grassland ecosystems and that continued fire management is important, whether the objective is to maintain the vitality and diversity of the natural ecosystem or to manage for other, agroeconomic, purposes. More recently, research has begun to refine the understanding of fire's role in grassland ecosystems with an increased focus on fie frequency (the number of years between bums) and fire season (the season during which fire is applied). Grassland tires occurred naturally at various times of the year, including summers (Moore 1972; Bragg 1982), thus the seasonal aspect of fire is important to understanding its role in the long-term management of this ecosystem. Studies comparing differences in effects of season of bum, however, have largely focused on the northerly, mixed-grass prairies of North and South Dakota. Few community-level studies on this specific aspect of tire ecology have been published for the tallgrass prairie.

Response of Grasses and Grass-Like Species

Many comparative studies on the effect of fire season on prairie vegetation have focused on either Spring or Fall, these being times most often appropriate for the management objective of cattle grazing. Burning during these seasons, particularly in the Spring, has also been carried over into ecological management of grasslands. Studies on the effects of tire often focus on grasses since they are the predominant vegetation type and since they have the greatest effect on forage production. When considered ecosystem-wide, the results of such studies have been found to be similar only in that they all differ considerably depending on season of burning, latitudinal location, and local climatic conditions. These differences on grass and grass-like species are reflected in two general areas of tire effects: productivity and species composition. For the sake of comparison of effects of season of burning, results are discussed separately for northern prairies (e.g. North and South Dakota) and for central (more southerly) prairies (e.g. Nebraska, Kansas, and Oklahoma).

Effect on Productivity

Native grass or grass-like species, for which studies on productivity have been conducted both under various burning regimes and at different locations, include the warm-season (C,) species blue grama [Bouteloua gracilis (H.B.K.) Lag. ex Griffiths] and cool-season (C,) species such as western wheatgrass (Agropyron smithii Rydb.), needle-and-thread (Stipa comata Trin. & Rupr.), and Kentucky bluegrass (Poa pratensis L.). Also included is threadleaf sedge (Carex filifolia Nutt.) although the carbon-fixation status of this species does not appear to have been determined.

As with most species, the effect of burning on blue grama differ by location and'with climatic conditions. In studies in South Dakota, for example, spring (April) burning was found to reduce the productivity of blue grama whereas the response to fall burning was variable, increasing production when precipitation was adequate and decreasing it when precipitation was low. In the mixed prairie of North Dakota, however, both spring (May) and fall (October) fires increased blue grama production with spring burning resulting in the

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[1] Professor of Biology, University of Nebraska at Omaha, Omaha, NE.

greater increase (Whisenant and Uresk 1989). For western wheatgrass in South Dakota, productivity increased with Fall burning but either increased or decreased in response to spring burning, again depending on precipitation. The response of this species to tire in the more northern North Dakota prairies, however, was an increase in production with both spring and fall burning (Whisenant and Uresk 1989). As with blue grama, spring burning resulted in the greater response.

Needle-and-thread is one native grass species for which productivity is generally reduced by tire throughout much of its range. In the mixed-grass prairies of both North and South Dakota, productivity of this cool-season grass declined with both spring and fall bums (Dix 1960; Wright and Klemmedson 1965; Engle and Bultsma 1984; Whisenant and Uresk 1989). Gartner et al. (1986), however, did report a greater productivity of this species with both spring and fall bums. In the central, more southerly, Nebraska tallgrass prairie, however, summer mowing (approximating summer burning) resulted in a higher canopy cover of the congeneric porcupine-grass (Stipa spartea Trin.) than in areas burned in the spring (Hover and Bragg 1982).

Threadleaf sedge, a species common in the mixed-grass prairies of the Dakotas is particularly informative. It has been reported to be unaffected by spring or fall burning (Schripsema 1977; Whisenant and Uresk 1989) although it is reduced by fall burning in North Dakota (Dix 1960; White and Currie 1983). The general response of this species to burning is similar to that of needle-and-thread, a C_3 species, but unlike that of western wheatgrass, another C_3 species. If this observation is extrapolated to other species, it suggests either that the response to burning may occurs independent of carbon-fixation pathway or that the fire conditions under which the previous studies were conducted are not fully known.

A summary of the effects of fire on grass productivity, then, suggests that the complexity of fire effect studies. Only two common denominators are suggested, first, tires in dry years reduce productivity, and second, not all C_3 and C_4 species can be expected to respond similarly to burning.

Effect on Composition.

Another aspect of the effect of season of bum is the response of the community as a whole, which is the principal focus of this study. Despite individual species responses, community level studies in the northern mixed-grass prairie have indicated that season of fire occurrence is not a sufficient factor to substantially alter community composition (Dix 1960) or to alter the C_3/C_4 ratio of the northern mixed-grass prairie (Steuter 1987).

The C, grasses of the northern mixed-prairie appear to be a fire-adapted guild (Steuter 1987). The tendency for cool-season grass species to increase or to be unaffected in the northern Great Plains, however, is opposite to the response in more southerly tallgrass prairies of Kansas and Oklahoma. In these tallgrass prairies, dominated by warm-season, C_4 species, spring bums more consistently decrease cool-season, C_3 species, including porcupine-grass, Kentucky bluegrass, Canada wild rye (Elymus canadensis L.), and Scribner dichanthelium [Dichanthelium oligosanthes (Schult.) Gould var. scribnerianum (Nash) Gould] (Hensel 1923; Ehrenreich 1959; Hadley and Kicckhefer 1963; Robocker and Miller 1955; Old 1969; Anderson and others 1983). The effect of fire at other seasons, however, has not been widely studied although it has been found that little bluestem (Andropogon scoparius Michx.), is most adversely affected by summer (July) bums (Adams et al. 1982)

Response of Forbs

General results on fire effects indicate that forbs are increasingly adversely affected as burning occurs at increasingly later spring dates. For example, late spring burning in the tallgrass prairies of Kansas reduced all forbs (McMurphy and Anderson 1965; Towne and Owensby 1984; Hulbert 1988) compared to earlier dates. However, while these studies reflect a reduction in cover (suggesting also a reduction in productivity), the actual composition of forbs is little effected (Anderson 1965). Similar effects related to season of bum are reflected in the shortgrass prairies of western Kansas. There, forbs are less effected by dormant season (fall/winter) bums than by spring bums which occur after they have initiated growth (Hopkins and others 1948).

One principal study on the response of individual forb species to seasonal effects of burning was conducted by Biondini and others (1989) in northern mixed prairie. In this study, the density of nine forbs was significantly effected by fire season. Species responses relevant to the present study include western ragweed (Ambrosia psilostachva DC.) and white aster (Aster ericoides L.), which were most positively affected by fall bums, blue lettuce (Lactuca oblongifolia Nutt.) most effected by summer bums, and stiff sunflower [Helianthus rigidus (Cass.) Desf.] and wavy-leaf thistle [Cirsium undulatum (Nutt.) Spreng.] most effected by spring bums. Only pasque flower (Anemone patens L.) had the highest density without burning. In another study in the northern prairie region, Schripsema (1977) recorded increases in species such as silver-leaf scurf-pea (Psoralea argophylla Pursh) with late spring (late May) burning whereas a winter (March) bum had the opposite effect.

In more southerly tallgrass prairies, fall burning increased rigid sunflower (Solidigo rigida L.) (Schwegman and McClain 1985) and leadplant (Amorpha canescens Pursh) (Towne and Owensby 1984) although the greatest increase was among the annual species such as grooved flax (Linum sulcatum Ridd.) and white sweet clover (Melilotus alba Medic. (Schwegman and McClain 1985). Whorled milkwort (Polygala verticilata L.) and grooved flax were best established in spring burned plots (Schwegman and McClain 1985) but late spring (mid-May) bums adversely affected species such as prairie violet (Viola pedatifida G. Don), white-eyed grass (Sisvrinchium camnestre Bickn.) and downy gentian (Gentiana puberulenta Pringle); gay-feather (Liatris aspera Michx.) and smooth blue aster (Aster laevis L.), however, had significantly more leaves with late than with early spring bums (Love11 and others 1983).

The results of previous studies on effects burning suggest that the basic characteristics (e.g. productivity and species composition) of grasslands of different latitudes should respond differently to fire and that the response will be further modified by season of burning and climatic conditions. The objective of this paper is to identify such differences by comparing the results from two grasslands that are similar physiognomically but that differ in both latitude and dominant species. Specifically, the study will compare a Loess Hills prairie of northwestern Iowa and a tallgrass prairie of eastern Nebraska in order to assess similarities in plant responses to fire. Further, the study is designed to assess the possible role of different seasons of burning and their implications for global application in long--term management of grassland ecosystems.

METHODS AND MATERIAL

The study involves unreplicated sites and unreplicated locations within each site. This design was necessitated by a combination of the travel distance, the absence of additional sites to which access could be controlled, and the time required for both fire treatment and field evaluation. Therefore, extrapolation of results to other sites of the same vegetation type can only be used in a speculative manner and then only with caution. However, in those instances where similar responses to burning are noted at each site, the response could be considered to be replicated (e.g. two prairie sites were evaluated) and thus it is more likely to be representative of general trends. In addition to limiting how broadly the results can be inferred, the lack of adequate replication limited the kind of statistical evaluations that could be appropriately applied.

An additional caution to extrapolation of results is necessary due to the absence of any fire treatment at either site for many years, probably decades, prior to the study. The plant communities that were burned, therefore, may not be the same as those that dominated historically when fires reoccurred with some regularity. Studies at these sites are continuing at least through the 1990's in order to assess this possibility.

Study Sites

The Loess Hills study site was located on Five Ridge Prairie (within Sections 20, 21 and 29, Township 91N, Range 48W) located in northwest Iowa approximately 20 kilometers north of Sioux City. The prairie is managed by the Plymouth County Conservation Board in cooperation with the Iowa Chapter of The Nature Conservancy. Treatment plots were located in the northwest quarter of Section 29 along a southwest facing, 20-26% slope on which native prairie vegetation prevailed. The site was dominated by grass species, particularly little bluestem and plains muhly [Muhlenbergia cuspidata (Torr.) Rydb.]. The soil of the site is a Hamburg silt loam (Typic Udoxthent soil subgroup, Entisol soil order). The Hamburg series consists of excessively drained, calcareous, silty soils formed on loess (Worster and Harvey 1976). Climate of the region is continental with normal daily highs of 30 C in July and a low of minus -14 C in January. Normal annual precipitation (based on 1951 to 1980 data) averages 64 centimeters with 74% occurring during the growing season (April through September). Climatic data are from National Oceanic and Atmospheric Association (1989a).

The tallgrass study site was located on Stolley Prairie, approximately 20 kilometers west of Omaha, Nebraska in Douglas County (NW 1/4 Section 15, Township 15N Range 11E) . Stolley prairie is privately owned, jointly leased for wildlife habitat by the Audubon Society of Omaha and the Papio-Missouri River Natural Resources District, and managed by the Biology Department, University of Nebraska at Omaha. The prairie had been mowed for more than 20 years until haying ceased in 1980 with leasing of the site. Treatment plots were located on a north-facing, 7-11% slope, tallgrass prairie dominated by big bluestem and porcupine-grass. The soil is a Marshall silty clay loam (Typic Hapludoll Subgroup, Mollisol Soil Order), a deep, well-drained soil formed in loess (Bartlett 1975). Climate of the region is continental with normal mean highs of 30 C in July and normal mean lows of minus 12 C in January. Normal annual precipitation (based on 1951 to 1980 data) averages 76 centimeters with 74% occurring during the growing season (April through September). Climatic data are from National Oceanic and Atmospheric Association (1989b).

Treatment

At each study site, treatment plots, approximately 20 by 20 meters in size, were established in a stratified, complete block design with plots situated at either upper-slope or mid-slope locations. A single, lo-meter (Tallgrass) or 20-meter (Loess Hills) transect was centrally located within each treatment plot and permanently established with two metal rods at each end. Differences in transect length were due to size of the area available for the study; the loess hills prairie was smaller in size due to woody plant invasion from lowland valleys. Along each transect, ten microplots were systematically placed. I was able to evaluate the same microplots each year of the study by extending a meter tape between the rods and using established intervals at each evaluation.

Neither of the study sites had been burned within recent memory. After preliminary data collection in 1981, randomly selected treatment plots at the Tallgrass site were burned in early May, early July, and mid-September 1983. With the exception of Fall treatments, all plots were resampled in the Fall of 1983, 1984, and 1986. Fall bum treatment plots were not sampled in 1983 since treatment had not yet been applied: evaluations for 1981 were used to represent pre-bum conditions for this treatment.

At the Loess Hills site, plots were burned in mid-October 1986 (after pretreatment data collection) and in late April and early July 1987; the fall bum was conducted in 1986 (rather than 1987) so that all fire treatment plots would be effected by the same (1987) growing season. Treatment plots were resampled the Fall of 1987, 1988, and 1989. At this site, spring evaluations were also conducted in each sampling year in order to record any species that were not visible in the Fall.

Data Collection

Because of different, site-specific characteristics of the plant canopy cover, microplot size varied for each site. Microplot size was 30 x 50 centimeters for the Tallgrass site and 50 x 100 centimeters for the Loess Hills site. The larger size used in the Loess Hills was needed due to lower total plant canopy cover and more widely spaced plants. The number of microplots to be evaluated was determined from preliminary sampling of each community type from which it was determined that ten microplots incorporated 90% of all species situated along each transect in each site. Microplots were systematically placed along each transect to facilitate relocation in subsequent years.

Within each microplot, canopy cover of each species was recorded as were the general cover categories of "bare soil" (soil devoid of surface litter; litter is dead plant matter that is no longer connected to a living plant) and "forb". Coverage was estimated based on procedures modified from Daubenmire (1959). Cover categories were 0%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-99%, and > 99%. Because of lack of adequate replicates and for the purpose of this broad scope paper, descriptive statistics (Mean ± Standard Error) were calculated for all species and used to compare effects of treatment.

RESULTS AND DISCUSSION

Site Differences

Site differences are characterized by data collected prior to the year of fire treatment. In addition to species differences, noteworthy pretreatment differences included significant differences (based on Standard Error) in bare soil (soil not covered with litter) (7% on the loess hills site compared to 1% on the tallgrass site) and in forb cover (38% loess hills; 45% tallgrass) (tables 1 and 2). In addition, 49 native species were recorded in loess hills, pretreatment microplots compared to 44 species for the tallgrass microplots. After adjusting for species observed at each site, but not necessarily present within microplots, 16 species were identified to be unique to the loess hills with 7 unique to the tallgrass site. This supports a qualitative observation made during field evaluations that the loess hills had higher plant species diversity than the tallgrass site and that this difference may be due to more niches afforded by the greater surface heterogeneity as reflected in bare soil. The tallgrass site, however, did have an active pocket gopher (Geomvs bursarius) population that has the potential to profoundly affect the ecosystem (Huntly and Inouye 1988) and is likely to afford some, continuous bare soil niches. Pocket gopher activity was not observed at the loess hills site.

Community-Level Responses

Some treatment effects were found to be similar at both sites of which the effect on forb cover and Species Richness (the total number of species) are most noteworthy. The fall following spring and summer treatment, forb cover declined from pre-treatment conditions in all microplots at both sites regardless of whether burned or unburned. The cause for this response is unclear except that precipitation does not appear to be the principal factor; both treatment years were followed by near average or above-average precipitation (fig. 1). While the decline in forb cover occurred at both study sites, it was greatest in unburned plots (-15%) at the tallgrass prairie and second greatest in the unburned plots (-33%) at the loess hills prairie where it was second only to summer burning (- 35%). Three growing seasons following fire treatment (4 seasons for the tallgrass prairie), the unburned plots continued to show the greatest loss of forb cover based on pre-treatment values (-18% for tallgrass; -21% for loess hills) (tables 1 and 2). It should be noted, however, that the decline in forb cover in the absence of tire, reflects only a change in the amount of a species and not necessarily changes in population size.

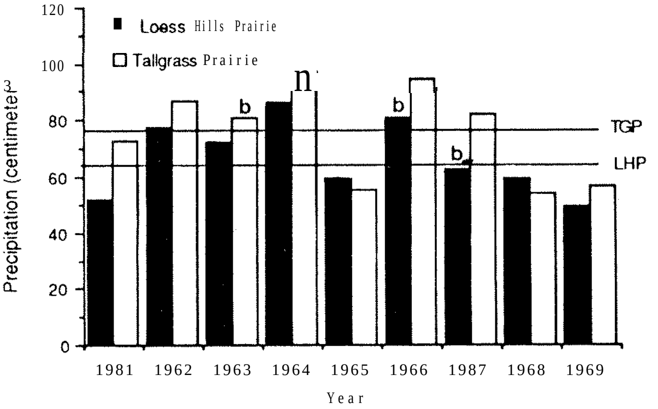


Fig. l.-Precipitation for Sioux City, Iowa [Loess Hills (= LHP) Prairie site] and North Omaha, Nebraska [Tallgrass (TGP) Prairie site] weather stations for the years 1981 through 1989. Horizontal lines represent normal precipitation (National Oceanic and Atmospheric Administration 1989a, 1989b). "b" = bum treatment year (For LHP, 1986 = Fall treatment and 1987 = Spring and Summer treatments)

Table 1. canopy cover (Mean ± Standard Error) of tallgrass prairie site species with frequency values greater then 50 percent, in either this or the loess hills prairie site. Values represent 20 microplots from two transects per treatment. Scientific and common names are from the Great Plains Flora Association (1986). "-" = no date; tr = co.5 percent cover.

species	Evaluation Year	season of Prescribed Burn Spring	Summer	Fall	Unburned
GENERAL CATEGORIES					
Number of Species	1981	29	32	29	31
	1983	34	24		31
	1984	32	30	30	26
	1986	27	32	29	31
Forb Cover	1981	39±3.6	49±5.2	44±3.8	49±5.9
	1983	21±3.0	14±2.7	-	16±2.4
	1984	19±3.8	32±5.3	50±3.6	24k.1
	1986	33±4.3	43±6.3	33±5.1	28±4.4
Bare Soil	1981	tr	2±1.0	2±1.9	tr
	1983	69±4.5	67±6.8		2±1.2
	1984	2±1.0	7±3.5	10+2.6	8±3.9
	1986	2±1.9	8±3.5	2±1.0	2±1.0
Achillea millefolium (yarrow)	1981	6±2.2	3±2.0	2±1.0	2±1.0
	1983	1±0.8	tr		2±1.0
	1984	1±0.8	7±3.6	1±0.8	tr
	1986	1±0.8	3±1.4	tr	tr
Canescens (leadplant)	19.31	0	2±1.2	2±1.2	tr
	1983	1±0.8	8±4.5	-	4±2.1
	1984	4±2.1	7±3.6	23±5.2	5±2.7
	1986	4±3.2	8x2.7	16±4.8	1±0.8
Andropogon gerardii (big bluestem)	1981	78±2.7	78±4.5	81±3.8	59±4.8
	1983	91±2.1	74±6.0		77±3.8
	1984	8122.7	85±5.0	86±1.7	60±6.0
	1986	77±2.9	74±5.6	83±2.6	74±5.3
Andropogon scoparius (Little bluestem)	1981	10±3.8	1±0.8	17±3.8	2±1.0
	1983	1±0.8	tr		1±0.8
	1984	0	0	0	0
	1986	1±0.8	2±1.9	1±0.8	4±2.1
Anemone cylindrica (candle anemone)	1981	tr	1±0.8	0	1±0.8
	1983	tr	tr		9±7.5
	1984	tr	0	0	3±2.0
	1986	0	1±0.8	0	3±2.1
Aster ericoides (white ester)	1981	tr	1±0.8	3±1.2	1±0.8
	1983	0	tr	-	0
	1984	0	3±3.1	2±1.9	0
	1986	1±0.8	6±2.7	9±3.9	0
Bouteloua curtipendula (sideoats grama)	1981	17±3.9	17±4.7	21±3.9	13±2.8
	1983	3±2.0	5±1.5		5±1.5
	1984	10±4.7	2±1.0	1±0.8	2±1.0
	1986	2±1.9	2±1,0	1±0.8	1±0.8
Carex spp. (sedge)	1981	10±1.6	12±1.4	13±1.2	10±1.6
	1983	19±3.3	15±2.1		6±1.7
	1984	16±3.7	18±3.2	13±1.9	10±2.2
	1986	421.5	10±3.8	3±1.4	5±2.2
Ceanothus herbaceous (New Jersey tea)	1981	11±4.7	5±3.6	1±0.8	1±0.8
	1983	10±5.3	3±3.1		6±4.6
	1984	13±5.9	6±3.6	0	4±3.1
	1986	9±5.3	4±3.1	0	6±3.6
Conyzansis (horse-weed)	1981	0	0	0	0
	1983	0	0		0
	1984	tr	4±1.3	tr	0
	1986	0	tr	1±0.8	2±1.0
Dichanthelium oligosanthes var. scribnerianum (Scribner dichanthelium)	1981	9±1.6	10~1.5	14±0.6	7±1.5
	1983	6±2.0	tr		3±1.2
	1984	1073.1	2±1.0	4±1.3	1±0.2
	1986	1±0.8	1±0.8	1±0.2	tr
Elymus canadensis (Canada wild rye)	1981	5±2.2	1±0.8	3±2.1	4±1.5
	1983	4±1.3	4±2.1	-	4±1.5
	1984	6±2.3	11±4.1	2±1.0	4±2.1
	1986	1±0.8	3±1.4	2±1.0	2±1.0
Equisetum laevigatum (smooth scouring rush)	1981	3±1.2	0	2±1.0	4±1.5
	1983	1±0.3	0		2±1.0
	1984	6±2.7	0	1±0.8	5±2.2
	1986	8±2.7	0	2±1.0	4±2.2

Table 1. (continued)

Species	Evaluation Year	Season of Prescribed Burn Spring	Summer	Fall	Unburned
Erigeron strigosus (daisy fleabane)	1981	0	2±1.2	0	1±0.8
	1983	tr	0		0
	1984	tr	1±0.8	3±1.2	0
	1986	0	1±0.8	2±1.0	0
Euphorbia (flowering spurge)	1981	5±1.6	3±1.4	5±1.6	8±2.8
	1983	8±3.2	5±2.2		5±1.6
	1984	6±3.1	2±1.9	4±2.1	10±4.2
	1986	10±3.4	9±3.8	8±3.8	13±3.2
Heliopsis helianthoides (false sunflower)	1981	0	4±1.5	1±0.8	tr
	1983	tr	2±1.2		2±1.9
	1984	1±0.8	9±4.5	tr	2±1.9
	1986	4±3.1	20±5.4	5±3.2	3±2.0
Kuhnia eupatoroides (false boneset)	1981	1±0.8	0	0	0
	1983	tr	0		1±0.8
	1984	tr	tr	tr	1±0.8
	1986	1±0.8	tr	0	3±2.1
Linum rigidum var. compactum (stiffstem flax)	1981	6±2.3	4±1.5	5±1.6	2±1.0
	1983	0	0		0
	1984	tr	5±1.6	20±4.2	0
	1986	0	1±0.8	0	0
Oxalis dellenii (gray-green wood sorrel)	1981	tr	tr	1±0.2	tr
	1983	3±1.0	0		0
	1984	tr	tr	1±0.2	0
	1986	tr	tr	tr	tr
Phlox pilosa (prairie phlox)	1981	6+1.7	1222.0	8±1.6	5±1.6
	1983	11F3.4	2±0.8		9±2.7
	1984	1073.2	6±1.5	16±3.6	8±2.7
	1986	16±4.0	13±2.4	20±3.4	10±3.1
Physalis virginiana (Virginia ground cherry)	1981	0	0	0	0
	1983	0	3±1.4		2±1.0
	1984	tr	2±1.0	0	0
	1986	4±2.6	1±0.8	1±0.8	2±1.2
Poa pratensis (Kentucky bluegrass)	1981	74±4.0	80±3.9	70±5.1	69+4.1
	1983	58±6.8	11±2.0		81±3.2
	1984	66±4.4	56±4.7	80±2.8	86±2.6
	1986	79±2.8	72±5.0	71±4.1	71±4.2
Rudbeckia t a (black-eyed susan)	1981	7±2.2	3±1.4	11±2.5	8+2.2
	1983	2±1.0	0		-0
	1984	2±1.0	10±4.1	14±3.5	0
	1986	0	3±1.2	2±1.0	0
Sorghastrum nutans (indiangrass)	1981	4+2.1	4±1.5	8±1.7	3±1.4
	1983	351.4	6±2.3		5+1.5
	1984	10±3.8	8±2.7	16±3.7	1654.8
	1986	22±5.4	8±3.1	20±5.0	23±6.0
Sporobolus asper (rough dropseed)	1981	2±1.0	4±1.6	8±1.7	0
	1983	0	0		1±0.8
	1984	0	1±0.8	0	2±1.9
	1986	0	0	0	tr
Stipa spartea (porcupine-grass)	1981	36+7.1	24+6.5	25±7.4	61+7.5
	1983	18±3.6	3±1.4		32-5.4
	1984	28±5.5	16+5,2	8+5,1	43±7.5
	1986	5±2.1	2±1.0	4±2.1	6±2.7
Taraxacum officinale (common dandelion)	1981	1+0.8	5±1.5	1±0.8	1±0.2
	1983	-0	1±0.8		0
	1984	0	0	0	0
	1986	0	tr	0	0
Trifolium pretense (red clover)	1981	36+4.1	43±5.5	35±3.7	42+4.9
	1983	9±2.1	0		1±0.8
	1984	3±1.3	10±3.5	3555.5	tr
	1986	tr	4±3.1	0	1±0.8
Viola pedatifida (prairie violet)	1981	1+0.8	1+0.8	1±0.8	tr
	1983	1±0.8	2±1.0		tr
	1984	2±1.0	2±1.9	3±1.2	tr
	1986	2±1.0	1±0.8	3±1.2	1±0.8

Table 2. Canopy cover (Mean ± Standard Error) of loess hills prairie site species with frequency values greater than 50 percent, in either this or the tallgrass prairie site. Values represent 20 microplots from two transects per treatment except for the Unburned plot which represents one transect. Scientific and common names are from the Great Plains Flora Association (1986). tr = <0.5 percent.

Table 2. (continued).

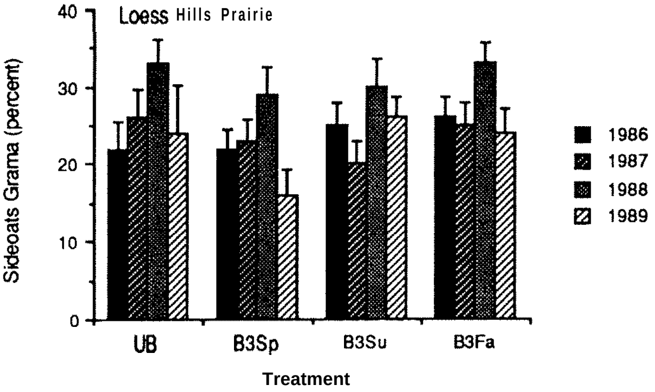
Species	Evaluation Year	Season of Prescribed Burn			
		Spring	Summer	Fall	Unburned
GENERAL CATEGORIES					
Number of Species	1986	38	32	34	24
	1987	35	25	34	20
	1988	33	33	34	20
	1989	33	32	32	20
Forb Cover	1986	32±3.7	34±3.3	39±3.1	47±7.1
	1987	22±2.4	21±2.6	32±2.6	32±4.2
	1988	18±2.6	25±3.3	30±3.5	30±6.6
	1989	21±2.8	28±4.1	33±2.1	29±5.4
Bare Soil	1986	4±1.4	9±2.1	8±2.2	7±2.2
	1987	23±2.8	37±1.8	35±2.5	2±0.2
	1988	11±2.1	40±1.7	30±2.5	1or2.1
	1989	8±2.6	23±2.5	21±3.0	1323.4
Andropogon gerardii (big bluestem)	1986	32±7.9	9±3.2	16±4.0	20±8.1
	1987	36±8.3	7±2.7	15±3.8	23±8.6
	1988	34±7.9	6±2.2	14±3.1	19±4.6
	1989	32±6.0	12±3.8	14±3.5	25±6.7
Andropogon scoparius (Little bluestem)	1986	66±4.7	83±1.7	84±2.0	78±5.8
	1987	49±5.3	80±2.1	79±2.9	78±5.0
	1988	46±6.0	82±2.6	79±2.7	80±3.1
	1989	36±4.8	80±2.7	73±3.6	78±3.5
Anemone patens (pasque flower)	1986	1±0.8	1±0.7	2±1.0	1±0.3
	1987	3±1.3	6±2.2	3±1.2	1±0.3
	1988	2±0.7	3±1.2	3±1.2	1±0.3
	1989	1±0.8	2±1.0	2±0.7	1±0.3
Aster sericeus (silky aster)	1986	5±1.5	10±2.1	11±3.0	27±4.6
	1987	3±1.4	5±1.4	7±1.6	25±4.6
	1988	3±1.2	8±1.6	8±1.6	27±5.8
	1989	3±1.2	7±1.5	6±1.5	23±4.4
Bouteloua curtipendula (sideoats grama)	1986	2222.4	25±3.0	26±2.6	22±3.5
	1987	23±2.8	20±2.9	25±2.9	26±3.8
	1988	29±3.5	30±3.5	33±2.7	33±3.1
	1909	16±3.3	26±2.6	24x3.1	24±6.3
Carex spp. (sedge)	1986	4±1.4	1±0.2	1±0.2	tr
	1987	9±2.6	1±0.8	4±1.4	tr
	1988	7±1.5	3±1.2	2±1.0	1±0.3
	1989	2±0.7	4±1.3	1±0.2	tr
Dalea spp. (prairie clover)	1986	1±0.8	7±2.7	2±1.0	tr
	1987	1±0.8	6±2.3	4±1.5	0
	1988	3±2.0	11±3.8	4±1.5	tr
	1989	2±1.0	12±4.0	3±2.0	tr
Dichanthelium oligosanthes var. *scribnerianum* (Scribner dichanthelium)	1986	tr	tr	tr	0
	1987	tr	tr	1±0.8	tr
	1988	1±0.9	tr	tr	tr
	1989	tr	tr	tr	tr
Dichanthelium wilcoxianum (Wilcox dichanthelium)	1986	1±0.2	tr	tr	tr
	1987	tr	tr	1±0.8	tr
	1988	tr	0	tr	0
	1989	tr	tr	tr	tr
Echinacea angustifolia (purple coneflower)	1986	tr	3±0.8	1±0.8	3±2.0
	1987	1±0.8	tr	3±1.4	tr
	1988	1±0.8	2±1.0	2±1.0	3±2.0
	1989	tr	1±0.8	2±1.0	2±1.5
Hedioma hispidum (rough false pennyroyal)	1986	1±0.3	2±0.4	2±0.4	1±0.3
	1987	0	0	0	tr
	1988	tr	0	0	0
	1989	0	tr	0	tr
Linum rigidum var. *compactum* (stiffstem flax)	1986	tr	2±1.2	1±0.8	tr
	1987	tr	0	tr	0
	1988	tr	tr	1±0.8	0
	1989	0	1±0.2	tr	tr
Lygodesmia juncea (skeletonweed)	1986	tr	4±1.5	6±1.5	6±2.4
	1987	tr	1±0.8	11±2.6	8±2.4
	1988	1±0.8	4±1.4	11±2.6	5±2.0
	1989	tr	2±1.0	5±1.4	7±2.3
Muhlenbergia cuspidata (plains muhly)	1986	8±2.7	6±1.6	4±1.5	tr
	1987	6±2.2	2±1.2	3±1.4	4±2.3
	1988	10±3.1	6±1.6	4±1.5	tr
	1989	10±3.4	5±2.2	421.5	tr
Psoralea tenuiflora (wild alfalfa)	1986	tr	tr	1±0.9	tr
	1987	tr	tr	0	tr
	1988	tr	1±0.9	0	0
	1989	tr	tr	0	tr
Rhus glabra (smooth sumac)	1986	18±6.8	2±1.2	7±3.6	7±4.0
	1987	23±6.6	2±1.0	5±2.2	6±3.9
	1988	18±4.6	2±1.0	6±3.2	6-3.9
	1989	15±4.1	1±0.8	4±2.1	32.0
Sisyrinchium campestre (white-eyed grass)	1986	5±2.1	6±1.a	7±2.0	6±2.0
	1987	tr	1±0.4	2±0.4	2±1.5
	1988	tr	1±0.4	2±0.9	-0
	1989	1±0.4	120.4	tr	0
Solidago nemoralis (gray goldenrod)	1986	9±2.7	9±1.6	7±1.6	7±2.3
	1987	4±1.3	3±1.1	7±1.6	6±2.4
	1988	3±1.4	1±0.2	8±1.6	1±0.3
	1989	3±1.2	1±0.2	5±1.4	tr
Solidago rigida (rigid goldenrod)	1986	4±1.3	3±1.2	4±1.4	tr
	1987	8±2.2	3±1.2	6±1.6	tr
	1988	6±1.6	1±0.8	6±1.6	2±2.0
	1989	6±1.6	1±0.8	6±1.6	2±1.5
Sorghastrum nutans (indiangrass)	1986	14±4.2	3±2.1	6±2.7	9±5.0
	1987	16±4.3	8±3.1	8±3.6	9±5.0
	1988	21±6.2	7±2.7	12±3.8	13±5.7
	1989	17±5.0	4±2.6	10±3.8	6±2.4
Verbena stricta (hoary vervain)	1986	1±0.2	tr	tr	tr
	1987	1±0.8	tr	1±0.8	tr
	1988	tr	0	tr	tr
	1989	0	0	tr	0

One consideration in the changes in species richness and forb cover with treatment is climate of which precipitation is an important component. Precipitation during all post-bum years at the loess hills site and during the second post-bum year at the tallgrass site averaged less than normal (fig. 1). The different responses of species diversity, both positive and negative, to season of burning, suggest that, while a drought year may be a poor time to bum prairies during some season of a year, some other season of the same year may be a reasonable time to bum. These results, if verified by further study, are particularly relevant to prairie management. Woody plant invasion threatens both loess hills (Heineman, 1982) and tallgrass (Bragg and Hulbert 1976) prairie areas. This study suggests that tire, a management tool that controls woody plant invasion, can be applied during appropriate seasons, even those of a drought year, without adversely affecting long-term species diversity. Further, results of this study that show increased diversity with different seasons of bum, suggest that any season of burning is better for maintaining grassland diversity than is fire exclusion. In the present study, this effect appears to be particularly true for the loess hills prairie ecosystem.

While one common effect between sites was a decline in forb cover without burning, another common effect was a short-term decrease in Species Richness with summer burning (-8% for tallgrass species; -7% for loess hills species); sufficient data were not available, however, to test for the statistical significance of this difference. This overall reduction in number with summer burning, however, did not persist beyond the second post-bum growing season (tables 1 and 2). For example, three growing seasons after burning in the loess hills, Summer treatment plots had recovered to pre-bum numbers. By this time, it was the Spring burned microplots that reflected the greatest loss of species (-5); unburned microplots averaged four less and fall burned plots averaged two less species. For the tallgrass prairie site, four growing seasons after treatment, species richness of all but the Spring treatment (-2 species) was at pre-bum numbers. Thus, for both the loess hills and the tallgrass prairie ecosystems, spring treatments, which represent the most widely applied time of tire management, showed the greatest long-term (3-4 year) loss of species.

Individual Species' Responses

The response of individual species provides further insight into the seasonal effect of burning on specific prairie types and on grassland ecosystems in general. Of the several species common to both sites, only big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], sideoats grama [*Bouteloua curtipendula* (Michx.) Ton.) , and sedge (*Carex* spp.) were sufficiently abundant to make comparisons between the tallgrass and loess hills sites. The responses of all but sideoats grama were similar between sites (tables 1 and 2). Sideoats grama, however, declined an average of 11 percent with all treatments at the tallgrass site but was maintained at or above prebum amounts both without burning and with all bum treatments except spring burning (fig. 2). The most likely explanation for this difference in



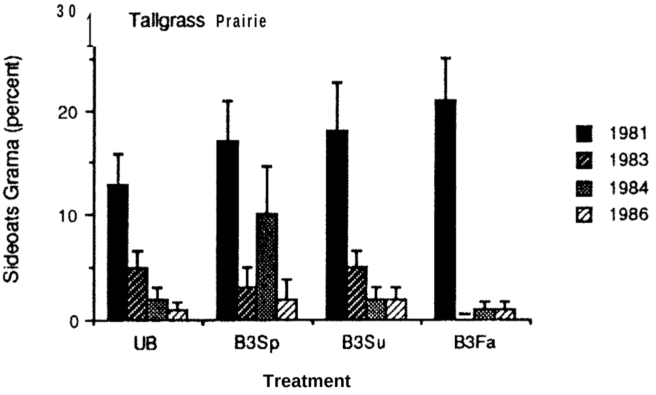
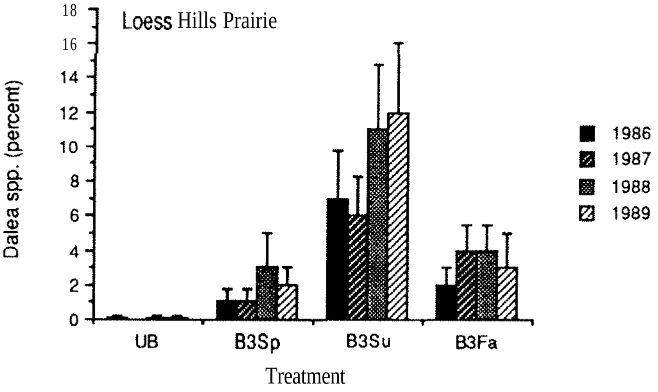


Fig. 2.-Sideoats grama cover for loess hills and tallgrass prairie sites contrasting the site-specific response of this species to burning. Vertical lines represent one Standard Error. B3 = three-year bum schedule, Sp = Spring, Su = Summer, Fa = Fall, UB = Unburned. Tallgrass site bum year = 1983; loess hills burn years = 1986 for Fall treatment and 1987 for Spring and Summer treatments; "-" for Tallgrass Prairie in 1983 indicates "no data".

response between sites is the long history of mowing management prior to the initiation of this study. Such management would have maintained a low canopy thus enabling sideoats grama, a mid-height grass, to persist in an ecosystem otherwise dominated by tall-statured species. With the cessation of mowing at the tallgrass prairie in 1980, canopy cover of the tall-statured component of the ecosystem increased as evidenced, for example, by the 15 percent increase in big bluestem and the 20 percent increase in indiangrass cover in unburned plots (table 1). The decline in mid-height and increase in tall-statured species were amplified by tire's tendency to favor tallgrass species (Ehrenreich 1959; Hadley 1970). At the loess hills site, however, tallgrass species were only a minor component of the ecosystem thus, tire's favoring of tallgrass species did not substantially affect the mid-height grasses such as sideoats grama and little bluestem (table 2). The effect of fire on a species (e.g. sideoats grama), therefore, may not operate directly on that species but rather may operate indirectly by favoring an intermediate species (e.g. indiangrass) that outcompetes the shorter grasses for some limited resource such as light.

Other species, either found only at one site or found in sufficient numbers only at one site, provide yet further insight on long-term management implications for prairies in general. One such insight of particular importance would be any evidence that fire encourages seedling establishment in a prairie ecosystem. Recruitment is one of the most critical facets of long-term prairie management since it ensures a replacement of a species' population, thereby maintaining ecosystem diversity over decades. No studies have been conducted on fire-affected seedling germination and establishment in the loess hills prairie but those in the tallgrass prairie generally show variable results. For example, Glenn-Lewin *et al.* (1990) found that, in years with adequate precipitation, burning resulted in higher seedling establishment than occurred without burning; one species that showed this effect was Scribner dichanthelium. In dry years, however, they found that burning reduced seedling establishment. Also noteworthy was that, with adequate precipitation, germination of some species (e.g. Kentucky bluegrass and prairie violet) was particularly high in either the unburned area or in areas burned the previous year.

While the present study did not focus on identification and establishment of seedlings, one might hypothesize that significant increases in canopy cover would be a logical consequence of such tire-initiated establishment. Initially being absent or having low cover (e.g. with seedlings) growth of new plants would be reflected in a significant increases in canopy cover over a few years. Evidence for such an effect of tire was found in the tallgrass prairie with summer burning of false sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fem.] (fig. 3), summer and fall burning of white aster, and fall burning of leadplant (table 1). In the loess hills, such a response was found for prairie clover (*Dalea* spp.) with summer and fall burning (fig. 3). Note that all of these seedling-initiation signatures occurred only with summer and fall burning, which are not the normal times for prairie management burning in the tallgrass or loess hills prairie regions. Rohn and Bragg (1989), for example, found that germinability of false sunflower and white prairie clover (*Dalea candida* Michx. *ex* Willd) declined with spring burning. These results suggest that, for the long-term maintenance of a diverse community, occasional bums of some portions of an area at times of the year other than spring may be important to ensuring the continuation of a full complement of species.



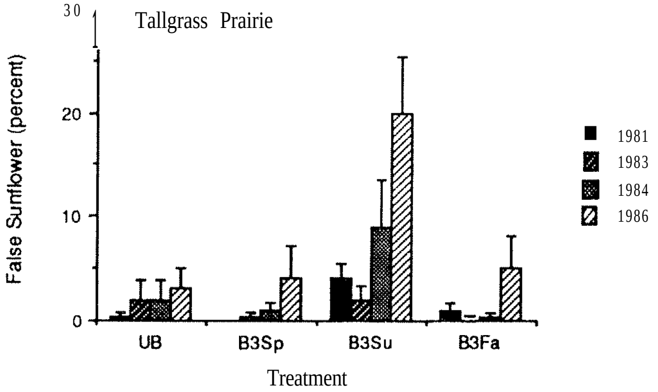


Fig. 3.-Canopy cover of Dalca spp. (prairie clover; loess hills prairie) and false sunflower (tallgrass prairie) showing the type of increase in cover hypothesized to reflect an increase in number of individuals in response to summer burning. Vertical lines represent one Standard Error. B3 = three-year bum schedule, Sp = Spring, Su = Summer, Fa = Fall, UB = Unburned; "-" for Tallgrass Prairie in 1983 indicates "no data". Tallgrass site burn year = 1983; loess hills burn years = 1986 for Fall treatment and 1987 for Spring and Summer treatments.

In addition to possibly encouraging seedling success, fires at different times of the year both in the loess hills and in the tallgrass prairie sites increased the cover of some species. Among the species that showed this response at the tallgrass prairie were white aster, stiffstem flax [Linum rigidum var. comnactum (A. Nels.) Rogers] (fig. 4), and black-eyed susan (Rudbeckia hirta L.), all of which increased with summer and fall burning; Stiffstem flax and black-eyed susan declined in cover without burning. At the loess hills site, other species showed a similar response pattern including gray goldenrod (Solidago nemoralis Ait.) with fall burning (fig. 4) and, as at the tallgrass site, stiffstem flax with summer and fall burning. Gray goldenrod, for example, declined during the four years of the study with all treatments except fall burning. Again, note the apparent importance of summer and fall burning to maximizing the canopy cover these species.

Significant declines with all seasons of burning were detected for sideoats grama and rough dropseed [Sporobolus asper (Michx.) Kunth] in the tallgrass prairie and silky aster (Aster sericeus Vent.) in the loess hills prairie. e bluestem declined with summer burning in the loess hills prairie. As has been pointed out above, note the particular role of summer and fall burning in affecting species' responses. Only candle anemone (Anemone cylindrica A. Gray) in the tallgrass prairie site increased significantly without some fire treatment.

Some species showed significant changes irrespective of treatment. For these, it appears that some factor other than fire is important in explaining their response. Species that decreased without regard to treatment included Scribner dichanthclium and porcupine-grass in the tallgrass prairie and white-eyed grass in the loess hills (tables 1 and 2). The one species that increased significantly was flowering spurge (Euphorbia corollata L.).

CONCLUSIONS

When taken in combination, the vegetative responses to tire reported at the tallgrass and loess hills study sites, suggest several considerations. First, the same species may respond differently in different ecosystems. This is a logical conclusion but one that needs to be carefully considered particularly when developing management plans for grasslands even within the same general geographic ares. Second, in order to maintain long-term (many decades long) diversity of a grassland ecosystem under relatively static climatic conditions, this study suggests that serious consideration bc given to some application of tire management at various times of the year. While further research is clearly needed, data from both the tallgrass and the loess hills grasslands suggest that successful seedling establishment, for example, might require different seasons of burning. Summer and fall burning seem to be times that are most likely to encourage such seedling success for several species. Higher biomass produced by some species with summer and fall burns further suggests the need for a consideration of occasional non-spring bums.

Thus, to maintain vegetative diversity both by seedling establishment and by maximizing species productivity, some areas or portions of areas within a preserve should be burned some time during the growing season. The size of such growing-season bums, however, should not be so extensive as to adversely affect the resident invertebrate population of the area. Such small scale summer bums are probably representative of the natural ecosystem in which sufficient fuel is present to support a fire (Bragg 1982) but where the amount of green matter in the fuel bed would not have supported a high intensity, widespread tire.

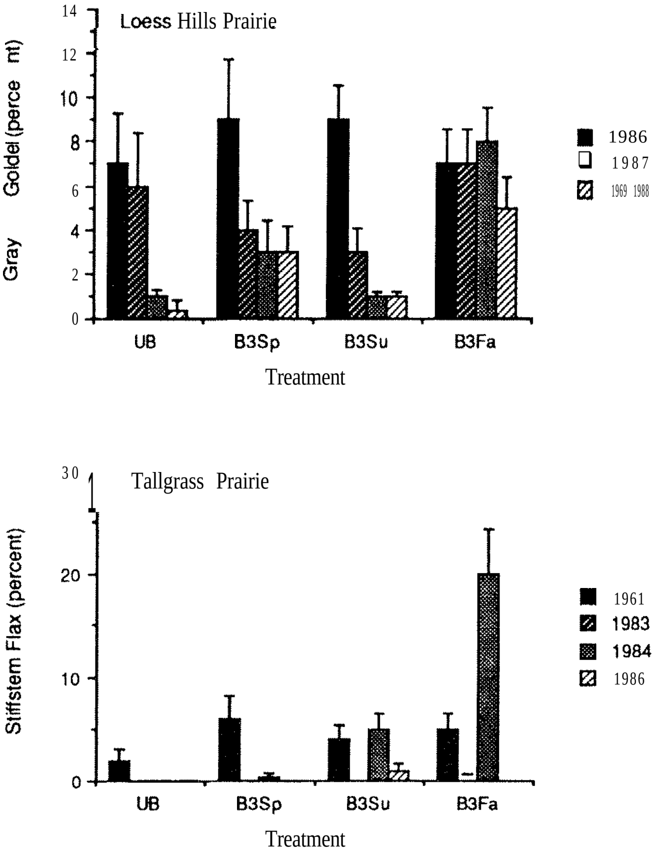


Fig. 4.-Canopy cover of grey goldenrod (loess hills prairie) and stiffstem flax (tallgrass prairie) indicating that their persistence may be dependent on summer or fall bums. Vertical lines represent one Standard Error. B3 = three-year bum schedule, Sp = Spring, Su = Summer, Fa = Fall, UB = Unburned; "-" for Tallgrass Prairie in 1983 indicates "no data". Tallgrass site bum year = 1983; locss hills bum years = 1986 for Fall treatment and 1987 for Spring and Summer treatments.

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LITERATURE CITED

Abrams, M.C. 1988. Effects of burning regime on burned seed banks and canopy coverage in a Kansas tallgrass prairie. The Southwestern Naturalist 33(1):76-70.

Adams, D.E., R.C. Anderson, and S.L. Collins. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. Southwestern Naturalist 27(1):55-61.

Anderson, K.L. 1965. Fire ecology - Some Kansas prairie forbs. In: Proceedings of the Tall Timbers Fire Ecology Conference 4:153-160.

Bartlett, P.A. 1975. Soil survey of Douglas and Sarpy Counties, Nebraska. U.S. Department of Agriculture, Soil Conservation Service and University of Nebraska Conservation and Survey Division. U.S. Government Printing Office, Washington D.C.; 79 pages plus maps.

Biondini, M.E., A.A. Steuter, and C.E. Grygiel. 1989. Seasonal tire effects on the diversity patterns, spatial distribution and community structure of forbs in the Northern Mixed Prairie, USA. Vegetatio 85(1-2):21-31.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29(1):19-24.

Bragg, T.B. 1982. Seasonal variations in fuel and fuel consumption by tires in a bluestem prairie. Ecology 63(1):7-11.

Daubenmire, R. 1968. Ecology of fire in grasslands Advances in Ecological Research 5:209-266.

Daubenmire, R. 1959. A canopy-cover method of vegetational analysis. Northwest Science 33:43-64.

Dix, R.L. 1960 The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. Ecology 41:49-56.

Ehrenreich, J.H. 1959. Effect of burning and clipping on growth of native prairie in Iowa. Journal of Range Management 12: 133-137.

Engle, D.M. and P.M. Bultsma. 1984. Burning of northern mixed prairie during drought. Journal of Range Management 37:398-401.

Gartner, F.R., R.I. Butterfield, W.W. Thompson, and L.R. Roath. 1978. Prescribed burning of range ecosystems in South Dakota. Pages 687-690 In: Proceedings of the First International Rangeland Congress, D.N. Hyder, editor. Society for Range Management, Denver.

Glenn-Lewin, D.C., L.A. Johnson, T.W. Jurik, A. Akey, M. Loeschke, and T. Rosburg. 1990. Fire in central North American grasslands: Vegetative reproduction, seed germination, and seedling establishment. Pages 28-45 In: Fire in North American tallgrass prairies (S.L. Collins and L.L. Wallace, editors). University of Oklahoma Press, Norman, OK. 175 pages.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS, 1392 pages.

Hadley, E.B. and B.J. Kieckhefer. 1963. Productivity of two prairie grasses in relation to fire frequency. Ecology 44:389-395.

Hadley, E.B. 1970. Net productivity and burning responses of native eastern North Dakota prairie communities. American Midland Naturalist 84:121-125.

Heineman, P.L. 1982. Woody plant invasion of Iowa loess bluff prairies. Masters Thesis, University of Nebraska at Omaha. 20 pages.

Henderson, R.A., D.L. Lovell, and E.A. Howell. 1983. The flowering responses of 7 grasses to seasonal timing of prescribed bums in remnant Wisconsin prairie. Pages 7-10 In Proceedings of the Eighth North American Prairie Conference, R. Brewer, editor. Department of Biology, Western Michigan University, Kalamazoo. 176 p.

Hensel, R.L. 1923. Recent studies on the effect of burning on grassland vegetation. Ecology 4:183-188

Hopkins, H., F.W. Albertson, and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. Kansas Academy of Science Transactions 51: 131-141.

Hover, E.I. and T.B. Bragg. 1981. Effect of season of burning and mowing on an eastern Nebraska Stipa-Andropogon prairie. American Midland Naturalist 105(1):13-18.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69(1):46-58.

Huntly, N. and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience 38(11):787-793.

Kozlowski, T.T. and C.E. Ahlgren. 1974. Fire and Ecosystems. Academic Press Inc., San Francisco. 542 p.

Lovell, D.L., R.A. Henderson, and E.A. Howell. 1983. The response of forb species to seasonal timing of prescribed bums in remnant Wisconsin prairies. Pages 11-15 In Proceedings of the Eighth North American Prairie Conference, R. Brewer, editor. Department of Biology, Western Michigan University, Kalamazoo. 176 p.

McMurphy, W.E. and K.L. Anderson. 1965. Burning Flint Hills range. Journal of Range Management 18:265-269.

Moore, C.T. 1972. Man and tire in the central North American Grassland, 1535--1890: A documentary historical geography. PhD Dissertation, University of California, Los Angeles, CA. 155 p.

National Oceanic and Atmospheric Administration. 1989a. Local climatological data: Annual summary with comparative data - Omaha (North), Nebraska. National Climatic Data Center, Asheville, NC. 8 p.

National Oceanic and Atmospheric Administration. 1989b. Local Climatological Data: Annual Summary with Comparative Data -- Sioux City, Iowa. National Climatic Data Center, Asheville, North Carolina. 8 pages.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monographs 39:355-384.

Risser, P.G., E.C. Bimey, H.D. Blocker, S.W. May, W.J. Parton, J.A. Wiens (editors). 1981. The true prairie ecosystem. Hutchinson Ross Publishing Co., Stroudsburg, PA. 557 p.

Robocker, C.W. and B.J. Miller. 1955. Effects of clipping, burning, and competition on establishment and survival of some native grasses in Wisconsin. Journal of Range Management 8: 117-121.

Rohn, S.R. and T.B. Bragg. 1989. Effect of burning on germination of tallgrass prairie plant species. Pages 169-171 In Proceedings of the Eleventh North American Prairie Conference, Bragg T.B. and J. Stubbendieck (editors). University of Nebraska Printing, Lincoln, NE. 293 pages

Ruyle, G.B., B.A. Roundy, and J.R. Cox. 1988. Effects of burning on germinability of Lehmann lovegrass. Journal of Range Management 41(5):404-406.

Schripsema, J.R. 1977. Ecological changes on pine-grassland burned in spring, late spring, and winter. M.A. Thesis, Biology and Botany Department, South Dakota State University, Brookings. 99 p.

Schwegman, J.E. and W.E. McClain. 1985. Vegetative effects and management implications of a fall prescribed bum on an Illinois hill prairie. Natural Areas Journal 5(3):4-8.

Steuter, A.A. 1987. C_3/C_4 production shift on seasonal bums - Northern Mixed Prairie. Journal of Range Management 40(1):27-3 1.

Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas Tallgrass prairie. Journal of Range Management 37(5):392-397.

Vogel, R.J. 1974. Effect of fire on grasslands. Pp. 139-194 In: Fire and Ecosystems, T.T. Kozlowski and C.E. Ahlgren, editors. Academic Press, NY. 542 p.

Whisenant, S.G. and D.W. Uresk. 1989. Burning upland, mixed prairie in Badlands National Park. Prairie Naturalist 21(4):221-227.

White R.S. and P.O. Currie. 1983. Prescribed burning in the northern Great Plains: Yield and cover responses of 3 forage species in the Mixed Grass Prairie. Journal of Range Management 36(2):179-l 83.

Worster, J.R. and E.H. Harvey. 1976. Soil Survey of Plymouth County, Iowa. U.S. Department of Agriculture, Soil Conservation Service, Iowa Agriculture and Home Economics Experiment Station and Cooperative Extension Service, Iowa State University, and Department of Soil Conservation, State of Iowa. U.S. Government Printing Office, Washington D.C. 75 pages plus maps.

Wright, H.A. and J.O. Klemmedson. 1965. Effect of fire in bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology 46:680-688.

Wright, H.A. and A.W. Bailey. 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, New York. 501 p.

FORTY YEARS OF PRESCRIBED BURNING ON THE SANTEE FIRE PLOTS: EFFECTS ON OVERSTORY AND MIDSTORY VEGETATION

Thomas A. Waldrop and F. Thomas Lloyd[1]

Abstract-Several combinations of season and frequency of burning were applied in Coastal Plain loblolly pine (Above-taeda L.) stands over a 40-year period. Pine growth was unaffected by treatment. ground portions of small hardwoods (less than 12.5 cm d.b.h.) were killed and replaced by numerous sprouts. With annual summer burning, sprouts were replaced by grasses and forbs. Study results emphasize the resilience of southern forests to low-intensity burning and that frequent burning over a long period is needed to produce significant changes to forest structure and species composition.

INTRODUCTION

It is well established in the literature and in other papers at this symposium that fire has been a major ecological force in the evolution of southern forests. Ecological and meteorological evidence suggest that lightning-caused fires were a major force in creating open pine forests in the Southeast (Komarek 1974). Archeological evidence has established the presence of Paleo-Indians in the region as early as 12,000 years ago (Chapman 1985). The movement of Indian tribes for game and cropland created variable patterns of fire frequency across the landscape, thus producing a mosaic of vegetation types and stand ages (Buckner 1989). Southeastern forests described by the first white settlers of the 1600's and 1700's were often open pine and hardwood stands with grasses underneath. Early writers suggested these open forests owed their existence to frequent burning (Bar-tram 1791; Harper 1962; Van Lear and Waldrop 1989). Frequent burning continued through the early 1900's, when tire protection policies of the U.S. Department of Agriculture, Forest Service, and cooperating State Forestry agencies attempted to prevent the use of fire. Prescribed burning for fuel reduction gained acceptance in the 1940's and 1950's, but only after a series of wildfires showed the disastrous consequences of fire exclusion (Pyne 1982). As a result, contemporary forests developed with a dense understory and a larger hardwood component.

It can be difficult to appreciate the important role of fire in shaping the species composition and structure of Southeastern forests. The changes tire causes in plant communities can be slow and depend on tire intensity, the season and frequency of burning, and the number of successive fires used. Opportunities to observe changes in vegetative characteristics over long periods are limited. A long-term study by the Southeastern Forest Experiment Station may give an indication of the ecological role fire once played. The experiment, known as the Santee Fire Plot Study, was established in 1946. Various combinations of season and frequency of burning were maintained for over 40 years. Previous papers have compared the effects of these various fire regimes on pine growth, understory vegetation, and soil properties at specific years during the study. This paper discusses changes to the structure and species composition of the overstory and midstory as they occurred over time and relates those changes to presettlement fire frequency and effects. Changes to understory vegetation after 43 years of burning are presented in another paper in these proceedings (White and others 1991).

DESCRIPTION OF THE STUDY

Study plots are on the Santee Experimental Forest in Berkeley County, SC, and on the Westvaco Woodlands in neighboring Georgetown County. Both areas are on a Pleistocene terrace on the Lower Coastal Plain at 7.5 to 9.0 m above sea level. Soils include a variety of series but are generally described as poorly drained Ultisols of medium to heavy texture (McKee 1982). Soils are considered productive with a site index of 27 to 30 m for loblolly pine at age 50. In 1946, the overstory of both study sites consisted of unmanaged, but well-stocked even-aged stands of loblolly pine. Common midstory species were dogwood (Comus florida L.), hickory (Carya sp.), southern red oak (Quercus falcata Michx.), post oak (Q. stellata Wangenh.), water oak (Q. nigra L.), and willow oak (Q. phellos L.). The Santee stand was 42 years old when the study was initiated, while the Westvaco stand was 36 years old. Both stands resulted from natural regeneration after logging. No evidence of previous burning was observed.

Six treatment plots, 0.1 ha in size, were established in each of live replications. Three replications are on the Santee Experimental Forest and two are on the Westvaco woodlands. Treatments include: (1) periodic winter burning, (2) periodic summer burning, (3) biennial summer burning, (4) annual winter burning, (5) annual summer burning, and (6) an unburned control. All winter burning was done on December 1 or as soon afterward as weather permitted. Summer burning was done on or soon after June 1. Periodic bums were conducted when 25 percent of the understory hardwood stems reached 2.5 cm in diameter at breast height (d.b.h.).

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[1] Research Forester and Project Leader, Southeastern Forest Experiment Station, USDA Forest Service, Clemson, SC.

This prescription resulted in variable burning intervals ranging from 3 to 7 years. Annual burning has not been interrupted since 1946. Biennial summer burning was added to the study in 1951.

To protect the study, burning techniques were selected to ensure low fire intensity. Selection was made at the time of burning based on prevalent fuel and weather conditions. In general, backing fires were used on periodically burned plots that had thick underbrush or when hot and dry weather increased the risk of high-intensity fires. Headfires or strip headfires were used on annually burned plots that had little underbrush or when fuels were too moist to support a backing fire.

OVERSTORY PINES

Loblolly pine remained the dominant overstory species in all study plots from 1946 to the present. However, growth rates may have been affected. The Santee Fire Plots were designed to study effects on understory vegetation with little consideration to tree growth. Detailed records of the number and size of trees were not kept throughout the history of the study. Therefore, comparisons of treatment effects on diameter and height growth were conducted through increment core analysis and stem analysis procedures, respectively. A more detailed description of these methods was given by Waldrop and others (1987).

Basal area per hectare for each burning treatment throughout the study is shown in figure 1. Since records of tree mortality were not kept, figure 1 represents the basal area of only those trees that survived until the time of sampling (1984). Differences in the levels of these curves represent differences in numbers and sizes of trees in treatment plots in 1984, rather than treatment effects. If burning treatments alter tree growth rates, the effect would be shown as differences in the slopes of these curves rather than differences in the relative heights. All curves in figure 1 are generally parallel, indicating that burning did not affect diameter growth. Basal area increment during each of four 10-year periods was subjected to analysis of covariance, using measured stand basal area to adjust growth rates for stocking effects. These tests indicated that differences between the slopes of lines were not significant for any period (alpha=0.05).

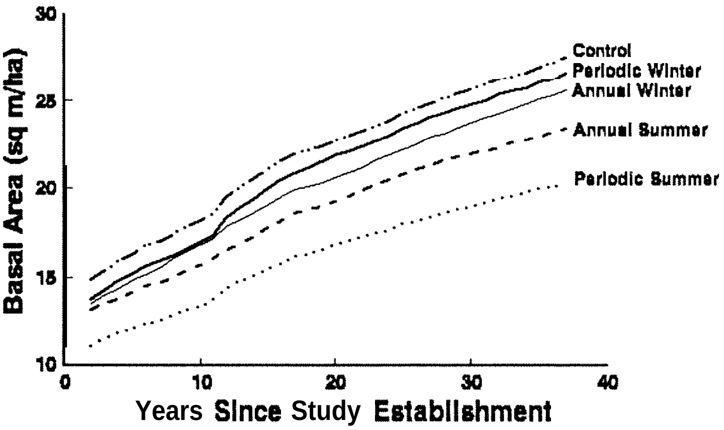


Figure 1.-Cumulative basal area of trees surviving from 1946 through 1984 by burning treatment.

Mean tree height for each treatment throughout the lives of these stands is shown in figure 2. Curves are very close together, indicating that trees in various treatment plots had similar height growth patterns. During the last 30 years, trees in plots burned annually in winter or summer appear to have slightly reduced height growth. These differences were not significant, however, when compared by analysis of variance (alpha=0.05).

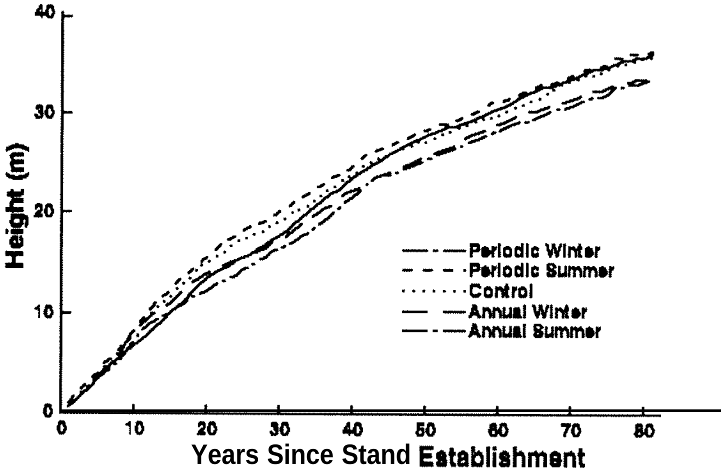


Figure 2.--Mean height of sampled trees by burning treatment from 1905 through 1984.

The lack of differences in diameter and height growth was unexpected. We expected that these low-intensity fires would not cause enough crown damage to reduce growth, and that vegetation control and increased soil fertility resulting from prescribed burning would improve growth. However, overstory pines averaged 40 years old at the beginning of the study and were probably too old to respond by the time these site changes reached meaningful levels. Even though McKee (1982) showed increases in phosphorus and calcium availability, no fertilization studies in the Coastal Plain have shown positive responses to these elements in trees of this age. In addition, soil moisture is rarely limiting to pine growth on these poorly drained Coastal Plain sites, even when competing vegetation is not controlled.

MIDSTORY

Diameter Distribution

Species composition of midstory vegetation changed little since study establishment. Dogwood, hickory, and oaks have remained common on all treatment plots since 1946. However, repeated measurements of the midstory show that diameter distribution of these hardwoods has been changed by the various combinations of season and frequency of burning. The d.b.h. of all hardwoods in all plots was measured at study establishment (1946), at year 20 (1966), and at year 30 (1976). Later descriptions are unavailable due to severe damage from Hurricane Hugo in September 1989. Stem numbers in each of five diameter classes (<2.5 cm, 2.6-7.5 cm, 7.6-12.5 cm, 12.6-17.5 cm, and 17.5+ cm) were used as dependent variables in a split-plot design of an analysis of variance to compare treatment differences over time. Whole-plot effects were those created by burning treatments while the years since study establishment were sub-plot effects. Mean separation was by linear contrast (alpha = 0.05).

At the beginning of the study, unburned control plots appeared to be undisturbed. Every size class of hardwoods from less than 2.5 cm to over 17.5 cm d.b.h. was present (fig. 3A). Diameter distribution followed a reverse-J pattern with numerous stems in small size classes and few stems in larger classes. The number of stems in each size class varied somewhat over time as individual trees grew into larger classes. However, the reverse-J pattern remained.

Hardwood diameter distributions were altered by periodic winter burns and periodic summer burns. For both treatments, the number of stems in the smallest size class (0-2.5 cm) increased significantly between year 0 and year 20 and between year 20 and year 30 (figs. 3B and 3C). Hardwood numbers in the next two classes (2.6-7.5 cm and 7.6-12.5 cm) decreased significantly over the same periods. With periodic summer burning, the smallest size class increased from approximately 11,000 to over 19,000 stems per hectare by year 30. The 2.6- to 7.5-cm size class was most affected, decreasing from over 1,100 to approximately 100 stems per hectare in both periodic treatments. Most changes occurred during the first 20 years, but the changes continued at a reduced rate through year 30.

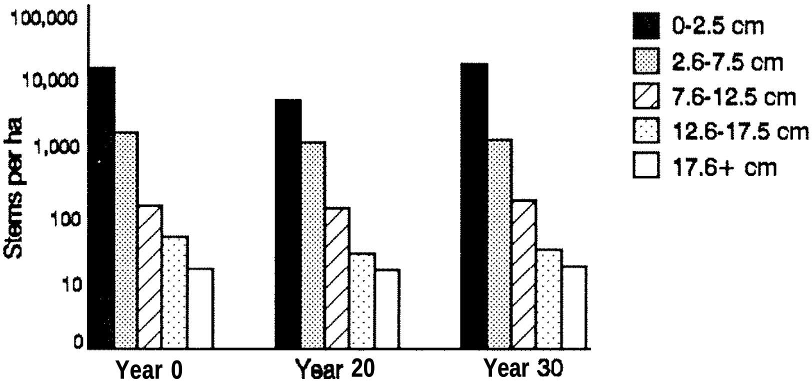
Hardwoods greater than 12.5 cm d.b.h. were generally unaffected by periodic winter and summer burning (figs. 3B and 3C). At the beginning of the study, these trees were old enough to be protected by thick bark and tall enough that their buds were protected. Most stems less than 12.5 cm d.b.h. were too small to survive burning. However, root systems of these smaller trees survived and produced multiple sprouts, causing the increase in stem numbers in the smallest size class. Burns were frequent enough to prevent the growth of sprouts into a larger size class. Fewer than 10 percent of the trees in the 2.6- to 7.5cm d.b.h. class survived until year 30. Trees of this intermediate size class are susceptible to top-kill from occasional flareups or hot spots. Since hot spots occur more often during the summer, fewer trees of this size class survived periodic summer burns than periodic winter burns.

Annual winter burning caused changes in the hardwood d.b.h. distribution similar to periodic winter and summer burning. Most stems in the 2.6- to 7.5cm d.b.h. class were top-killed or girdled during the first few years. Stem numbers in this size class were significantly reduced (from approximately 1,200 per hectare to less than 100) by year 20, with no additional reduction through year 30 (fig. 3D). The number of stems per hectare in the smallest d.b.h. class (0-2.5 cm) increased dramatically over the 30-year period. By year 20, this size class had increased significantly from 16,000 to 21,000 stems per hectare. Between years 20 and 30, that number increased to over 47,000 per hectare. Most of these stems were sprouts less than 1 m tall. Since annual winter burns allow sprouts a full growing season to recover from fire, many root systems survived and produced larger numbers of sprouts after each fire. In year 44, White and others (1991) found a slight decrease in the number of stems per hectare in annual winter burn plots and a substantial decrease in cover by woody plants. Even though sprouts are still numerous, these decreases may indicate declining sprout vigor.

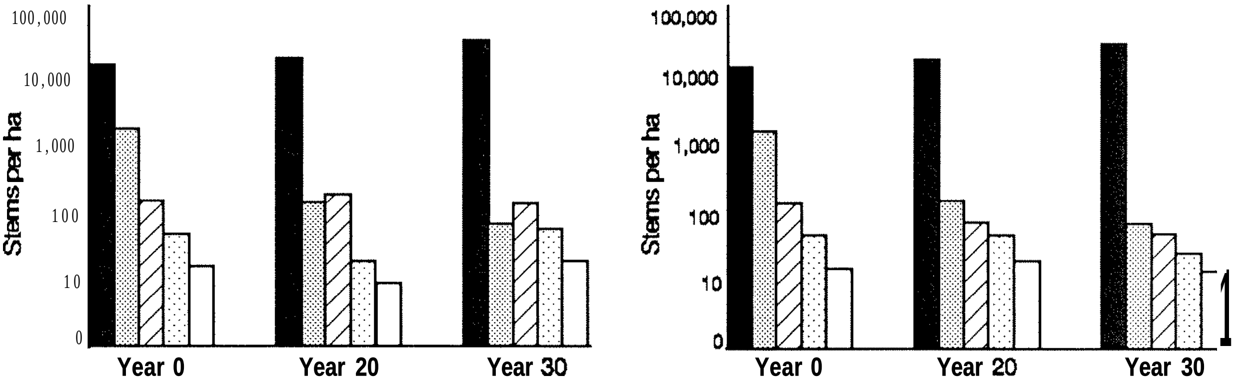
Annual summer burning has nearly eliminated woody vegetation in the 0- to 2.5-cm d.b.h. class (fig. 3E). Root systems were probably weakened by burning during the growing season when carbohydrate reserves were low. Burning was frequent enough to kill root systems of all hardwoods less than 7.5 cm d.b.h. during the first 20 years. A few hardwood seedlings appeared each spring but did not survive the next fire. As with other treatments, the number of stems between 2.6 and 12.5 cm d.b.h. was significantly reduced by annual summer burning and the majority of the change occurred during the first 20 years. Stem numbers of hardwoods over 12.5 cm d.b.h. were unaffected by annual summer burning.

Root Mortality

Patterns of hardwood rootstock mortality observed during the first few years on the Santee Fire Plots prompted investigators to expand the study. In 1951, biennial summer burning was added to provide a comparison with annual summer burning to study root system survival for four hardwood species (Langdon 1981). Individual trees were observed repeatedly to

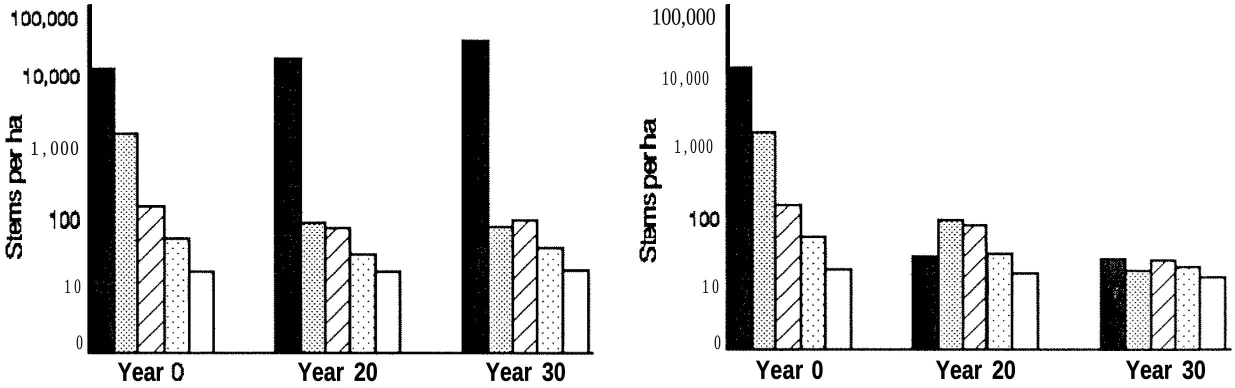


A Unburned Controls



B. Periodic Winter Burns

C. Periodic Summer Burns



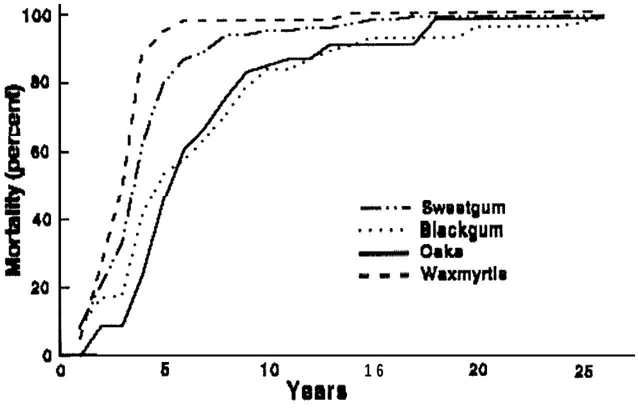
D. Annual Winter Burns

E. Annual Summer Burns

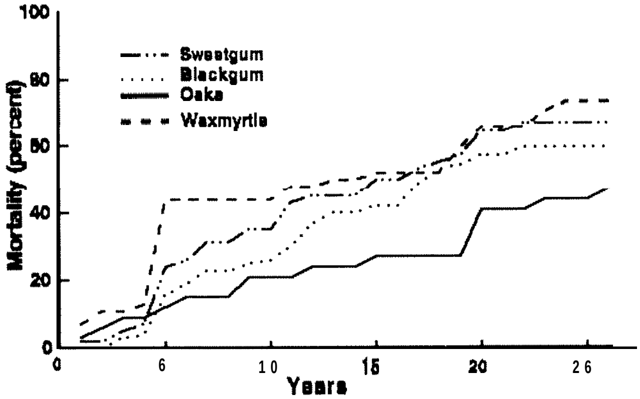
Figure 3.--Diameter distribution of all hardwoods at selected years for (a) unburned control plots, (b) period winter burn plots, (c) periodic summer burn plots, (d) annual winter burn plots, and (e) annual summer bum plots.

determine the number of bums required to kill their root systems. With annual summer burning (fig. 4A), mortality was rapid for sweetgum (Liouidambar stvraciflua L.) and waxmyrtle (Myrica cerifera L.), nearing 100 percent within 8 years. Oaks and blackgum (Nyssa svlvatica Marsh.) were more difficult to kill, requiring approximately 20 years to reach 100 percent mortality. Biennial summer burning (fig. 4B) was less effective in killing root systems of all species tested. After 26 years (13 bums), mortality among the oak species remained less than 50 percent. With biennial burning, root systems have an entire growing season to recover.

Apparently, that time is sufficient for carbohydrate reserves to accumulate enough to allow some resistance to fire.



A. **Annual** Summer Burn



B. Biennial Summer Burn

Figure 4.--Cumulative mortality of hardwood roots over 26 years of (a) annual summer burning and (b) biennial summer burning (Langdon 1981).

Species Composition

Survival of hardwoods over 12.5 cm d.b.h. was unaffected by burning treatments and, therefore, changes in species composition among larger trees were not observed. The major effect of burning treatments was to kill the aboveground portion of stems smaller than 12.5 cm d.b.h. With most burning treatments, however, root systems survived and sprouted. If burning was stopped or delayed, sprouts would eventually grow into the midstory producing a stand with species similar to unburned controls. Variations among species in plants' abilities to regenerate after tire created changes in the species composition of regeneration (fig. 5). In year 44, control plots were covered mostly by shrubs with some grasses and hardwoods (White and others 1991). Total coverage was increased by periodic winter and summer bums due to increased sprouting of hardwoods and shrubs. Total coverage after annual winter bums was greater than in control plots, but species composition had changed. Burning greatly reduced the shrub component, which was replaced by grasses and forbs. However, numerous hardwood sprouts remained. Annual summer burning was the only treatment which eliminated regeneration of hardwoods. In these plots, the shrubs and hardwoods that were dominant in 1946 were replaced entirely by grasses and forbs.

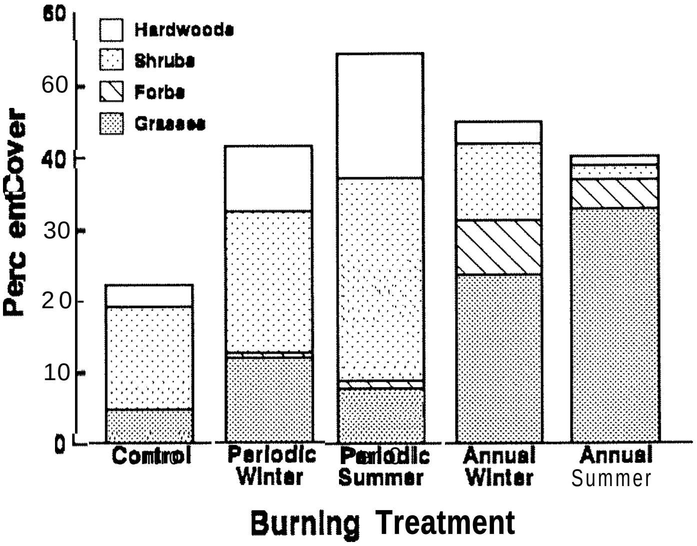


Figure S.--Percent crown coverage of all understory plants after 44 years of prescribed burning (White and others 1991).

DISCUSSION AND CONCLUSIONS

All tree species on the Santee Fire Plots were well adapted to frequent low-intensity burning. Thick bark and high crowns protected the pines from damage and no growth loss was detected. Hardwoods over 12.5 cm d.b.h. were protected by thick bark and most survived. During the first few years of the study, most hardwoods below 12.5 cm d.b.h. were either top killed or girdled, particularly by summer burning. However, root systems survived and produced multiple sprouts. Annual summer burning over a 20-year period was the only treatment that eliminated hardwood sprouts.

The response of tree species to these long-term prescribed burning treatments was considered minimal. Only one major trend was observed. Small hardwoods were replaced by large numbers of sprouts during the early years of the study. Later, those sprouts were replaced by grasses and forbs. The gradual change from small hardwoods to grasses and forbs was completed by only the most intensive treatment, annual summer burning. White and others (1991) provide evidence that sprout vigor is decreased by annual winter burning, suggesting that these sprouts may eventually be eliminated. However, a large regeneration pool of hardwoods still exists after 44 years of treatment. Periodic bums did little to reduce numbers or vigor of hardwood sprouts.

Hardwood sprout survival was affected by the season and frequency of burning (Langdon 1981). Hot summer fires conducted each year when carbohydrate reserves are low produced relatively rapid (20 years) mortality of hardwood rootstocks. Periodic winter, periodic summer, and annual winter burning allow at least one growing season for sprouts to store carbohydrate reserves in root systems and, therefore, resist mortality. Without annual summer fires, it is questionable whether hardwood sprouts can be eliminated by fire.

This study emphasizes that frequent fires over long periods are needed to create and maintain the open character of pine forests described by early explorers in the Southeast. Periodic burning over 40 years did little to eliminate hardwoods and supported a dense understory shrub layer. Annual winter bums maintain an open understory with vegetation generally less than 1 m tall. However, that understory includes numerous woody sprouts and a dense hardwood midstory would return if burning was delayed a few years. Of all treatments tested, only annual summer bums produced an open understory with no hardwood regeneration. However, presettlement forests did not support the midstory hardwoods present in study plots. In addition to frequent low-intensity fires, an occasional high-intensity tire or other disturbance would eliminate large hardwoods.

Although the Santee Fire Plot Study provides information on the frequency and number of fives required to create and maintain open pine forests, differences exist between its controlled experimental conditions and the environment of presettlement fires. Annual fires set by Indians were controlled only by weather and geographic barriers. Therefore, fire intensity was probably higher than in the Santee study. Also, large herds of deer (Odocoileus virginianus) browsed the open forests and grasslands. Hotter tires and intense browsing would cause higher mortality rates of hardwood sprouts. The Santee Fire Plots were dominated by loblolly pine, which was much less common than longleaf pine (Pinus palustris Mill.) prior to the 20th century. Since loblolly pine seedlings are susceptible to fue, pine regeneration is unlikely to escape the frequent fires on study plots. Seedlings of longleaf pine are resistant to fire during the grass stage. Prior to the 20th century, longleaf pine seedlings probably escaped to form the overstory during short gaps in fire frequency or in localized areas where fire intensity was low.

LITERATURE CITED

Bartram, William. 1791. Travel through North and South Carolina, Georgia, East and West Florida. New York: Dover Publications, Inc. 414 pp.

Buckner, Edward. 1989. Evolution of forest types in the Southeast. In: Waldrop, Thomas A., ed. Proceedings of pine-hardwood mixtures: a symposium on management and ecology of the type; 1989 April 18-19; Atlanta, GA. Gen. Tech. Rep. SE-58. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 27-33.

Chapman, Jefferson. 1985. Telico archeology: 12,000 years of Native American history. Knoxville: Tennessee Valley Authority.

Harper, Roland M. 1962. Historical notes on the relation of fires to forests. In: Proceedings, Tall Timbers fire ecology conference 1: 1 l-29.

Komarek, E.V., Sr. 1974. Effects of fire on temperate forests and related ecosystems: Southeastern United States. pp. 251-277. In: Kozlowski, T.T. ; Ahlgren, C.E., eds. Fire and Ecosystems. New York: Academic Press.

Langdon, 0. Gordon. 1981. Some effects of prescribed fire on understory vegetation in loblolly pine stands. pp. 143-153. In: Wood, Gene W., ed. Prescribed fire and wildlife in southern forests: Proceedings of a symposium. Georgetown, SC: The Belle W. Baruch Institute of Clemson University.

McKee, William H., Jr. 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites. Res. Pap. SE-234. Asheville, NC: U. S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 pp.

Pyne, Stephen J. 1982. Fire in America. Princeton, NJ: Princeton University Press. 654 pp.

Van Lear, David H.; Waldrop, Thomas A. 1989. History, use, and effects of fue in the Appalachians. Gen. Tech. Rep. SE-54. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 20 pp.

Waldrop, Thomas A.; Van Lear, David H.; Lloyd, F. Thomas; Harms, William R. 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. Gen. Tech. Rep. SE-45. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 pp.

White, David L.; Waldrop, Thomas A.; Jones, Steven M. 1991. Forty years of prescribed burning on the Santee Fire Plots: effects on understory vegetation. [These proceedings.].

FORTY YEARS OF PRESCRIBED BURNING ON THE SANTEE FIRE PLOTS: EFFECTS ON UNDERSTORY VEGETATION

David L. White, Thomas A. Waldrop, and Steven M. Jones[1]

Abstract--The effects of 43 years of repeated prescribed burning on crown cover, species composition, species richness, and diversity in the lower understory strata of the Santee Fire Plots were examined. Five study treatments, installed in 1946, include an unburned control, periodic winter and summer burns, and annual winter and summer bums. Understory cover has not changed in the past 20 years except in the annual winter bum plots where cover of trees $\leq$ 1.5 m in height declined and grass cover increased. Detrended correspondence analysis indentified four distinct undcrstory plant communitites corresponding to season and frequency of bum. Distribution of understory species across a tire disturbance gradient is discussed in terms of varying plant adaptations to fire. Species richness, when separated into herbaceous and woody species groups, and Shannon's diversity index varied significantly across treatments.

INTRODUCTION

The Santee Fire Plot (SFP) study in the Francis Marion National Forest provides a unique opportunity to examine the response of understory vegetation to long-term use of several combinations of season and frequency of burning. Several studies have examined the effects of single or repeated prescribed fires on understory vegetation (Abrahamson 1984; Conde and others 1983; Cushwa and others 1966, 1969; DeSelm and others 1974; Fox and Fox 1986; Gilliam and Christensen 1986; Grano 1970; Grelen 1975; Hodgkins 1958; Lemon 1949, 1967), but none of these studies was conducted over a period as long as the period of the SFP study. Prescribed burning in loblolly pine stands on the SFP was initiated in 1946 and continued without interruption until 1989, when the overstory pines were destroyed by Hurricane Hugo.

Previous SFP studies focused on the effect of prescribed fire on understory vegetation (Langdon 1971, 1981; Lewis and Harshbarger 1976; Lotti 1955, 1956; Lotti and others 1960), benefits to wildlife (Lewis and Harshbarger 1976) and soil chemical changes (Wells 1971; McKee 1982). Waldrop and others (1987) summarized the effects of the various treatments on the growth of overstory pines after 40 years. Lewis and Harshbarger (1976) reported the effects of prescribed fire on shrub and herbaceous vegetation in the plots after 20 years. On the basis of information developed by Lewis and Harshbarger (1976), Langdon (1981), Waldrop and others (1987), and Waldrop and Lloyd (1991), the following generalizations can be made regarding the effects of long-term use of prescribed fire on understory vegetation in the SFP: (1) the unburned control plots were dominated by several size classes of shrub and hardwood species and contained only small numbers of grasses and virtually no forbs; (2) plots that were burned periodically contained two distinct size classes of understory hardwoods (> 15 cm and <5 cm d.b.h.) and herbaceous species, most of which were grasses; (3) annual winter and biennial summer bums resulted in large numbers of woody stems < 1 m tall and many grasses and forbs; and (4) annual summer burning virtually eliminated understory woody vegetation, and produced an understory dominated by grasses and forbs.

This paper describes differences among plant communities in the Santee Fire Plots after 43 years of prescribed burning. More specifically, we compare the understory plant communities in the context of plant species composition, species richness, and diversity. We also sought to determine whether there have been any changes in understory species composition since year 20 (1967).

METHODS

Site Description

The SFP study was originally designed with three replications on the Santee Experimental Forest in Berkeley County, SC, and two replications on the Westvaco Woodlands in Georgetown, SC. The Westvaco plots were regenerated in 1984 so the present study is confined to the three Santee replications. Study plots are located on the upper terrace of the coastal flatwoods region of the Flatwoods Coastal Plain Province, at an elevation of 9.0 m above sea level (Meyers and others 1986). They contain a variety of soil series, which are generally described as poorly drained Ultisols of medium to heavy texture.

Study Design

The SFP study was initiated in 1946 in 42-year-old naturally regenerated loblolly pine with a well-developed understory of hardwoods (post oak, blackjack oak, southern red oak,

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[1] Ecologist, Southeastern Forest Experiment Station, Clemson, SC; Research Forester, Southeastern Forest Experiment Station, Clemson, SC; and Assistant Professor, Department of Forest Resources, Clemson University, Clemson, SC.

dogwood, American holly, miscellaneous hickories, sweetgum, and blackgum) and shrubs (bayberry, pepperbush, and gallberry). Initially, five treatments were installed: (1) no-burn control, (2) periodic winter burn, (3) periodic summer burn, (4) annual winter burn and (5) annual summer burn. An additional treatment, biennial summer burn, was installed in 1951. Because of recent insect-related mortality in some plots of the biennial summer burn, it was not included in this study.

Winter burning was conducted as soon as possible after December 1 of each year when the temperature was 16 °C (60 “F) or higher. Summer burning was conducted after June 1 when the temperature was 32 °C (90 “F) or higher. Burning was conducted only when relative humidity was less than 50 percent, wind speed was 1 to 7 mi/h and fuel moisture was < 10 percent. Backing fires were used initially; later, head fires (strip and flanking) were used in the annual burn plots. Periodic burns were conducted when 25 percent of the understory stems reached 2.5 cm dbh. The average burn interval for periodic burns was 5 years. More detailed site descriptions can be found in Lotti (1960) and Waldrop and others (1987).

For sampling understory vegetation, a 25- by 25-m sample plot was established within each of the 32- by 32-m treatment plots. Two 25-m line transects were randomly located in each sample plot to determine percent crown cover for the following species groups: grasses, legumes, other herbs, woody vines, shrubs, and trees. The vegetation sampled in this study was the lower understory, which was defined as plants $\leq$ 1.5 m tall or plants having a majority of their crown at or below a height of 1.5 m. Cover was determined along a 25-m line transect by measuring the portion of a crown intersected by the 25-m line. Where two or more crowns overlapped, the overlapping sections of the lower crown(s) were not included.

Two OS- by 2-m subplots were randomly located along each 25-m transect (four subplots per plot) to measure stem density or abundance. All plants were identified to species or genus and the number of plants per species or genus was recorded. In measuring abundance of plants that sprout from roots or rhizomes, no attempt was made to determine whether a clump of stems was associated with just one individual or many. Species not encountered in the four subplots were tallied in two 1- by 25-m subplots, each of which was located adjacent to a 25-m transect. The larger subplots (1- by 25-m) were used primarily to sample relatively uncommon species. Species not encountered in subplots of either size but occurring in a 25- by 25-m sample plot were listed as present but not tallied. The species and density data were used to determine species diversity and richness.

Data Analysis

Analysis of variance was used to test for significant treatment and block effects on species richness and diversity. Mean separation was by Fisher’s unprotected LSD test (Statistical Analysis System (SAS) 1987). Species richness is the total number of species in a given area. The Shannon-Weaver index was used as a measure of species diversity and was calculated as:

$$H' = - \sum (p_i \ln p_i)$$

where p_i = proportion of individuals of species i to the total number of individuals of all species (base e logarithms are used here).

Detrended Correspondence Analysis (Gauche 1982; Hill 1979; Hill and Gauche 1980) was used to interpret the variation in vegetation composition among treatments. The technique groups plots or communities based on similarity of species composition and relative abundance. The degree of difference between plots is indicated by standard deviation (S.D.) units. A separation of communities by four S.D. units generally indicates that the two communities have no species in common, while one S.D. unit indicates approximately a 50-percent difference in species composition (Hill 1979; Hill and Gauche 1980).

RESULTS AND DISCUSSION

Changes in Understory Cover Between 1967 and 1989

Lewis and Harshbarger (1976) reported on the status of herbaceous and shrub vegetation after 20 years of prescribed burning on the SFP. We chose to compare percent cover by species group at year 43 with their data to determine whether vegetation changes had occurred since their 1967 study. Only the no-burn, periodic summer, and annual winter treatments were compared, because the interval between burning and sampling was not always the same in both studies.

In the no-burn treatments (fig. 1a), both shrub and tree cover declined over the 23-year period. Some trees and shrubs formerly in the understory grew into the midstory. Also, midstory hardwoods that were present in 1967 continued to grow, further reducing the amount of light reaching the forest floor.

In the periodic summer burn plots (fig. 1b), there were few changes between years 20 and 43. At both times, the understory was dominated by shrubs and trees. A slight increase in total cover (all species) may have been caused by increased sprouting of trees and shrubs (Langdon 1981).

Greater changes were observed in the annual winter burn plots (fig. 1c). From year 20 to year 43, tree cover declined and grass cover increased. Little change was observed for the other species groups. Although tree cover declined, the number of hardwood stems (44,700 stems ha^{-1}) was similar to

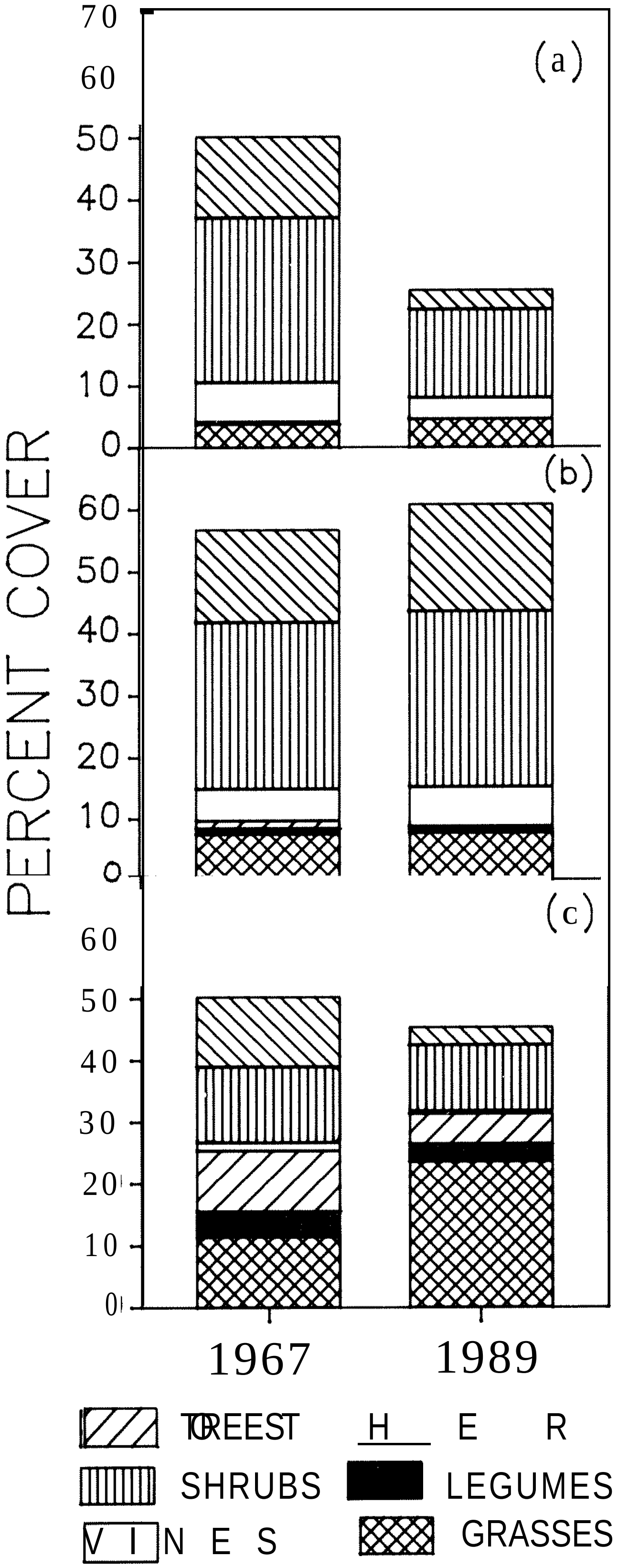


Figure 1--Understory cover by treatment, 1967 and 1989. Treatments: (a) no-bum control, (b) Periodic summer bum, (c) annual winter bum. 1967 data are from Lewis and Harshbarger (1976).

the number reported by Langdon (1981) at year 30 (47,000 stems ha-‘). This pattern suggests that hardwood sprouts are smaller than before and that frequent winter burning may reduce sprout vigor over time. The increased importance of grasses in these plots may be a response to the decline in tree cover or it may have contributed to that decline. While the majority of vegetation changes in annual winter bum plots occurred early in the SFP study, our results indicate that the frequent but relatively mild disturbance associated with this treatment continues to cause changes in vegetation over extended periods of time.

Plant Community Differences

Community Analysis

Detrended correspondence analysis identified four distinct vegetative communities that were associated with season and frequency of burning (fig. 2). Annual summer bums, annual winter bums, periodic bums, and no-burn controls produced distinctive communities. Differences between treatments were less distinct for the periodically burned plots and the control plots, where woody vegetation predominated. The understory communities produced by periodic winter and summer burning were very similar. The distribution of plots along the X axis leads us to interpret this axis as a fire-mediated disturbance gradient. The relatively large magnitude of difference across treatments (3.5 S.D. units) indicates that beta diversity, or between-community diversity, is high and is affected by season and frequency of burning. Separations along the Y axis are less easily understood, but are interpreted as representing a natural variability gradient. Variability in species composition within a community type decreases as the level of burning increases.

The distribution of species along a fire disturbance gradient reflects the species fire tolerance and competitive vigor. Table 1 is a species synthesis table, as described by Mueller-Dombois and Ellenburg (1974), showing the relative abundance of each species in each treatment plot. This list has been edited to contain only differential species, or those species that demonstrate clear associations for a given treatment or treatments. The 32 species in this table were placed in 5 groups based on their affinity for a given treatment or treatments. Detrended correspondence analysis indicated that the periodic winter and summer bum plots were vegetatively similar and since our sampling of the vegetation took place during the growing season following the burning of the periodic winter plots, only the periodic summer bum treatment is shown in table 1.

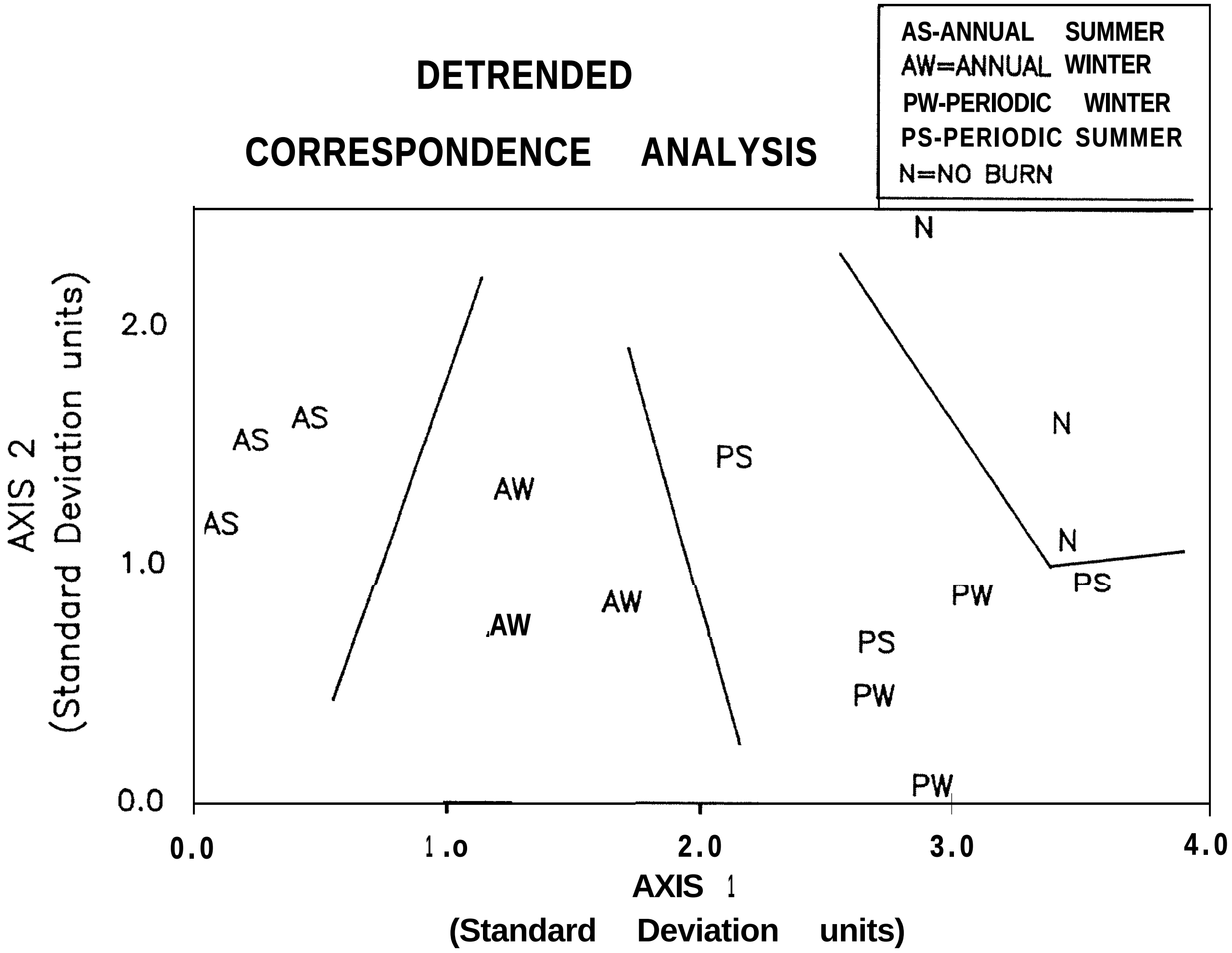


Figure 'L--Results of detrended correspondence analysis of all understory plants in all treatment plots. Treatments indicated by the following codes: AS=annual summer burn, AW=annual winter burn, PS=periodic summer burn, PW=periodic winter burn, N=no-burn control. Lines are drawn to show separation between dissimilar groups of plots. See text for explanation of axes.

With few exceptions, groups 1, 2, and 3 are herbaceous plants that have been described as “fire followers” (Lemon 1949, 1967). Many of these plants are also associated with early successional plant communities following non-fire disturbance. Other species, such as the legumes, are known to benefit directly from the effects of fire (Cushwa and others 1969; Martin and Cushwa 1966; Martin and others 1975). The species in group 1 are found almost entirely in the annual summer burn plots. These are generally opportunistic species that lack the competitive vigor to become established in other burned plots, where more vigorous grasses and woody plants predominate. Species in group 2 are most common in the annual winter burn plots, but some of the legume species are also common in the periodic summer or annual summer burn plots. Generally, group 2 species are less tolerant of annual summer burning and do not compete well with the hardier woody vegetation characteristic of the periodically burned plots. The relatively low abundance of legumes in plots that have been burned every summer may result from the lack of full growing seasons in which to partition photosynthate into perennial rootstocks. Plants in group 3 were common in all burned plots but absent in the no-burn control plots, indicating a dependence on frequent disturbance. Four composite species, two grasses (Panicum species and Andropogon virginicus), and three woody plants (Hypericum species, Rubus species, and Rhus coppalina) comprised this group. Most species in group 3 disperse their seed broadly and compete vigorously for resources and this enables them to become established quickly after fire.

Groups 4 and 5 (table 1) contain all woody plants with the exception of one grass (Uniola laxa) and one perennial (Mitchella repens). Most of the species in this group reproduce vegetatively - but with varying degrees of vigor, as is indicated by the absence of some species from either the annually or periodically burned plots. Group 4 species are relatively abundant in all but the annual summer plots, maintaining their abundance primarily through vegetative reproduction. About half of these species occurred rarely or infrequently in the annual summer plots; however, their occurence in the annual summer plots is probably due to germination from seed that was transported to the plot by

Table l--Species synthesis table showing relative abundance[a] of each species across treatments (three plots per treatment)

Species[b]	Group	Treatment											
		Unburned control			Periodic summer			Annua 1 winter			Annua l summer		
Paspatum species	1										9	R	
Polygala tutea											9	R	3
Hypoxis micrantha										R	1	9	7
Rhexia species									R	+	9	R	R
Coreopsis major	2							+	9	1	+		
Cassia nictitans								5		5	9		
Stylosanthes biftora								4	1	8	4	9	
Gatactia macreei								9		1			
Desmodium species							2	+		9	+	R	
Tephrosia hispidula					R		R		R	9	1		
Centrosema virginianum					R		R	9		9			
Lespedeza species						+	+	+	+	9			
Lobelia nuttattii	3				+				9	R	+	6	4
Aster species					1			1	9	2	1	+	+
Solidago species					+		R	9	+	4 2		1	
Eupatorium species					+	+	+	9	+	7	2	3	+
Elaphantopus species					3		1	6	9		1	1	+
Panicum species						+	+			3	6	2	3
Andropogon virginicus					+		8		6	9	5	9	3
Hypericum species					+				8		+	2	1
Rubus species				1	+	5	5	+	1	5	+	R	
Rhus coppatina			+		8		R	2	R	1	1	R	R
Pinus taeda	4		+	1		+	+	R	+	+	7	9	6
Gavlussacia species		+	+	+	+	3	1	+	1	4	R		+
Vaccinium species			1	+	1	1	6	+	3	9	+		+
Uniota laxa		+	+	+	3	+	+	9	3	5			+
Myrica cerifera		1	+	+	9	2	1	1	R		+		
Liquidambar styraciftua		+	+	+	5	1	+	4	1	9			
Smitax species		9	1	1	2	+	R	1	+				
Vitis species		+	1	+	1	1	+	+		+	R		
Puercus species		+	+	+	643			+		9			+
Gelsemium sempervi rens		+	+	+	7	9	1				+		+
Cornus ftorida	5		3	2	7	a	9				R		
Mitchella repens			4	+	3	9	2						
Persea borbonia		9	+	+			R						
Lyonia tucida			+	9									

[a] Relative abundance indicated as deciles:"+"=1-10 percent of the maximum abundance value for a given species,"1"=11-20 percent; etc. "R" indicates that a species was rare in the vegetation plot (i.e., was present only).

[b] Nomenclature follows Radford and others (1968).

wind or animals. Species in group 5 were relatively intolerant of frequent burning. Comus florida (dogwood) and Mitchella repens (partridge berry) were absent from annual bum plots, while Persea borbonia (redbay) and Lvonia lucida (fetterbush) were absent from both periodic and annual plots. Fetterbush has been previously mentioned as one of several shrubs on the SFP that sprout prolifically after fire (Langdon 1981). Data from other studies (Cypert 1973; Abrahamson 1984) also suggest that this species is tolerant of tire. The absence of this species in year 43 may indicate that the species is intolerant of long-term frequent burning, at least on sites similar to those in the SFP study area.

Species Abundance

Understory species abundance (number of plants 0.1 ha^{-1}) for woody plants is shown in figure 3. Abundance of hardwoods, shrubs, and vines was dramatically reduced by annual summer burning. In the periodic bum plots and the annual winter burn plots, understory hardwood abundance was slightly greater than in unburned controls. Only the annual summer burn plots had lower shrub abundance than the control plots. The large values for shrubs are attributable primarily to the rhizomatous shrubs, Gavlusaccia spp. (Huckleberry) and Vaccinium spp. (blueberry), which sprout prolifically after fire. The greater abundance of all three woody plant groups in periodic winter bum plots was due to the fact that these plots had been burned the winter prior to sampling, which illustrates the immediate response to tire by this predominantly woody understory.

Abundance of grasses, legumes, and other forbs is shown in figure 4. Herbaceous plant abundance increased with increasing fire frequency, and abundance of all three groups was greatest in the annual winter bum plots. The annual winter treatment yielded a substantially higher number of legume stems than all the other treatments. Legume abundance in the annual winter burn plots was higher than values reported from other studies in the South (Buckner and Landers 1979; Cushwa and Jones 1969; Cushwa and others 1970, 1971; Hendricks 1989; Speake and others 1975). Legume abundance in the periodic and the annual summer bum plots was in the range found in the studies cited above, most of which were conducted after single or periodic bums.

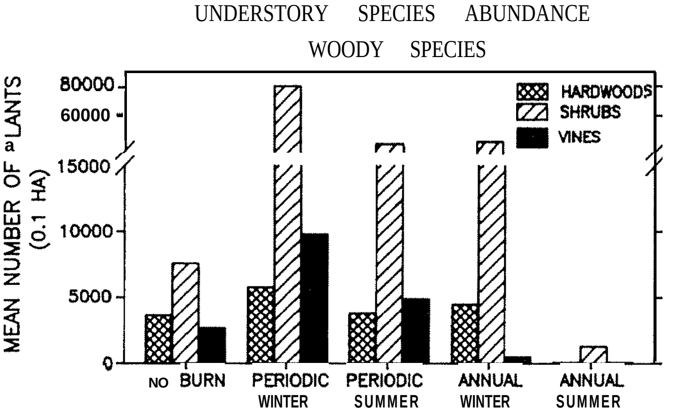


Figure 3--Mean number of stems 0.1 ha^{-1} for understory woody plant groups across all treatments. Note axis scale change.

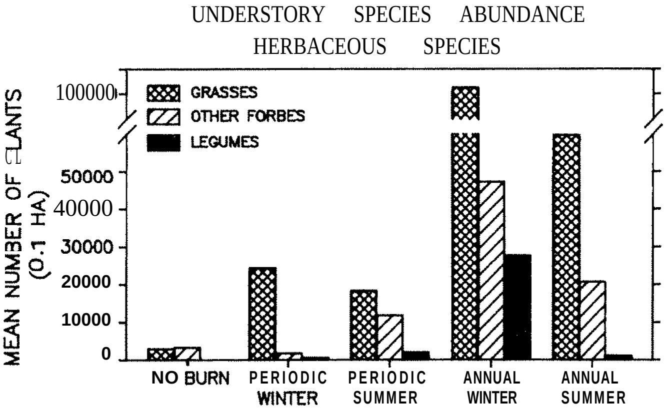
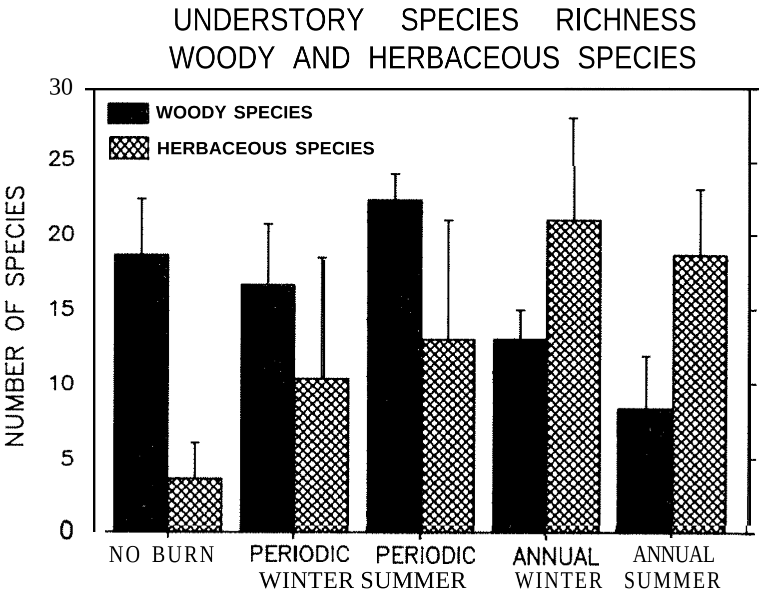


Figure 4--Mean number of stems per 0.1 ha^{-1} for understory herbaceous plant groups across all treatments. Note axis scale change.

Species Richness and Diversity

Understory species richness was not significantly affected by treatment. When species richness was separated into woody and herbaceous categories, treatment effects were significant (fig. 5). Woody species richness was significantly higher for the no-burn and periodic burn treatments than for either of the annual burn treatments. In contrast, herbaceous species richness increased with increasing burning frequency and was significantly higher for the annual winter burn treatment than for the periodic winter and the no-burn treatments.

Shannon diversity, calculated using all understory species, was significantly affected by treatment (table 2). Understory species diversity was significantly higher for the annual winter burn treatment than for the annual summer and periodic winter burn treatment but not higher than for the periodic summer and no-burn treatments. It is significant that differences in richness and diversity among treatments were not more distinct. As burning frequency increased, herbaceous species importance increased and there was an associated decline of woody species. This species replacement resulted in relatively small differences in diversity and richness between most treatments. Annual winter burning resulted in higher richness and diversity values because woody biomass was reduced to a level sufficient to allow establishment of herbaceous plants, many of which responded positively to the conditions created by fire.



(Error Bars represent 2 standard errors)

Figure 5--Understory species richness. Error bars represent two standard errors

Table 2--Shannon diversity indices for under-story plant communities from each treatment

Treatment	Diversity Index[a]
Annual winter burn	2.40 a
Periodic summer burn	2.28 ab
No burn control	2.07 abc
Annual summer burn	1.88 bc
Periodic winter burn	1.70 c

[a] Means with different Letters are significantly different at the 0.05 level.

CONCLUSIONS

While all plants in this southern pine ecosystem arc well adapted to fire, it is the fire regime--incorporating intensity, frequency, and season--rather than fire itself, to which plant species are adapted (Gill 1975). Observed differences in species composition of understory plant communities along a fire disturbance gradient were explained by reference to differences in tire tolerance and competitive vigor. Differences in frequency and season of fire produced four distinct plant communities which, when viewed as communities distributed over the landscape, resulted in relatively high beta diversity.

Land managers are faced with increasingly complex problems as the concept of multiple resource management expands to include compositional, structural, and functional biodiversity. Our increased understanding of the “natural” or historical role of fire in shaping forested ecosystems should enable us to better incorporate the use of fire in the management of whole landscapes to accomplish multiple resource objectives.

ACKNOWLEDGMENTS

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LITERATURE CITED

Abrahamson, Warren G. 1984. Post fire recovery of Florida Lake Wales Ridge vegetation. American Journal of Botany 71(1):9-21.

Buckner, James L.; Landers, J. Larry. 1979. Fire and disking effects on herbaceous food plants and seed supplies. Journal of Wildlife Management 43(3):807-811.

Conde, Louis F.; Swindel, Benee F.; Smith, Joel E. 1983. Plant species cover, frequency and biomass: early responses to clearcutting, burning, windrowing, discing and bedding in *Pinus elliottii* flatwoods. Forest Ecology and Management 6:3 19-33 1.

Cushwa, Charles T.; Brender, Ernst V.; Cooper, Robert W. 1966. The response of herbaceous vegetation to prescribed burning. Res. Note SE-53. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 2 pp.

Cushwa, Charles T.; Czuhai, Eugene; Cooper, Robert W.; Julian, William H. 1969. Burning clearcut openings in loblolly pine to improve wildlife habitat. Res. Pap. 61. Georgia Forestry Research Council. 5 pp.

Cushwa, Charles T.; Jones, M.B.; 1969. Wildlife food plants on chopped areas in the Piedmont of South Carolina. Res. Note SE-119. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 4 pp.

Cushwa, Charles T.; Hopkins, Melvin; McGinnes, Burd S. 1970. Response of legumes to prescibed bums in loblolly pine stands of the South Carolina Piedmont. Res. Note SE-140. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 6 pp.

Cushwa, Charles T.; Martin, Robert E.; Hopkins, Melvin. 1971. Management of bobwhite quail habitat in pine forests of the Atlantic Piedmont. Res. Pap. 65. Georgia Forestry Research Council. 5 pp.

Cypert, Eugene. 1973. Plant succession on burned areas of the Okefenokee Swamp following the tires of 1954 and 1955. In: Proceedings, Tall Timbers fire ecology conference 12; 1972 June 8-9; Lubbock, TX. Tallahassee, FL :Tall Timbers Research Station: 199-217.

DeSelm, H.R.; Clebsh, E.E.C.; Nichols, G.M.; Thor, E. 1974. Response of herbs, shrubs and tree sprouts in prescibed burned hardwoods in Tennessee. In: Proceedings, Tall Timbers fire ecology conference 13; Tallahassee, FL: Tall Timbers Research Station: 331-344.

Fox, Marilyn D.; Fox, Barry J. 1986. The effect of fire frequency on the structure and floristic composition of a woodland understorey. Australian Journal of Ecology 11:77-85.

Gauch, Hugh G., Jr.; 1982. Multivariate analysis in community ecology. Beck, E.; Birks, H.J.B.; Connor, E.F., eds. New York: Cambridge University Press. 298 pp.

Gill, A.M. 1975. Fire and the Australian flora: a review. Australian Forestry 38:4-25.

Gilliam, Frank S.; Christensen, Norman L. 1986. Herb layer response to burning in pine-flatwoods of the lower Coastal Plain of South Carolina. Bulletin of the Torrey Botanical Club 113(1):42-45.

Grano, Charles X. 1970. Eradicating understory hardwoods by repeated prescribed burning. Res. Pap. SO-56. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 11 pp.

Grelen, Harold E. 1975. Vegetative response to 12 years of seasonal burning on a Louisiana longleaf pine site. Res. Note SO-192. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 4 pp.

Hendricks, J.J. 1989. Nitrogen fixation and litter quality of understory legumes in a burned pine forest of the Georgia Piedmont. Athens: University of Georgia. 90 pp. Thesis.

Hill, M.O. 1979. DECORANA--A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ithaca, NY: Cornell University. 52 pp.

Hill, M.O.; Gauch, H.G., Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47-58.

Hodgkins, Earl J. 1958. Effects of tire on undergrowth vegetation in upland southern pine forests. Ecology 39(1):36-46.

Langdon, 0. Gordon. 1971. Effects of prescribed burning on timber species in the southeastern Coastal Plain. In: Proceedings, Prescribed burning symposium; 1971 April 14-16; Charleston, SC. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 34-44.

Langdon, 0. Gordon. 1981. Some effects of prescribed tire on understory vegetation in loblolly pine stands. In: Wood, Gene W., ed. Prescribed fire and wildlife in southern forests: Proceedings of a symposium; 1981 April 6-8; Myrtle Beach, SC. Georgetown, SC: Clemson University, Belle W. Baruch Institute: 143-153.

Lemon, Paul C. 1949. Successional responses of herbs in longleaf-slash pine forest after tire. Ecology 30:135-145.

Lemon, Paul C. 1967. Effects of fire on herbs of the southeastern United States and central Africa. In: Proceedings, Tall Timbers fire ecology conference 6; Tallahassee, FL: Tall Timbers Research Station: 113-127.

Lewis, Clifford E.; Harshbarger, Thomas J. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. Journal of Range Management 29(1):13-18.

Lotti, Thomas. 1955. Summer tires kill understory hardwoods. Res. Paper SE-71. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 2 pp.

Lotti, Thomas. 1956. Eliminating understory hardwoods with summer prescribed tires in Coastal Plain loblolly pine stands. Journal of Forestry 54:191-192.

Lotti, Thomas.; Klawittcr, Ralph A.; LeGrande, W.P. 1960. Prescribed burning for understory control in loblolly pine stands of the Coastal Plain. Res. Paper SE-116. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 19 pp.

Martin, Robert E.; Cushwa, Charles T. 1966. Effects of heat and moisture on leguminous seed. In: Proceedings, Tall Timbers fire ecology conference 5; Tallahassee, FL: Tall Timbers Research Station: 159-175.

Martin, Robert E.; Miller, Robert L.; Cushwa, Charles T. 1975. Germination response of legume seeds subjected to moist and dry heat. Ecology 56:1441-1445.

McKee, William H., Jr. 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites. Res. Paper SE-234. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 pp.

Mueller-Dombois, Dieter; Ellenberg, Heinz. 1974. Aims and Methods of Vegetation Ecology. New York: John Wiley and Sons. 547 pp.

Myers, Richard K.; Zahner, Robert; Jones, Steven M. 1986. Forest habitat regions of South Carolina. Res. Ser. 42. Clemson, SC: Clemson University Department of Forestry. 31 pp. Map supplement, scale 1:1,000,000.

Radford, Albert E.; Ahles, Harry E.; Bell, C. Ritchie. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill, NC: The University of North Carolina Press. 1183 pp.

Statistical Analysis System (SAS) 1987. SAS/STAT guide for personal computers. SAS Institute Inc., Cary, NC. 1028 pp.

Speake, D.W.; Hill, E.P.; Carter, V.E. 1975. Aspects of land management with regard to production of wood and wildlife in the southeastern United States. In: Forest soils and forest land management, Proceedings of the fourth North American forest soils conference; 1973 August; Quebec, Canada: Lava1 University: 333-349.

Waldrop, Thomas A.; Van Lear, David H.; Lioyd, F. Thomas; Harms, William R. 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. Gen. Tech. Rep. SE-45. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 pp.

Waldrop, Thomas A.; Lloyd, F. Thomas. 1991. Forty years of prescribed burning on the Santee fire plots: effects on overstory and midstory vegetation. [These Proceedings].

Wells, Carol G. 1971. Effects of prescribed burning on soil chemical properties and nutrient availability. pp. 86-97. In: Proceedings, Prescribed Burning Symposium; 1971 April 14-16; Charleston, SC. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 160 pp.

FOREST DEVELOPMENT FOLLOWING DISTURBANCES BY FIRE AND BY TIMBER CUTTING FOR CHARCOAL PRODUCTION

Wayne K. Clatterbuck'

Abstract-Stand reconstruction techniques and historical documentation were used to analyze present species composition, stand structure, and successional trends on forest lands on the Western Highland Rim of Tennessee. These lands were affected by tire and cutting practices during the late 1800's, when local wood was burned to make charcoal fuel for use at a nearby iron forge. The present two-aged stand structure indicates that there was a discriminatory cutting pattern in which white oak (Ouercus alba L.) and hickories (Carya spp.) were selectively harvested for charcoal. Trees of other species, whatever their size and location, were often left to form the residual stand. Iron forgers apparently favored the hotter burning charcoal of white oak and hickories for producing wrought iron. These results are in contrast to those from other areas, where all tree species were cut and burned to provide charcoal fuel wood for the production of crude pig iron in iron furnaces.

INTRODUCTION

The iron industry flourished on the Western Highland Rim in middle Tennessee during the 19th century. Historical documentation of this industry has focused on the iron-making process, community and social development, and biographies of leading men associated with the industry. Little information is available about the production of charcoal, which was the fuel used to smelt the iron ore and forge wrought iron. Vast timber reserves were necessary to produce sufficient quantities of charcoal as one ton of charcoal was required for each ton of iron produced (Baker 1985). Luther (1977) states that

> "an early chronicler of the industry estimated that to keep a furnace with a 12-ton-per-day iron production going for a year required the cutting of 500 acres of forest, and that to keep one going permanently . . . would require about 16,000 acres (25 square miles) per furnace, allowing 30 years for timber to grow back before the next cutting. In the year 1873 there were 11 furnaces in blast on the Rim, producing iron at the rate of about 50,000 tons per year. In order for all of these furnaces to operate on a 'permanent' basis, then, something on the order of 375 square miles of timber would have been necessary to support them."

Thus, large units of forest land were affected by the charcoal activity. This paper reports on the present species composition, stand structure, and successional trends on forest lands that were affected by (1) cutting during the 1800's for the production of charcoal, (2) fire and grazing during and after the charcoal activities until 1938, and (3) stable State ownership, management, and protection from 1938 to present.

STUDY AREA

The study was conducted on the 19,887-acre Cheatham Wildlife Management Area (CWMA), which is located 25 miles west of Nashville, TN (36" 12'N, 87° 5'W), on the Western Highland Rim Physiographic Region (Fenneman 1938).

Braun (1950) describes the Western Highland Rim as part of the Western Mesophytic Forest, a transition area between the Mixed Mesophytic Forest Region of the mountains to the east and the Oak-Hickory Forest Region to the west. CWMA is located on the strongly dissected, mature plateau of the Western Highland Rim and consists of narrow to broad ridges, steep dissected side slopes, and V-shaped upland stream valleys (Smalley 1980). Elevations range from 480 to 820 feet. The climate is classified as humid mesothermal (Thomthwaite 1948). Mean annual precipitation is 50 inches and is fairly well distributed throughout the year with slight deficits in late summer and early fall and surpluses during the winter months. Average daily temperature is 15" C with mean temperatures of 2" C in January and 26" C in July (Smalley 1980).

The CWMA was logged and burned in the 19th century during the production of charcoal for a nearby iron forge. Trees were harvested on the ridges and ridge margins where timber was abundant and where the charcoal could easily be transported by wagon downhill to the forge. Most of the land in the broader valleys had been cleared previously for agriculture. Many of the "charcoal hearths" or "fire circles" where the charcoal was produced are still evident on the study area. For more details on charcoal making and iron production processes, see Smith and others (1988) and Ash (1986).

During and after the decline of the iron industry in the 1880's, these cutover areas were periodically, if not annually, burned to promote production of forage for livestock and to retard the advance of woody undergrowth. Fires were also

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'Staff Forester, Forest Resource Planning, Tennessee Division of Forestry, Nashville, TN.

used locally to control snakes and ticks and to expose mast for grazing livestock. Open-range laws were also in effect at that time. Scattered logging for firewood, local building materials, railroad ties, and to clear forest land for agriculture continued, primarily near homesites. The loss of American chestnut (Castanea dentata (Marsh.) Borkh.) to chestnut blight (Endothia parasitica (Murr.) P.J. & H.W. And.) also shaped the composition and structure of the present forest.

In 1938, the State of Tennessee acquired the land for a wildlife management area. The area supports a heavy deer (Odocoileus virginianus L.) population which is intensively managed through controlled hunts. CWMA has been protected from fire and livestock grazing since 1940. Apart from hunting and occasional scattered timber harvesting (mainly in the last 10 years), there has been little disturbance by man. Currently, dieback and mortality associated with "oak decline" are present in varying degrees.

Vegetation on two adjacent narrow ridges (A and B) was studied. Ridge A and Ridge B contained 6 and 5 charcoal hearths, respectively. The hearths were located about 200 yards apart along the ridges. The ridges were two miles from the Narrows of the Harpeth River, a historical landmark and the site of the iron forge.

Soils on these ridges and ridge margins are either of the Bodine or Mountview series (North 1981). Both soils are Typic Paleudults and are deep, well-drained, and fine textured. Mountview soils developed in 2 to 3 feet of loess over limestone residuum, while Bodine soils developed in limestone residuum without the loess. Chert fragments are frequent on the surface and throughout the soil mass. Site index (base age 50) for upland oaks is 65 to 70 feet (Schnur 1937). The primary tree species on these ridges are white oak, black oak (Q. velutina Lam.), hickories, flowering dogwood (Comus florida L.), sourwood (Oxvdcndrum arboreum L. DC.), and sassafras (Sassafras albidum (Nutt.) Nees.). Other associated species are northern red oak (Q. rubra L.), yellow-poplar (Liriodendron tulipifera L.), white ash (Fraxinus americana L.), scarlet oak (Q. coccinea Mucnchh.), and blackgum (Nyssa svlvatica Marsh.).

PROCEDURES

In 1986, a total of 12 one-fifth-acre circular plots were used to sample existing vegetation. Six plots were established on each ridge. Three plots on each ridge had their outer boundary adjacent to a charcoal hearth, while the other three were located in relatively undisturbed areas not affected by charcoal cutting. On each plot, the following data were recorded for each tree with diameters at breast height (4.5 feet) of 5.5 inches and greater: species, azimuth and distance from plot center, l-inch diameter class, and crown class (dominant, codominant, intermediate, or suppressed). Trees with diameters from 1.6 to 5.4 inches were tallied by l-inch diameter class and species. Total heights were measured, and increment cores at DBH were taken from at least three overstory trees on each plot for site productivity assessments, diameter growth profiles, and to determine total age. Point basal area was estimated from plot center with a lo-factor prism. Data from each of the two ridges were pooled by disturbance class (cut for charcoal or not) because the ridges were similar in disturbance history and site quality.

Stem analysis to reconstruct height and diameter growth patterns, to reference fire scars, and to determine age structure was conducted on 12 trees from two plots, one plot from each ridge. Each tree was sectioned at 0.5 feet above the ground and at 4-foot intervals along the bole to the tallest centrally located growing tip. The number of annual rings in each section was subtracted from the tree's total age to determine how old the tree was when its terminal leader was at or near the height of each section. Heights were plotted over corresponding ages to illustrate the height growth pattern of each tree. Diameter growth at 4.5 feet was determined by measuring the annual increment along four perpendicular radii. Height and diameter data were analyzed using accepted stand reconstruction and graphical procedures (Oliver 1982, Clatterbuck and Hodges 1988). Only height and diameter relationships of individual trees are presented in this paper because the small sample size prevents making statistically testable generalizations.

Historical documentation was used as much as possible to reference forest development. Local newspapers, magazines, and books were searched for relevant information about early iron and charcoal production as were county survey records. The earliest aerial photographs of the study area, which were taken in 1938, were obtained. Local residents were interviewed concerning their recollections of land use events.

RESULTS AND DISCUSSION

Plot Data

Data from the study plots indicated that areas cut for charcoal and the uncut areas had different age structures (table 1). The dominant and codominant trees in the uncut areas were even-aged and averaged 125 years old. White oak, black oak, hickories, and occasional yellow-poplar and blackgum composed the overstory, while dogwood and sourwood made up the midstory. These areas were in the understory reinitiation stage (Oliver 1981): the dominant overstory trees were beginning to decline, allowing a more favorable understory environment for herbaceous and woody vegetation, especially advanced reproduction of tree species.

Table 1.- Stand parameters, based on trees greater than 5.5 inches in diameter, from six sample plots in areas cut for charcoal and from six sample plots in uncut areas.

	DBH (inches)		Age (years)		Density (stems/acre)	
	mean	range	mean	range	mean	range
			AREAS CUT FOR CHARCOAL			
Black oak	22	12-29	130	106-139	24	14-32
White oak	12	6-16	60	48-75	42	30-60
Hickories	9	6-14	58	52-68	10	4-19
Other species”	10	6-21	75	40-13s	11	6-24
			UNCUT AREAS			
Black oak	19	8-27	130	110-136	18	8-32
White oak	13	6-31	127	115-132	26	17-50
Hickories		6-22	91	63-125	8	3-16
Other species”	10	6-24	115	55-130	11	6-17

“Includes yellow-poplar, blackgum, scarlet oak, northern red oak, white ash, flowering dogwood, and sourwood.

In contrast, the areas cut for charcoal were two-aged, with 60- and 130-year age classes (table 1). More surprising was the species segregation in these stands. One might hypothesize that any tree species that was easy to cut and transport would have been used to make charcoal. However, the charcoal producers were discriminating enough to cut only white oak and hickories, presumably because they judged that these species made the best and hottest burning charcoal for forging iron. Black oak and other species were not cut. Black oaks adjacent to the charcoal hearths have diameters of 20 to 28 inches and many possess fire scars caused by the charcoal activities and subsequent burning for grazing. Many suppressed black oaks were released by the charcoal cutting contributing to their poor, open-grown form. White oak and hickories near the charcoal hearths are 60 to 70 years old. They originated from sprouts or seeds after cutting and burning ceased, and are in the large pole to small sawtimber size classes. Although two-aged, the cut areas were also in the understory reinitiation stage.

The charcoal hearths, with their circular shape, black soil, and absence of overstory vegetation, were conspicuous on the landscape. The soils in these hearths had lost their structure and were nearly sterile as a result of the intense heat associated with charcoal production. The only tree species to colonize these areas were sassafras and dogwood. These trees averaged 32 feet in height, 3 inches in diameter, and 55 years of age.

Stem Analysis

Cumulative height and diameter growth patterns were reconstructed using stem analysis information. Data from trees on the uncut areas are not presented here because these areas exhibited structure and growth patterns typically associated with even-aged stands (Smith 1962). Figure 1 shows the height and diameter growth for the following representative trees on a plot in an area where trees were cut for charcoal: (1) a 132-year-old black oak located 20 feet from the edge of the charcoal hearth, (2) a 132-year-old white oak located 75 feet from the hearth, (3) a 55-year-old sassafras present in the hearth, and (4) a 54-year-old white oak located 30 feet from the hearth. The 132-year-old oaks are residuals left from the charcoal cutting. The older white oak probably was not cut for charcoal because of its distance from the hearth. The younger white oak and sassafras regenerated once the burning and grazing ceased in the 1930’s.

Stem analysis supplemented and corroborated the plot data for the area that was cut for charcoal. In 1885, the present 132-year-old oaks were 31 years old, 3 to 4 inches in diameter, and 32 to 40 feet tall (fig. la). By most accounts, charcoal production had stopped by that time (Smith and others 1988). These stems grew slowly and were probably suppressed resulting in spindly form and flat-topped crowns. These trees were probably released when the overstory was cut for charcoal. However, little increase in height occurred between 1885 and 1935 for two possible reasons: (1) the annual burning of the area to enhance grazing and (2) the time necessary for suppressed trees to respond to release. The combination of these two factors is hypothesized to have hindered trees from increasing their crown volumes and altering their crown shapes enough to allow substantial increase in height over this 50-year period.

However, with a slow buildup in crown volume, substantial increases in total height began to occur in the 1930’s (fig. la) when these stands were protected from fire and open-range grazing was prohibited. Total height increased 35 percent for each of the older oaks for the 50 years from 1935 to 1985. For the previous SO-year period (1885 to 1935) when fire and grazing was common, total height only increased 18 to 20 percent for both trees.

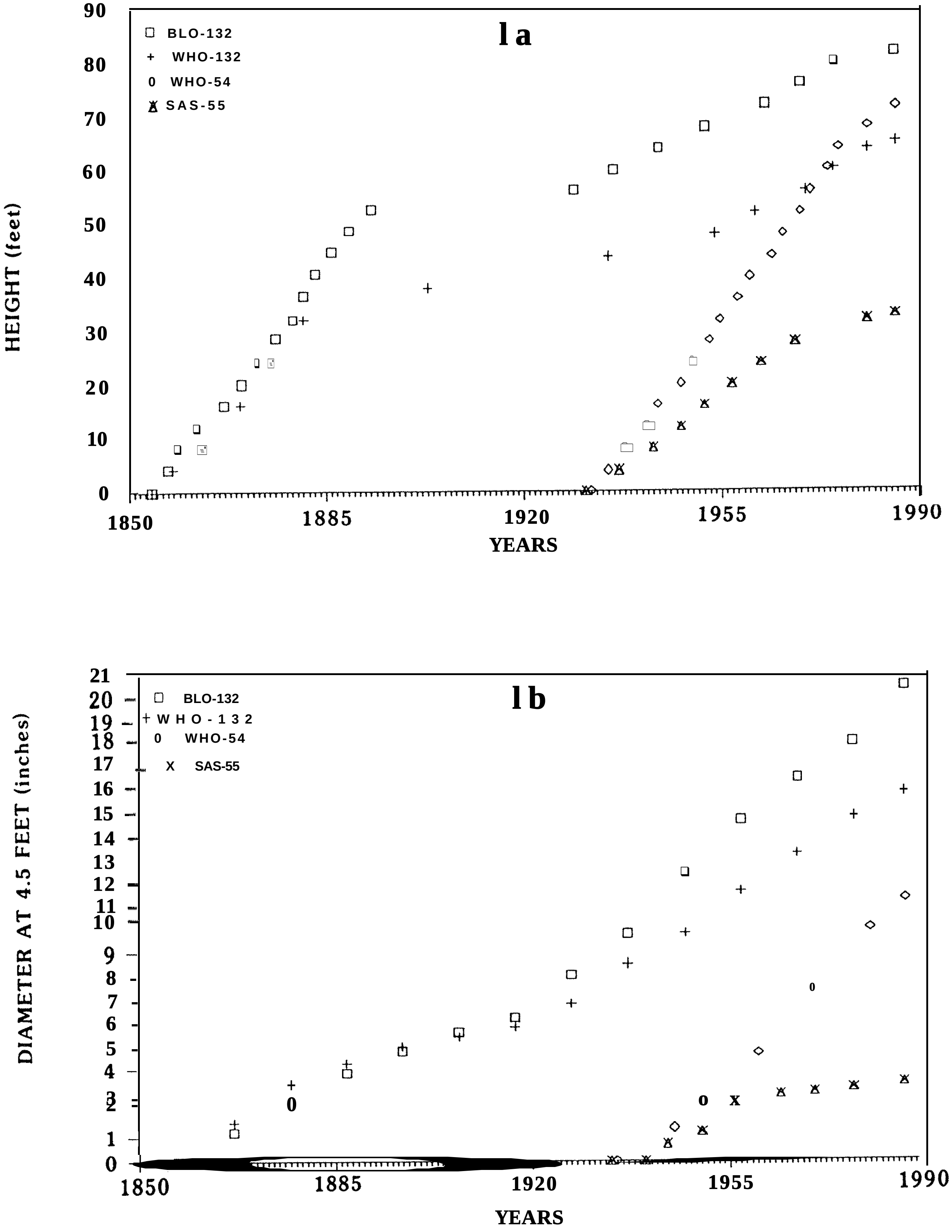

Figure 1.-Cumulative height (la) and diameter (lb) growth patterns of a 132-year-old white oak (WHO-132), a 132-year-old black oak, a 54-year-old white oak (WHO-54), and a 55-year-old sassafras (SAS-55) from an area that was cut for charcoal.

Height growth of the 54-year-old white oak was almost linear, increasing in height at an average of 1.3 feet per year. This oak regenerated in a cutover open area that had been burned and grazed for many years. Older trees were not close enough to affect its growth, form, and development. The sassafras was 33 feet tall at age 55; its slow growth is indicative of low soil productivity in the charcoal hearth.

The diameter growth patterns of these stem-analyzed trees are similar to the height growth patterns (fig. lb). Both the older white oak and black oak had diameters of 4 inches in the 1880's when they were released from overstory vegetation, 8 and 10 inches, respectively in 1940 following the grazing and burning, and presently are 16 and 21 inches, respectively. The 54-year-old white oak with its uninhibited growth had a steady diameter growth rate of 2.1 inches per decade. The sassafras in the charcoal hearth was only 3.5 inches in diameter at 55 years of age.

Fire scars were numerous in the basal cross-sections of the older oaks. For both trees, the most severe scarring occurred in 1872, 1894, and 1922. These major fire occurrences probably were localized because they were not referenced in the local literature. However, the abundance of fire scars on these older oaks suggests that burning the forest was common practice in this area prior to 1940.

Historical Documentation

The 1938 aerial photographs of the study area showed a series of patchlike 1- to 3-acre openings along the ridges. Although the charcoal hearths could not be distinguished on the black and white photographs, the centers of the openings were devoid of trees. Isolated individual trees were scattered in these openings; the majority of these were black oaks that were not cut for charcoal and that survived the numerous ground fires.

Long-time local residents verified that fire had been used on a annual basis to "green-up" the herbaceous vegetation for grazing and to control encroachment of woody vegetation into open areas. Both cattle and hogs roamed freely and grazed in the forest until fence laws were passed and enforced. It has been verified that cattle were transported by rail from Texas to the study area during the Dust Bowl years of the 1930's.

American chestnut was a component of these forests and was valued not only for local uses such as firewood, building materials, and mast, but also as a cash product. A manufacturing plant near Nashville, TN purchased chestnut wood in quantity and extracted tannin from it. The tannin was then used to fix coloring in dyes, wine, and beer and to produce an astringent drug. Chestnut logs, whether green, affected with blight, or dead and lying on the forest floor, were used by this industry. The decayed remains of American chestnut logs that are evident in other areas of Tennessee are not present on or in the immediate vicinity of CWMA. The frequent use of fire, chestnut blight, and this specialized industrial use of chestnut logs all influenced stand development in the study area before 1940. American chestnut may have also been used to produce charcoal, but that could not be determined from this study.

Implications

Forest development following charcoal cutting in the study area was unlike forest development in other places where charcoal has been produced and used to fuel iron furnaces. The iron forgers who operated at the Narrows of the Harpeth River used only those species that they judged would produce the best and hottest burning charcoal, primarily white oak and hickories. Other species were intentionally left, and this cutting pattern eventually created a two-aged forest. This unique two-aged species segregation does not occur in areas where all trees, regardless of species, were cut and burned to produce charcoal for iron furnaces. Where charcoal has been produced for use in iron furnaces, larger areas of land, approaching 100 acres, have been cut. The same charcoal hearths were generally used several times, and on many areas the woody even-aged regrowth was cut two or three times (Ash 1986; Smith et al. 1988; Martin 1989). On the study area, the forest was cut once, the charcoal hearths were used once, and a mosaic of 1- to 3-acre cuts resulted.

Oak decline and associated mortality have been prevalent at CWMA for the last decade. Mostly black oaks and scarlet oaks have died, but so have other oak species and hickories. Generally, mortality occurs on the poorer sites -- the drier upper side slopes, ridge margins, and ridge crests. Several stress-related factors including senescence, insect defoliation, disease pathogens, climatic fluctuations (particularly drought), and above average stand densities have been proposed as causes for oak decline and mortality. Although none of these hypotheses has been adequately proven, it is probable that a complex of factors contribute to the mortality (Starkey and Oak 1989). On CWMA, the large, fire scarred, overmature black oaks that survived the charcoal cutting and the subsequent tires and grazing are the trees most susceptible to decline and mortality. The younger, more vigorous oaks, for the most part, have not been affected. Thus, current oak decline and mortality may be attributed at least in part to the older age classes and the species segregation initiated by the charcoal cutting.

Data from this study reflect the ability of oaks and hickories to persist in areas that are grazed and burned repeatedly following timber harvesting. Although burning and grazing usually precludes the establishment of woody vegetation, the rootstocks of oaks and hickories have the ability to resprout repeatedly from suppressed buds at or below ground level.

Thus, periodic burning and associated grazing promotes advanced regeneration and establishment of oaks and hickories and gives them an ecological advantage over their associates (Van Lear and Waldrop 1989). Even though research has not determined the precise combination of season, frequency, and number of bums needed to promote oaks through silvicultural practices, it is evident that the land use events on CWMA have favored the development of an oak-hickory forest.

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LITERATURE CITED

Ash, Stephen V. 1986. Tennessee's iron industry revisited: the Stewart County story. Land Between the Lakes Association and Tennessee Valley Authority, Land Between the Lakes Cultural Resource Program, Golden Pond, KY. 41 p.

Baker, A.J. 1985. Charcoal industry in the U.S.A. In: Symposium on Forest Products Research International--Achievements and the Future; Vol. 5. 1985 April 22-26; Pretoria, Republic of South Africa. South African Council for Scientific and Industrial Research, National Timber Research Institute. 15 p.

Braun, E.L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia. 596 p.

Clatterbuck, W.K.; Hodges, John D. 1988. Development of cherrybark oak and sweetgum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. Canadian Journal of Forest Research 18(1):12-18.

Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill Co., New York. 714 p.

Luther, Edward T. 1977. Our restless earth. University of Tennessee Press, Knoxville. 94 p.

Martin, W.H. 1989. The role and history of fire in the Daniel Boone National Forest. U.S. Department of Agriculture, Forest Service, Daniel Boone National Forest, Winchester, KY. 131 p.

North, Olin L. 1981. Soil survey of Davidson County, Tennessee. U.S. Department of Agriculture, Soil Conservation Service, Washington, DC. 116 p.

Oliver, Chadwick Dearing. 1981. Forest development in North America following major disturbances. Forest Ecology and Management 3:153-168.

Oliver, Chadwick Dearing. 1982. Stand development--its uses and methods of study. p. 100-112. In: Means, Joseph E., ed. Forest succession and stand development research in the Pacific Northwest; 1981 March 26; Corvallis, OR. Corvallis: Forest Research Laboratory, Oregon State University.

Schnur, G.L. 1937. Yield, stand, and volume tables for even-aged upland oak forests. Agric. Tech. Bull. 560. Washington, DC: U.S. Department of Agriculture. 87 p.

Smalley, Glendon W. 1980. Classification and evaluation of forest sites on the Western Highland Rim and Pennyroyal Gen. Tech. Rep. SO-30. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 120 p.

Smith, David Martyn. 1962. The practice of silviculture. John Wiley & Sons, Inc., New York. 578 p.

Smith, Samuel D.; Stripling, Charles P.; Brannon, James M. 1988. A cultural resource survey of Tennessee's Western Highland Rim iron industry, 1790s-1930s. Research Series No. 8. Nashville, TN: Tennessee Department of Conservation, Division of Archaeology. 209 p.

Starkey, Dale A.; Oak, Steven W. 1989. Silvicultural implications of factors associated with oak decline in southern upland hardwoods. p. 579-586. In: Miller, James H., compiler. Proceedings of the Fifth Biennial Southern Silvicultural Research Conference; 1988 November l-3; Memphis, TN. Gen. Tech Rep. SO-74. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station.

Thomthwaite, C.W. 1948. An approach toward rational classification of climate. Geographical Review 38:55-94.

Van Lear, David H.; Waldrop, Thomas A. 1989. History, uses, and effects of tire in the Appalachians. Gen. Tech Rep. SE-54. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 20 p.

NATURAL REVEGETATION OF BURNED AND UNBURNED CLEARCUTS IN WESTERN LARCH FORESTS OF NORTHWEST MONTANA

Raymond C. Shearer and Peter F. Stickney’

Abstract-In 1967 and 1968, seven south- and east-facing units, averaging 4-ha each, in a western larch forest of northwest Montana were (1) clearcut and burned by prescribed tire or wildfire, (2) clearcut and unburned, or (3) uncut and burned by wildfire. More than 20 years of forest succession data from permanent transects show that tire caused a marked change in composition of all vegetation. Herb cover, mostly tireweed, dominated burned sites through the fifth year. Shrub cover (such as from willow or shiny leaf ceanothus) dominated burned sites from the 6th through the 20th years, but the herb cover changed little during this period. Trees rapidly regenerated burned sites, and height of pioneer species, such as western larch and lodgepole pine, exceeded that of shrubs about 7 years after treatment. But the percentage of conifer cover increased slowly and usually required at least 20 years to equal shrub cover. Without fire, the herb and shrub component remained relatively stable; trees were limited to the smaller, more shade-tolerant uncut conifers. Trees established slowly on unburned sites, and most were shade-tolerant subalpine fir and Engelmann spruce.

INTRODUCTION

Disturbance reinitiates the plant succession cycle. Fire has been the agent of the most extensive disturbances in the Northern Rocky Mountains. Land managers can predict successional pathways on the basis of early responses to prescribed burning. Postfire vegetation is composed of “survivor” and “colonizer” species (Stickney 1982). Survivors are established plants capable of regrowth after fire, and colonizers are new plants that establish from seed on the burned site. Seeds of residual colonizers are already on the site and survive fire either in seedbanks in the ground (Baker 1989) or in tree crowns. Seeds of offsite colonizers disperse onto burned areas, usually from nearby unburned sites.

Stickney (1986) attributes early stages of forest succession after fire to differential development of species present in the initial community. Prebum species composition and severity of burning largely determine what survivor and residual colonizer species will be present. Establishment of offsite colonizers depends on the production and dispersal of seed, mostly from nearby sources, and on favorable site conditions for germination and establishment. Once the initial vegetation is established, successional development usually is limited to changes in species abundance,

Establishment of trees may begin immediately after disturbance, but trees develop more slowly than do some herbs and shrubs. Conifer regeneration in the Northern Rockies continues, sometimes in large numbers, for at least 15 years after burning (Shearer 1989). The faster growing herbs and shrubs dominate the conifers until the trees begin sustained rapid height growth.

This paper describes differences in natural revegetation of south- and east-facing burned and unburned clearcuts in a western larch (Larix occidentalis) forest. Revegetation of a wildfire-burned uncut stand is also compared.

STUDY AREA

The experimental work was conducted in the Miller Creek Demonstration Forest (MC) in western Montana, at latitude 48” 31’ N., longitude 114” 43’ W. MC is a research and demonstration area in the Flathead National Forest.

Elevations of the treated units are 1,424 to 1,654 m, and slopes average 24 percent (12 to 37 percent). The local climate is cool and moist; mean annual temperature is 5 °C, and mean annual precipitation is 635 mm. The growing season (May to August) has a high proportion of clear, hot days and only 17 to 30 percent of the yearly precipitation falls during this period (Schmidt and others 1976). Soils have developed in glacial till composed of argillites and quartzites of the Wallace (Belt) Formation and overlain with 13 to 140 mm of loess (DeByle 1981).

Forest cover is of the western larch type (Eyre 1980). Percent conifer composition (based on volume of the uncut forest) was: Engelmann spruce (Picea engelmannii) 3 1, Douglas-fir (Pseudotsuga menziesii var. glauca) 31, western larch 26, subalpine fir (Abies lasiocarpa) 6, and lodgepole pine (Pinus contorta) 6 (Beaufait and others 1977). The predominant potential climax vegetation is classified as the Abies lasiocarpa/Clintonia uniflora (ABLA/CLUN) habitat type (Pfister and others 1977). Three phases are represented: Xerophvllum tenax (XETE) on the drier south- and west-facing slopes, Menziesia ferruainea (MEFE) on the cooler middle and upper east- and north-facing terrain, and Clintonia uniflora (CLUN) on west-, east-, and north-facing slopes on the remaining sites.

‘Principal Silviculturist and Associate Plant Ecologist, respectively, U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Forestry Sciences Laboratory, Missoula, MT.

Table 1.--Site and fire effects description of four units on south-facing slopes, Miller Creek Demonstration Forest

	Unburned	Prescr. fire May 18. 1968	Prescr. fire Aug. 8, 1967	Wildfire Aug. 23, 1967
SITE				
Elevation (m)	1456	1498	1479	1424
Slope (%)	12	22	21	24
Azimuth (deg.)	210	196	193	189
Dry slope (%)	100	88	91	94
Habitat type	ABLA/CLUN,XETE	ABLA/CLUN,XETE	ABLA/CLUN,XETE	ABLA/CLUN,XETE
FIRE EFFECTS				
Fine fuel red. (%)	N/A	82	74	ca 90
Duff red. (%)	N/A	16	84	100
Unburned duff (cm)	N/A	4.3	0.5	0
Soil exposure (%)	N/A	14	84	100

METHODS

This paper reports on portions of two studies that describe herb, shrub, and tree development on south- and east-facing experimental burning units that were (1) clearcut and burned by prescribed broadcast burning or wildfire, (2) clearcut without burning, or (3) uncut but burned by wildfire. The burning units averaged 4-ha in area.

Three south-facing units were clearcut in 1967; the fourth was not cut (table 1). Two of the south-facing clearcuts were prescribed burned (one in early August 1967, the other in mid-May 1968), and the third was not burned. A wildfire burned the uncut unit in late August 1967. The three east-facing units were clearcut in 1967 (table 2). Two of these units were prescribed burned in early October 1967 and early August 1968; the third unit was not burned.

Successional Development

The postfire development of vegetation was measured annually (most units) on permanent plots located within the 4-ha experimental burning units. The permanent plots within a burning unit were referenced to two 25-m baselines, usually arranged end to end (Stickney 1980). Each baseline served as the base for five contiguous 5 x 5 m plots. Within each 5-m plot, three smaller plots were nested to accommodate the sampling of lower/shorter woody plants and herbaceous vegetation. Shrubs and trees were sampled according to height as: (1) 2.5 m and taller on 5 x 5 m plots, (2) height 1.5 to 2.45 m on 3 x 3 m plots, and (3) height 0.5 to 1.45 m on 1.5 x 1.5 m plots. Herbs (irrespective of height) and low woody plants (including shrubs and trees <0.5 m high) were sampled in two 0.5 x 0.5 m plots nested in each 5 x 5 m plot along the baseline. Cover (aerial crown) by plant species was measured to quantify the successional development of shrubs and trees and ocularly estimated for herbaceous and low woody plants.

The total number of conifer seedlings and saplings and the number of plots with at least one conifer seedling or sapling were determined at 5-year intervals on 31 to 74 temporary 0.0004-ha circular plots systematically installed throughout each unit. Each of these circular plots was enlarged to

Table 2.--Site and fire effects description of three units on east-facing slopes, Miller Creek Demonstration Forest

	Unburned	Prescr. fire Aug. 7. 1968	Prescr. fire Oct. 2. 1967
SITE			
Elevation (m)	1585	1654	1448
Slope (%)	37	29	22
Azimuth (deg.)	59	72	63
Moist slope (%)	92	78	80
Habitat type	ABLA/CLUN,MEFE	ABLA/CLUN,MEFE	ABLA/CLUN,CLUN
FIRE EFFECTS			
Fine fuel red. (%)	N/A	92	44
Duff red. (%)	N/A	60	49
Unburned duff (cm)	N/A	2.5	2.8
Soil exposure (%)	N/A	72	88

0.0013 ha to determine the number of (1) established (at least 30.5 cm tall for larch and lodgepole pine or 15 cm for other species) and (2) plots with one tree present. Also, the height of the tallest conifer of each species was recorded for each plot.

The data presented in this paper were not analyzed statistically.

Severity of Fire Treatment

Assessment of fire severity treatment to vegetation follows the Ryan-Noste Fire Severity Index (Ryan and Noste 1985, p. 232) as the standard. Severity, as defined by Ryan and Noste, differs from "fire intensity" because it incorporates the downward heat pulse to site in addition to the upward heat pulse. Expressed as ground char depth, the downward heat pulse is the critical one so far as understory vegetation is concerned. The postfire manifestations of ground char class are expressed in the depth reduction of the litter/duff layer/mantle. On the experimental burning units being reported here, ground char classes ranged from light for most of the broadcast burned units to moderate for the wildfire and summer burned units.

RESULTS

Fire caused changes in composition of all vegetation. The degree of modification varied with severity of the fire treatment as shown by changes on units receiving differing tire treatments on south- and east-facing slopes.

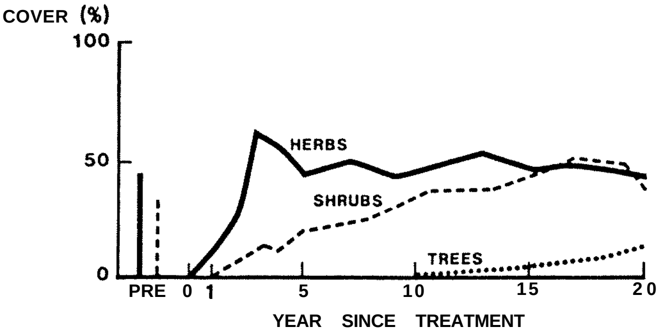
Reforestation of South-Facing Slopes

Overstory trees common in 200- to 250-year-old virgin forests on south-facing slopes at MC include Douglas-fir, western larch, Engelmann spruce, subalpine fir, and less frequently lodgepole pine. The more prominent understory plants include the shrubs huckleberry (Vaccinium globulare), mountain maple (Acer glabrum), and spirea (Spiraea betulifolia); and the herbs arnica (Arnica latifolia), beargrass (Xerouhvllum tenax), and prince's pine (Chimanhilia umbellata). Clearcutting removes the overstory conifers and, when followed by slash burning, eliminates any onsite seed source for trees.

Clearcut and a spring prescribed fire.

Following clearcutting, a prescribed tire on May 18, 1968 (when the lower half of the duff was still wet from snowmelt and rain) left a continuous, intact, duff mantle as a seedbed and killed the aerial portions of understory herbs and shrubs. Many topkilled herbs and shrubs quickly regrew from root crowns and rootstocks. Forest succession began with the regrowth of an abundant survivor component of arnica and beargrass and the establishment of the offsite colonizers Iircweed (Epilobium angustifolium) and bullthistle (Cirsium vulgare). Herbaceous cover developed rapidly. Fireweed quickly established; beargrass regrew less rapidly but more persistently than did tireweed, and was a major component of the herbaceous cover. The herb stage dominated the first 15 years of succession (fig. 1) because shrub development was dependent on the slow recovery of huckleberry and sparse colonization by Scouler's willow (Salix scouleriana). Conifers regenerated slowly because of unfavorable seedbed and harsh site. Regeneration may also have been limited by infrequent good seed crops and the distance from the seed source.

Hcrbaceous cover and shrub cover were similar (45 to 50 percent) from the 15th through the 20th years. Tree cover developed slowly; increasing to about 10 percent after 20 years (fig. 1). In 1984, 17 growing seasons after treatment, at least one conifer seedling or sapling grew on 79 percent of the plots. There were more than 1,900 total and established trees/ha (fig. 2). Most of these were Douglas-fu, larch, Engelmann spruce, and subalpine fir (table 3). Conifer density was greatest close to the nearby uncut timber; overstocking occurred in patches. There were few trees on a drier slope in the interior of the clearcut. Many of the conifers growing on that slope were exposed to direct sunlight. Most conifers originated from the 1971 cone crop that was rated good for all species.



	PRE	0–1	5	10	15	20
Survivor :						
XETE (H)	13	3	12	15	18	25
ARLA (H)	14	7	11	1	<1	4
VAGL (S)	29	<1	3	8	16	11
Colonizer :						
EPAN (H)	0	<1	17	22	12	8
SASC (S)	0	0	5	4	5	2

Figure 1. - Early successional development (cover) of major life form groups and prominent species from 1968 through 1988 on a south-facing clearcut, prescribed burned May 18, 1968, Miller Creek Demonstration Forest; ARLA = arnica, EPAN = fireweed, SASC = willow, VAGL = huckleberry, XETE = beargrass; H = herb, S = shrub.

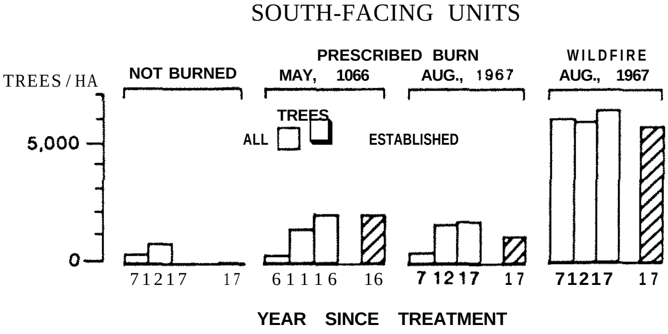


Figure 2. - Average number of all conifer seedlings and saplings per hectare (open bars) by years since treatment and number of established conifers (larch and pine at least 30.5 cm tall, others at least 15 cm) at the most recent measurement (crosshatched bar) on four south-facing units, Miller Creek Demonstration Forest, 1984.

Because all of the important nonconiferous species present in 1988 are traceable to the plant community established in the first postfire year, it may be several decades before seeds from other shrubs or tree species influence succession on this site.

Clearcut and a summer prescribed fire.
In contrast to the spring burning, a prescribed fire on August 8, 1967, when duff moisture was low, consumed most of the duff and as a consequence, killed many plants by burning their aerial portions and lethally heating their roots within the surface 3 cm of soil. A wildfire reburning the area on August 23 consumed the remaining duff, thereby increasing plant mortality. Consequently, the postfire community resulting from this double-burn treatment contained few survivor plants and revegetation was largely in the form of colonization by pioneer plants. Predominant colonizers were shinyleaf ceanothus (Ceanothus velutinus) originating from seed in a ground-stored seedbank emplaced well prior to the fire and fireweed whose seed dispersed onto the burn in the fall following the fire. A few seeds of conifers dispersed long distances from outside the burn.

Forest succession began with the germination of these seeds and the regrowth of spirea, beargrass, and huckleberry. Early dominance by herbaceous plants, mainly fireweed, was of short duration. Shrub seedlings of ceanothus, germinating profusely from the seedbanks, dominated the site after about 7 years of postfire development. Once the herb and shrub layer provided shade on this south-facing site, more conifer seedlings became established, especially from the good cone crop of 1971 4 years after the fire. Cover estimates are not available for this unit, but shrubs still dominate after 20 *years* although scattered conifers have overtopped the shrubs. In 1984, most of the 1,500 total and the 970 established trees/ha were Douglas-fir and larch (fig. 2, table 3). Conifers grew on nearly half of the plots.

In spite of an ash seedbed, tree density on most of the clearcut has remained low because there is no onsite seed source. A few trees on a ridge above the unit survived the wildfire and provided some seed for regeneration. High temperature at the soil-air interface and low moisture in the surface 10 cm limited early conifer seedling survival. Lack of moisture and competition with shrubs limited recent survival. The number of established shade-intolerant larch

Table 3.--Percent composition of established conifer regeneration[a] on south- and east-facing slopes by treatment[b], Miller Creek Demonstration Forest, 1984

Treatment	Tree composition				
	LAOC	PSME	PIEN	ABLA	PICO
		SOUTH-FACING UNITS			
CC, NB	0	0	0	0	0
CC, PB May 1968	21	41	22	13	3
CC, PB Aug. 1967	32	45	9	10	4
UC, WF Aug. 1967	10	2	1	1	86
		EAST-FACING CLEARCUTS			
CC, NB	0	67	33	0	0
CC, PB Aug. 1968	8	12	57	22	1
CC, PB Oct. 1967	28	29	21	22	0

[a] Based on data from 0.0013-ha circular plots that recorded all subsequent natural regeneration >30.5 cm tall for western larch and lodgepole pine and >15.0 cm tall for all other species. ABLA = subalpine fir, LAOC = western larch, PICO = lodgepole pine, PIEN = Engelmann spruce, PSME = Douglas-fir.

[b] CC = clearcut, UC = uncut;
PB = prescribed burned, WF = wildfire, NB = not burned

and lodgepole pine decreased by 40 percent from 1979 through 1984, while numbers of shade-tolerant Douglas-fir increased 192 percent.

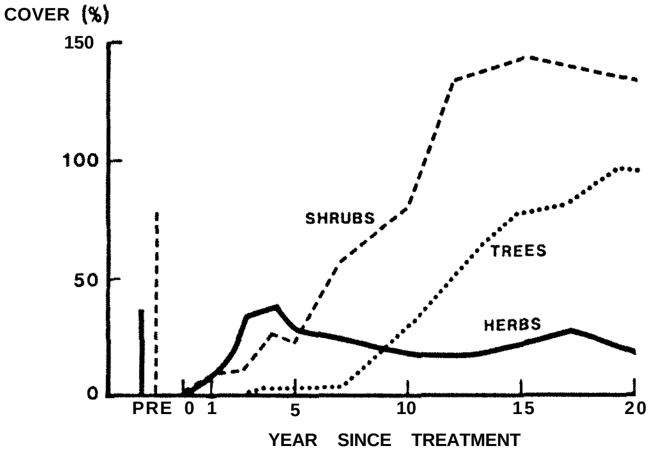
Clearcut without fire.

A third clearcut was slashed but received no fire treatment. Logging and slashing removed all overstory trees but did not remove the small-diameter understory trees, most of which were subalpine fir. The initial post treatment community was composed almost exclusively of species that were present in the prelogged forest (fireweed was the exception). Alder and menziesia were important shrubs, both before and after logging and site treatment. During the 20 years since disturbance, only a few subalpine fir and Engelmann spruce have regenerated (fig. 2, table 3).

Uncut, summer wildfire.

On August 23, 1967, a wildfire burned a virgin stand of larch, Douglas-fir, and lodgepole pine that was designated for logging later in the summer. The fire killed the overstory trees (except two larch), burned the aerial portion of all other vegetation, and ashcd the litter/duff layer to the soil surface. High mortality of huckleberry and beargrass, the major shrub and herb species, resulted from this fire. Because few plants survived the fire, the site was available for colonization by pioneer species. Colonizers in the first postfire year were fireweed (herb), ceanothus (shrub), and lodgepole pine and larch (tree). Seed sources for these initial colonizers were onsite seedbanks for ceanothus (ground-stored) and lodgepole pine and larch (tree crowns) and offsite for fireweed. Forest succession began with the germination and establishment of these tree species coupled with regrowth of surviving spirea, beargrass, and huckleberry. The fast initial growth of herb cover was due mostly to the rapid development of fireweed. Herb cover peaked at 4 years and shrub cover dominated after only 7 years, mainly because spirea and ceanothus grew rapidly (fig. 3). Although most conifers established in the first year at the same time as fireweed and ceanothus, their height did not begin to exceed that of the shrubs until the ninth year. After 20 years, shrub cover still was twice as great as that of conifers (fig. 3). It is expected that increased shading resulting from height growth and crown development of conifers will cause reductions in ceanothus cover. During the winter of 1986-87, low temperature coupled with lower-than-average snow cover killed a large proportion of ceanothus crowns. Some recovery was noted in 1989.

In 1984 (succession year 17), more than 6,400 total and 5,600 established trees/ha, mostly lodgepole pine and western larch, covered the ares (fig. 3, table 3). Trees occurred in 97 percent of the plots--the result of seedfall from tire-killed onsite trees.



Survivor:						
XETE (H)	23	2	5	10	10	8
SPBE (S)	9	2	11	18	23	28
VAGL (S)	54	0	1	4	5	8
Colonizer:						
EPAN (H)	0	0	16	8	5	3
CEVE (S)	0	<1	<1	55	100	75
PICO (T)		0	2	22	58	82

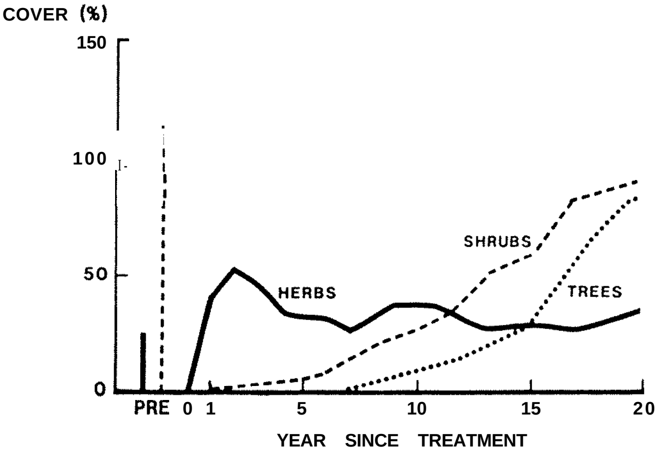
Figure 3. - Early succession development (cover) of major life form groups and prominent species from 1967 through 1987 of a south-facing uncut forest burned by wildfire on August 23, 1967, Miller Creek Demonstration Forest; CEVE = ceanothus, EPAN = fireweed, PICO = lodgepole pine, SPBE = spirea, VAGL = huckleberry, XETE = beargrass; H = herb, S = shrub, T = tree.

Reforestation of East-Facing Slopes

Tree species found on the south-facing slopes at MC are also characteristic of virgin forests on more mesic east-facing slopes. The understory shrub and herb species found on the east-facing slopes are typical of moister sites. Prominent shrubs include yew (Taxus brevifolia), menziesia (Menziesia ferruginea), and alder (Alnus sinuata), in addition to huckleberry; important herbs were arnica and oak fern (Gymnocarpium dryopteris). south aspects, clearcutting and burning eliminated onsite sources for coniferous seed. Burning decreased or eliminated potential sources for seed in the slash. Where slash is not burned, advance coniferous regeneration survived on the site.

Clearcut and a fall prescribed fire.

After a record-dry summer, a prescribed fire on October 2, 1967 (during the first major storm since late June) burned half of the freshly moistened 5.8 cm duff layer. The fire eliminated western yew, the major understory species, and greatly reduced the cover percentages of the other principal understory species, huckleberry and arnica (fig. 4). The reduced duff layer and poor survival of understory shrubs and herbs combined to provide a conducive site for colonization. Five offsite colonizers attained prominence in early succession: tireweed, Scouler's willow, western larch, Douglas-fir, and subalpine fir. As on the south-facing slopes, fireweed showed the most rapid development and attained 47 percent canopy cover by the second year after fire. It remained the most abundant cover species for the duration of the herb stage. Recovery of huckleberry survivors and development of initial colonizer Scouler's willow were primarily responsible for succession to the shrub stage in the 13th year. Shrubs remained the most abundant life form through 1989. Some conifer seeds germinated the first year after the fire but most of them originated as secondary offsite colonizers from the seed crop of 1971, 4 years after burning. Because two edges of the unit bordered uncut forest, thousands of conifer seedlings per hectare germinated in 1972. More than 12,600 seedlings/ha, mostly larch and Douglas-fir, survived in 1974 (fig. 5, table 3). Regeneration more than doubled over the next 10 years because of large increases in Douglas-fir, Engelmann spruce, and subalpine fir. During this period the number of shade-intolerant western larch decreased about 22 percent. More than 22,000 conifer seedlings and saplings/ha were counted in 1984, and more than 21,000 of these were considered established. In the 20th year of succession, percentages of cover of trees and of shrubs were high and almost equal, while percentages of herb cover were much less (fig. 4).



Survivor :						
ARLA (H)	12	2	1	2	6	9
VAGL (S)	26	1	2	9	21	38
ALSI (S)	7	0	0	0	3	12
TABR (S)	63	0	0	0	0	0
Colonizer :						
EPAN (H)	0	41	30	17	9	12
SASC (S)	0	0	CI	7	14	15
LAOC (T)	0	<1	<1	6	20	44

Figure 4. - Early successional development (cover) of major life form groups and prominent species from 1967 through 1987 of an east-facing clearcut, prescribed burned October 2, 1967, Miller Creek Demonstration Forest; ALSI = alder, ARLA = arnica, EPAN = fireweed, LAOC = western larch, SASC = willow, TABR = yew, VAGL = huckleberry; H = herb, S = shrub, T = tree.

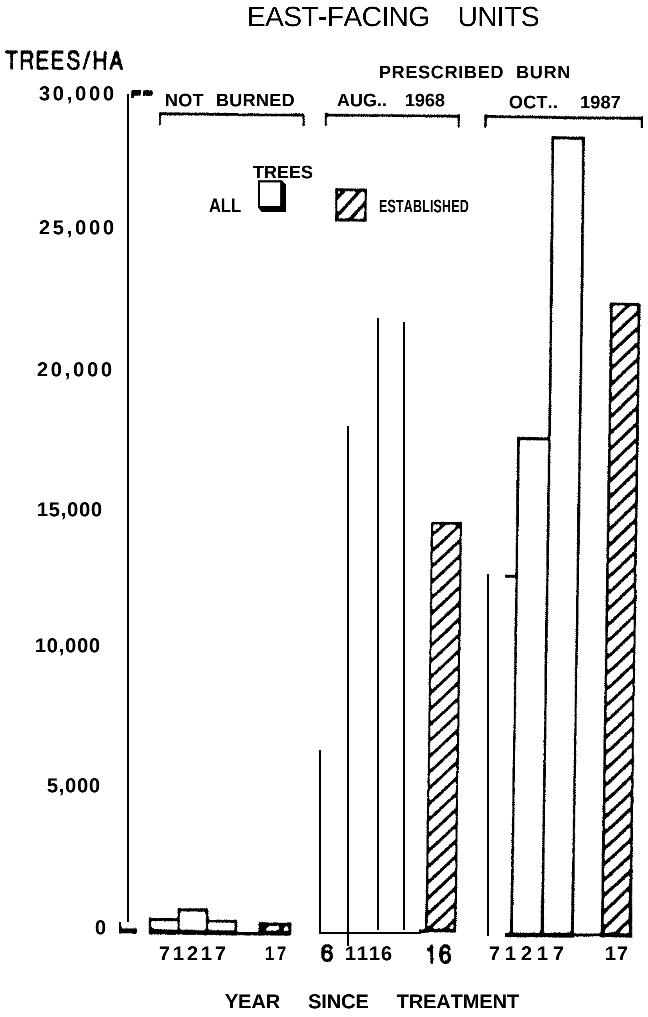


Figure 5. - Average number of all conifer seedlings and saplings per hectare by years (open bars) since treatment and number of established conifers (larch and pine at least 30.5 cm tall, others at least 15 cm) at the most recent measurement (crosshatched bar) on three east-facing units, Miller Creek Demonstration Forest, 1984.

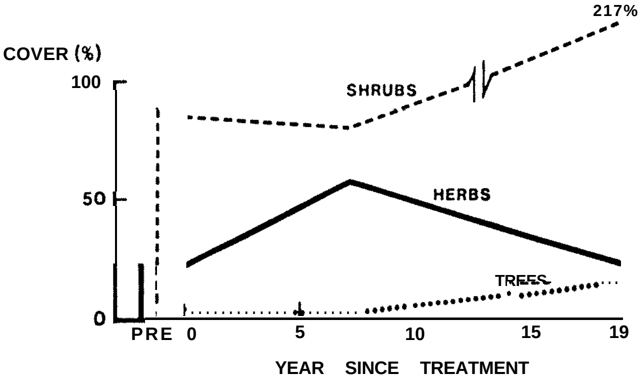
Clearcut and a summer prescribed fire.

After the onsite conifer seed source was removed by clearcutting and slashing, the August 7, 1968, prescribed fire burned the aerial portions of the understory vegetation and removed the upper 60 percent of the duff layer. The tire substantially reduced cover of most of the shade-tolerant understory species, especially huckleberry, alder, and menziesia. Herbs responded quickly, covering 68 percent of the freshly burned site by the second year of succession. Arnica, a rhizomatous herb, attained 19 percent cover by regrowth; tireweed, which grew from seed from offsite sources, attained 47 percent coverage. The few survivor shrubs regrew slowly in early succession, and cover of herbs was five times as great as cover of shrubs by the sixth year, the last year for which data are available.

Conifers regenerated quickly from seed of offsite trees bordering two sides of the clearcut. Most seedlings resulted from the abundant 1971 seedfall. The moderate or good cone crops of 1974, 1976, and 1980 provided seed for additional seedling establishment. In 1974, 6 years after the tire, there were 6,300 seedlings/ha (fig. 5). This increased to more than 18,100 in 1984 and 21,800 in 1989. About two-thirds of the tree seedlings counted in 1984 were considered established--there were seven times more established seedlings in 1984 as there were in 1979. Of the established conifers, 57 percent were Engelmann spruce, 22 percent suablpinc fir, 12 percent Douglas-fir, 8 percent larch, and 1 percent lodgepole pine (table 3). Only the Engelmann spruce were as tall here as they were on the other clearcuts. The few established lodgepole pine were much shorter than elsewhere, but they were 0.6 m taller than the other species. In contrast, height growth of Engelmann spruce was greater than on other burned clearcuts at Miller.

Clearcut and no fire.

An cast-facing unit bordering the clearcut prescribed burned on August 7, 1968, provided an unburned contrast. The unmerchantable trees were cut but not removed after clearcutting, but many small subalpine fir and a few other shade-tolerant conifers were not cut. With no further disturbance, the understory alder, menziesia, arnica, and small conifers constituted the initial community with species composition little changed from the prelogging forest (fig. 6). The major exception, tireweed, colonized sites where removal of overstory trees revealed gaps in the shrub layer. Because shrubs constituted the most important cover group both before and after logging, forest succession began with an initial shrub stage that has continued for 20 years. Possibly some secondary colonization of alder and menziesia from onsite seed sources occurred during the middle of the first decade. Alder and menziesia have become codominant for the shrub stage. Twenty years after logging, iireweed represents a minor component overall but maintains higher coverage in the openings of the shrub stand. Although adjacent uncut stands supplied much seed, competition for light and moisture is intense and few conifers became established. The current tree component is sparse and consists of subalpine fir that were established before the stand was clearcut and were too small for slashing in 1967 and about 62 Douglas-fir and Engelmann spruce/ha (table 3, fig. 5). A few western larch and lodgepole pine are present, probably growing on small areas disturbed during timber harvest.



Survivor :

ARLA (H)	5	19	8
VAGL (S)	25	18	20
MEFE (S)	28	23	90
ALSI (S)	26	34	90

Colonizer :

EPAN (H)	0	34	8

Figure 6. • Early successional development (cover) of major life form groups and prominent survivor and colonizer species from 1968 through 1987 on an east-facing clearcut that was not burned, Miller Creek Demonstration Forest; ALSI = alder, ARLA = arnica, EPAN = fireweed; MEFE = menziesia, VAGL = huckleberry; H = herb, S = shrub.

DISCUSSION

Maturing forests are inhospitable to the establishment and growth of many native species. Fire renews and rejuvenates aging ecosystems following years of successional changes and the accumulation of duff and litter. The potential for tire to alter succession depends mainly on the composition of the forest community, the onsite seed source, and the severity of the tire. Low-severity fires leave a high survivor component and do little to change species composition, leaving sites in a later stage of succession. As fire severity increases, the burned area becomes more favorable to colonizers. Severe tires kill more of the existing vegetation and have the potential to greatly change the course of subsequent succession, that is, set succession back to an earlier stage. Fire similarly affects succession after clearcutting. Without fire or other site modification after timber harvest, conifer regeneration is slow and often excludes shade-intolerant species. The MC study showed response of vegetation to a wide range of fire characteristics. On south aspects conifer regeneration was successful on an uncut unit burned during the August 1967 wildfire, less so on prescribed burned clearcuts, and unsuccessful on an unburned clearcut. On the east-facing slopes conifer regeneration was successful on prescribed burned clearcuts but was also unsuccessful on an unburned clearcut. Ryan and Noste (1985’) show that when plenty of conifer seed is present, regeneration on clearcuts following fire depends on the severity of burning treatment.

Clearcutting followed by prescribed burning can deplete the surface of most of the woody residues. Although conifer regeneration following clearcutting was usually most successful when the duff layer was removed by fire, research has shown that most conifers successfully regenerate through 1.3 cm of duff in the western larch forest type (DeByle 1981). Retention of a shallow duff layer and other organic matter, especially the woody component, protects the soil from intense summer rainfall for the first few years (DeByle 1981) and helps maintain the productivity of the site (Harvey and others 1987).

Many trees that burned during the wildfire on the south-facing uncut unit bore mature cones. Some cones burned and their seeds were lost while other cones were singed and their undamaged seeds dispersed on the ash covered surface a few days after the fire. Seeds with unburned wings could disperse farther than seeds with partly burned wings. Overhead shade from dead and surviving trees promoted seedling survival through decreased surface soil temperatures and reduced evapotranspiration. Prompt conifer seedfall permitted establishment before shrub and herb competition for moisture and light became extreme. Following less severe wildfire, more overstory trees survive and serve as a continuing onsite seed source. The availability of onsite seed to affect regeneration depends on the regularity and amount of seed crops and the duration of a receptive seedbed after burning.

Burned seedbed had greater conifer germination and seedling establishment than on unburned sites. Regeneration usually increased where the duff layer was reduced most. Sparse conifer establishment on the two presecribed burned clearcuts on south aspects resulted from the harsh site conditions. Without shading, the soil surface dried quickly and temperatures as high as 79 °C were measured in June and July (Shearer 1976). The combination of lethal temperature and rapid drying of surface soil soon after germination often causes high mortality of new seedlings (Shearer 1976). The May prescribed fire left a 4-cm-deep residual duff layer that was unfavorable for seedling survival. Cracks developed in the duff as it warmed and dried during the sunny, dry season following site treatment. In subsequent years, seedlings survived much better in the enlarging cracks than on the surface of duff. The August prescribed fire nearly eliminated all of the duff layer on the other clearcut and left it exposed to extremes in light and temperature. Seedfall was deficient because few trees grew nearby.

The east-facing clearcuts were less influenced by long periods of intense radiation. Each of the clearcuts had one or two sides bordering uncut timber that provided abundant seed for natural regeneration. Both prescribed burned clearcuts regenerated readily and conifers now account for a substantial percentage of the plant cover. Subsequent regeneration failed on the unburned clearcut where no exposed mineral seedbed was left after logging.

Lodgepole pine have serotinous cones, but the other conifers present depend on the current cone crop to provide seeds after late summer or early fall burning. A fair or good cone crop usually provides sufficient seed to regenerate the site the spring after the fire. But for stands that are burned when few or no onsite cones are available, regeneration is dependent on offsite seed sources. The number of new seedlings decreases as distance to the trees increases.

If clearcutting occurs near the time of cone maturity, the cones will open and disperse their seeds. Severe slash fires burn much of the duff layer and destroy all or most of the seed, preparing a substrate free of heavy duff and favorable for seed germination. If seeds are present in nearby stands and disseminate into the units, as they did on the east-facing clearcuts that were burned by the summer and fall prescribed fires, prompt regeneration occurs. If seed is unavailable, as in the south-facing clearcut prescribed burned in August 1967, regeneration is delayed. Cutting without slash burning maintains the viable seed, but does not prepare a seedbed conducive to seedling establishment (examples are east- and south-facing clearcuts where fire was excluded).

Exposed charred duff apparently decomposed rapidly. Within a few years, the depth of this layer decreased sufficiently so that significant numbers of conifer seedlings became established. After some early seedling establishment, the abundant seed crop of 1971 dispersed onto the 5-year-old nearly duff-free ground surface and a substantial pulse of new conifer seedlings established.

If these new forests were to burn with a tree-killing fire, the initial postfire community would be composed mostly of survivor species. Principal shrubs would be ceanothus, spirea, and huckleberry; principal herbs would be fireweed and beargrass. Tree species probably would be excluded from the site for lack of an onsite seed source. This condition would be equivalent to the double burn situation in the Northern Rocky Mountains that created large shrubfields as noted by foresters at the turn of the century (Lieberg 1897).

LITERATURE CITED

Baker, Herbert G. 1989. Some aspects of the natural history of seed banks. In: Leck, Mary Allessio; Parker, V. Thomas; Simpson, Robert L. eds. Ecology of soil seed banks. Academic Press, Inc. San Diego, CA: 9-21.

Beaufait, William R.; Hardy, Charles E.; Fischer, William C. 1977. Broadcast burning in larch-fir clearcuts: The Miller Creek - Newman Ridge Study. Research Paper INT-175. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 53 p.

DeByle, Norbert V. 1981. Clearcutting and fire in the larch/Douglas-fir forests of western Montana--a multifaceted research summary. General Technical Report INT-99. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 73 p.

Eyre, F. H., ed. 1980. Forest cover types of the United States and Canada. Society of American Foresters. 148 p.

Harvey, Alan E.; Jurgensen, M.F.; Larsen, M.J.; Graham. R.T. 1987. Decaying organic materials and soil quality in the Inland Northwest: a management opportunity. General Technical Report INT-225. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 15 p.

Leiberg, John B. 1897. General report on a botanical survey of the Coeur d'Alene Mountains in Idaho during the summer of 1895. Contributions from the U.S. National Herbarium. Washington, DC: U.S. Department of Agriculture, Division of Botany. 5(1):5-81.

Pfister, Robert D.; Kovalchik, Bernard L.; Amo, Stephen F.; Presby, Richard C. 1977. Forest habitat types of Montana. General Technical Report INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Ryan, Kevin C.; Noste, Nonan V. 198.5. Evaluating prescribed fires. In: Lotan, James E.; Kilgore, Bruce M.; Fischer, William C.; Mutch, Robert W. tech. coords. Proceedings--Symposium and workshop on wilderness fire; 1983 November 15-18; Missoula, MT. General Technical Report INT-182. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 230-238.

Schmidt, Wyman C.; Shearer, Raymond C.; Roe, Arthur L. 1976. Ecology and silviculture of western larch forests. Technical Bulletin 1520. Washington, DC: U.S. Department of Agriculture. 96 p.

Shearer, Raymond C. 1976. Early establishment of conifers following prescribed broadcast burning in western larch/Douglas-fir forests. Proceedings, Tall Timbers Fire Ecology Conference; 4:481-500.

Shearer, Raymond C. 1989. Fire effects on natural conifer regeneration in Montana. In: Baumgartner, David M.; Breuer, David W.; Zamora, Benjamin A.; Neuenschwander, Leon F.; Wakimoto, Ronald H. compilers and eds. Prescribed fire in the Intermountain Region--forest site preparation and range improvement. 1986 March 3-5; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 19-33.

Stickney, Peter F. 1980. Data base for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. General Technical Report INT-62. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 133 p.

Stickney, Peter F. 1982. Vegetation response to clearcutting and broadcast burning on north and south slopes at Newman Ridge. In: Site preparation and fuels management on steep terrain: Proceedings of symposium; 1982 February 15-17; Spokane, WA. Pullman, WA: Washington State University, Inland Empire Reforestation Council: 119-124.

Stickney, Peter F. 1986. First decade plant succession following the Sundance Fire, northern Idaho. General Technical Report INT-197. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 26 p.

CHANGES IN WOODY VEGETATION IN FLORIDA DRY PRAIRIE AND WETLANDS DURING A PERIOD OF FIRE EXCLUSION, AND AFTER DRY-GROWING-SEASON FIRE

Jean M. Huffman and S.W. Blanchard[1]

Abstract-South Florida dry prairie and herbaceous wetlands are recognized as fire maintained communities. Aerial photography was used to show how the woody vegetation in Myakka River State Park (Sarasota County, Florida) changed over approximately thirty years of fire exclusion (1939-1968). Rapid increases occurred in Quercus virginiana and Serenoa repens uplands and in forested and shrubby wetland associations. Corresponding decreases occurred in dry prairies and herbaceous wetlands. Present management goals are to maintain and restore fire-dependant plant communities. Drought-condition burns early in the growing season appear to be more effective in reducing woody species cover than traditional dormant-season burns or wet growing-season burns.

INTRODUCTION

Increases in woody vegetation are known to occur in many southeastern Coastal Plain plant communities following fire excusion or when fire frequency is *reduced* (Heyward 1939; Alexander 1973; Platt and Schwartz 1990; Wade and others 1980).

We mapped vegetation change over a thirty-year period of fire exclusion in two areas within Myakka River State Park, a 11,686 ha. preserve of dry prairie, pine flatwoods, marshes and oak-palm (Quercus virginiana, Q. laurifolia and Sabal palmetto) hammock located in Sarasota and Manatee Counties in Southwest Florida (Fig.1).

Vegetation changes that have occurred following fire exclusion in Florida dry prairies and imbedded wetlands were documented. We also mapped changes resulting from attempts at restoration using the reintroduction of different types of prescribed fires. Restoration efforts over the past several decades suggest that not just fire, but fire at a specific time of year and under specific moisture conditions is critical for restoration of dry prairie habitats invaded by woody species during periods of fire suppression.

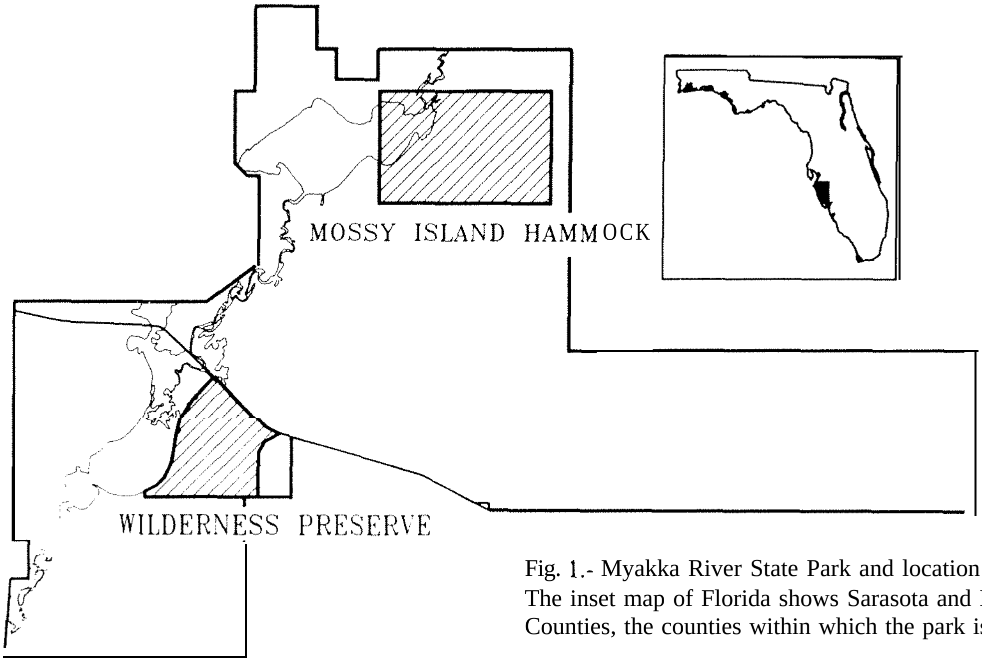


Fig. 1.- Myakka River State Park and location of study sites The inset map of Florida shows Sarasota and Manatee Counties, the counties within which the park is located.

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[1] Park Biologist, Myakka River State Park, Florida Department of Natural Resources, Division of Recreation and Parks, Sarasota, Florida; and Research Assistant, Myakka River State Park, Sarasota Florida.

STUDY AREA

Climate

The climate of Southwest Florida is characterized by an annual cycle that includes a dry season from October through May and a wet season from June through September (Chen and Gerber 1990). At Myakka River State Park, 61 percent of the average total annual rainfall (144 cm) occurs during the wet season (Fitzgerald 1990). The wet season does not correspond exactly to the growing season, which typically occurs from April through October. Therefore, at the time that growth of plants is initiated in the spring, the dry season has not yet ended.

Fire History

Myakka River State Park lies within an area that has a long history of lightning-ignited fires and fires set by cattlemen. The thunderstorm (lightning) season typically occurs from May through September in south Florida, and approximately 95 percent of total annual thunderstorm days occur during this period (Robbins and Meyers 1989). Fire records from southwest Florida indicate that naturally-ignited tires burn the largest areas at the end of the dry season in early spring (Miller and others 1983). Presumably this was the historic pattern of burning in this region before European settlement. For the last 100 years or more cattlemen and ranchers have burned primarily in the winter, in the beginning and middle of the dry season. These bums usually occur after the passage of a cold front brings rain, when fuel moistures, and often water tables, are high and seasonal wetlands have standing water.

The State Park was established in 1934, a period of strong anti-fire sentiment in the Southeastern United States. During the late 1930's and early 1940's the Civilian Conservation Corps made the lighting of tires at Myakka a high priority. Hundreds of miles of firebreaks were cut throughout the park and tires were extinguished whenever possible. Although many lightning fires were ignited, they were suppressed as quickly as possible. The result was not total tire exclusion but a much reduced tire frequency in most areas. This fire-suppression policy continued in effect through the late 1960's when prescribed burning was accepted as a management tool. Prescribed fire was not regularly used within the park until the late 1970's, when winter-burning was initiated. Spring and summer growing season bums were initiated in the early 1980's (Robert Dye pers. comm.).

Plant Communities

Early accounts of the Myakka region suggest an almost treeless landscape of dry and wet prairies, and scattered pine flatwoods in which closed canopy hardwood forest occurred only as scattered, small "islands" and narrow borders along the river and lake systems. (Townshend 1875; Reid 1843). These are still the major habitat types present in Myakka River State Park today.

A large portion of the park (6,0000-7,000 ha.) consists of dry prairie, which contains a highly diverse mix of grasses (e.g. Aristida stricta, Schizachvrium scoparium, and Sorghastrum secundum) forbs (e.g. Rhynchospora plumosa, Lachnocaulon anceps, Pityopsis graminifolia, and Carphephorous odoritissima) low shrubs (e.g. Quercus geminata, Vaccinium darrowii, Ilex glabra, and Lvonia fruticosa), and saw palmetto (Serenoa repens). Florida dry prairie is a tire-maintained plant community that occurs only in south central and southwest Florida (Davis 1967, Harper 1927). This community has been globally ranked (G2) as threatened by The Nature Conservancy (Florida Natural Areas Inventory 1990). Dry prairie is the native habitat for several species of listed animals including Crested Caracara, Florida Grasshopper Sparrow and Florida Burrowing Owl, all species or subspecies which were common in the 1940's (Van Duyn 1941) but do not regularly occur in Myakka River State Park today.

Hundreds of small wetlands are scattered within dry prairie and flatwoods areas. These wetlands have seasonally fluctuating water levels, typically drying near the end of the dry season. Dominant species include Hypericum fasciculatum, Panicum hcmitomon, and Pontederia cordata.

Hammocks are closed canopy forests that are dominated by Quercus virginiana and Sabal palmetto. They occur along the Myakka River and lakes, and, in smaller patches adjacent to other wetlands. Groundcover is generally lacking or consisting of a sparse cover of herbs.

METHODS

We used Soil Conservation Service and Florida Department of Transportation aerial photos from the 1940's and 1980's to map vegetation in two selected areas within the park. We selected sites that currently have large amounts of dry prairie-hammock edge. The Wilderness Preserve site covers approximately 850 acres and the Mossy Island Hammock site covers approximately 1,500 acres. Site locations are shown in figure 1. In the earlier photographs, boundaries between areas with and those without canopy cover were quite distinct, as most canopied areas had 90 percent or greater tree cover. Boundaries between forested and nonforested communities were very sharp. In photos from the later series, these boundaries were not as clear. Ground-truthing was used for the 1990 series.

Wilderness Preserve areas with greater than 75 percent canopy cover in March 1948 and March 1985 were delineated. The majority of cover consisted of live oaks (Quercus virginiana), laurel oaks (Q. laurifolia), sabal palms (Sabal palmetto), and smaller numbers of South Florida slash pines (Pinus elliottii var. densa). Wetlands with woody cover of red maple (Acer rubrum), buttonbush (Cephalanthus occidentalis), willow (Salix caroliniana), or popash (Fraxinus caroliniana) were also included in the canopy-covered category. Wherever oaks (especially laurel oaks in wetter areas) invaded wetlands, the area was then classified as forested upland.

Mossy Island aerials taken in April 1940 and January 1986 were used both to delineate canopy-covered areas and to distinguish between forested and open wetlands. Species comprising upland and wetland woody cover in Mossy Island were the same as those comprising Wilderness Preserve upland and wetland cover.

Fires that occur during the growing season, after an extended dry period are hereafter referred to as dry growing-season bums. Reductions in the cover of woody vegetation after one dry growing-season bum in the Wilderness Preserve study area, and after two, or in some sections three, dry-growing-season bums in the Mossy Island Hammock area, are shown using the same mapping methods on aerial photography from November 1990.

Community boundaries were mapped and digitized into a PC ARC/INFO Geographic Information System computer database. The digital maps were transformed into state plane coordinates, and areas occupied by the vegetation types were calculated. The aerial photographs were not rectified; because landmarks had changed during the course of 40 years, it was sometimes difficult to locate registration points precisely. Transforming maps to state plane coordinates helped minimize errors resulting from the use of unrectified aerials. We also used percentage of area covered rather than total acreage to compensate for unrectified aerials.

Field observations were used for descriptions of vegetation composition and change in the mapped areas. Fire and weather records kept at Myakka River State Park were consulted for information on fire conditions.

RESULTS

Before Fire Suppression (1940's Maps)

In the 1940's vegetation cover of the two study areas was predominantly open, with non-woody vegetation the dominant cover type. Open prairie reached to the lake shore in both series (see Figs. 2 and 3). Most wetlands were open, with very few forested or woody wetlands. Hardwood hammocks occurred in small areas closely associated with wetlands.

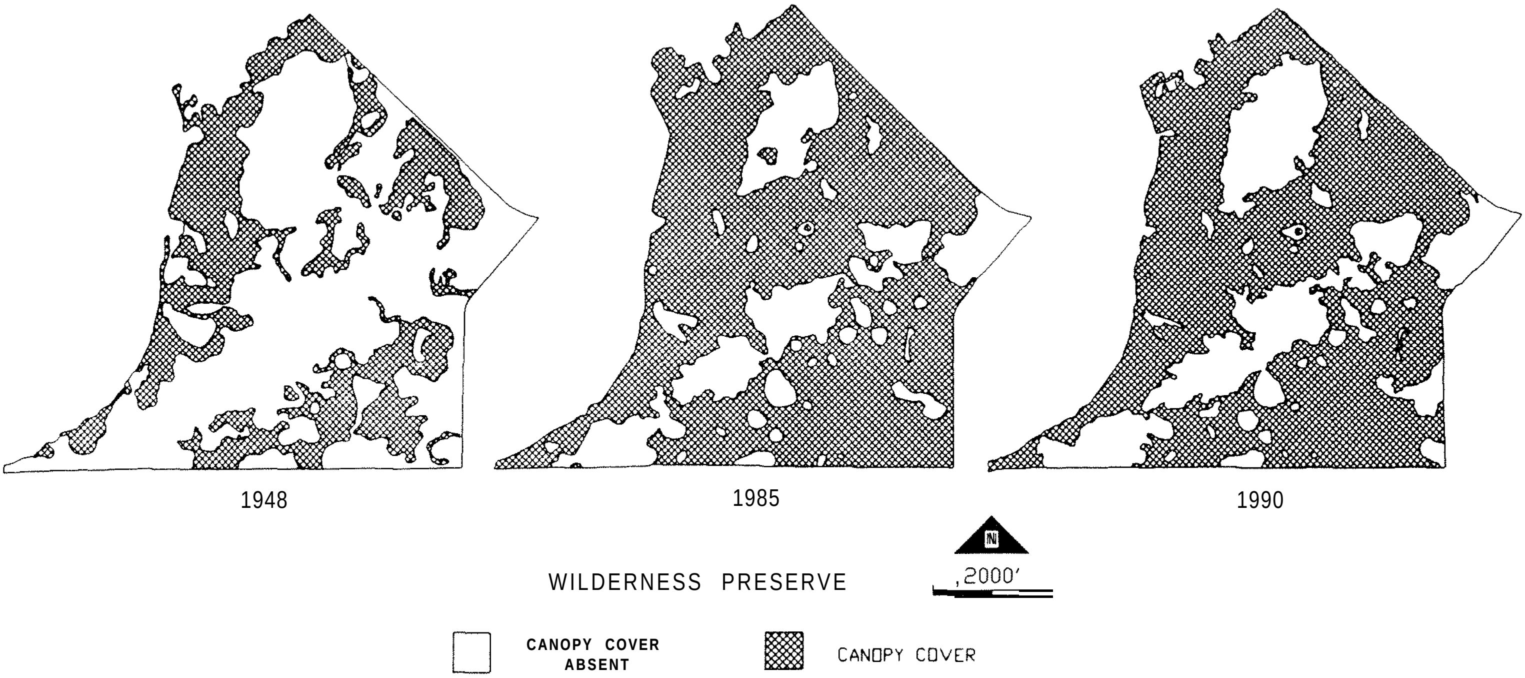
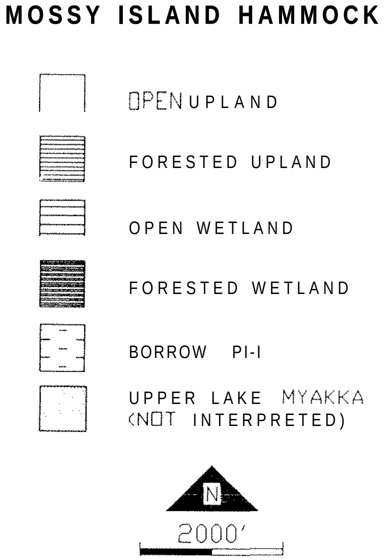


Fig. 2.- Wilderness Preserve canopy cover in 1948 before fire exclusion; in 1985, after fire exclusion; and in 1990, after one dry-growing season bum. Shaded areas indicate canopy cover. The north, east and southern edges are bounded by roads. The west side is bordered by the marshes of the Lower Lake Myakka.



After Fire Suppression (1980's)

Uplands - In both sites woody canopy coverage (mostly *Quercus virginiana* and Q. laurifolia) increased dramatically from 1948 to 1986.

Where oaks were adjacent to dry prairie or pine flatwoods they expanded into these habitats (Figs. 2,3). In the Wilderness Preserve Series (fig. 2) open areas decreased from 66 percent to 26 percent of the total area (fig. 4). In the Mossy Island series (fig. 5) dry prairie decreased from 58 to 39 percent of the total mapped area. Nearly all of this decrease is traceable to the large increases oak stands. It is important to note that oak canopy stands that have expanded into dry prairie since the 1940's are very different from the original oak hammocks. Oak stands that have developed during fire exclusion have a dense palmetto understory (Fig. 6). In contrast, the older, pre-fire-exclusion hammock has an open understory or a sabal palm understory (Fig. 7), with palmettos only along hammock fringes. It is this border fringe of oaks and palmettos that have expanded tremendously during the period of fire suppression.

Wetlands - Nearly half of open wetlands were lost between the 1940's and 1986 (Figs. 2 and 3). In the Mossy Island series in 1940 most wetlands were open and grassy, and wetlands of this type constituted 14 percent of the total area. In 1986 many wetlands were dominated by trees or shrubs and open wetlands constituted only 8 percent of the total area.

Areas of forested wetlands increased from 1 to 4 percent of the total area. This change accounts for 37.5 percent of open wetland loss. Fifty-one percent of open wetland reduction

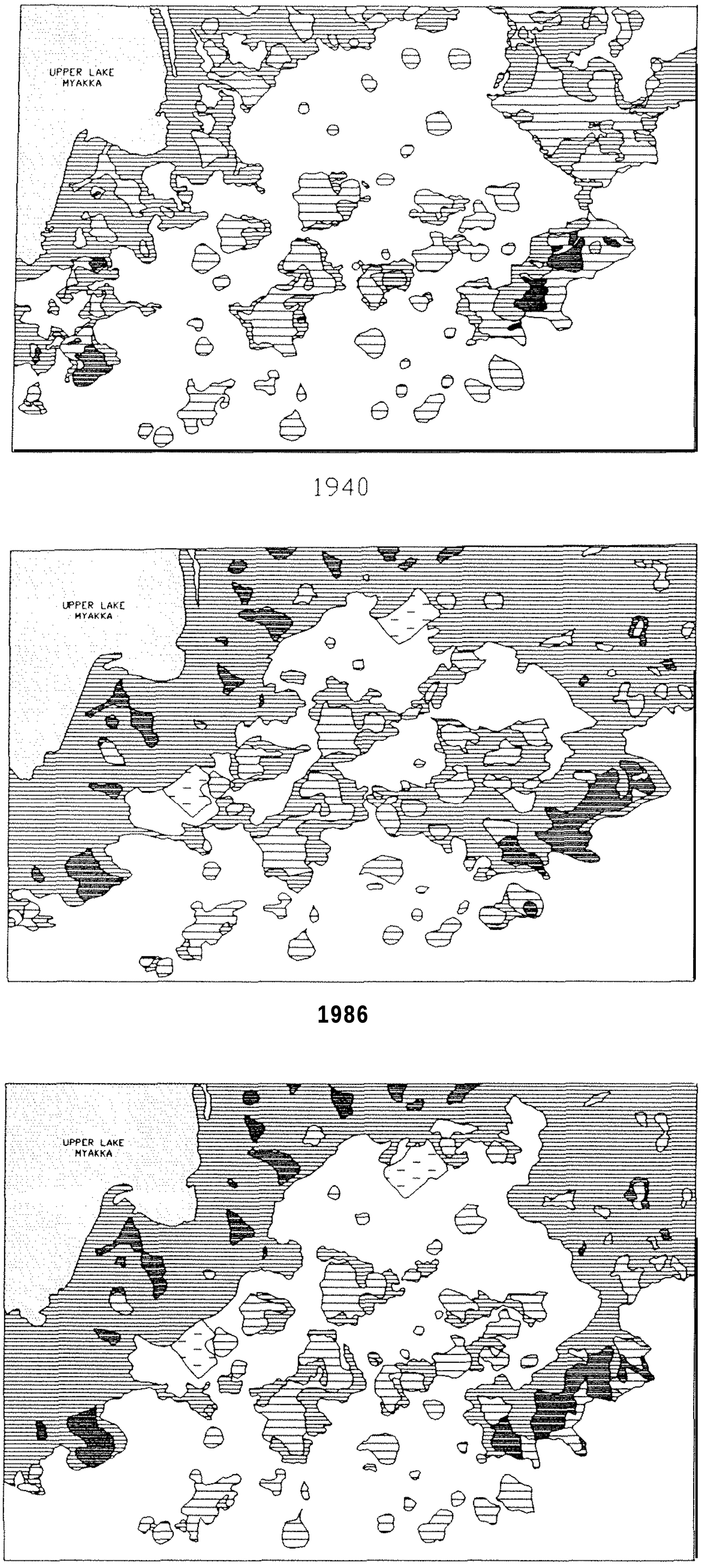


Fig. 3.- Mossy Island Hammock study site vegetation in 1940 before fire exclusion; in 1986 after fire exclusion; and in 1990, after two dry-growing season bums.

represents shifts to the forested upland category. Construction of a shallow drainage ditch (combined with fire exclusion) contributed to the extensive change from wetland to oak cover in the northeast section of the map. The remaining open wetland reduction is represented by the open wetland area that was converted to shallow borrow pits.

All woody species were mapped as a group, however there were several patterns apparent in woody species increase in wetlands. Open wetlands that are surrounded by hammock are less likely to bum as often as wetlands surrounded by dry prairie. These wetlands were the most likely to change from open herbaceous to woody cover during the period of fire exclusion. This change was especially rapid in floodplain wetlands along the river and lake, and in other wetlands that contained areas of hardwoods in 1940 (compare 1940 and 1986 maps in Fig. 3).

Woody species, including Mvrica cerifera (wax myrtle), Fraxinus caroliniana (popash), Salix caroliniana (willow), and Cephalanthus occidentalis (buttonbush), expanded their coverage of formerly grassy wetlands. The most common woody colonizer of small floodplain marshes was popash. This species was not observed, however, to colonize isolated, prairie wetlands. Laurel oaks often moved into the outer zones of wetlands bordered by hammocks. Very little oak cover increase occurred in wetlands that did not have adjacent hammock.

Cover type	Percentage of cover	
	1948	1986
Open uplands and wetlands	66	26
Closed canopy uplands and uet lands	34	74

Fig. 4.-Vegetation cover Wilderness Preserve, Myakka River State Park.

Cover type	Percentage of cover	
	1940	1986
Open upland	58	39
Forested upland	18	39
Open wetland	14	8
Forested wetland	1	4
Borrow pits	0	1
Upper lake	9	9

Fig. 5.- Vegetation cover of Mossy Island Hammock, Myakka River State Park.

Fig. 6.- Live oaks with dense saw palmetto understory typical of areas where oak has expanded into dry prairie since the 1940's.

In both floodplain hammock and prairie-bordered ponds wax myrtle sometimes established in the outer zones. Willow, buttonbush or more rarely, maple, colonized or expanded coverage in the deeper, more central wetland zones.

After Reintroduction of Fire (1990 maps)

Prescribed burning was initiated at Myakka River State Park in the late 1960's. Burning in the sixties and seventies halted the expansion of young oaks but resulted in little or no reduction of existing canopy cover. Because fires were conducted in the traditional manner during the dormant-season (winter), at times when fuel moisture and water table levels were relatively high, fires did not move into the oak-palmetto areas. Fire also did not move into wetlands with increased woody vegetation. Growing-season prescribed bums were initiated in the park in 1983, but it was not until 1986 that a bum moved into oak-palmetto and woody wetland areas.

Mossy Island Hammock. Three bums have occurred in the Mossy Island Hammock area between 1986 and 1990. On May 31, 1986, at the end of a long dry season a fire, resulting from a natural ignition, occurred in the Mossy Island Hammock area. Prior to this fire, the area was last partially burned by a lightning-ignited tire which occurred on August 21, 1985. This fire occurred late in the afternoon and was accompanied by high humidities and rain. Typical of earlier bums it did not result in any significant reduction in oak or woody wetland species cover (Robert Dye pers. comm.). The effects of the May, 1986 bum were quite different from those of previous bums. Many oaks that had invaded dry prairie since 1940 were damaged severely. Some individuals with d.b.h. over 12 inches were killed outright; epicormic and basal resprouting occurred on others. This tire was the first to cause substantial reductions in oak canopy cover.

A second growing-season headfire burned into the same area on June 30, 1988. This fire took place under only moderately dry conditions but also killed many oaks that presumably had already been weakened by the first fire. These bums demonstrated that fire can cause mortality of large oaks when a palmetto understory is present. Slash pine also survived the fire (Figure 8). No oaks in the older hammock areas without palmetto understory were killed. Areas in which oak cover burned corresponded to areas that were dry prairie in 1948 (see figs. 4 and 5).

The Mossy Island Hammock series also shows changes in woody-wetland vegetation. Wetland water levels at the time of these fires were low, especially during the 1988 bum. This allowed fire to sweep across wetlands, reducing woody species cover.

The western portion of the Mossy Island Hammock study area burned once more, on May 11, 1990, with an intense bum. The remainder of the area burned on May 24 and 3 1, 1990 with a milder bum. The 1990 map of the Mossy Island Hammock series (fig. 3) shows the extent of woody species cover reduction following the 3 bums of June 1986, June 1988 and May 1990.

Wilderness Preserve. The Wilderness Preserve area was burned in May 1983 under high humidities without any significant reduction of oak cover (Robert Dye, park manager, pers. comm.). The first growing-season fire under dry conditions occurred in this area on June 1, 1989. This fire occurred during a period of very low wetland water levels and low humidities and reduced oak canopy coverage in oak-palmetto areas that had established during the period of fire exclusion. The 1990 Wilderness Preserve series map in figure 2 shows the extent of hardwood canopy reduction in 1990 after the dry growing-season tire of June 1, 1989.

This fire occurred 90 days after the last 1/2 inch rain when nearly all wetlands were without standing water. The fire burned into wax myrtle, willow, popash and buttonbush in areas that had increased in cover since 1948. The fire reduced woody cover in wetlands and resulted in a return of characteristic herbaceous species such as Panicum hemitomom (maidencane) and Polygonum punctatum (smartweed). No previous prescribed bum had touched these areas.

DISCUSSION

Fire suppression and vegetation change

When fire suppression occurs the boundaries between habitat types change (Myers 1985; Platt and Schwartz 1990). Our data suggests an expansion of a habitat type with elements of dry prairie and hammock but which is actually neither. This oak-savanna, fringing habitat type only, not the original hammock, increased during the thirty-year period of tire exclusion. The dense cover of palmetto still present in the understory of this new habitat type burned under dry-condition prescribed fires and contributed the fuel that resulted in oak mortality. These processes cause this boundary type habitat between dry prairie and oak-palm hammock to be very dynamic, expanding and contracting with varying fire regimes, while true hammock areas remained more stable.

While aerial photography can be used to illustrate oak canopy cover increases and decreases, the changes within dry prairies are more difficult to document. In the absence of fire shrubs and palmetto are known to increase, both in cover and height (Givens and others 1982; Hilmon 1969). These increases may occur at the expense of the herbaceous element of the dry prairie flora. The increase in palmetto and woody shrubs alters fire intensity and behavior, causing less frequent, more

Fig. 7.- Original hammock with live oaks and sabal palms, note absence of saw palmetto understory.

Fig. 8.- Fire kill and stress of live oaks in Mossy Island Hammock area, 1991. South Florida slash pines survived fires that killed large oaks.

intense tires, which may contribute to oak mortality. However the reintroduction of fire, even during the dry growing-season, does not appear to be sufficient to control increased amounts of saw palmetto occurring as a result of altered fire regimes (pers. obs.).

Fire and Hardwood Mortality

Only dry growing-season fires were observed to move into shrub-dominated wetlands. Although other tires occasionally impacted the edge of the oak palmetto zone only dry growing-season fires were observed to move far into this zone and cause mortality in large oaks. These results are similar to those found by (Platt and others 1991), who found that spring fires caused the highest mortality rates for oaks in sandhill habitats in north Florida. They found that tire temperature was not a significant factor in their study of oak mortality but suggested that the phenological state of the vegetation was the most critical factor. We suggest that dry conditions appear to cause added stress to oaks making them even more vulnerable to fire during the growing season.

Management Considerations

Fire management plans often are implemented in areas that have previously had a history of fire suppression. When managing a natural area it is important to consider the vegetation changes that occurred during these fire suppression periods.

When reversal of fire exclusion changes is a management goal growing season bums are very useful for obtaining hardwood control. The growing season is recognized as the “natural” fire season in Florida. Growing season bums are known to stimulate flowering of some species and kill invading oaks (Platt and others 1991). Our present study demonstrates the success of dry growing season fues in restoring herbaceous wetlands and reducing oak-palmetto fringe habitat. Many recognize the probable significance of spring drought fires (Robbins and Meyers 1989; Wade and others 1980), however, few managers of natural areas use prescribed tire under spring drought conditions.

Fires occurring under very dry conditions are more difficult to control and more likely to spot for long distances. These considerations must be taken into account but experienced fire managers can conduct successful bums in very dry conditions.

A dry growing-season bum should not be implemented in areas with large fuel accumulations. A fuel reduction bum may be required in these cases and it may be necessary to take special precautions such as removing fuel that has accumulated around the bases of pines before attempting a dry growing-season fire. General sensitivity of pines should be considered. It is important to think about any other possible sensitive elements before conducting bums under very dry conditions.

CONCLUSIONS

In the absence of frequent tire, oaks colonize dry prairie and wetland edges, and hardwood wetland species increase dramatically within wetlands. Where plant communities depend on frequent fire for maintenance, even a few decades of fire exclusion can cause major changes in dominant woody vegetation. The maintenance of open, grassy, dry prairie and wetlands in South Florida is dependent on frequent burning.

The reintroduction of fue after an extended period of tire exclusion, however, does not always reverse the abundance of woody species that have increased as a result of altered fire regimes. Prescribed fire usually does not move into long excluded areas that have oak canopy cover. Even when tire does occur in these areas usually very low or no mortality of well-established hardwoods occurs.

Observations of dry growing-season bums at Myakka indicate that such bums, which usually occur in South Florida at the end of the dry season and the beginning of the lightning season (April and May) may be an important element of habitat management. Conducting all bums under conditions when fuel moisture and water levels are high may be causing significant shifts to occur in vegetation, especially in wetlands. Growing season bums under dry conditions at the end of the dry season, were almost certainly part of the presettlement fire regime. At least a periodic bums of this type may be necessary for the long-term maintenance of wetland plant communities.

Dry growing-season bums have also been observed to kill well-established hardwoods -- large oaks in dry prairie and various woody species in wetlands. In areas where hardwood cover has increased as a result of long-term fire exclusion or long intervals between fires, dry growing-season fire therefore is an important component of a fire management plan where restoration and reversal of tire-exclusion effects is a management goal.

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LITERATURE CITED

Alexander, T.R., and A.G. Crook. 1973. Recent and long-term vegetation changes and patterns in south Florida. Final Rep. Part 1. USDI Natl. Park Serv. NTIS No. PB 231939.

Chen E. and J.F. Gerber. 1990. In (R. Myers and J. Ewel, eds., Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

Davis, J. H., Jr. 1967. General map of the natural vegetation of Florida. Circ. S-178, Inst. Food Agric. Sci., Agric. Exp. Stn., University of Florida, Gainesville.

Fitzgerald, S.M. 1990. Small mammal, bird and plant responses to the rehabilitation of a dry prairie grassland association using fire and roller chopping applied in two seasons. Unpublished thesis, Univ. of Florida. Gainesville.

Florida Natural Areas Inventory and FL. D.N.R. 1990. Guide to the natural communities of Florida. Tallahassee, Florida.

Givens, K. T., J. N. Layne, W. G. Abrahamson and S. C. White-Schuller. 1982. "Structural changes and successional relationships of live Florida Lake Wales Ridge plant communities". Bulletin of the Torrey Botanical Club. 111:8-18.

Harper, R. M. 1927. Natural resources of Southern Florida. 18th Annual Report of the Florida State Geological Survey.

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20:287-304.

Hilmon, J. B. 1969. Autecology of saw palmetto (Serenoa repens (Bartram) Small). Phd. Dissertation. Duke University.

Myers, R.L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bull. of the Torrey Bot. Club 112:241-252.

Miller, J., J. Huffman and J. Morris. 1983. The changing landscape of North Port, Florida. Unpublished Report, Environmental Studies Program, New College of the Univ. of S. Florida. Sarasota, Florida.

Platt, W.J. and M.W. Schwartz. 1990. Temperate hardwood forests. In (R. Myers and J. Ewel, eds.), Ecosystems of Florida. University of Central Florida Press, Orlando.

Platt, W.J., J.S. Glitzenstein and D.R. Streng. 1991. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. In Proceedings of the Annual Tall Timbers Fire Ecology Conference 1989. Tallahassee, Florida.

Reid, S. 1843. U.S. survey notes and plats for Township 37 South Range 20 East and Township 36 South Range 20 East. Florida Department of Natural Resources, Tallahassee.

Robbins, L.E. and R.L. Myers. 1989. Seasonal effects of prescribed burning in florida: a review. Nongame Wildlife Report. Florida Game and Freshwater Fish Commission Nongame Wildlife Program. Tallahassee, Florida.

Townshend, F.T. 1875. Wildlife in Florida. Hurst and Blackett London, England.

Van Duyn, G. 1941. Biological reconnaissance, Myakka River State Park, Florida, with preliminary check lists of vertebrate fauna. Unpublished Report Florida Park Service.

Wade, D., J. Ewel and R. Hofstetter. 1980. Fire in South Florida eosystems. U.S.D.A. Forest Service General Technical Report SE-17. Southeastern Forest Experiment Station Asheville, North Carolina.

LIVESTOCK GRAZING ALTERS SUCCESSION AFTER FIRE IN A COLORADO SUBALPINE FOREST

William L. Baker[1]

Abstract-Plant succession after tires is often considered a relatively predictable process, yet the possibility of alternative outcomes, or multiple stable states, has not been thoroughly studied. The present study makes use of field data collected along a livestock exclosure fence on a site near Pikes Peak, CO, at an elevation of about 3350 m. These data suggest that the west-facing part of the site was once occupied by a subalpine forest dominated by *Picea engelmannii* and that this forest was burned in about A.D. 1867. Livestock grazing discouraged tree regeneration until a major decrease in use in the mid-1940's. On the grazed side of the fence, the forest became dominated by *Pinus aristata,* a tree commonly found on drier, rockier sites like that produced on this moister site by heavy grazing. On the ungrazed side of the fence *Picea engelmannii* appears to be regaining its dominance. This is an example of extrinsically produced alternative outcomes, a successional result that warrants further study.

INTRODUCTION

Plant succession after fires and other natural disturbances has traditionally been viewed as a relatively predictable process ending in reestablishment of the predisturbance climatic climax vegetation. This traditional postfire succession model, which derives from the ideas of Clements (1916), has formed the basis for much research on postfire succession (e.g. Fischer and Bradley 1987). The possibility of relatively permanent alternative outcomes, or multiple stable states (Holling 1973), has been raised (Jameson 1987) but has not been demonstrated with empirical data.

The multiple stable states model was developed to account for the observation that some ecological systems can be moved into alternative states by insect outbreaks, overgrazing, overfishing, pollution, and other disturbances. The essential characteristics of a system with multiple stable states is that the original state is not regained once the disturbance is discontinued (Holling 1973). The existence of multiple stable states can be demonstrated theoretically (e.g. May 1977), but the empirical evidence for their existence has been challenged (Conncll and Sousa 1983). Connell and Sousa suggest that all purported examples fail for one or more of three reasons: (1) the physical environment is different in the different alternate states; (2) the alternate states persist only when disturbances are maintained; or (3) the evidence is simply inadequate.

Succession after fires in southern Rocky Mountain subalpine forests is often slow and variable (Stahelin 1943; Veblen and Lorcnz 1986). There is some evidence of failure to restore pre-fire tree composition (Veblen and Lorcnz 1986), but no clear evidence of multiple stable states. The evidence presented here suggests that livestock grazing following a fire can alter the course of succession, and that the result may be a potentially stable alternative forest.

STUDY SITE

The study site consists of two hillsides in a subalpine forest about 7 km south-southeast of the summit of Pies Peak, Colorado (figs. 1 and 2). The forest is now dominated by bristlecone pine (*Pinus aristata*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Smaller numbers of limber pine (*Pinus flexilis*) are present. Elevation of the sloping study area ranges from 3,290 to 3,400 m. Treeline is at about 3,650 m.

The study is focused on vegetation on two sides of a fence that prevents livestock that graze on a U.S.D.A. Forest Service allotment south of the fence from entering a protected watershed owned by the City of Colorado Springs (fig. 1). The fence was installed between 1890 and 1902, and the watershed on the north side has not been grazed by livestock since that time (Personal communication, Bennie Baucom, Superintendent, Water System Operations, City of Colorado Springs). The Forest Service lands south of the fence are part of the Deer Park Unit of the Beaver C&H Allotment, which has been a designated cattle allotment since the early 1900's (U.S.D.A. Forest Service, Pikes Peak Ranger District records). Forest Service records of grazing levels in this allotment are spotty, but by the 1950's grazing had been reduced to less than 20 percent of the 1930 level (fig. 3a). Evidence of excessive use was apparent by the 1930's. In 1934, Forest Ranger William Cochran commented in a memo to the Forest Supervisor that "...a very heavy reduction of the present use must be made" (Working Plans, Pikes Peak District Office, Colorado Springs). The site was burned by a large forest fire, which is discussed below. The fire burned both sides of the fence and much of the area in figure 2.

METHODS

Six 20- by 50-m (0.1 ha) plots were sampled. Plots 1, 3, and 5 were on the south (grazed) side of the fence, and plots 2, 4, and 6 were on the north (ungrazed) side of the fence.

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[1] Assistant Professor of Geography and Recreation, University of Wyoming, Laramie, WY 82071.

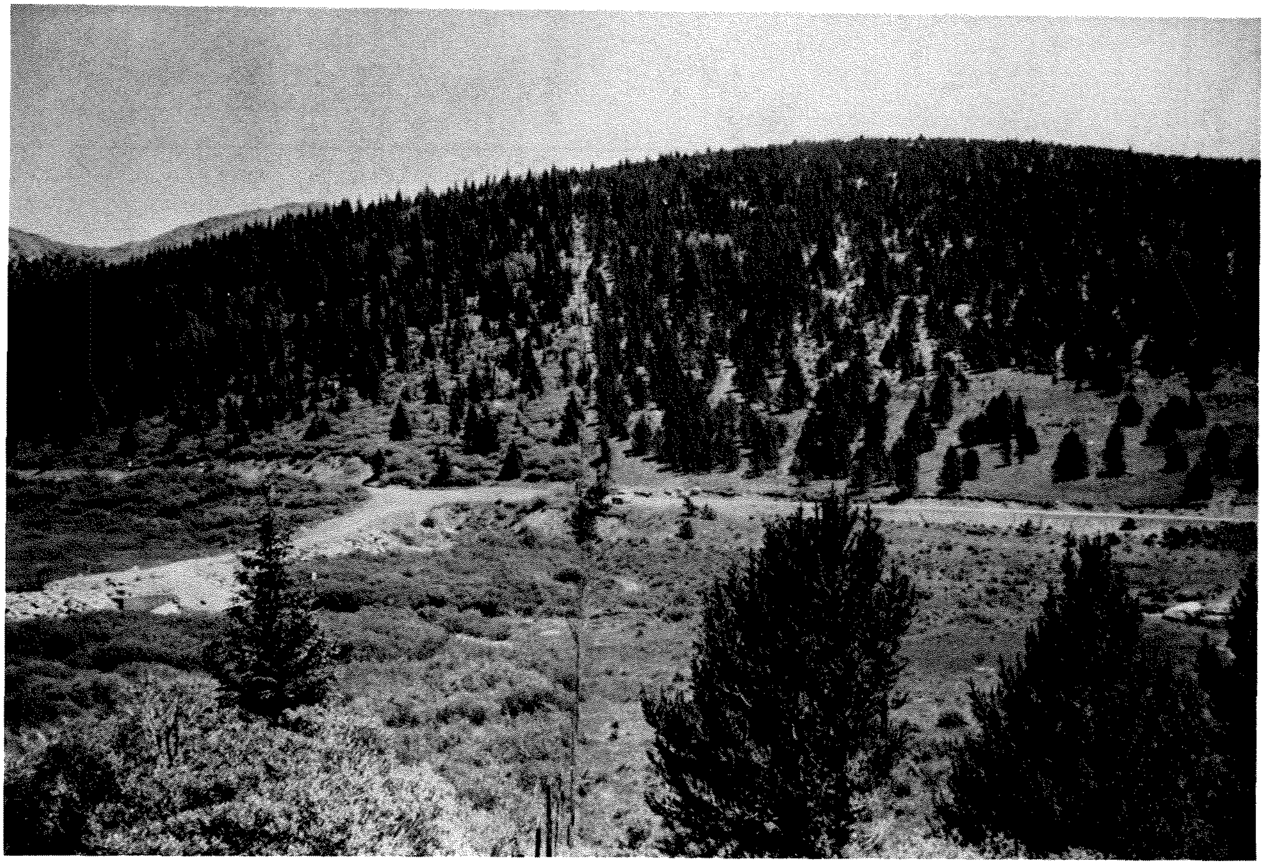

Figure 1.-Looking east along the fenceline at the west-facing part of the site. The ungrazed side, with abundant *Picea engelmannii* and *Salix*, is on the left, and the grazed side, with abundant *Pinus aristata* is on the right. The fire burned across the entire hillside.

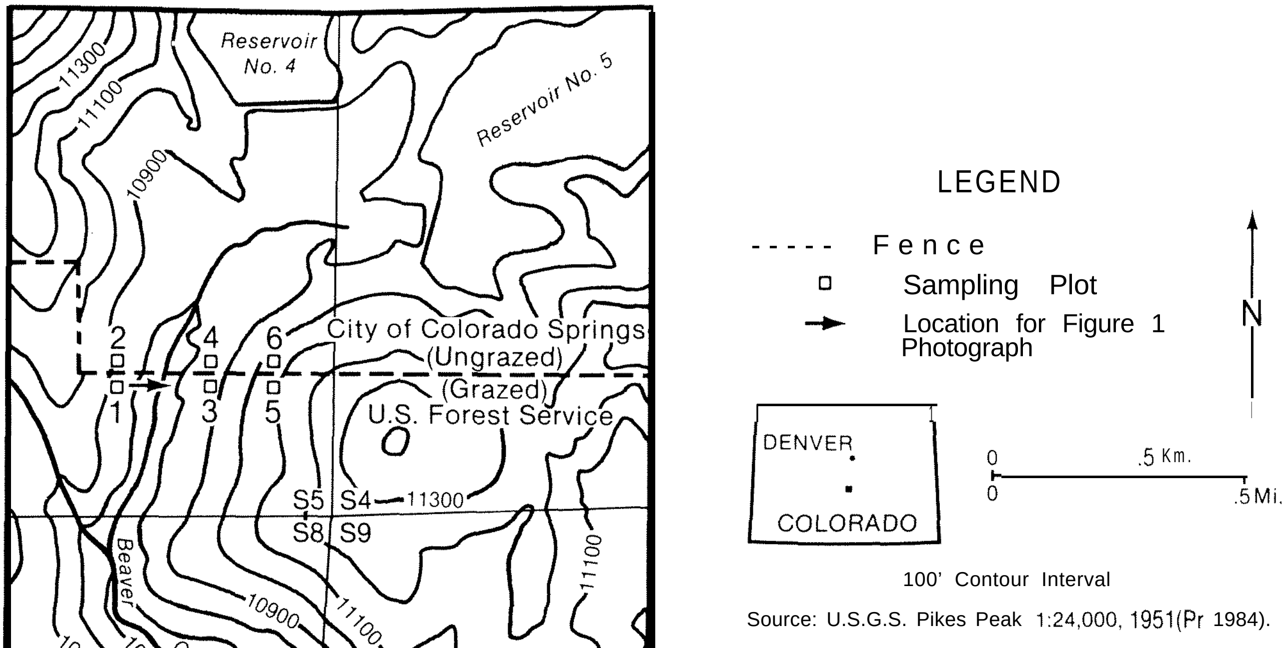

Figure Z.-Study area map.

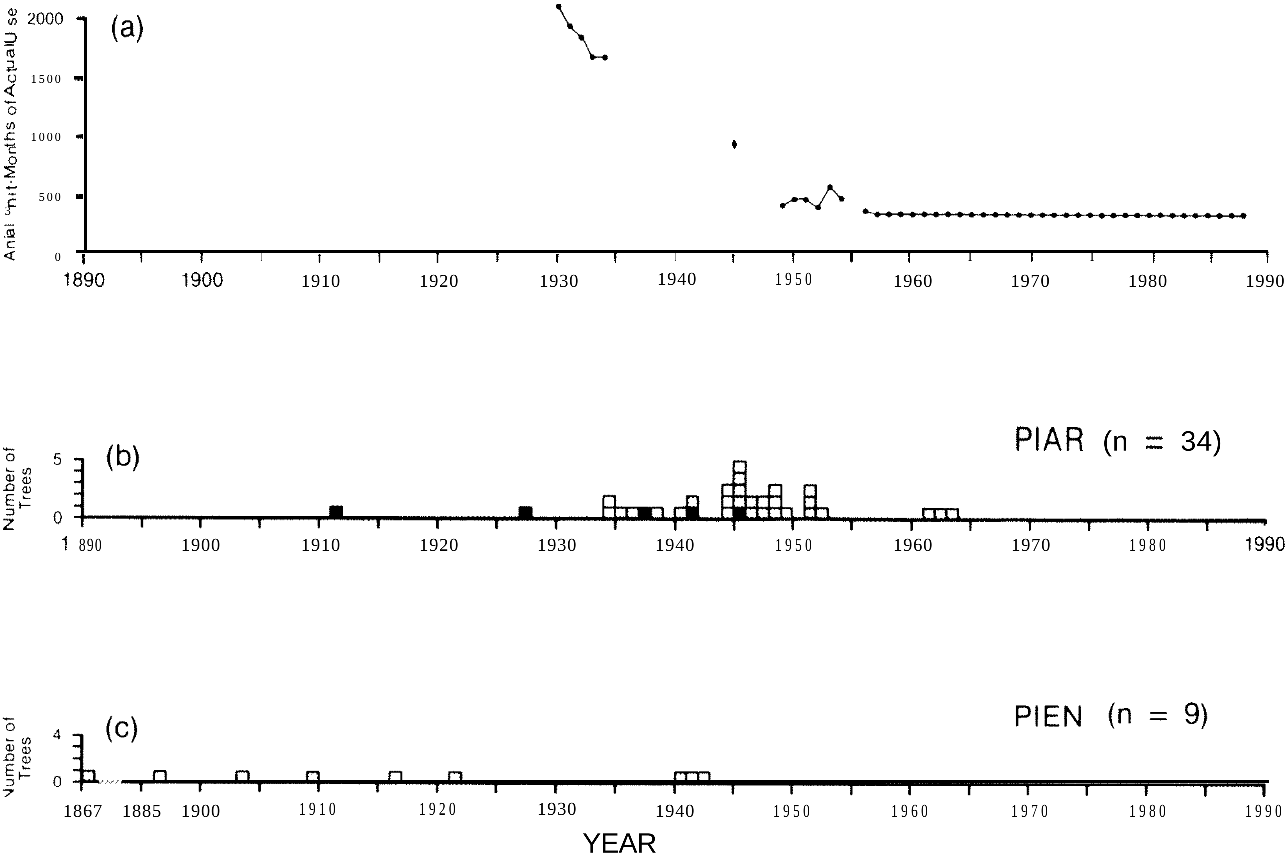

Figure 3.-(a) History of cattle use on the Deer Park Unit of the Beaver C&H Allotment. Data are from U.S. Forest Service-Pikes Peak Ranger District records. (b) Dates of establishment of largest Pinus aristata. Solid bars are dates from cores that contained the actual center of the tree. Shaded bars are dates estimated from cores that were close to containing the center (three or fewer years added to estimate the date). Unshaded bars are dates from cores that were an estimated 4-8 years from containing the center. (c) Dates of establishment of largest Picea engelmannii. The shading is as in (b).

Elevation, aspect, and slope were identical in adjoining plots (table 1). In each plot I tallied all trees, including seedlings and saplings, by size class. Seedlings are defined as stems <5 cm diameter and < 1 m tall. Saplings are <5 cm diameter and > 1 m tall. The remaining size classes, beginning at 5.0 cm diameter, are all 5 cm wide (e.g. 5 to 9.99 cm).

To determine the composition and structure of the prefire forest, we tallied by size classes the standing dead 'and downed trees killed by the fire in plots 5 and 6. Standing dead trees were not sufficiently abundant in the other plots. Nearly all the trees killed in the fire could be identified to species, and most stems remained intact, although smaller trees probably were consumed by the fire.

To determine the approximate date when trees became established following the fire, we removed increment cores from the bases of 34 of the largest P. aristata and 9 of the largest P. engelmannii. The cores were sanded, and each core's rings were counted under a stereomicroscope. When the core did not extend to the center of a stem, the number of additional rings needed to reach the center was estimated.

Table 1. --Environmental data for the six fenceline plots.

Plot	Environmental variables		
	Elevation	Aspect	Slope
	Meters	-----Degrees-----	
1	3,307	100	22
2	3,307	100	22
3	3,307	285	20
4	3,307	285	20
5	3,377	270	19
6	3,377	270	19

First the radius of the circle that contained the first ring on the core was estimated. Then the number of rings that might occur within that radius was estimated by multiplying the radius in cm by the average density of rings over the length of the core (rings/cm of core).

The date of the forest fire was determined by cross correlating tree-ring width variations in 14 standing dead burned trees with ring-width variations in the Almagre Mountain master chronology developed by the University of Arizona's Laboratory of Tree-Ring Research (Drew 1974). This chronology is from a site approximately 2 km east of the study area. Tree-ring widths were measured with a stereomicroscope and a computer-assisted Henson incremental measuring machine. Ring-width time series were corrected for growth trends by fitting a negative exponential or straight line to each series. The series were then standardized. INDEX, a program produced by the University of Arizona's Laboratory of Tree-Ring Research (Graybill 1979), was used to perform these computations. Each series, including the Almagre Mountain series, was then pre-whitened by fitting standard autoregressive-moving average (ARMA) time series models. This is necessary to avoid spurious results from cross-correlation (Yamaguchi 1986). The last year of growth present on each burned tree was then determined by floating each time series against the Almagre Mountain chronology and locating the highest cross-correlation coefficient.

RESULTS

The fire probably occurred in A.D. 1867. Many of the last years of growth present on the burned trees, based on the ring-width cross correlations, are near that date. Last years of growth for 14 burned trees were: 1867, 1867, 1866, 1866, 1861, 1861, 1860, 1858, 1856, 1851, 1847, 1840, 1828, and 1815. The last year of growth is not necessarily the fire year, as the fire might have burned into the stem, removing the outer part of the core. Thus the evidence from the burned trees only suggests that the fire occurred in or after 1867. The abundance of dates in the 1860's suggests that the fire occurred within a few years of 1867. The oldest living tree (P. engelmannii) contained 121 rings and an estimated one additional ring to the center, for a pith date of A.D. 1867, suggesting that 1867 was the actual fire year.

The prefire forest on the west-facing part of the site was dominated by P. engelmannii. Stems in diameter classes from about 15 to 25 cm were most numerous, and only a few P. aristata were present (fig. 4). The null hypothesis that the prefire size class distribution for P. engelmannii in plot 5 does not differ from the prefire distribution in plot 6 (across the fence) cannot be rejected at the 0.05 level of significance (chi-square=8.70 and d.f. =6).

Five of eight postfire P. engelmannii became established between 1886 and 1921, whereas most of the largest P. aristata originated between 1934 and 1952 (Fig. 3c, 3b).

While prefire size class distributions in adjoining plots on opposite sides of the fence had not differed significantly, there were significant differences between postfire size class distributions (fig. 4). In general, P. aristata was much more abundant on the grazed side of the fence, particularly in the west-facing plots (3-6). The null hypothesis, that P. aristata age class distributions were the same on both sides of the fence, was rejected at the 0.05 level of significance (chi-square=51.86 and d.f. =6), for paired plots 1 and 2, but could not be tested for the remaining plots (too many zero entries). Nonetheless, these distributions are completely different (fig. 4). P. aristata is much more common on the grazed side of the fence, and P. engelmannii was generally much more abundant on the ungrazed side of the fence (fig. 4). The null hypothesis, that P. engelmannii distributions were the same on both sides of the fence, was rejected at the 0.05 level of significance for paired plots 3 and 4 (chi-square=16.41 and d.f. =5) and paired plots 5 and 6 (chi-square=53.59 and d.f. =6), but could not be tested for paired plots 1 and 2. Populus tremuloides was also more abundant on the ungrazed side of the fence, but was absent from both plots 3 and 4 (fig. 4). The null hypothesis, that P. tremuloides distributions were the same on both sides of the fence, was rejected at the 0.05 level of significance for paired plots 1 and 2 (chi-square=22.36 and d.f. =3).

DISCUSSION

These data suggest that a wildfire in A.D. 1867 burned a west-facing hillside subalpine forest that was dominated by P. engelmannii. P. engelmannii began reestablishing on the burned hillside immediately after the fire, but had not fully reoccupied the site when livestock grazing began. Grazing probably occurred on both sides of the fence until the fence was installed sometime between 1890 and 1902. P. engelmannii continued to reestablish on both sides of the fence, but at a slower rate on the south side due to livestock use. When the intensity of livestock use was decreased to 20 percent of its former level, in the 1940's, the environment had been modified by the effects of grazing on the vegetation. As a consequence, the site probably had lower cover of Salix and other subalpine plants (as is apparent now--fig. 1), and thus greater insolation received at ground level, resulting in an effectively drier site. P. aristata is typically found on drier, more southerly-facing, rockier sites, often in close proximity to moister, more northerly-facing, less rocky P. engelmannii sites (Baker, unpublished data). The grazing may thus have shifted the environment on this site toward one favoring P. aristata establishment. When grazing was decreased, establishment was not possible. Pearson (1934) has described a similar pattern in which Pinus ponderosa establishment was favored when heavy grazing, which decreased competition from grass, was followed by lighter grazing, that allowed tree seedlings to survive.

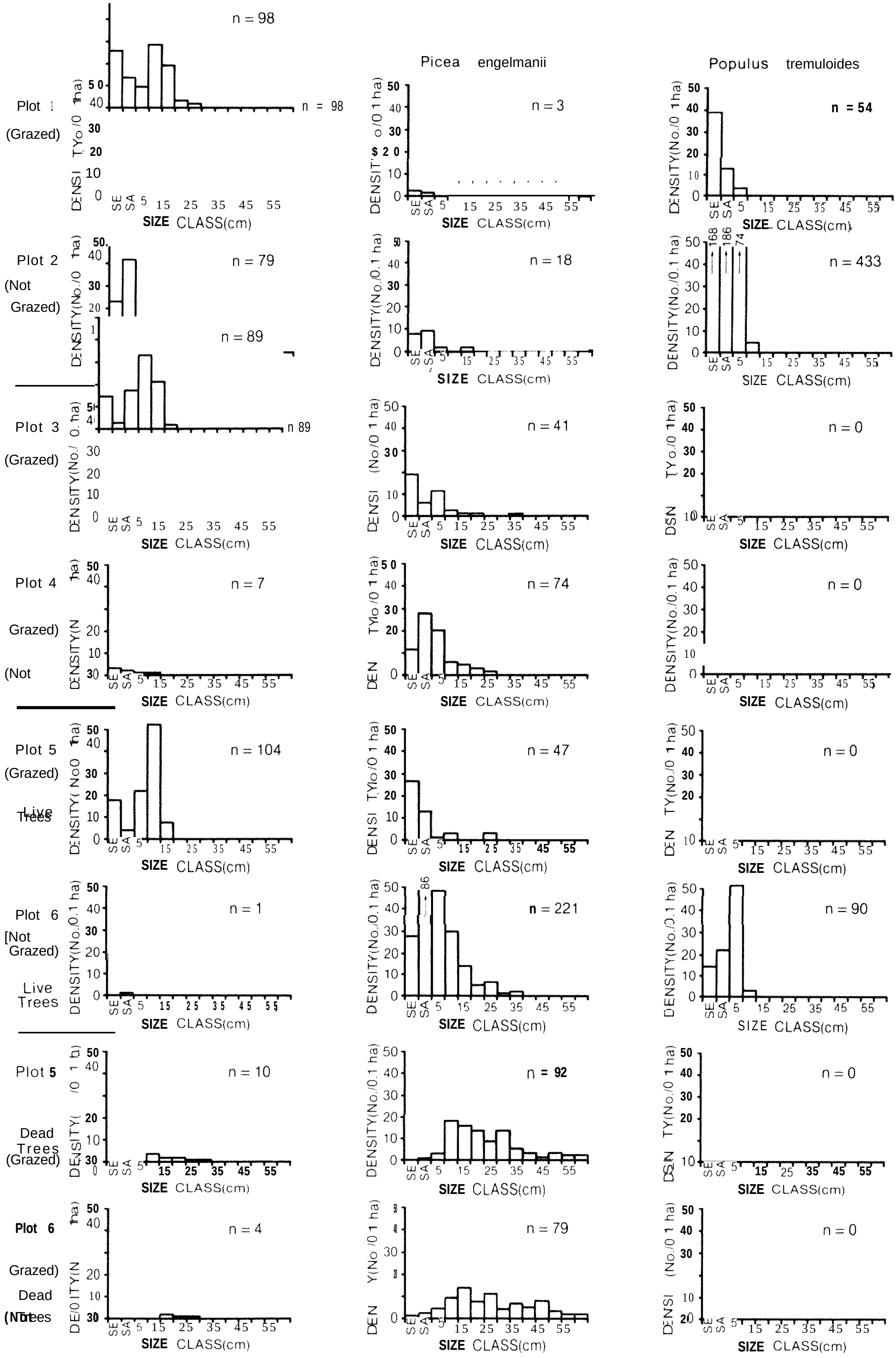

Figure 4.-Size class distributions for all live trees present in the six fenceline plots and for dead and downed trees in plots 5 and 6. Size classes are: SE=Seedlings (< 1 m tall and <5 cm diameter), SA=Saplings (> 1 m tall and <5 cm diameter). Other size classes are 5.0 cm wide, with the label indicating the lower limit of the size class.

It is not known whether the P. aristata and P. tremuloides postfire forest on the east-facing part of the site (plots 1 and 2) represents reestablishment of the prefire forest. The prefire composition is unknown. P. aristata is common in the postfire forest on both the grazed and ungrazed sides of the fence, suggesting that on this part of the site grazing is not the primary reason for P. aristata abundance. This part of the site is probably drier, however, because its aspect is somewhat more southerly than that in plots 3 to 6. This drier environment may have favored P. aristata postfire establishment even without grazing.

The pattern of succession on the ungrazed part of the west-facing burned hillside has been as expected. P. engelmannii has returned and has reestablished dominance. In the grazed area on this hillside, however, P. engelmannii has not reestablished dominance. P. aristata has achieved dominance and will likely retain it for some time. The traditional successional model is not appropriate in this case.

Is this, then, an example of multiple stable states? The case described here fails to fulfill Connell and Sousa's (1983) first criterion, as the environment is different on opposite sides of the fence and the difference is the result of an extrinsic influence--overgrazing. The environment is different because Salix is nearly absent from the grazed side of the fence (Fig. 1). This results in a different microenvironment on the two sides of the fence at ground level. The case described here does, however, meet the second criterion of Connell and Sousa, as the alternative state would persist if the disturbance were excluded. Excluding livestock from the south side of the fence could conceivably reverse most of the abiotic effects of grazing and even some of the biotic changes, but the P. aristata population is firmly established and is not likely to die if livestock are removed. Moreover, the coincidence of peak P. aristata invasion with a decline in grazing intensity (fig. 3), suggests that the alternative state of P. aristata dominance is now favored by removal of the disturbance source.

Connell and Sousa also argue that the persistence of the alternative state must be demonstrated through at least one turnover of the population. P. aristata has a maximum lifespan of over 1,500 years (Krebs 1972), and forests containing trees that are 400 or more years old are common (Baker, unpublished data). Connell and Sousa's requirement for persistence is theoretically sound, but neither persistence nor the lack of it can be demonstrated in the near future. The alternative state of P. aristata dominance has already persisted for about 50 years, however, a duration that is significant in terms of forest management. I suggest that a true alternative state should persist following removal of the disturbance agent, but that a variety of inferential evidence of this persistence should be acceptable.

The multiple stable states described by Connell and Sousa (1983), where the alternate state must be maintained intrinsically (by the biota), have yet to be clearly demonstrated to occur in nature. The rigorous criterion of intrinsic maintenance these authors use may be justified from a theoretical standpoint, but it is important not to discourage further study of extrinsically produced and maintained multiple stable states.

Environmental changes accompany most kinds of natural disturbances and human land uses. The possibility of unexpected outcomes following these disturbances and land uses is thus of considerable interest. This possibility has previously been raised in connection with various human influences on vegetation, including effects of fire suppression (Vale 1982), overgrazing (Anderson and Holte 1981; Walker and others 1981; Westoby and others 1989), and clearcut logging (Vale 1988). The failure of trees to regenerate following fires (e.g. Payette and Gagnon 1985) due to climatic change may also produce alternative states. Other potential examples of extrinsic multiple stable states have been reviewed by Holling (1973), Vale (1982), and Connell and Sousa (1983).

In an increasingly managed world in which environmental changes accompany many ordinary human land uses, it is critical to understand how and why persisting alternative states may arise. Livestock grazing following fires may produce unexpected and persistent alternative outcomes.

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LITERATURE CITED

Anderson, J. E. and Holte, K. E. 1981. Vegetation development over 25 years without grazing on sagebrush-dominated rangeland in southeastern Idaho. Journal of Range Management 34:25-29.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institute of Washington Publication 242, Washington, D.C.

Connell, J. H. and Sousa, W. P. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist 121:789-824.

Drew, L. G., ed. 1974. Tree-ring chronologies of western America. IV. Colorado, Utah, Nebraska and South Dakota. Chronology Series 1, Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ. 41 pp.

Fischer, W. C. and Bradley, A. F. 1987. Fire ecology of western Montana forest habitat types. U.S. Department of Agriculture, Forest Service, General Technical Report INT-223, Intermountain Research Station, Ogden, UT. 95 pp.

Graybill, D. A. 1979. Revised computer programs for tree-ring research. Tree-Ring Bulletin 39:77-82.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-23.

Jameson, D. A. 1987. Climax or alternative steady states in woodland ecology. p. 9-13 In: Everett, R. L., compiler. Proceedings-pinyon-juniper conference [Reno, NV-Jan. 13-16, 1986]. U.S. Department of Agriculture, Forest Service, General Technical Report INT-21.5, Intermountain Research Station, Ogden, UT. 581 pp.

Krebs, P. V. H. 1972. Dendrochronology and the distribution of bristlecone pine (Pinus aristata Engelm.) in Colorado. PhD. Dissertation, University of Colorado, Boulder, CO. 211 pp.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471-477.

Payette, S. and Gagnon, R. 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Quebec. Nature 313:570-572.

Pearson, G. A. 1934. Grass, pine seedlings, and grazing. Journal of Forestry 32:545-555.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude bums by coniferous trees in the central Rocky Mountains. Ecology 24:19-30.

Vale, T. R. 1982. Plants and people: vegetation change in North America. Resource Publications in Geography, Association of American Geographers, Washington, D.C. 88 pp.

Vale, T. R. 1988. Clearcut logging, vegetation dynamics, and human wisdom. Geographical Review 78:375-386.

Veblen, T. T. and Lorenz, D. C. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography 7: l-24.

Walker, B. H., Ludwig, D., Holling, C. S., and Peterman, R. M. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology 69:473-498.

Westoby, M., Walker, B., and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42(4):266-274.

Yamaguchi, D. K. 1986. Interpretation of cross correlation between tree-ring series. Tree-Ring Bulletin 46:47-54.

CLIMATIC CHANGE AND THE MODELING OF FIRE EFFECTS IN COASTAL SAGE SCRUB AND CHAPARRAL

George P. Malanson and Walter E. Westman[1]

Abstract-Human-inducedclimatic change will affect the processes and rates of species growth and thus the rates of accumulation and the composition of fuel loads. The combination of altered fuel loads and altered weather patterns will result in altered fire regimes. Altered fire regimes will in turn affect species growth and community composition. This feedback can be incorporated in computer simulation models of the response of vegetation to a changing climate, but the ways species will grow in climates in which they do not now exist and the way this growth can be translated into fuel loads are not well understood. for California shrublands, in which the continual production of basal sprouts allows shrubs to continue life while some branches die, we propose that the apportionment of biomass into live and dead fuel classes is the critical issue in modeling this feedback.

INTRODUCTION

It is becoming increasingly clear that minimizing the risk of wildfires and maximizing natural processes in wildlands are often incompatible goals for land managers (cf. Malanson 1985a). This realization has come with increasing understanding of the history and processes both of wildfire and of ecosystems. If land managers are to resolve these conflicts, it is necessary that the relationship between wildfires and biotic elements of wild ecosystems be understood. In this paper we discuss how human-induced climatic changes may affect wildfire-vegetation interactions and how some aspects of the wildfire-vegetation relationship might be addressed in future research. We examine computer simulation models of population dynamics in California shrublands in which fire intensity is important, and we consider the way in which ecosystem processes must be translated into fuel dynamics.

The relationship between ecological processes and quantitative estimates of fire intensity has been addressed in a number of ecological studies. WC used a calculation of fire intensity to assess the impacts of fire regime on Californian costal sage scrub (Westman and others 1981; Malanson and O'Leary 1982), chaparral (Malanson and O'Leary 1985), and French garriguc (Malanson and Trabaud 1987). We have also attempted to determine what ecological processes produce fuel loads different enough to result in different fire intensities and rates of spread (Malanson and Butler 1984; Malanson and Trabaud 1988). The incorporation of fire behavior into an iterative computer simulation model of species dynamics is, however, elementary. We modeled the dynamics of Californian coastal sage scrub over periods of 200 years under a variety of fire regimes, and we included the effects of altered fire intensity at different fire intervals in this model (Malanson 1983, 1985b). These studies and others like them, have shown that the dynamics of species populations and individual growth affect fuel loads, and that these fuel loads affect fire behavior which in turn affects species dynamics.

CLIMATIC CHANGE

Projected Changes and Responses

If the global climate changes, our present understanding of the feedbacks between ecological processes and fire behavior maybe inadequate for the purposes of managing fire regimes. Projections of general circulation models (GCM's) indicate that the global climate may warm from 1 to 5 °C in the next century due to emissions of radiatively-active trace gases (Schneider 1991). Species responses to a change in climate are not easily predicted. The rate of change in climate at the Pleistocene-Holocene boundary was not as rapid as that projected for the next century, and so analogs from the fossil record may not be applicable. We know that species can live in less stressful (warmer and moister?) conditions than those occurring in their natural range (Darwin 1859, MacArthur 1972, Woodward 1991); yet we do not know how well species will grow in their present locations if and when the climate changes. The inertia of biogeographic response, which results from the advantage to species already occupying sites, is likely to be important (cf. Cole 1985; Hanson and others 1989). But eventually climatic change will alter relative abundances in given locales and also the production of fuel (e.g., Suffling, this volume). The changes will also alter the frequency of the conditions under which fires are ignited and spread (Beer and others 1988). These changes in frequency will not be directly analogous to those that occurred during the Holocene (cf. Clark 1985). Current conceptions of the problems of suppression and prescribed burning are based on the pattern of fuel development and tire weather from the recent past. These concepts may not fit the patterns of the future (cf. Van Wagener 1987).

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[1] Associate Professor of Geography, University of Iowa, Iowa City, IA; and Staff Scientist, Applied Science Division, Lawrence Berkeley Laboratory, Berkeley, CA (Walt Westman died 1/2/91).

First-Generation Model for Coastal Sage Scrub

Research on the effects of climatic change on Californian coastal sage scrub suggests that altered fire regimes may result in greater changes in species composition than the direct effects of climatic change (Malanson and Westman 1991; Westman and Malanson 1991). We used a computer simulation model that was designed to examine the effects of different fire regimes under a constant climate and altered the fire intensities and ecological functions to include the effects of climatic change. In this model, however, we simulated conditions at a new equilibrium climate, and we did not include a feedback connecting plant growth, fuel, fire, and regeneration. We had previously made observations and estimated fuel loads in Californian coastal sage scrub (Westman and others 1981; Malanson 1985); we altered these estimates as we judged appropriate to reflect climatic changes projected by two different GCM's. These GCM's, the GISS (Hansen and others 1981) and GFDL (Manabe and Wetherald 1980), project warmer temperatures and increased precipitation in southern California. To analyze the effects of altered temperature (Temperature runs), we changed the fuel loads by the same proportion as the change in total foliar cover projected for the species in question in a direct gradient analysis: fuel load was reduced by 13 % . To analyze the effects of increased winter precipitation (Composite Moisture Index, CMI runs), we increased the dead fuel linearly from zero at the time of fire up to double that currently found on 40-year-old sites. Albini's FIREMODS program (1976a), which makes use of Rothermel's fire model (1972), was used to calculate new fire intensities on the basis of the new total fuel loads. As an index of fire intensity we used the total heat release (Joules per square meter) calculated by the program (fig. 1). Albini (1976b) recommended total heat release as the best indicator of the effects of tire on vegetation. Because of the complexity of fire behavior and the lack of functions describing the flux of heat from the fire to the regeneration organs of the plants, this index of intensity is best considered to be a surrogate measure of fire effect.

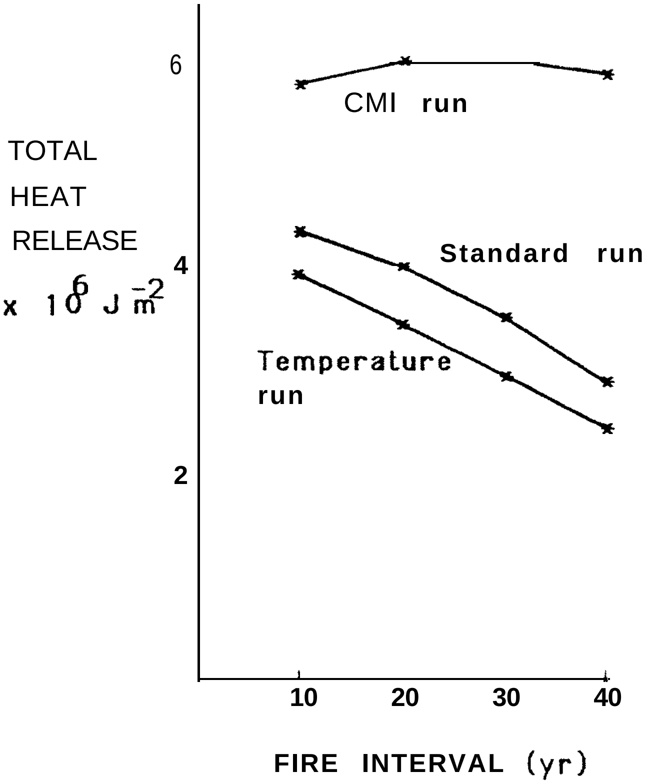

Figure 1. Fire intensities projected for coastal sage scrub under assumptions of altered climate (doubled carbon dioxide levels, GISS model). The Standard run is produced for current observed fuel loads; the Temperature run indicates the results of a decrease in fuel load assumed for an increase in temperature; the CMI (Composite Moisture Index) run indicates the results of an increase in fuel load assumed for an increase in precipitation.

These tire intensities were used to alter the rates of resprouting of the component species for the new climates through previously described response functions based on field observations (Malanson and Westman 1991). Under these fire regimes thee are changes in the relative abundances of the five species involved. However, overall cover changes only when a lo-year fire interval, i.e., a short interval, is assumed; in this case, cover declines throughout the 200-year period simulated. This result indicates that the increases in dead fuel may be the most realistic assumption for most conditions. But this assumption does not address the issue of declining fuel loads under the lo-year-interval fire regime, which indicates that increasing fire intensities are not the only impact. Neither does it address the fuel load changes that would occur if species with different physiognomies were considered. If the area were occupied by increasing cover of grasses or chaparral shrubs, the fuel loads would have to be altered in a different ay than to simply assume change in the growth of the coastal sage scrub species. Therefore, it is necessary to include the feedback between species composition and growth in the iterative process of modeling tire in the simulation (e.g., fig 2).

FUEL RESPONSES

The concept that the growth of plants in a simulation should determine the fuel load at the next fire seems straightforward. The fuel load, however, is more complex than a direct measure of foliar cover or of biomass would indicate. First, the distribution of wood in different branch sizes, with different surface to volume ratios and thus different rates of combustion, is known for present shrub species, but both the species and their growth forms may be altered under a different climate. Second, the heat content of the fuel, especially in Mediterranean-type ecosystems where the content of volatile oils is high, may change in anew climate. Third, the spatial distribution of fuels in three dimensions (e.g., grass-shrub proximity or fuel packing) could change with changing grass/shrub biomass ratio. These three factors could result in changes in both tire behavior and intensity, and thus in potential effects on vegetation. For the present, however, we will discuss one change in the fuel load: the ratio of live to dead biomass.

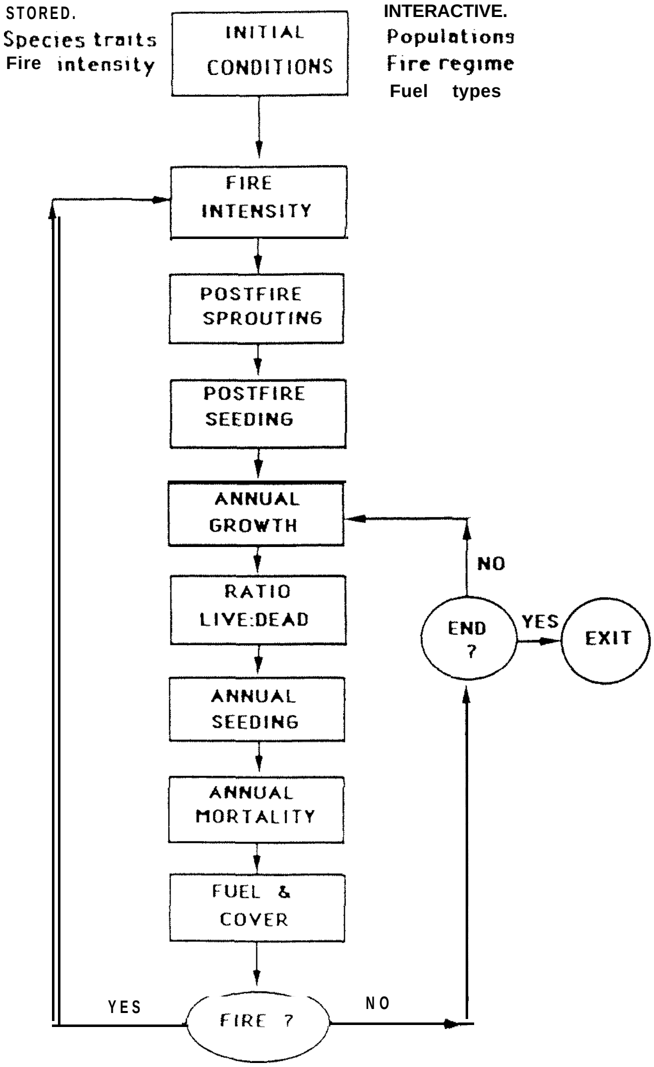

Figure 2. Vegetative response to fire and climate with a feedback to fire intensity through fuel load.

Importance of Dead Fuel

Calculations of fire intensity show that the live:dead ratio is of great importance. Using the fuel loads reported by countryman (1964) for light, medium, and heavy chaparral, we divided these fuels into six categories of live to dead fuel ratios, and entered them into FIREMODS. The results indicate that especially at high fuel loads, when larger stems that are live contribute less to combustion, the proportion of dead fuel greatly affects the estimation of fire intensity (fig. 3). These results are not always consistent with our simulations of fire intensity (total heat release) in coastal sage scrub in an altered climate: our estimates of fire intensity under conditions of increased moisture availability (approximately 6 x 10^6J m^{-2}) may be too high (fig. 1), while our calculations based on Countryman's estimates of fuel load for light chaparral (approximately 2.4 x 10^6J m^{-2}) may be too low (fig. 3).

Dead Fuel in Coastal Sage Scrub and Chaparral

Both chaparral and coastal sage scrub can produce considerable amounts of dead fuel during long fire-free periods. Chaparral has been noted for this feature, which is often referred to as senescence. In coastal sage scrub, we observed that individual shrubs continually produce new basal branches during the fire-free period (Malanson and Westman 1985). Keeley and Keeley (1988) observed the same characteristic in certain chaparral species. A plant with this trait can replace its dead branches with live ones, and thus can produce new growth without expanding its area. This ability is critical for the continued production of dead standing fuel. In the Mediterranean climate, standing dead fuel does not decompose rapidly, although fuel falling to the ground does not seem to accumulate, since litter loads are not heavy. This trait of coastal sage and chaparral shrubs, while indicating the importance of recording the change in fuel characteristics through time, may also indicate a pathway for assessing the potential effects of climatic change on standing dead fuel.

Standing dead fuel becomes common in these shrublands after the canopy has closed. This indicates that as the site becomes crowded, and perhaps as nutrient and moisture reserves become more finely divided among individual shrubs and even among the branches of a single shrub, the ratio of production to respiration (Ps/Pr) in and individual branch becomes critical and that branch may then die. Under a

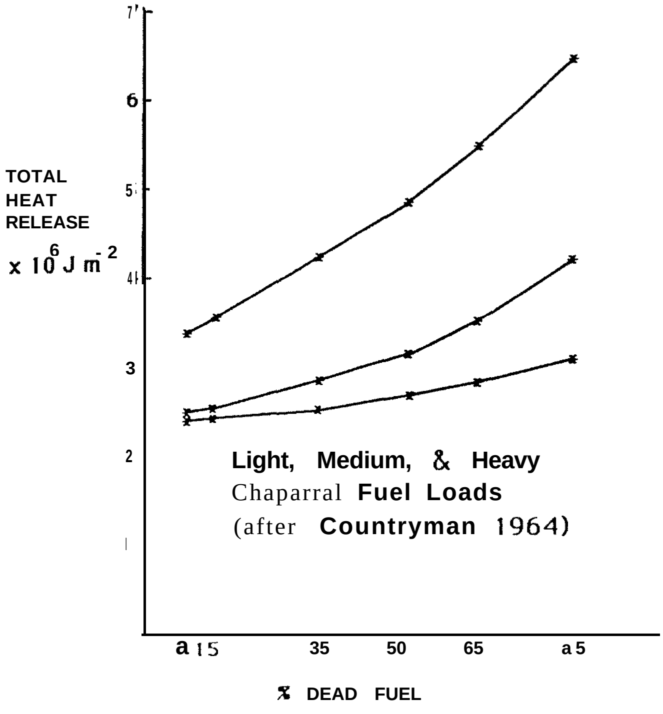

Figure 3. Fire intensities projected for three fuel loads apportioned into six classes of live-to-dead fuel ratio.

closed canopy, light levels for subcanopy leaves may be insufficient to support a net positive Ps/Pr ratio. This reasoning allows us o link the production of dead fuel to the overall crowding, or foliar cover, and a site--the abundance variable most easily assessed.

Proposed Modeling of Fuel Loads

In our current modeling work for both coastal sage scrub and chaparral, we are incorporating the dynamics of dead fuel. In our previous model of coastal sage scrub (Malanson 1984; Malanson and Westman 1991), and in other models of shrub and forest dynamics (e.g., Botkin and others 1972; van Tongeren and Prentice 1986) growth is limited by crowding. In our previous model, when foliar cover reaches 90 percent, no further growth occurs in any iteration until enough mortality has occurred to reduce cover below this threshold. In other models, and in our own current work, growth is limited much as population growth is limited in the logistic, i.e., exponential growth is increasingly reduced as an upper limit, in our case of total foliar cover, is approached. In order to apportion this growth between live and dead fuels, it is necessary to assume that a proportion of the growth produced during an iteration is in replacement of a branch that has died. We propose to set the upper limit of total foliar cover at 150 percent on a site. When cover exceeds 100 percent, however, an increasing proportion of the decreasing amount of growth is considered to be replacement only (fig. 4). The increase in fuel will proceed as follows: following fire, live growth will begin to fill a site; as the site fills, the rate of growth will slow; once the canopy closes, the rate of growth continues to slow and much of the growth will be recorded as an accumulation of dead fuel; no upper limit for dead fuel is specified a priori. In this function, climate has no direct effect on the quantity of dead fuel, but affects it only indirectly by influencing growth.

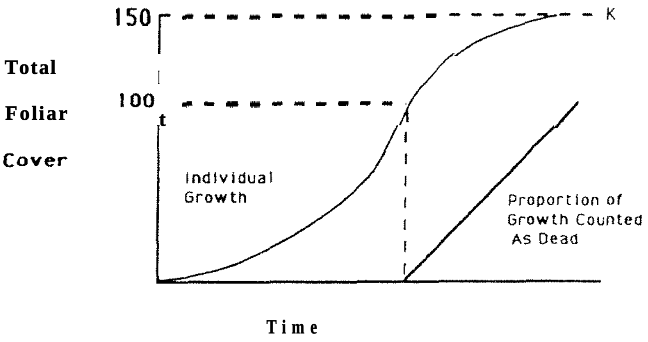

Figure 4. Apportionment of growth into live and dead fuel as overall growth is limited by crowding.

There is another route to modeling dead fuel, however. In earlier models, individuals or proportions of cohorts die: in the forest dynamic models, individual trees die if their rate of growth drops below a threshold; in our earlier simulation, mortality was a function of age. We propose to use the threshold approach in new models of California shrublands. If growth is reduced below a threshold as climate changes, a proportion of the cohort, which is the unit of record in our model, will die and that proportion of the biomass will be added to the dead fuel category. Thus if climates become more harsh, mortality will increase and add to dead fuel, while simultaneously releasing extant shrubs from competition and allowing continued growth.

In our present mode, fuel loads, both in terms of the biomass and the live-to-dead ratio, can then be calculated in a simulation as the growth of species responds to climatic change. Fire behavior simulations that make use of models like FIREMODS require a great deal of computation; it will therefore be best to calculate a matrix of fire intensities for fuel mixtures that vary in live-to-dead ratio, biomass, and the content of chaparral, coastal sage, and grass species (the different physiognomic types vary in their fuel packing and surface to volume ratios). When a hypothetical fire is to occur in hypothetical vegetation, the tire intensity that is appropriate for the projected vegetation can be selected from the matrix. In this way the feedback between fuel and regeneration can be completed.

CONCLUSIONS

These models of species growth and fuel load cannot predict with certainty the abundances of species in climates that do not now exist. They can indicate the general direction and magnitude of changes we might expect. They certainly will help to pinpoint areas in which additional empirical work is needed. While uncertainties do exist, it is probable that the rates at which ecological processes operate in fire environments and the current patterns of fire regime and of species distributions wilt change with climatic change (cf. Clark 1988). Investments in the planning and implementation of wildland and tire management programs can be more efficient if models of the system in altered climatic conditions are incorporated in the planning process.

ACKNOWLEDGMENTS

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LITERATURE CITED

Albini, F.A. 1976a. Computer-Based Models of Wildland Fire Behavior: A User's Manual. Ogden, UT: U.S. Forest Service.

Albini, F.A. 1976b. Estimating wildfire behavior and effects. U.S. Forest Service General Technical Report INT-30.

Beer, T., Gill, A.M. and Moore, P.H.R. 1988. Australian bushfire danger under changing climatic regimes. In Pearman, G.I., ed. Greenhouse, Planning for Climate Change. Canberra: CSIRO Division of Atmospheric Research, pp. 421-427.

Botkin, D.B., Janak, J.F. and Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60: 849-872.

Clark, J.S. 1988. Effect of climate change on tire regimes in northwestern Minnesota. Nature 334: 233-235.

Cole, K. 1985. past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. American Naturalist 12.5: 289-303.

Countryman, C.M. 1964. Mass fires and tire behavior. U.S. Forest Service Research Paper PSW-19.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. London: John Murray.

Hansen, J.E., Johnson, D., Lacis, A., Lebedeff, S., Lee, P., Rind, D. and Russell, G. 1981. Climate impact of increasing carbon dioxide. Science 213: 957-966.

Hanson, J.S., Malanson, G.P. and Armstrong, M.P. 1989. Spatial constraints on the response of forest communities to climate change. In: Malanson, G.P., ed. Natural Areas Facing Climate Change. The Hague: SPB Academic, pp. l-23.

Keeley, J.E. and Keeley, S.C. 1988. Chaparral. In: Barbour, M.G. and Billings, W.D., eds. North American Terrestrial Vegetation. New York: Wiley, pp. 417-469.

MacArthur, R.H. Geographical Ecology. Princeton, NJ: Princeton University Press.

Malanson, G.P. 1984. Linked Leslie matrices for the simulation of succession. Ecological Modelling 21: 13-20.

Malanson, G.P. 1985a. Fire management in coastal sage scrub, southern California, USA. Environmental Conservation 12: 141-146.

Malanson, G.P. 1985b. Simulation of competition between alternative shrub life history strategies through recurrent tires. Ecological Modelling 27: 271-283

Malanson, G.P. and Butler, D.R. 1984. Avalanche paths as fuel breaks: implications for fire management. Journal of Environmental Management 19: 229-238.

Malanson, G.P. and O'Leary, J.F. 1982. Post-fire regeneration strategies of Californian coastal sage shrubs. Oecologia 53: 355-358.

Malanson, G.P. and O'Leary, J.F. 1985. Effects of tire and habitat on regeneration in Mediterranean-type ecosystems: <u>Ceanothus spinosus</u> chaparral and coastal sage scrub. Oecologia Plantarum 6: 183-195.

Malanson, G.P. and Trabaud, L. 1987. Ordination analysis of components of resilience of <u>Quercus coccifera</u> garrigue. Ecology 68: 463-473.

Malanson, G.P. and Trabaud, L. 1988. Computer simulations of fire behavior in garrigue in southern France. Applied Geography 8: 53-64.

Malanson, G.P. and Westman, W.E. 1985. Post-fire succession in Californian coastal sage scrub: the role of continual basal sprouting. American Midland Naturalist 113: 309-318.

Malanson, G.P. and Westman, W.E. 1990. Modeling interactive effects of climate change, air pollution, and fire on a California shrubland. Climatic Change, in press.

Manabe, S. and Wetherald, R.T. 1980. On the distribution of climatic change resulting from an increase in the CO, content of the atmosphere. Journal of Atmospheric Sciences 37: 99-118.

Rothermel, R.C. 1972. A mathematical model for predicting fire spread rate and intensity in wildland fuels. U.S. Forest Service Research Report INT-115.

Schneider, S.H. 1991. Review of the climate scenario and discussion of current climate knowledge. In Peters, R.L. and Lovejoy, T., eds. Consequences of the Greenhouse Effect for Biological Diversity. New Haven: Yale University Press, in press.

van Tongeren, 0. and Prentice, I.C. 1986. A spatial simulation model for vegetation dynamics. Vegetatio 6.5: 163-173.

Van Wagener, C.E. 1987. Forest fire research - hindsight and foresight. In: Davis, J.B. and Martin, R.E., eds. Wildland Fire 2000. Berkeley, CA: U.S. Forest Service, pp. 115-120.

Westman, W.E. and Malanson, G.P. 1991. Effects of climate change on Mediterranean-type ecosystems in California and Baja California. In Peters, R.L. and Lovejoy, T., eds. Consequences of the Greenhouse Effect for Biological Diversity. New Haven: Yale University Press, in press.

Westman, W.E., O'Leary, J.F. and Malanson, G.P. 1981. The effects of tire intensity, aspect, and substrate on postfire growth of Californian coastal sage scrub. In Margaris, N.S. and Mooney, H.A., eds. Components of Productivity of Mediterranean Regions. The Hague: W. Junk, pp. 151-179.

Woodward, F.I. 1991. Review of effects of climate on vegetation: ranges, competition, and composition. In Peters, R.L. and Lovejoy, T., eds. Consequences of the Greenhouse Effect for Biological Diversity. New Haven: Yale University Press, in press.

WILDLAND FIRE MANAGEMENT AND LANDSCAPE DIVERSITY IN THE BOREAL FOREST OF NORTHWESTERN ONTARIO DURING AN ERA OF CLIMATIC WARMING

Roger Suffling[1]

Abstract-A climatic gradient across Northwestern Ontario induces a spatial gradient in fire incidence, with few fires in the Northeastern part and many in the Southwestern part. The resultant landscape mosaics exhibit maximum landscape (beta) diversity with intermediate disturbance frequency, as predicted by a theoretical model. This implies that the results of fire suppression on landscape-scale habitat diversity differ qualitatively, depending on previous fire occurrence. Diversity is promoted by fire in fire-free areas, and suppressed by tire where fire occurs frequently. Fire occurrence has fluctuated wildly, however, over periods shorter and longer than the life span of forest trees and, with anticipated anthropogenic global climate warming, tire occurrence may depart from the norms of living memory. Thus the future lightning-fire regime cannot necessarily be regarded as an unmodified feature of the natural environment. Because temporal variation in fire frequency makes estimation of a "natural" fire frequency almost meaningless, wildland fire management policies should not be aimed at maintaining vegetation in a state that is representative of a particular historical time. Policy objectives can be set, however, to retain a minimum area of each ecosystem type, with the minimum defined by reference to historical variation.

INTRODUCTION

Fire management by Europeans in North American forests has proceeded through a number of philosophical phases: from no management, to complete fire suppression, to a mixed model with fire suppression in some areas under some circumstances and fire tolerance or fire setting under others (e.g. Dubé 1977; Elfring 1989; Van Wagner 1990). Change in attitude has been most dramatic in some designated wilderness areas in fire-prone regions where fire is no longer seen as destructive and tends to be viewed as an integral component of the natural environment (e.g. Woods and Day 1977; Houston 1973; Van Wagner and Methven 1980; Romme and Knight 1982; Hemstrom and Franklin 1982; Lopoukhine 1991). In such areas, fires are often categorized as of natural origin and therefore to be left to burn if possible, or of human origin and thus to be suppressed (e.g. Anon 1975; Elfring 1989; Schullery 1989). Not everyone endorses this approach, however, as the aftermath of the 1988 Yellowstone fires has demonstrated (Bonnicksen 1989; Buck 1989). In overtly modified landscapes, fire is usually suppressed, but is also used as a tool for deliberate modification of the landscape (e.g. Rego and others 1988; Arno and Gruel1 1986), or for reduction of unnatural fuel accumulation (e.g. Wade and others 1980; Pehl and others 1986; Birk and Bridges 1989).

There is a widespread belief that fire promotes what is variously described as landscape diversity or heterogeneity in both wilderness and overtly modified landscapes (e.g. Wright 1974; Romme and Knight 1982; White 1987; Hannson 1979; Forman and Godron 1986; Loucks 1970 ; Agee and others 1990). The first part of this paper calls into question the universality of this notion. It is hypothesized that fire, whether natural or otherwise, can promote landscape diversity, but can also suppress it in definable circumstances.

These ideas are of more compelling concern in view of anticipated global climate change. Atmospheric carbon dioxide concentration will probably reach double the pre-industrial revolution level in the next 50 to 100 years (Bolin 1986), thus trapping more heat in the lower atmosphere. Various general circulation models suggest that a doubled CO_2 concentration will increase global mean equilibrium surface temperature by 1.5 to 5.5°C in this period (Bolin and others 1986; Flavin 1989; Anon 1990).

Studies by Van Wagner (1988) and Suffling (1990) confirm the general belief the area of forest burnt in Northern Hemisphere regions is greater during warm summers. Thus climate warming is of direct concern to fire managers, as the fire climate will probably deviate from that of living memory. The second part of the paper addresses possible fire management responses to climate warming and landscape diversity questions in wildland areas.

A MODEL OF LANDSCAPE DIVERSITY

Many landscapes, including continental boreal forests, can be thought of as disturbance mosaics or, in more abstract terms, as populations of ecosystems. Heinselman (1973) introduced this notion when he redefined fire as normal but infrequent in temperate forest landscapes. This led to the attractive notion of Temperate Zone wildland forested landscapes in which "Fire rotation controls the distribution of age classes of stands and the succession within stands. The resulting diversity may represent long range stability, as implied by the

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[1] Associate Professor, School of Urban and Regional Planning, University of Waterloo, Waterloo, On., Canada.

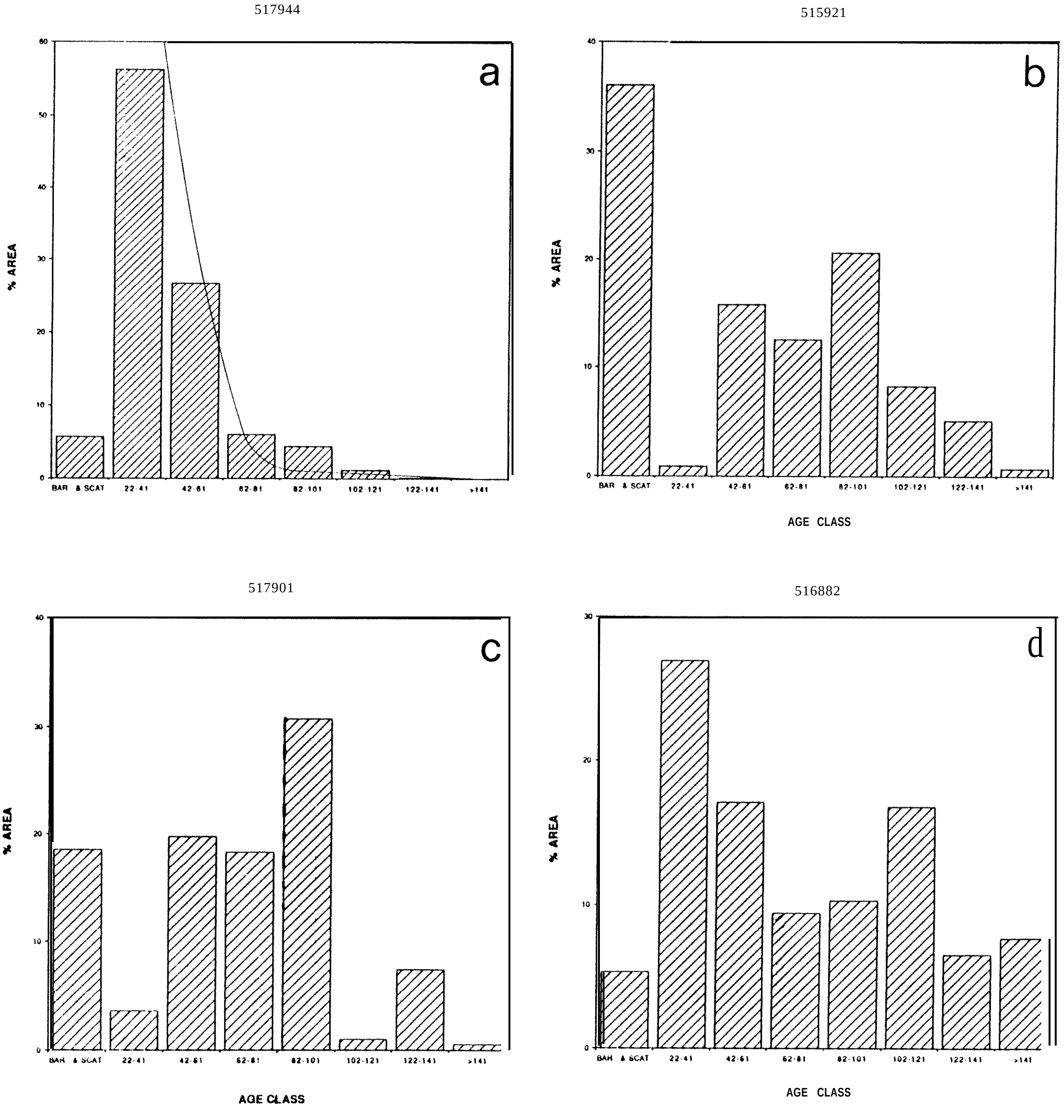


Figure 1 --Stand age-class distributions for Northwest Ontario for four areas ranging from most tire prone (la) to least tire-prone (Id). The data for the 4 graphs are stand ages of main stands since disturbance recorded on 1:15840 Ontario Forestry Resource Inventory maps at the 8 locations shown on figure 2. Map titles indicate longitude and latitude (e.g. 516882 = 51.6°N 88.2°W). A negative exponential curve (Van Wagner 1978) is fitted for figure la ($r^2=0.81$), but omitting the "barren and scattered" category which is an amalgam of recently regenerated stands and sparsely treed areas such as rock barrens.

palaeoecological record" (Wright 1974). This theory was given quantitative form by Van Wagner (1978) who showed, for the same Minnesota Great Lakes mixed forest landscape, that the distribution of stand ages followed a negative exponential curve (see figure la for an example of this distribution). The model applies if the chance of disturbance of any stand is equal throughout its life and if the amount of disturbance remains substantially unaltered in the long term. Some subsequent investigations confirmed the model (Yaric 1979; Harmon 1984), but other studies and data did not support it, or applied inconsistently (e.g. Hemstrom and Franklin 1982; Suffling 1983; Tande 1979; Antonovski and Ter-Mikhaelian 1987). This is leading to increasing support for a shifting-state concept of forest landscape. These latter results tend to demonstrate what palaeoecologists have long claimed, that the areal amount of disturbance fluctuates widely over time, not only in the short term, but also over periods as long as or longer than the life span of individual trees (e.g. MacDonald and others 1991; Romme and Knight 1982; Romme and Despain 1989). Figure 1 shows a typical range of age-class distributions encountered in Northwest Ontario, Canada, where change in fire occurrence over time disrupts the negative exponential pattern, especially where the overall fire return period is long, as in figure 1d.

The disturbance mosaic can be used to calculate the landscape diversity, or beta diversity associated with differences between stands in the mosaic (Suffling 1983). This diversity has a richness component (essentially the number of kinds of stand), and an evenness component expressing the relative amount of different kinds of forest (Suffling and others 1988). The two measures are commonly combined in the Shannon equation (Shannon 1948).

Landscape diversity is a function of inherent differences between sites based, for instance, on aspect or drainage. It also depends on the forest age class distribution that has been created by disturbance. Simulation models of stand-age distributions over time predict that landscapes with intermediate frequency of disturbance should have higher landscape diversity than those with very frequent disturbance and those that have almost no disturbance (Suffling and others 1988). This is the case whether fire occurs equally in all age classes or is concentrated on older ones.

The continental boreal forest of Northwest Ontario (fig. 2) was used to test the model (Suffling and others 1988). This huge, more-or-less flat glacial peneplain, exhibits spatial climatic variation that is little affected by altitude, and its

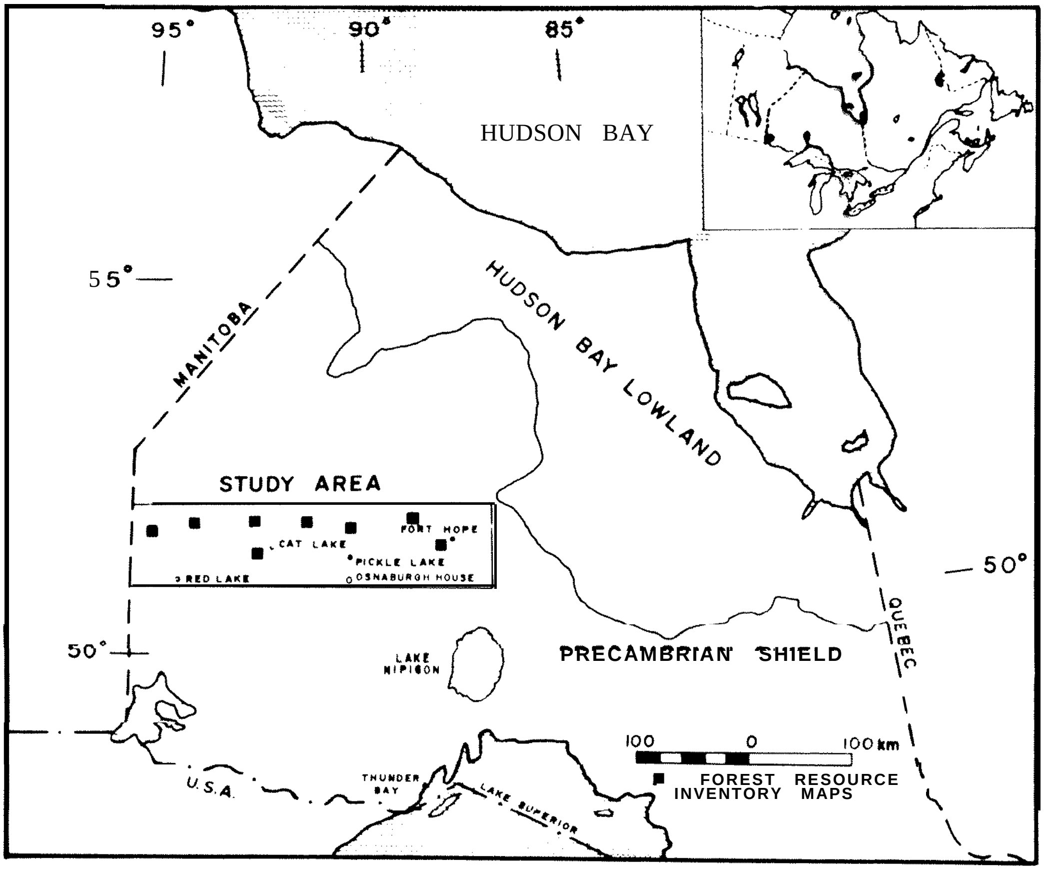


Figure ?--The location of the study area in Northwest Ontario geology is sufficiently uniform that climate variation begins to show consistently across the landscape. The area adjacent to the Hudson Bay Lowland is cooler and more humid than that against the Manitoba border. The amount of fire reflects this climatic variation, grading from a high of over 1 percent of land area burnt per year in the Southwest to almost no fire at all in the Northeast (Fig. 3). Most tires are stand-replacing crown tires, and the size of the disturbance patch created can vary from less than 1 to over 100,000 ha. There has, thus far, been very little logging in this area.

The fire gradient induces a cline in vegetation. Forests in the southwest are generally young and are dominated by fire-adapted jack pine (*Pinus banksiana* Lamb.) and aspen (*Populus trernrcloides* Michx.). Those in the northwest are generally much older and balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) are much commoner there (figs. 1 and 4). In the center of the region, a mixture of these forest types prevails (Suffling 1988). Measurements of landscape diversity (fig. 5) confirm the theoretical predictions that diversity will be highest in the center of the area, where frequency of disturbance is intermediate (Suffling and others 1988).

EFFECTS OF PRESCRIBED FIRE AND FIRE SUPPRESSION ON LANDSCAPE DIVERSITY

Predictions that the model generates, and the empirical confirmation of its applicability, justify several generalizations concerning tire management. In a landscape with little previous disturbance, prescribed burning will increase landscape diversity by creating patches of immature habitat in the primarily mature mosaic. Conversely, application of more tire in an already frequently burnt landscape will reduce the diversity of the landscape. In a landscape previously experiencing intermediate disturbance that has produced maximal landscape diversity, either fire suppression or increased prescribed or natural fire will reduce the landscape's diversity.

Land managers are thus faced with a problem: Promoting maximal landscape diversity is not necessarily synonymous with keeping an area pristine. By managing for some primeval wilderness condition with a different fire occurrence from the present one, a manager might actually reduce landscape diversity. In reality, however, many wildland areas have for many years been managed under fire exclusion policies that have eliminated or reduced both lightning tires and aboriginal burning patterns (Barrett and Arno 1982; Lewis 1977), and have tended to result in a bell-shaped distribution of stand age classes (Van Wagner and Methven 1980).

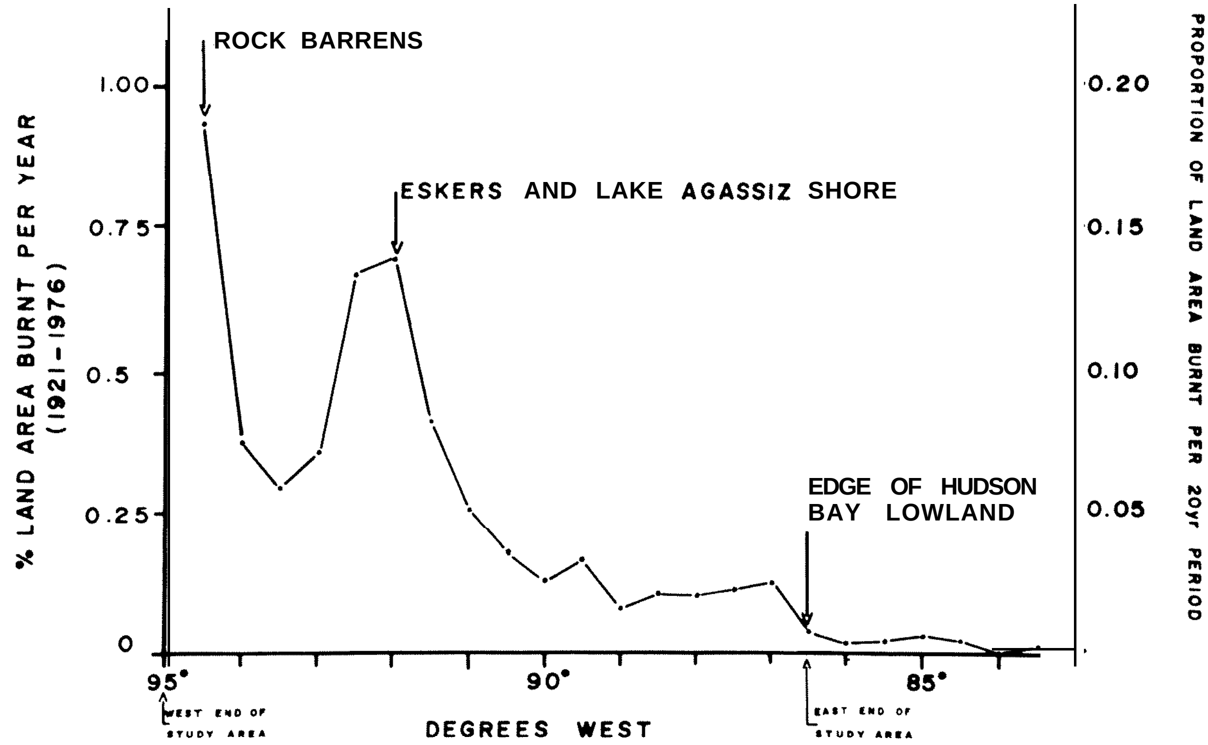


Figure 3--The gradient in fire occurrence across the study area in Northwest Ontario. (After Suffling and others 1988)

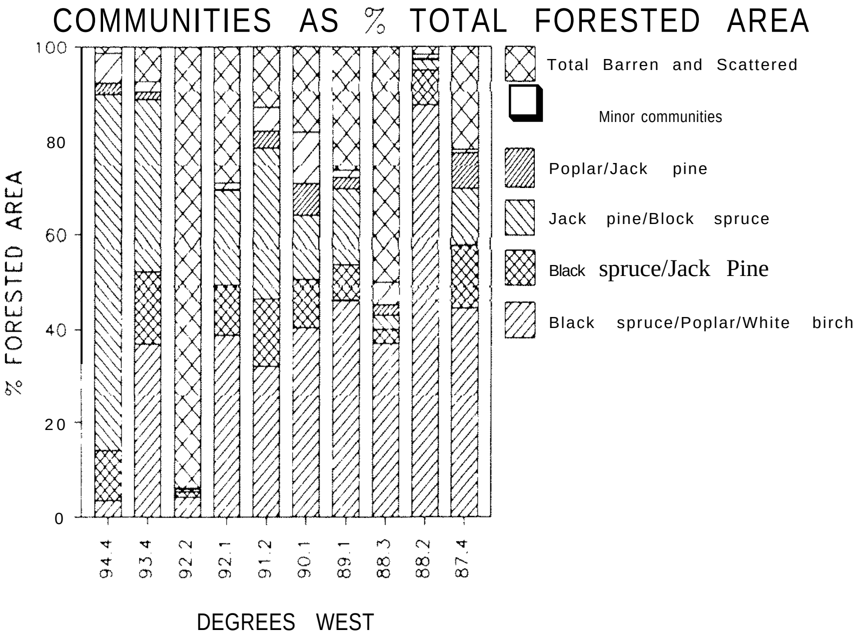


Figure 4--The change in community composition of forested upland sites across the study area in Northwest Ontario.(After Suffling 1988).

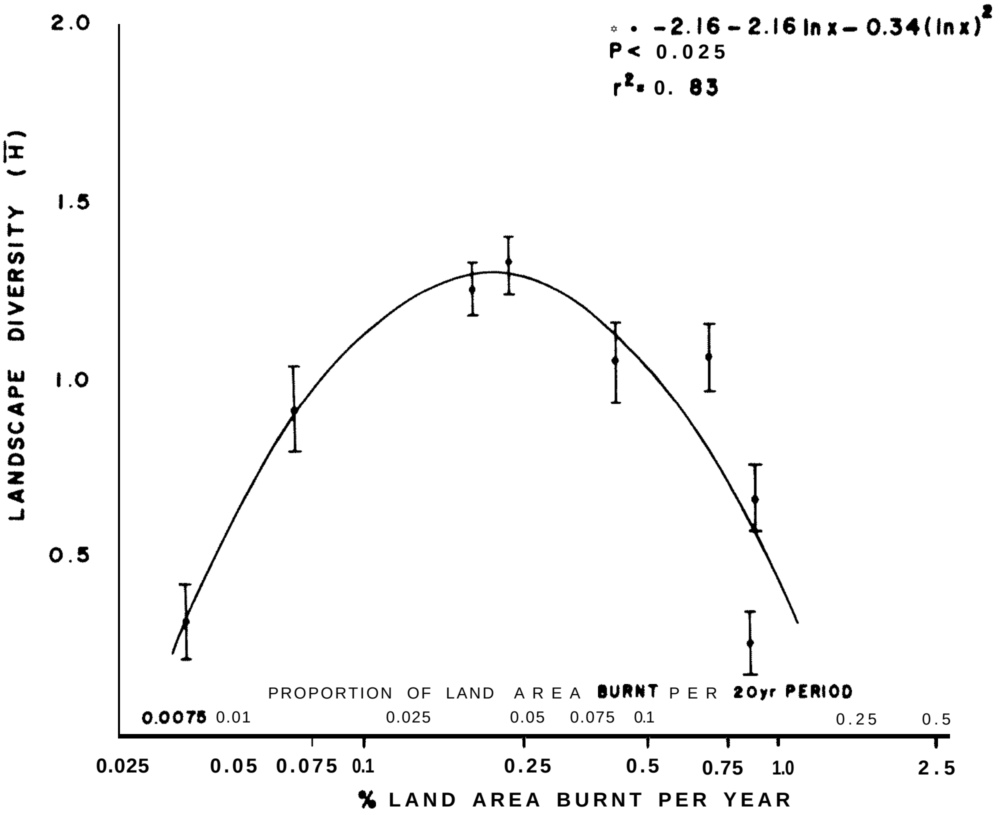


Fig. S--The relationship of landscape diversity (Shannon's H statistic) in the Northwest Ontario study area, to disturbance by forest fires (After Suffling and others 1988).

FIRE MANAGEMENT IN AN ERA OF CLIMATE CHANGE

The policy of allowing natural fires to burn while suppressing human-caused fires (if they can be recognized as such!) relies on a premise that the climate that starts fires or encourages them to spread is an unmodified component of the natural system. Now, however, there are predictions that climate will be anthropogenically warmed. The amount of change is debated and the "control" situation without greenhouse warming is not clearly definable for several reasons: First, natural climatic fluctuation will certainly occur anyway. Second, we presently have much less reliable information about anthropogenic change in precipitation than wc do about temperature. Third, regional forecasts from the present generation of general circulation models (GCM's) are not thought to be very accurate, and good regional analogues of GCM's will be 3 to 5 years in the making. Fourth, there is the possibility of deliberately ameliorating anthropogenic climate change, but it is generally agreed that some warming is now inevitable. The "predictions" are thus scenarios. Those who make them are under no illusion that they represent anything other than options or a range of possible futures.

Given these complications, one can only be reasonably sure that there will be more fire in many forest regions than is natural, so that a "let bum" policy will no longer promote a natural fire regime. There will be changes in the relative amounts of different habitats, in landscape diversity, in the kinds and amounts of tire ecotone, and in the spatial relationships and patch sizes of different habitats (Suffling and others 1988; Turner 1989; Turner and others 1989).

The wildland tire manager's first reaction might be to attempt to control tires to an extent that approximates the historical pristine condition (e.g. Hawkes 1980), so as to preserve a "vignette of primitive America" (Leopold and others 1963). The development of landscape-based fire ecology models (e.g. Heinselman 1973; Wright 1974; Van Wagner 1978; Johnson and Van Wagner 1985; Parks and Alig 1988) gave much theoretical support to this philosophy. However, considerable research aimed at defining a pristine condition (either today's, or an earlier era's), has often demonstrated that there has been considerable variation in fire occurrence even the last hundred years (e.g. Romme and Despain 1982; Suffling 1988). Thus, the objective of recreating the pristine has been reinterpreted as not... "trying to hold nature steady but rather maintaining natural dynamics and discouraging anthropogenic deterioration" (Noss 1987). Where one is able, however, to assemble a history that predates the end of the little ice age (1820-1835 in many areas of North America), the variation between present and the fire past regimes is sufficiently enormous to render unworkable even Noss' interpretation of Leopold's concept.

Fire records from Northwest Ontario demonstrate this clearly. Government records provide a history of fire only since 1926 (fig. 6) and demonstrate a steady diminution of fire until the 1940's. Except in 1961, a disastrous fire year, very little forest was burnt until 1974. Fire areas increased dramatically thereafter in response to some of the warmest and driest summers of this century.

Because of the fierce, stand-replacing nature of fires in this region, it is difficult to establish a reliable quantitative history from fire scar information. Our attempts to establish a regional fire history from charcoal in lake sediments have proved fruitless because varves are not formed in the area's oligotrophic lakes. Fortunately, however, historical information from Hudson's Bay Company fur trade journals for Osnaburgh House spans the period from 1786 to 1911, and demonstrates a massive outbreak of forest fires in the 1820's, a relatively quiescent period from 1830 to 1860, and then a steadily increasing fire incidence until the turn of the century. While much of this variation was climatically driven, we know that a large proportion of the recorded fires were started by people (Suffling and others in press), and that this activity was intimately bound up with economic, social, and attitudinal changes associated with the fur trade. This information on the temporal distribution of tires tallies well with the stand-age distributions for this area (fig. 1) that show many present-day stands dating from between 1860 and about 1900. (The data for figure 1 largely predate the post-1974 fire outbreak, so this latter outbreak does not show on these figures).

If one wished to manage the fire regime of this Northwest Ontario area, what information base should be used to identify the "natural" condition? The present high fire activity is anomalous if considered in the context of the period of government statistics from 1927 to the present, and would thus require suppression, but the current increase in tires is driven by climatic variation rather than by some change in human-set fires. (We do not yet have the advantage of hindsight, however, and cannot say whether the recent fire outbreak is just a major fluctuation, or represents the beginning of anthropogenic climate warming). Conversely, if one used the stand age distribution to establish a "natural" baseline, one would conclude that fire was virtually absent from the 1920's but was common before that. If one used the Hudson's Bay Company record (which does not allow a quantitative determination of fire frequency), one could use the low fire period at the end of the little ice age or the high tire period of the 1820's (though there is a strong suspicion that numerous large fires of the 1820's resulted from both climatic influence and human activity). Alternatively, one could pick any of the subsequent high or low fire eras.

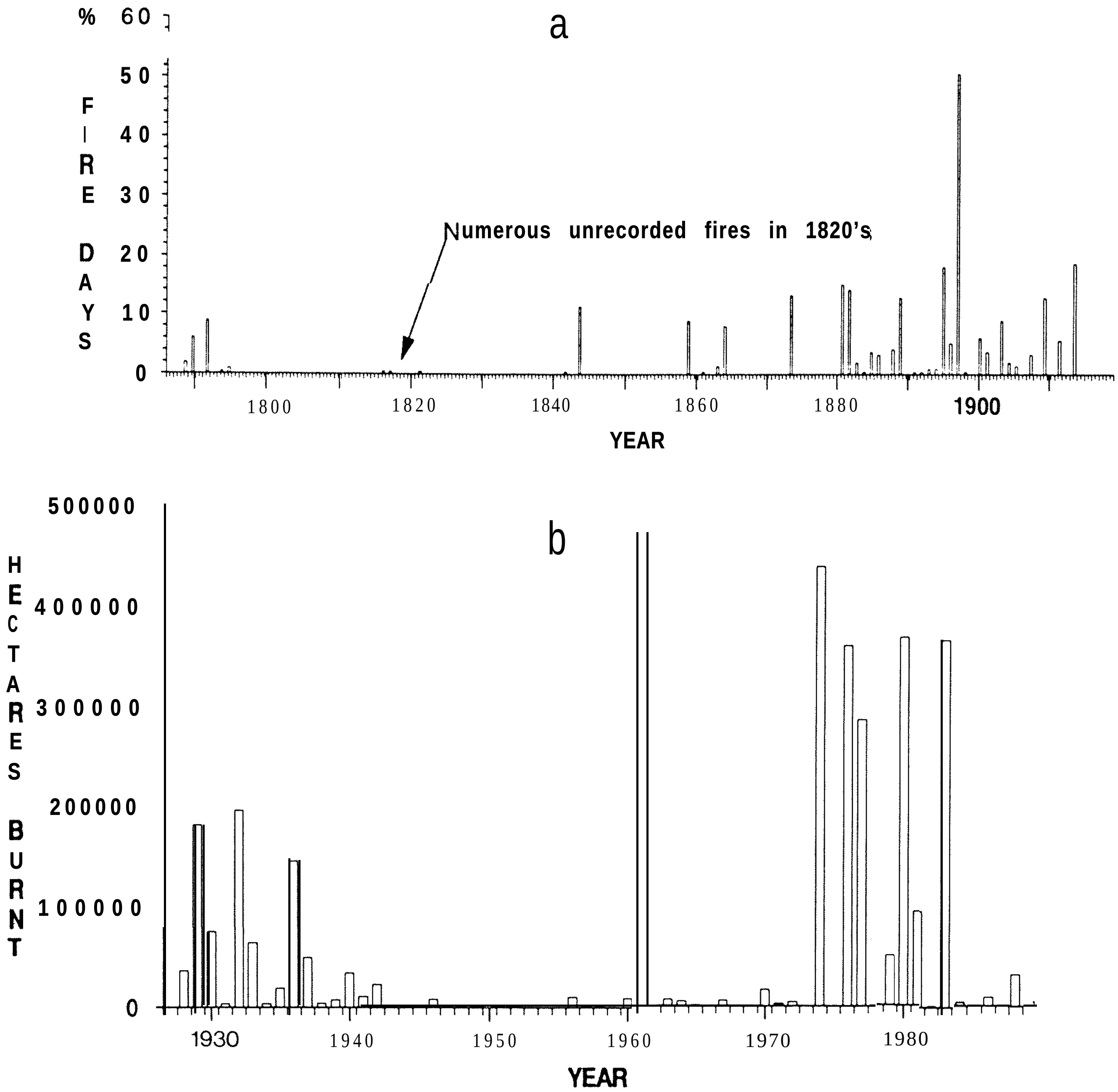


Fig. 6- Historical variation in fire occurrence in Northwest Ontario. a: Fire occurrence as represented by "fire days" (Suffling 1988) at Osnaburgh House. b: Ontario government statistics for area burnt in the Kenora District, 1927.1989 (Ontario Ministry of Natural Resources 1928-1990).

It is possible that the outbreaks of fire in Northwest Ontario follow about a 50-year cycle, with high fire eras in the 1820's, 1870's, and 1980's. There is little information for the early 1920's but oral tradition suggests that tires were frequent at that time. Data from other regions support the possibility that cyclical tire occurrence is commonplace at a landscape scale. Charcoal fragment counts in varved lake sediments in the boreal forest of Wood Buffalo National Park in Canada's Northwest Territories (MacDonald 1990 pers. comm.) imply a 100 to 200 year cycle of fire in the landscape over a 2000 year period. Similarly, the conifer forests of the Yellowstone Plateau in Wyoming have experienced long quiescent periods punctuated by major cyclic fire outbreaks about every 300 to 400 years, as in 1988 (Romme and Knight 1982; Romme and Despain 1989). Current research on the effects of spatial landscape patterns is beginning to explain these temporal variations (Antonovski and Ter-Mikhaelian 1987; Turner 1989).

In none of the cases noted above is there any indication that the major fire outbreaks are merely extremely large events in a stochastic series. In each case, fire occurrence appears to have "flipped" between high and low states without the appearance of an intermediate condition. Thus, adoption of an average fire return period would be arbitrary, and would not mimic nature. Likewise, any attempt to "fix" the landscape adopting a particular fire frequency from a high or low fire period will be unnatural.

How can the *fire* manager resolve this dilemma? One approach is to identify acceptable limits of variation in the disturbance mosaic over time -an ecosystem supply strategy. For instance, if one decides that it is desirable to retain some mature stands of jack pine over 100 years old, fire management policy can be tailored to protect such stands if their total area falls below a defined limit represented by a certain percentage of potential jack pine site area. Conversely, one might set prescribed bums in potential jack pine areas if the total area of jack pine under 20 years old were to fall below a defined limit. Acceptable limits could be set on the basis of the historical representation of ecosystem types in the landscape, on aesthetic or other cultural values, or on the need to preserve certain ecosystem types for their valued flora or fauna.

CONCLUSION

Fire managers should not assume, *a priori*, that forest fires (or, for that matter, any other patch disturbance) will increase landscape diversity, or that they will reduce it. The effect of fire on landscape diversity depends on the current status of the landscape mosaic and, thus, on previous disturbance. Because global climate warming will increase forest fire occurrence in the boreal and other biomes, wildland fire managers should no longer assume that the lightning fire regime as non-anthropogenic. The timing and extent of increase in fire, as well as the "control" fire regime that might occur without global climate warming are currently unknown. One might wish to maintain the status quo in wildland areas in terms of proportions of different ecosystem types. However, these proportions shift constantly over time, even at the landscape scale, in response to natural climate variation and the spatial pattern in the landscape (Antonovski and Ter-Mikhaelian 1987; Turner 1989), which links to endogenous fuel processes. Thus, one must decide what fire is to create and what to protect from fire. This can mean determining what minimum area of each ecosystem type should exist in the landscape. Such definitions can be based on the status quo, on historical variation, or on culturally defined values. Sadly, in an era of climate warming the ethic of leaving nature to continue without human interference becomes illusory.

LITERATURE CITED

Agee, J.K.; Finney, M.; DeGouvenain, R. 1990. Forest fire history of Desolation Peak, Washington. Canadian Journal of Forest Research 20:350-356.

Antonovski, M. Ya; Ter-Mikhaelian, M.T. 1987. On spatial modelling of long-term fire dynamics. IIASA Working Paper WP-87-105. International Institute for Applied Systems Analysis, Laxenburg, Austria.

Arno, S.F.; Gruell, G.E. 1986. Douglas fir encroachment into mountain grasslands in southwestern Montana. Journal of Range Management 39:272-276.

Barrett, S.W.; Arno, S.F. 1982. Indian Fires as an ecological influence in the Northern Rockies. Journal of Forestry 80:647-651.

Birk, E.M.; Bridges, R.G. 1989. Recurrent fires and fuel accumulation in even-aged blackbutt *(Eucalyptus pilularis)* forests. Forest Ecology and Management 29:59-79.

Bonnicksen, T.M. 1989. Nature vs. Man(agement): "Fire" is not a management value. Journal of Forestry 87:41-43.

Buck, B. 1989. A Yellowstone critique: Something did go wrong. Journal of Forestry 87:38-40.

Dubé, D.E., ed. 1978. Proceedings workshop, fire ecology in resource management. 1977 December 6-7; Information report NOR-X-210. Edmonton, Alta., Canada: Northern Forest Research Centre, Canadian Forestry Service, Environment Canada.

Elfring, C. 1989. Yellowstone: Firestorm over fire management. Bioscience 39:667-672.

Environment Canada 1990. The Canadian Climate Centre "2 x CO_2" experiment: Preliminary results. CO_2/Climate Report 90-01:1-2.

Flavin, C. 1989. Slowing global warming: A worldwide strategy. Worldwatch paper 91. Washington, D.C.: Worldwatch Institute.

Forman, R.T.; Godron, M. 1986. Landscapeecology. New York: John Wiley and Sons. 619 pp.

Hannson, L. 1979. On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. Oikos 33:182-189.

Harmon, M.E. 1984. Survival of trees after low-intensity surface fires in Great Smoky Mountains National Park. Ecology 6:796-802.

Hawkes, B.C. 1980. Fire history of Kananaskis Provincial Park - Mean fire return intervals. In: Stokes, M.A.; Dietrich, J.H., eds. Proceedings, The fire history workshop; 1980 October 20-24; Tucson, Ariz. Gen. Tech. Rep. RM-81. Fort Collins, Colorado: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station. pp. 42-45

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329-382.

Hemstrom, M.A.; Franklin, J.F. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Research 18:32-51.

Houston, D.B. 1973. Wildfires in Northern Yellowstone National Park. Ecology 54:1111-1117.

Johnson, E.A.; Van Wagner, C.E. 1985. The theory and use of two fire history models. Canadian Journal of Forest Research 15:214-220.

Leopold, A.S.; Cain, S.A.; Cottam, C.M.; Gabrielson, I.N.; Kimball,T.L. 1963. Wildlife management in the national Parks. Washington, D.C.: U.S. Dept. of the Interior.

Lewis, H.T. 1977. Maskuta: The ecology of Indian fires in Northern Alberta. Western Canadian Journal of Anthropology 7: 15-52.

Lopoukhine, N. 1991. A Canadian view of fire management in the greater Yellowstone area. In: Proceedings, The Greater Yellowstone Ecosystem Symposium; 1989 April 12-14; University of Wyoming, Laramie, Wyo.: Yale Press, Newhaven, Conn.: In press.

Loucks, O.L. 1970. Evolution of diversity, efficiency and community stability. American Zoologist 10:17-25.

MacDonald, G.M.; Larsen, C.P.S.; Szeicz, J.M.; Moser, K.A. 1991. The reconstruction of boreal forest fire history from lake sediments: A comparison of charcoal, pollen, sedimentological and geochemical indices. Quaternary Science Reviews 10:53-71.

Noss, R.F. 1987. Protecting natural areas in fragmented landscapes. Natural Areas Journal 7:2-13.

Ontario Ministry of Natural Resources 1928-1990. Statistical supplement to the annual report of the Minister of Natural Resources for the year ending 19xx. Toronto, On., Canada. (The earlier parts of this statistical series were issued by various forerunners of the Ministry such as the Ontario Department of Lands and Forests under a number of different titles).

Parks, P.J.; Alig, R.J. 1988. Land based models for forest resource supply analysis: A critical review. Canadian Journal of Forest Research 18:965-973.

Pehl, C.E.; Red, J.T.; Shelnutt ,H.E. 1986. Controlled burning and land treatment influences on chemical properties of a forest soil. Forest Ecology and Management 17:119-128.

Rego, F.C.; Bunting, S.C.; Barreira, M.G. 1988. Effects of prescribed fire on *Chamaespartium tridentatum* ((L. P. Gibbs) in *Pinus pinaster* (Aiton) forests. Journal of Range Management 41:410-412.

Romme, W.H. ; Despain, D.G. 1989. Historical perspective on the Yellowstone fires of 1988. Bioscience 39:695-699.

Romme, W.H.; Knight, D.H. 1982. Landscape Diversity: The concept applied to Yellowstone Park. Bioscience 32:664-670.

Schullery, P. 1989. The fires and fire policy. Bioscience 39:686-694.

Shannon, C.E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:379-423

Suffling, R. 1983. Stability and diversity in boreal and mixed-temperate forests: A demographic approach. Journal of Environmental Management 17:359-371.

Suffling, R. 1988. Catastrophic disturbance and landscape diversity. In: The implications of tire control and climate change in subarctic forests. In: Moss, M. ed. Landscape Ecology and Management : Proceedings, 1st Symposium of the Canadian Society for Landscape Ecology and Management; May 1987. University of Guelph, On., Canada: Polyscience Publications, Montreal, Canada: pp. 111-120.

Suffling, R. 1989. Climatic change, forest fires and the boreal forest.In: Boer, M.M.; Groot, R.S. eds. Discussion Report on: Fennoscandian Region. European Conference on Landscape Ecological Impact of Climatic Change; 1989 Dec 3-7; Lunteren, Netherlands: Universities of Wageningen, Utrecht and Amsterdam; Wageningen, Netherlands: pp. 112-130.

Suffling, R.; Lihou, K.; Morand, Y. 1988. Control of Landscape diversity by Catastrophic disturbance: A theory and a case study of fire in a Canadian Boreal forest. Environmental Management 12:73-78.

Tande, G.F. 1979. Fire history and vegetation pattern of coniferous forests in Jasper National Park, Alberta. Canadian Journal of Botany 57:1912-1931.

Taylor, D.L. 1980. Fire history and man-induced tire problems in subtropical South Florida. In: Stokes, M.A; Dieterich, J.H. eds. Proceedings, Fire History Workshop; 1980 Oct 20-24; Tucson, Ariz. U.S. Department of Agriculture, Forest Service. Gen. Tech. Rep. RM-81. Fort Collins, Co.: Rocky Mountain Forest and Range Experimental Station. pp. 63-68.

Turner, M.G. 1989. Landscape ecology: The effect of pattern on process. Annual Review of Ecology and Systematics 20: 171-197.

Turner, M.G.; Gardner, R.H.; Dale, V.H.; O'Neill, R.V. 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55:121-129.

U.S. National Park Service 1975. The Natural role of fire: A fire management plan for Yellowstone National Park. Unpublished report, Yellowstone National Park, Wy.

Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research 8:220-227.

Van Wagner, C.E. 1988. The historical pattern of annual burned area in Canada. Forestry Chronicle 63:182-185.

Van Wagner, C.E. 1990. Six decades of forest fire science in Canada. Forestry Chronicle 66: 133-137.

Van Wagner, C.E.; Methven, I. 1980. Fire in the Management of Canada's National Parks: Philosophy and Strategy. National Parks Occasional Paper R61-2/8-1E. Ottawa, On., Canada: Environment Canada.

Wade, D.J.; Ewel, J.; Hofstetter, R. 1980. Fire in south Florida ecosystems. Gen. Tech. Rep. SE-17. Asheville, N.C.: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experimental Station. 125 pp.

White, P.S. 1987. Natural disturbance, patch dynamics and landscape pattern in natural areas. Natural Areas Journal 7: 14-22.

Woods, G.T.; Day, R.J. 1977. A summary of the tire ecology study of Quetico Provincial Park. Report 8, Fire Ecology Study, Quetico Provincial Park. Toronto, On., Canada: Ontario Ministry of Natural Resources.

Wright, H.E., Jr. 1974. Landscape development, forest tires, and wilderness management. Science 186:487-495.

Yarie, J. 1979. A preliminary analysis of stand age distribution in the Porcupine unit. Proceedings, Alaskan Science Conference 30: 12

HAZEL PISTOL EROSION PLOT STUDY ON THE SISKIYOU NATIONAL FOREST IN SOUTHWEST OREGON

William F. Hansen'

Abstract-In November 1977, small erosion plots were installed on 30, 50 and 70 percent slopes following forest management activities in southwest Oregon. Activities included clearcutting using a skyline yarding system, followed by burning to reduce logging debris and hardwood competition in 1976. Little of the soil was exposed prior to burning because one end of the logs was suspended during the yarding operation. The burning intensity was severe due to the high amounts of logging debris and the relatively dry conditions with low fuel moistures. After burning, mineral soils were exposed on over 75 percent of the area. Rainfall measured 111 and 150 inches after 3 months and 12 months, respectively. Surface runoff and erosion leaving the plots were collected and measured. Some data loss occurred due to pipes plugging or container overflow. During the first 3 months, surface runoff measured from the burned area varied from 27.6 to 33.4 inches on 30 percent plots, 35.0 to 51.6 inches on 50 percent plots and 43.9 to 44.3 inches on 70 percent plots. The unburned 70 percent plots had water movement of 22.4 to 34.2 inches. Soil loss (<2mm) was 2.02 to 3.57 tons/acre on 30 percent plots, 2.18 to 5.89 tons/acre on 50 percent plots and 4.04 to 18.68 tons/acre on 70 percent slopes. Plots on 70 percent slopes within the clearcut area that were not burned had erosion ranging from 1.26 to 3.09 tons/acre. Surface runoff and erosion figures after one year are also presented. The magnitude of erosion was partly due to wind-driven rains near the Pacific Ocean and the highly erosive siltstone soils of the Dothan Formation. This study was helpful in changing attitudes about the effects of burning and requiring burning prescriptions that protect soils (e.g., by burning under conditions with greater fuel and soil moistures or requiring more fuel removed during the yarding operation). Visual indicators of surface erosion and methods for minimizing or mitigating the effects of prescribed burning are also discussed.

INTRODUCTION

Relatively little information was available on surface erosion quantities following forest practices in southwest Oregon when this study was conducted on the Siskiyou National Forest (SNF) in 1977 and 1978. During that time, the SNF was a leader in developing and implementing technology to reduce environmental impacts from forest practices. Resource values and constraints were extremely high with steep slopes covered with old growth Douglas-fir (Pseudotsuga menziesii) and beautiful streams with some of the most valuable salmon and steelhead habitat in the nation.

Prior to the study, the Siskiyou National Forest had identified many sensitive environmental issues. In response to the critical issues, forest practices were being carefully scrutinized to reduce environmental impacts. Road construction was a primary concern because of its potential effects to the soil, water and fishery resources. Access roads were typically kept near ridges to avoid stream crossings and reduce surface and mass soil movement into streams. Side casting of soils during road construction was minimized or even hauled away in very steep terrain. An aggressive program to provide road surface drainage and to revegctate the bare soils adjacent to roads was also being implemented. Skyline yarding systems, which partially or totally suspend logs on steep slopes or in streamside areas, were being successfully used to reduce the logging impacts associated with conventional ground-based skidders on steep slopes.

Fire management practices were addressed after the major contributors to erosion and stream sedimentation had been identified and were being *reduced.* The effects of post-logging bums became a concern of watershed specialists during monitoring trips on the SNF. Observations causing concern included loss of surface organic layer, exposure of mineral soil, soil pedestals, fresh silt *in* streams, and turbid water during storm events. Burning practices and attitudes about burning would be difficult to change without some evidence to back up observations. The challenge to "prove it" or at least "measure it" was a necessary and reasonable request by the unconvinced majority.

The concerns about erosion following prescribed bums would have been reduced if erosion was *not* measured under severe conditions. The SNF was an ideal testing ground to measure erosion in the late 1970's, and severe conditions following prescribed bums were not hard to find. The usual objectives of burning *were* to *reduce* heavy fuel loading from logging debris and to reduce competing vegetation with the next generation of Douglas-fir seedlings. These objectives were usually accomplished with hot bums, in the summer or early fall. Soil litter and the organic layer were often consumed.

'Forest Hydrologist, National Forests in South Carolina and Georgia, Forest Service, U.S. Department of Agriculture, Columbia, S.C. (formerly Forest Hydrologist on the Siskiyou National Forest in Grants Pass, Oregon).

To the untrained eye, overland flow and erosion were not problems because the streams usually carry little sediment. Soil erosion and water quality changes occur rapidly in response to rainfall intensity and duration. These processes are not easy to measure. Small plots were chosen to collect surface runoff and erosion realizing potential problems with variability within an area and impact from the plot edge. Advantages included the low cost, ability to collect and measure all the soil and water leaving each plot and ease with which photos could be used to show plot and sampling details.

DESCRIPTION OF THE STUDY

Location

The study was conducted on the Chetco Ranger District of the SNF in southwest Oregon, (specifically the north side of unit 2 of the Hazel-Pistol timber sale, Township 38S, Range 13W, section 28, NE 1/4 of the SW 1/4, Willamette Meridian). The study area is about 8 miles from the Pacific Ocean in the Pistol River basin between Brookings and Gold Beach, Oregon. The aspect was generally southwest to southeast.

Background Information

Following clearcutting using skyline yarding with one-end log suspension, the unit was burned in the fall of 1976 to reduce fuel residue and vegetation competition. Although not measured, over 75 percent of the mineral soils were exposed. Unusually dry conditions persisted until the fall of 1977 when the plots were installed.

The coastal landscape is typically deeply dissected by streams with boulders, bedrock or debris, which prevent further channel degradation (downcutting). Adjacent slopes often have high potential for erosion or instability due to soil materials, high rainfall, steep slopes and loss of support from channel erosion. The soils are also extremely complex due to numerous geologic changes. Average annual rainfall is over 100 inches (2.5 m) for much of the National Forest. Dry, hot summers with periodic lightning storms and burning by early natives and settlers have caused many past wildtires. In many cases, the litter layer and organic surface soils are shallow to non-existent. High decomposition rates and erosion are contributing factors. Such harsh site conditions present revegetation and regeneration problems, especially on the south-facing, skeletal (gravelly) soils. The study area selected has some of the most severe conditions on the SNF and in Oregon.

Geology and Soils

The bedrock of the study area consists of bedded layers of moderately hard siltstone, massive to slightly fractured mudstone and sandstone rocks of the Dothan formation. The soils were derived from colluvial and residual material. Soils of the area are primarily thin gravelly loams on slopes over 40 percent and thick silt and clay loams on slopes under 40 percent. Slopes in the unit arc locally highly dissected and range from 20 to 90 percent. The soils are moderately unstable and highly erosive.

Climate

The temperature extremes of cold winters and hot summers in southwest Oregon are moderated somewhat due to the close proximity to the Pacific Ocean. Warm, moist air masses are cooled as they are pushed upward by the coastal mountains. At an elevation of 2600 feet and only 8 miles from the coast, the study area is subject to high wind speeds and precipitation. Winds typically blow from the west to southwest with speeds occasionally exceeding 50 miles per hour. The average annual precipitation for the study area is estimated at over 125 inches and occurs primarily between November and May. Rainfall events are usually long duration with low to moderate intensity. Temperature differences from the coast may be present when the coast is fogged in and the study area is clear. Winter freeze-thaw cycles occur with few snow events.

METHODS

Experimental Design

The sampling methods were designed to test the effectiveness of grass seeding in reducing water movement and surface erosion on an area clearcut and broadcast burned. The experimental design was a 3 X 2 factorial analysis with one replication, or 12 plots total. The factors varied were slope and grass seed. Slopes used were 30, 50 and 70 percent and grass seeding was either 0 or 7 pounds per acre.

Plot Design

The plot boundaries consisted of 2 X 4 lumber with a 2 X 8 for the upper boundary. Each plot was designed to be 112500 of an acre (17.4 square feet) and the plot dimensions varied according to the slope. Each plot was drained into 6 inch fascia gutter scraps along the lower boundary. The gutter with end caps was nailed to the wooden boundary with the gutter lip bent down about 1/2 inch. The wooden boundary with gutter was eased into the correct position on the plot and staked to the ground at several locations outside the plot. The bent gutter lip was pressed into the soil. On the outside of the wooden boundary, a small ditch about 4 inches deep was constructed and filled with concrete to provide a good seal to prevent surface water from entering or leaving. Concrete was also placed by hand above the bent gutter inside the plot to prevent water from bypassing the gutter. A small trench above each plot diverted other runoff away from the plot.

Soil and Water Measurements

Surface water from the plot drained into a 55 gallon drum using 3/4 inch black plastic tubing. However, after continuous clogging problems, 1 1/2 inch black plastic tubing was installed. Plastic tubing fittings were used to go from the gutter into the 55 gallon drum lid. A 500 ml plastic bottle was placed over the tubing outlet to collect the heavier sediment. The lighter sediment was collected in the drum with the water from the plot. The water in the drum was measured, mixed and sampled. The concentration in the sample multiplied by the volume in the drum gave the amount of sediment in the drum. Larger or heavier materials often settled out in the gutter. This material was collected, oven-dried, sieved into soil (<2mm) or large particles (>2mm), weighed separately and added to the estimated sediment from the drum. Large particles included rocks or pebbles, Douglas-fir cones, needles, leaves and other debris. The collection gutters were cleaned out in February 1978 and November 1978, respectively, approximately 3 months and 12 months after installation. Rainfall measurements were made using a Belfort recording raingage. Under $5,000 was spent to collect this information.

RESULTS AND DISCUSSION

Some adjustments in the data analysis had to be made due to unforeseen problems. The grass failed to germinate properly within the plots and only scattered depressions had any success. Two plots were accidently located on an unburned portion of the burned unit. Another plot flooded with water and filled with sediment from an ephemeral microchannel which had not been diverted away from the plot. Lost data from plugged tubing and drum overflows from large storm events posed additional problems. The statistical efficiency of the factorial plot design was lost with these problems, but the information collected provided valuable insight to surface erosion and water movement after typical forest practices of the time.

Information was intensively collected on the study plots from November 11, 1977 to February 22, 1978 (104 days).

Fourteen separate rainfall events were identified during this period, ranging from 1.1 to 18.4 inches. Rainfall totaled 111 inches (2.8m) Average storm intensities were less than 0.25 inches per hour, while peak 2-hour intensity reached 0.82 inches per hour. During the first year, over 143 inches of rainfall was measured and about 7 inches was estimated, for a total of 150 inches (3.8m).

Figure 1 presents data to compare rainfall and runoff by plot slope and treatment for only those dates when collectors did not plug or overflow. There were a few discrepancies when runoff exceeded rainfall (the raingage opening was level while the plot openings were not) during individual storms. Whether the raingage caught less of the windblown rain, or the plots caught more, is not known. The amount of overland flow from the plots was alarming and provided strong evidence that surface erosion mechanisms existed. The following table presents the measured rainfall and runoff summarized at two points in time over a year. Since the collectors occasionally plugged or overflowed, estimates of runoff are low by approximately 10 percent for all treatments, except the 70B treatment data are 30 percent low.

Time Period	Time	Rainfall	Average Plot Runoff (in) by Treatment			
	(months)	(in)	30B	50B	70B	7ou
11/77-2/78	3.4	111	30.7	41.8	44.1	28.3
11/77-11/78	12	150	57.8	71.5	63.8	48.8

(30, 50, 70= % slopes, B=Burned, U=Unburned, 1 in=2.54 cm)

Figure 2 presents the measured erosion by treatment for the one year. Due to collection problems, some data was probably lost. The amount lost is believed to be much less than the amount of runoff lost because the gutters were effective sediment traps when pipes clogged. The following table summarizes soil and total erosion after 3 months and one year.

Time Period	Time	Rainfall	Total Erosion (tons/ac) by Treatment			
	(months)	(in)	30B	50B	70B	70U
11/77-2/78	3.4	111	2.5(2.7)	4.6(5.8)	11.4(20.0)	2.2(3.8)
11/77-11/78	12	150	3.8(4.3)	6.2(9.1)	12.8(23.2)	2.7(6.0)

(same symbols as previous table, 1 ton/acre = 2240 kg/ha)

Poor record keeping after November 1978 made the data collected after one year questionable. However, visual indications of continued surface water and erosion occurred because vegetative cover was slow to develop. In 1983, seven years after the burn, signs of accelerated erosion of litter, mineral soil and rock fragments on the 70 percent unburned plots were disturbing.

Several types of erosion processes were observed on the area, including raindrop, sheet, and rill erosion. These were detected or inferred by close observations during intense rainfall periods or inspection during the study period on the erosion plots.

Raindrop erosion occurred when large amounts of kinetic energy were expended on the soil surface by falling raindrops. In an undisturbed forest, vegetation and litter absorb this energy. Soil particles exposed during management activities are susceptible to detachment by the raindrop impact. The wind driven rain supplies additional velocity and energy. Raindrop erosion may clog surface pores thereby reducing infiltration. Soil pedestals formed under the protection of pebbles or wood were another indicator of soil remaining in place when shielded from raindrop impact.

Sheet erosion occurred as thin layers of surface materials were gradually removed. This was noticed as a fine root network was eventually exposed on the 30 percent plots. Larger roots and gravel were also exposed on the steeper sites as fines were removed. Soil delivery to the collection device was diffuse and defined water movement was difficult to observe.

Rill erosion was apparent during one heavy rainfall event on plot 6 (70 percent burn slope). Microchannels no more than an inch in cross section developed. Soil was being removed by running water of sufficient volume and velocity to generate

Figure 1
CUMULATIVE RAINFALL AND RUNOFF BY TREATMENT FOR SELECTED DATES

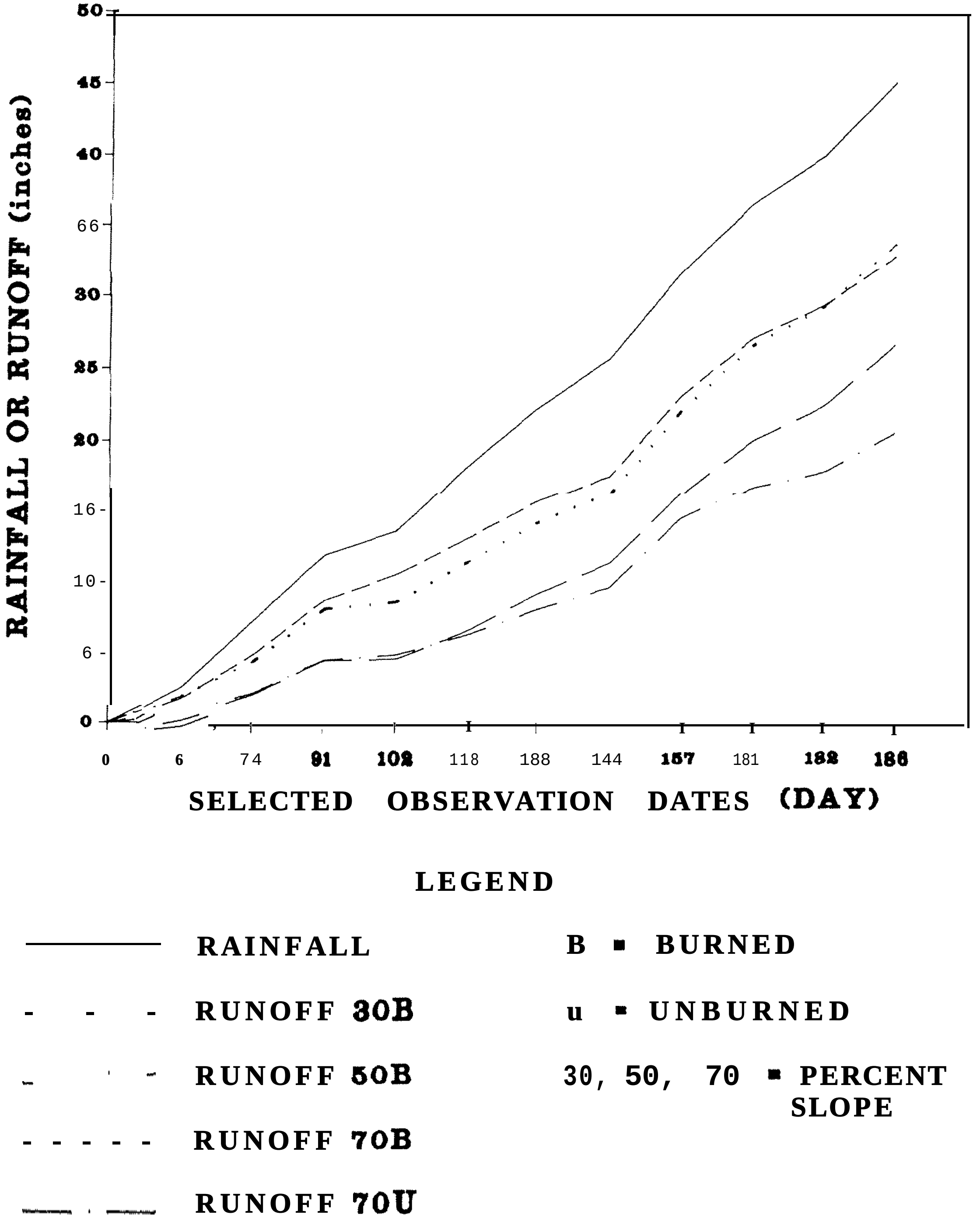
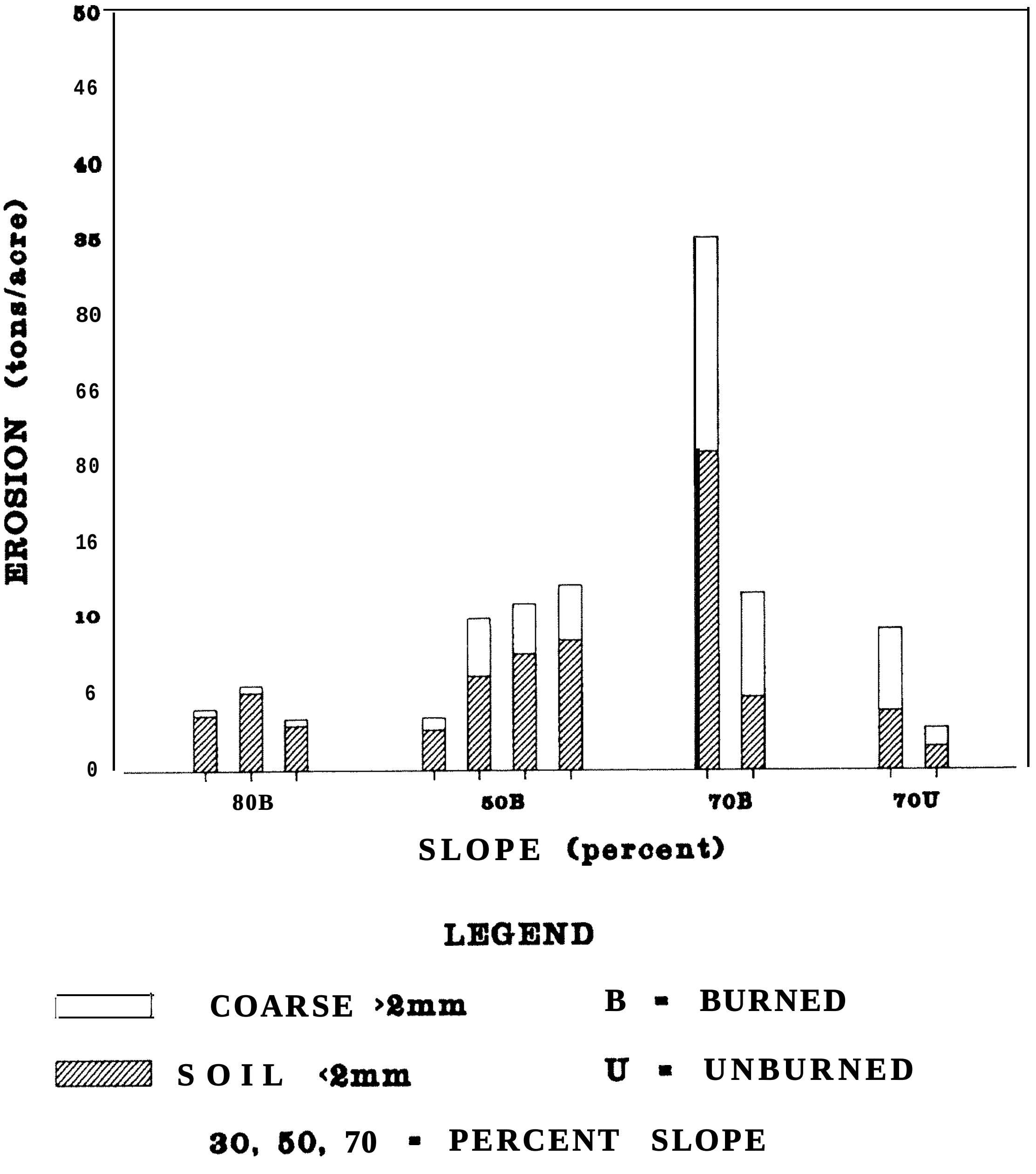


Figure 2
SOIL EROSION BY SLOPE
AND TREATMENT 11/77 TO 11/78



cutting power. As the soil particles eroded away, pebbles and small rocks could be seen and heard tumbling down the slope as they were moved by water and gravity.

Other visual observations of erosion were made outside of the erosion plots, within the harvest unit. Examples of exposed roots could be found on all slope classes. Fine roots were often exposed on 30 percent slopes and larger roots were sometimes exposed on steeper areas. These roots were not fire scarred and were apparently buried at the time of the prescribed bum. Fire scars on trees were occasionally above the soil surface, indicating measurable soil erosion. An increase in surface rock content was noticeable on slopes exceeding 50 percent or more. Soil deposition occurred in surface depressions, above woody debris and in pool areas within the stream channels. Soil protected from the burn under large woody debris or rocks had about 112 to 1 inch of litter and organic soil. Small rocks were suspended on soil pedestals. Streams would rapidly change in turbidity and sediment loads in response to rainfall intensity.

Part of the results include management's reaction to information collected on the study area. This study was an eye opener to forest managers, who previously perceived that surface erosion and overland flow effects were negligible following prescribed burning. After some initial deliberations and reactions to change, adjustments were made to strengthen the prescribed burning program.

Prescribed burning plans were adjusted to protect the surface soil and organic layer, including its ability to take up and store water. Burning is accomplished when the duff layer is moist (usually a few days after a soaking rain in the spring). Directional falling of the old growth trees on steep slopes reduced breakage of logs, prevented high debris loads in streams and increased the tree utilization. Required yarding of unutilized material (YUM), is another method to reduce the logging waste and fire intensity.

Burning specialists began to receive additional training in measuring weather, fuel moisture, fuel load, and flame height values to reduce fire impacts to soil resources. Strategies such as helicopter lighting also reduced tire intensity. Monitoring post-burning conditions also help evaluate the bum. When areas are accidently burned too hot, grass seeding with fertilization helped mitigate burning effects. The grass species mixture can help provide immediate cover needs with soil improvement and wildlife benefits.

CONCLUSIONS

This study was undertaken to document the presence or absence of surface runoff and erosion following typical clearcut and prescribed burning practices in southwest Oregon during the late 1970s. Severe conditions were chosen to test whether surface runoff and erosion were valid concerns. The effects of using grass seeding as possible mitigation was not possible because much of the grass was apparently lost due to erosion. During the intensive 104-day study of the burned area, 111 inches of precipitation occurred, producing surface runoff in excess of 30 to 50 inches and soil erosion from 2 to over 18 tons/acre. In contrast, the steep unburned areas produced substantially less runoff (20 to 30 inches) and soil erosion (1 to 3 tons/acre).

The results of this study convinced forest managers that some adjustments in prescribed burning practices were needed to protect soil, water and fishery resources. Resetting burning objectives to protect these resources was the first step. Methods designed at minimizing potential impacts to both onsite resources, such as soil productivity, and offsite resources such as downstream water quality, fishery habitat and air quality, were included in prescribed burning plans. Practices were implemented to reduce fuel loading through greater utilization and adjust burning intensity to protect soil resources.

Burning is a useful and necessary tool in forest management, but it can cause unacceptable adverse impacts if not properly applied. With adequate planning, timber harvest and burning practices can be adjusted to achieve soil and water resource objectives, with good success at residue abatement and temporary vegetation control. Soil, slope, climatic and historic land use factors should be assessed to help evaluate the erosion potential of an area prior to burning. When burning under conditions with severe erosion potential cannot be avoided, aggressive efforts to revegetate exposed mineral soils are needed.

Despite the limited application of small plot studies, they are helpful in this case to identify and measure site specific processes that are difficult to measure on a large scale. However, several factors should be considered before applying the results of this study to other conditions. The presence of abundant wind-blown rain, highly erodible soils, steep slopes and exposed mineral soil from a combination of forest logging and burning practices were all important contributing factors in the severity of the study results.

ACKNOWLEDGEMENTS

Foremost, I recognize and thank Malcolm Drake, Hydrologic Technician, for his valuable assistance and hard work in the installation and service of the plots. Other USDA-Forest Service employees that I want to recognize include John Millet (retired), encouraged and supported this study; Harvey Timeus, Joe Waller, and Ed Gross, Chetco Ranger District, helped service the erosion plots; Roy Meyer and Mike Amaranthus, described the soils; Bob Ettner, encouraged reporting of these findings; Luis Mundo helped with the computer graphics and Lynda Hansen helped with typing and editing.

THE SIGNIFICANCE OF FIRE IN AN OLIGOTROPHIC FOREST ECOSYSTEM

Frank S. Gilliam'

Abstract-Past and present climate conditions have interacted with soil development to result in distinctly oligotrophic (nutrient-poor) conditions in many southeastern U. S. Coastal Plain ecosystems. Fire historically has been an important abiotic component in these systems favoring the dominance of plant species which require fire for successful regeneration and growth. This study examined the role of periodic tire in several components of an oligotrophic lower Coastal Plain pine flatwoods ecosystem. Except for some loss of nitrogen (N) from the forest floor, experimental bums had slight effects on nutrient loss from the system. Fires volatilized an average of 24 kilograms N per hectare. Much of this loss is balanced by annual net (precipitation input minus stream flow output) ecosystem increases in N. Fire increased nutrient availability in the soil, an increase which coincided with increases in the biomass and species diversity of the herbaceous layer. Thus, fire is important in maintaining nutrient availability in these nutrient-poor soils. Evidence presented in this study support the idea that pine flatwoods are especially limited by phosphorus(P) and potassium (K) availability and that fire significantly increases available levels of P and K in the soil. Fire is considered here a characteristic property of the ecosystem, one which integrates all hierarchical levels of organization of the system.

INTRODUCTION

General hypotheses concerning the importance or role of fire in ecosystems appear difficult to make, given the great variety of ecosystem types wherein fire occurs at a sufficient frequency to be considered a component of the system. It is a reasonable hypothesis, however, that a predominant role of fire, regardless of ecosystem type, is to increase or maintain the availability of an essential (usually growth-limiting) resource, either energy (sunlight), nutrients, or water. The specific role of fire would be determined by which resource, or combination of resources, is limiting in a particular ecosystem. For example, in tallgrass prairie, which has nutrient-rich soils, but experiences substantial build-up of plant detritus which intercepts both light and water, fire appears to be important in maintaining availability of energy and water, but not nutrients.

The Coastal Plain of the southeastern United States has long been a region of great interest to fire ecologists, as evidenced by earlier reviews by Wells (1942) and Garren (1943), and more recently by Christensen (1981). This is a region wherein past and present climatic factors have influenced soil development in a way that resulted in oligotrophic (nutrient-poor) conditions (Gilliam 1990). Such conditions have, in turn, favored the dominance of plant species, such as pines, which require fire for successful reproduction and growth. These species, adapted to low soil fertility, produce acidic, low-nutrient detritus, thus maintaining oligotrophic conditions, a scheme that represents co-development of biotic and abiotic components of the ecosystem (Jenny 1980).

The main objective of this study was to examine the effects of fire on several components of a pine flatwoods ecosystem of the lower Coastal Plain of South Carolina. These results were used to address the hypothesis that fire, as an integral part of the system, serves a significant function in increasing nutrient availability. A second objective of this study is to look at the specific role of fire at each hierarchical level of organization of the system (ecosystem, community, and population) to address the contention that fire is "incorporated" (*sensu* O'Neill and others 1986) at the level of the ecosystem.

In addition to the presentation of previously unpublished data, this paper provides a brief synthesis of several aspects of the Santee Watershed Study. These include studies on the effects of fire on water quality (Richter and others 1982, 1984), precipitation chemistry (Richter and others 1983), soil nutrients (Gilliam and Richter 1985, 1988; Gilliam 1990), and effects of fire on herbaceous layer vegetation (Gilliam and Christensen 1986; Gilliam 1988).

MATERIALS AND METHODS

Study Site

The study was carried out on Watershed 77 (WS77) of the Santee Experimental Forest. This forest is within the Francis Marion National Forest in South Carolina, approximately 50 kilometers north-northwest of Charleston (33°N, 80°W). WS77 is 165 hectares in area and is typical of lower Coastal Plain pine flatwoods ecosystems. Topographic relief of this and other first-order watersheds of the region varies by 5.5 meters. Prior to the start of the study, WS77 had not been burned for 40 years.

'Assistant Professor of Biological Sciences, Marshall University, Huntington, WV

WS77 soils are clayey, mixed, thermic, vertic Aquults of the Bayboro, Bethera, Carolina, and Wahee series. Although these soils are of mixed minerologies they are generally derived from old and highly-weathered secondary sediments of an alluvial origin and from montmorillonitic deposits of a marine origin. The soils tend to be extremely acidic, infertile, and low in weatherable minerals (Gilliam 1990). Each of the four series are described as very strongly acidic in reaction to at least 130 centimeters (Hatchell and Henderson 1976).

Vegetation of WS77 is characteristic of Coastal Plain pine flatwoods. The dominant overstory species were pines, loblolly pine (*Pinus taeda* L.--75 percent of the overstory basal area) and longleaf pine (II. *palustris* Miller--l7 percent). Other canopy species were sweetgum (*Liquidambar styraciflua* L.--4 percent), black gum (*Nyssa sylvatica* Marshall--3 percent), and shortleaf pine (*P. echinata* Miller--2 percent). Dominant shrub species included nearly equal mixtures of wax myrtle (*Myrica cerifera* L.), gallberry (*Ilex glabra* (L.) Gray), and lowbush blueberry (*Vaccinum tenellum* Aiton.). The herb layer was dominated by broom sedge (*Andropogon virginicus* L.), with switch cane (*Arundinaria gigantea* (Walter) Muhl.) abundant along seeps and stream channels.

The climate for this region is classified as humid mesothermal (Trewartha 1954), with mild winters and warm, moist summers. Mean monthly minimum temperatures for January and July (extreme months) are 4 and 20°C, respectively, whereas mean monthly maximum temperatures are 12 and 32°C. Seasonal patterns of precipitation, stream flow, and evapotranspiration for WS77 are shown in fig. 1. Precipitation averaged 135 centimeters annually, while stream flow averaged 35 centimeters annually. Precipitation typically exceeded evapotranspiration throughout the year (fig. 1).

Sampling

Precipitation and Stream Flow

Nutrient inputs were estimated from weekly precipitation sampling and chemical analysis. Precipitation was sampled with a network of nine bulk collectors and volume was determined directly using a method described in Thiessen (1911).

Similarly, nutrient outputs were estimated from chemical analysis of weekly stream flow grab samples taken behind the calibrated weir at WS77. Weekly flow volume was calculated from continuous stream height monitoring. Daily flow volume was calculated from these readings by U. S. D. A. Forest Service Computations. All sampling (precipitation and stream flow) was carried out for 6 years

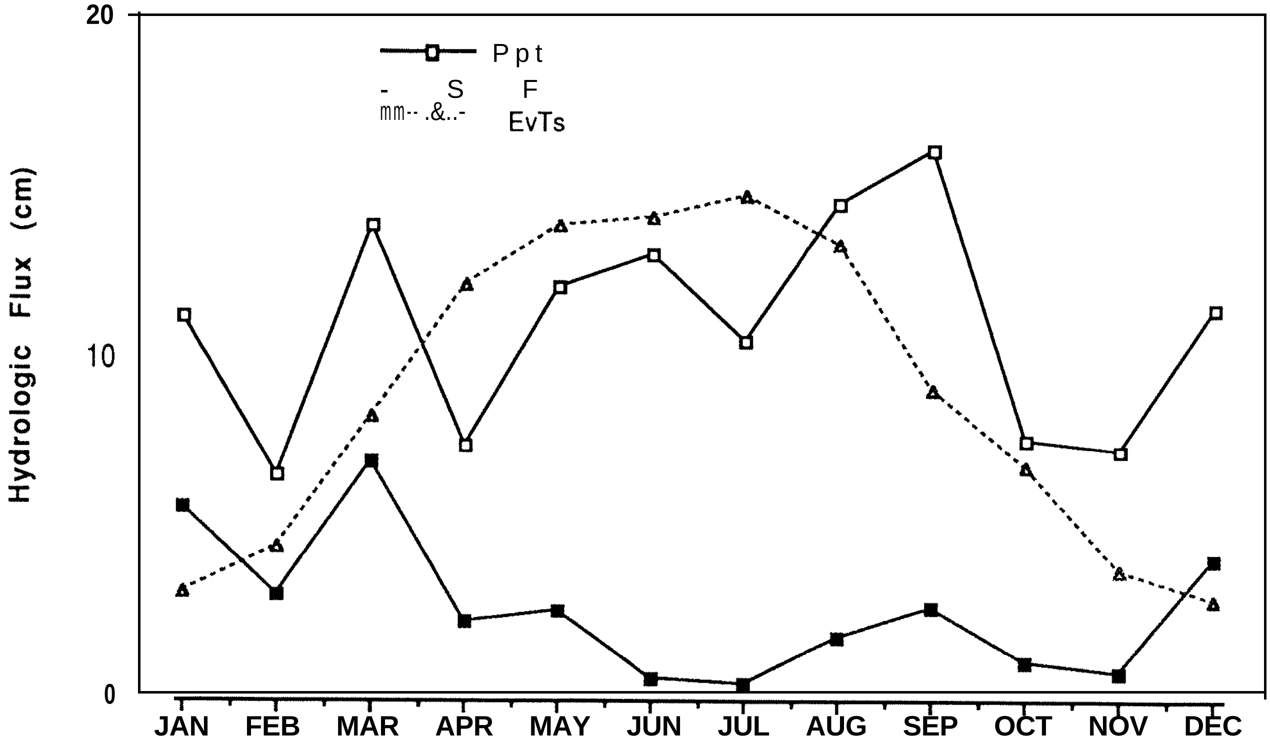


Figure l.-Mean monthly fluxes of precipitation (Ppt), stream flow (SF), and evapotranspiration (EvTs) for WS77.

Fire Effects

WS77 was divided into 20 compartments of approximately 8 hectares. Fires were administered as summer or winter prescribed fires, largely as backing fires. A total of nine tires administered during this study. See Cilliam and Christensen (1986) for **a** complete description of compartments and fire treatments. Briefly, nine compartments receiving either winter-only tires, winter and summer fires, or no fire (control) were chosen randomly from the 20 compartments of the watershed.

Effects of fire were estimated from sampling (usually both before and after the fire) within 10 lo-meter x lo-meter plots in each compartment. Forest floor and mineral soil were sampled both before and after the bum. Forest floor was sampled with a 14.7-centimeter diameter litter cutter; mineral soil was sampled with a 2.0-centimeter diameter soil corer to a depth of 20 centimeters and cores were divided into O-5 centimeters, 5-10 centimeters, and 10-20 centimeters depths. Five subsamples taken randomly within each plot were composited for each sample type.

Overstory and shrub layer vegetation were sampled once prior to burning. All stems >0.6 centimeters diameter (at 1.5 meter in height) within each plot were identified and measured, either for diameter (trees) or canopy cover (shrubs).

The herbaceous layer, defined as all vascular plants ≤ 1 meter in height, was sampled in live of the 10 plots in each compartment to determine 1) herb layer cover and biomass, 2) species richness and diversity, and 3) nutrient content. Herb layer cover was estimated non-destructively in two 0.5 meter x lo-meter transects in each of the live sample plots. The transects were subdivided to yield 10 l-square meter subplots. Per cent cover was estimated visually for each species in all subplots. Biomass was estimated by harvesting three separate 50-meter x OS-meter transects. These transects were subdivided into 75 0.5-meter x 2-meter subplots.

A separate design was used to determine nutrient concentrations of herb layer vegetation in burned and unburned areas. Ten pairs of sample plots were established in the topographic extremes of WS77, five in upslope areas and five in lowland areas. One plot of each pair was burned and the other was left unburned. Herb layer vegetation was sampled by harvesting all above-ground parts within the two transects as described previously. All herb sampling (cover estimates, biomass harvests, and nutrient analysis harvests) was carried out in the summer.

Analyses

Precipitation and Stream Flow

Precipitation and stream flow were analyzed for pH with a glass electrode. Metal cations $(Na^+, K^+, Ca^{++}, Mg^{++})$ were determined with atomic absorption spectrophotometry (Isaac and Kerber 1971). Ammonium $(NH4^+)$ was determined by isocyanurate colorimetry (Reardon and others 1966), NO; by Cd reduction and azo-dye colorimetry (APHA 1976), PO_4^{3-} by molybdenum blue colorimetry (Mehlich 1953), and SO,” by turbidimetry (Schlesinger and others 1982).

Mineral Soil

Samples of mineral soil were air-dried and ground in a hammer mill to pass a ‘L-millimeter screen. Measured samples of about 10 grams each were extracted with a dilute double-acid solution at a 1:5 soil/solution ratio according to Mehlich (1953), a method established for acid, clay soils. Extractable elements were determined as described above.

Herb Layer Vegetation

Harvested herb layer material was oven-dried and ground in a Wiley mill. Plant tissue was digested using a H_2SO_4-H_2O_2 method (Lowther 1980) and analyzed for Ca, Mg, K, N, and P as described above.

Data Analysis

Fire effects on soil were tested using t-tests to compare pre-bum soil pH and nutrient cation concentrations and those of post-bum soils. T-tests were also used to test the effects of tire on plant tissue nutrient concentrations by comparing burned and unburned means. In each case the level of significance was $p < 0.05$. Linear regression analysis was used to generate a model relating herb layer cover to biomass. The level of significance was $p < 0.01$ (Zar 1974).

RESULTS AND DISCUSSION

Ecosystem-Level Effects of Fire

Although nutrient budgets are somewhat incomplete in this study, the components studied provide reasonable estimates of total nutrient flux. For example, soil surveys suggest minimal deep seepage loss because of poorly drained throughout WS77 (U.S.D.A. 1980). Denitrification should also be minimal, due to low NO; production in these extremely acidic soils. Finally, N fixation is probably low because of the low frequency of legumes in the forest (Gilliam and Christensen 1986) and because non-symbiotic N fixers are generally rare in acidic forest soils (Alexander 1977). Thus, input/output data may be strongly indicative of the nutrient status of the

Table 1. Input-output budgets for cations in precipitation and stream flow for WS77. Data represent averages from 19761982.

Input-Output	H^+	Ha'	K^+	Ca^{++}	Mg^{++}	NH_4	NO,'	so,=	Cl^-	PO_4^{3-}
	keq/ha/yr									
Precipitation	0.54	0.27	0.03	0.26	0.13	0.06	0.12	0.50	0.45	0.01
Stream Flow	0.05	0.49	0.03	0.37	0.22	0.01	0.00	0.51	0.61	0.01
Net (I-O)	+.49	-.22	0	-.11	-.09	+.05	+.12	-.01	-.16	0

ecosystem. Table 1 shows precipitation and stream flow nutrient budgets for the entire 6-year period of the study. Hydrogen ion was greatly conserved by the system, with precipitation H^+ inputs exceeding stream flow outputs by an order of magnitude. Also conserved were $NH4^+$ and NO;. Although such patterns are not conclusive, these data suggest that N, commonly limiting in forest ecosystems, may be a limiting nutrient in this forest.

There were net annual outputs of Na^+, Ca^{++}, Mg^{++}, $SO4^=$, and Cl^- over the study period (table 1). Although many of the soils of this region were derived from highly-weathered sediments of an alluvial origin, net outputs of these ions indicates that, for WS77, further weathering is taking place and that these parent material sediments were largely of a marine origin.

None of the nine fires in the six years of the study had any significant effect on stream flow nutrient output (Richter and others 1982). The main loss of nutrients due to fire was an average volatilization of 24 kilograms N per hectare from the forest floor (Richter, and others 1984). Assuming a fire cycle of 5 to 7 years (Christensen 1981), however, this loss is balanced by annual accumulations of inorganic N (2.4 kilograms per hectare per year--calculated from table 1) and organic N (approximately 2 kilograms per hectare per year--Richter 1980) from precipitation.

Nutrient budgets werebalanced for K and P (table 1), suggesting strongly that K and P (in addition to N) may be growth-limiting in these soils. As discussed in Gilliam (1988), this contention is supported further by comparisons of nutrient concentrations in herb layer vegetation from similar and contrasting ecosystems (table 2). Among these sites, including hardwood forests and other conifer forests, K, N, and P concentrations were typically lowest for herb layer vegetation from WS77 (table 2).

Table 2. Herbaceous Layer nutrient concentrations for various sites.

Site/Study	K	Ca	Mg	N	P
			%		
Eastern Illinois hardwoods/ Peterson and Rolfe (1982)	3.79	1.17	0.42	2.32	0.36
Northern hardwood forest/ Siccama, and others (1970)	3.18	0.74	0.33	2.38	0.18
Northeast Minnesota/ Grigal and Ohmann (1980)	3.25	2.28	0.50	1.38	0.34
Central New York State/ Bard (1949)	3.01	2.00	----	1.93	0.21
Boreal forest/ Gagnon, and others (1958)	0.51	0.81	0.24	----	0.19
Lower Coastal Plain/ Garten (1978)	0.60	0.85	0.16	----	0.18
Coastal Plain flatwoods/ Gilliam (1988)	0.84	0.77	0.20	1.19	0.06

Nutrient Availability and Uptake

The effect of fire on extractable soil nutrients was minimal and varied with season of burn (table 3). Summer burns seemed to have little influence on soil nutrients, except for a significant decrease in extractable NH4’. For winter burns, however, there were significant increases in pH and extractable K^+, Ca^{++}, and NH,+. Although data for extractable P are not shown here, increases in extractable P in these soils in response to fire has been demonstrated (Gilliam 1983). Therefore, there is an indication that fire may increase availability of limiting nutrients.

Gilliam and Christensen (1986) summarized the response of herb layer cover and species richness of WS77 to tire. They sampled nine randomly chosen compartments representing six fire treatments, including winter- and summer-burned compartments and unburned control compartments. They found that only (but not all) winter fires had appreciable effects on the herb layer. Thus, it should be stressed that, depending on the ecosystem component being studied, fire effects may be seasonal and highly variable. Furthermore, such variability itself can have great significance on the level of the ecosystem (Christensen 1981). For the purpose of comparison, specific results for a particular winter tire will be presented in this paper.

Tissue nutrient concentrations for herb layer vegetation were significantly ($p < 0.05$) higher in burned plots than unburned plots for K, N, and P (fig. 2). There were no significant differences for Ca and Mg. This pattern suggests that fire may increase the availability of K, N, and P.

The relationship of herb layer cover and harvested biomass for each species in the three harvest transects is shown in fig. 3. This relationship yielded the equation

$$y = -0.03 + 1.81x \qquad (1)$$

where y is herb biomass in grams per square meter and x is herb cover in per cent. The correlation coefficient was 0.94 and was significant at $p < 0.01$. The relationship is based on mean values for individual species. Thus, given the highly significant correlation, equation (1) can be used to estimate biomass for individual species in plots of the burned and unburned compartments, Biomass was summed for all species in each plot to yield total herb layer biomass per plot.

Average cover was significantly ($p < 0.05$) higher in the winter burn plots compared to the control plots (37 percent vs. 16 percent, respectively; table 4). Using equation (1) for each individual species in these plots, this difference translated to a greater than two-fold increase in herb layer above-ground biomass (65 grams per square meter versus 28 grams per square meter).

Table 3. T-test comparisons of pre- vs. post-burn soils at different depths and seasons of burning.

Sumner burn

Depth/Treatment	pH	K^+	Ca"	Mg^{++}	NH_4
	μeq/g				
		0.7			
O-5 cm/Pre-burn	4.38	0.7	12.2	5.5	1.1
O-5 cm/Post-burn	4.35		11.0	5.4	0.6*
5-10 cm/Pre-burn	4.48	0.3	6.6	4.1	0.7
5-10 cm/Post-burn	4.48	0.3	6.4	4.0	0.2*
IO-20 cm/Pre-burn	4.58	0.2	6.1	4.7	0.4
IO-20 cm/Post-burn	4.65	0.2	5.8	4.4	0.1*

* indicates significant difference ($p<0.05$) between pre- and post-burn means

Uinter burn

Depth/Treatment	pH	K^+	Ca^{++}	Mg	NH_4
	μeq/g				
O-5 cm/Pre-burn	4.16	0.9	4.8	2.5	0.7
O-5 cm/Post-burn	4.26*	1.1*	7.3*	3.0	0.9*
		0.5			
5-10 cm/Pre-burn	4.35	0.5	3.4	2.2	0.3
5-10 cm/Post-burn	4.45*		3.2	1.9	0.4*
IO-20 cm/Pre-burn	4.48	0.4	3.6	2.8	0.3
IO-20 cm/Post-burn	4.58	0.3	2.6	2.3	0.4*

* indicates significant difference ($p<0.05$) between pre- and post-burn means

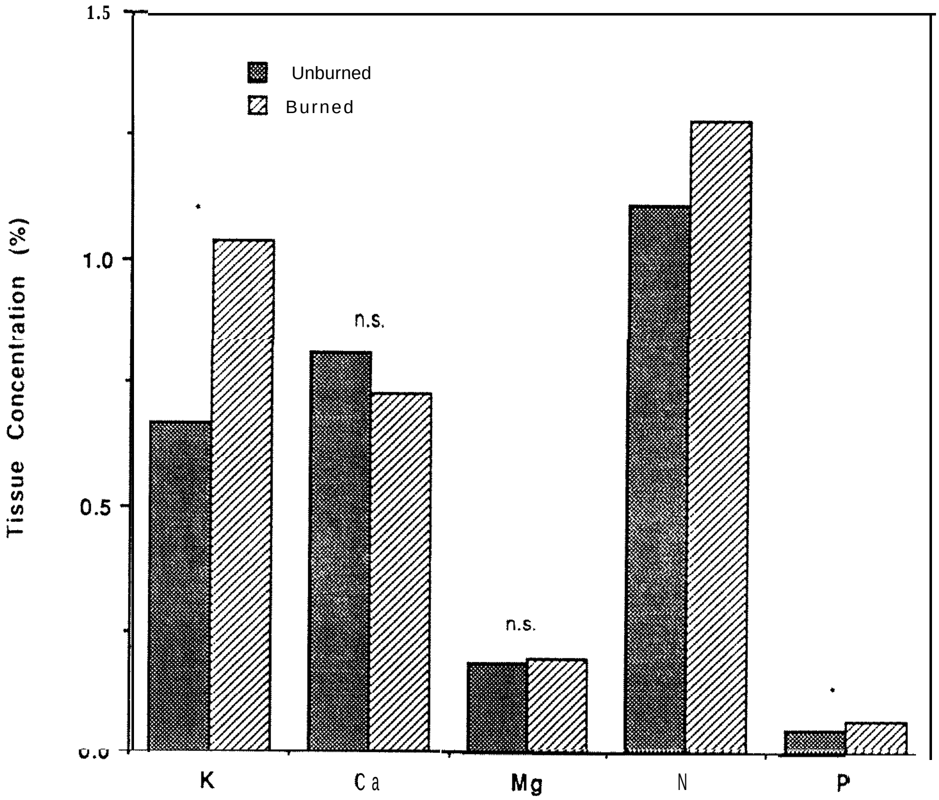


Figure 2.-Nutrient concentrations of burned and unburned plot herb layer vegetation. *Indicates significant difference between burned and unburned treatments at $p < 0.05$.

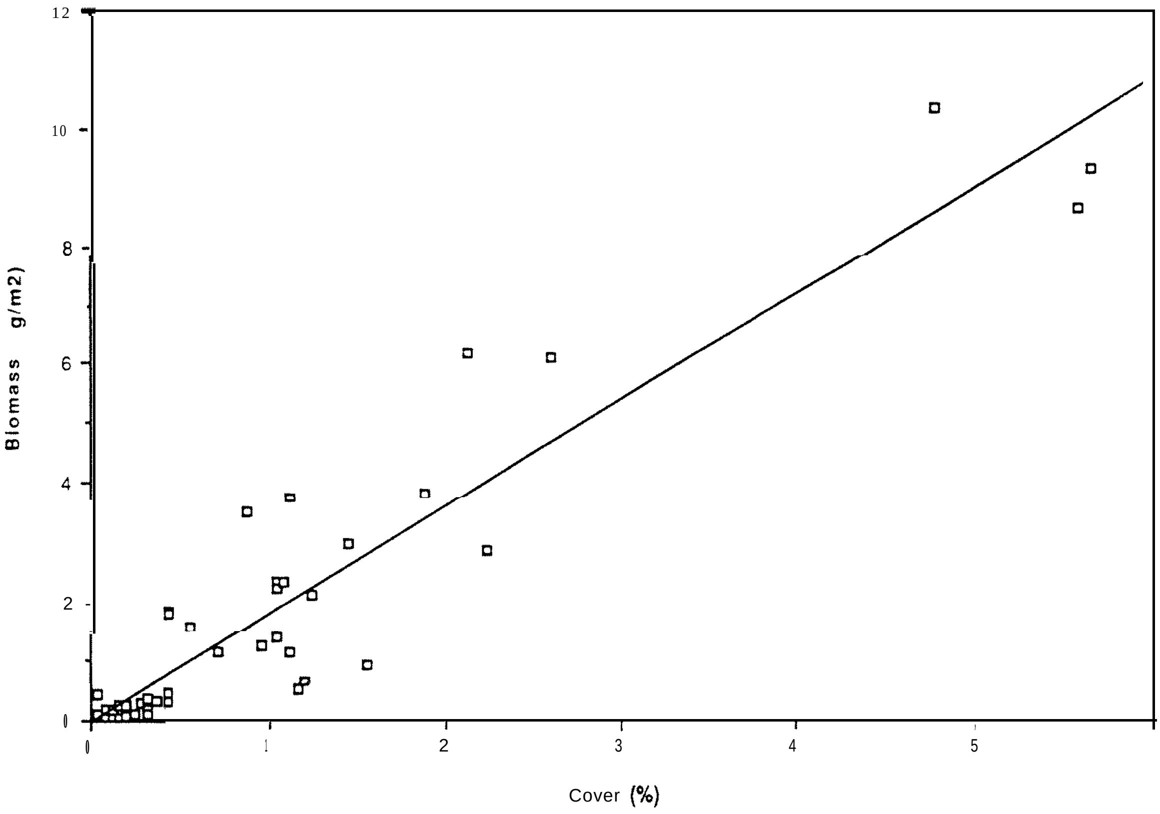


Figure 3.-Relationship of herb cover and harvested herb biomass for WS77. Each point represents average biomass and cover values for individual species. See text for equation.

Table 4. Herbaceous Layer cover, biomass, species richness, Shannon-Weiner diversity, and nutrient content for burned and unburned plots of WS77. Error values are one standard error of the mean.

Treatment	Cover (%)	Biomass (g/m^2)	K	Ca	Mg	N	P	Diversity	Richness (spp./plot)
			kg/ha						
Control	16.2 ± 2.7	28.3 ± 4.7	1.9	2.2	0.5	3.1	0.2	1.95 ± 0.15	16.5 ± 2.3
Winter burn	36.7 ± 3.7	65.1 ± 6.3	6.8	5.0	1.3	8.3	0.5	2.50 ± 0.10	29.5 ± 1.9

Herb layer nutrient content was approximated by applying the appropriate nutrient concentration data from fig. 2 to unburned and burned herb layer biomass means in table 4; i.e., "burned" K, N, and P values from fig. 2 were used with "winter burn" biomass from table 4 and "unburned" values in fig. 2 were used with "control" biomass. Since fire did not significantly influence Ca and Mg concentrations, overall mean values from fig. 2 for these nutrients were used with mean biomass values from table 4.

Not surprisingly, using this method, increases in herb layer nutrient content were especially pronounced for K, N, and P. These increases were >3.5-fold, 2.7-fold, and >2.5-fold for K, N, and P, respectively (table 4).

It merits repeating that these degrees of differences, whether for herb cover, biomass, or nutrient content, are not indicative of all fires in this ecosystem, since some fires (especially summer fires) had no appreciable influence on the herb layer. These data, therefor, provide a meaningful comparison representative of the potential effects of fire in this system.

Community-Level Effects of Fire

Although the major emphasis of much of this work has been on ecosystem-level effects of fire, the herbaceous layer is also useful in assessing the effects of fire on the level of the plant community, especially with respect to effects on species diversity and composition. Herb layer species diversity was measured for each plot in winter burn and control compartments as the Shannon-Weiner Diversity Index (H), using the equation

$$H = - \sum_{i=1}^{n} [p_i \ln(p_i)] \qquad (2)$$

where p_i is the decimal fraction of individuals of the ith species and n is the total number of species.

Fire significantly increased species diversity of the herb layer for this particular winter burn (table 4), a response typical for other winter fires of WS77 (Gilliam and Christensen 1986). The value of H reflects both numbers of species present as well as their relative importance, measured here as relative cover. Thus, much of the increase in the diversity index was from a significant increase in species richness, from 17 species per plot in control compartments to 30 species per plot in winter burn compartments (table 4).

In addition to increasing the numbers of species in burned plots, fire altered species composition as well (table 5). Grass species in particular increased in importance in burned areas. Indeed, for the species listed in table 5, fire did not so much alter which species were important as it altered species cover, on both an absolute and a relative basis.

Table 5. Important species for the herbaceous layer in burned and unburned plots of US77. Nomenclature follows Radford, and others (1968).

Control		Winter burn	
Species	Relative Cover (%)	Species	Relative Cover (%)
Lonicera japonica	16.3	Andropogon virginicus	21.4
Andropogon virginicus	15.2	Liquidambar styraciflua	8.5
Ilex glabra	12.1	Vaccinum tenellum	5.9
Vaccinum tenellum	8.8	Vitis rotundifolia	5.8
Myrica cerifera	7.6	Vaccinium elliottii	5.4
Liquidambar styraciflua	6.5	Rubus betulifolius	5.1
Rubus betulifolius	4.3	Ilex glabra	4.0
Pinus taeda	2.7	Myrica cerifera	3.2
Mitchella repens	2.3	Festuca elatior	2.7
Vitis rotundifolia	2.1	Lonicera japonica	2.7

Population-Level Effects of Fire

Fire will affect populations of plant species differentially, depending on the species' life history characteristics and resource requirements. Many species in southeastern Coastal Plain ecosystem not only respond positively to relatively high tire frequencies, but actually are dependent on tire for successful reproduction and growth. A well-documented example of such a fire-dependent species is longleaf pine. There are excellent accounts of the relationship between fire and longleaf pine, the most recent of which focuses on the importance of tire in several aspects of its population dynamics (Platt and others 1988).

Woody species data for WS77 provides an example of the effects of long-term fire exclusion on longleaf pine, since WS77 had not been burned for approximately 40 year prior to the initiation of the study. Figure 4 is a size class frequency distribution comparing longleaf pine to loblolly pine, which is a much less fire-dependent species. The distribution pattern for loblolly pine is typical of a successfully regenerating species, with high frequencies of small stems and attenuating numbers toward larger size classes. In contrast, the pattern for longleaf pine (e.g., extremely low frequencies of small stems) is indicative of greatly suppressed regeneration. Thus, long-term fire exclusion and greatly reduced tire frequencies cause sharp declines in longleaf pine populations.

Conclusions

This Coastal Plain pine flatwoods ecosystem is distinctly oligotrophic and fue, as an integral part of the system, serves a significant role in increasing nutrient availability. It is thus notable that P and K typically increase in availability after tire.

The importance of tire on the plant community level was evident in its effects on the herbaceous layer. Although these effects were variable (especially varying with season of bum), tire can cause substantial increases in species diversity, apparently by altering microenvironments and ultimately increasing resource availability.

Fire also plays a vital role in the life history and population dynamics of several plant species in pine flatwoods systems. Data presented here demonstrate the importance of tire in maintaining successful regeneration of the canopy co-dominant species, longleaf pine.

Thus, fire effects appear to be integrated across all hierarchical levels of organization, from the population to the community to the ecosystem. Fire serves significant functions that are both required and unique at each level.

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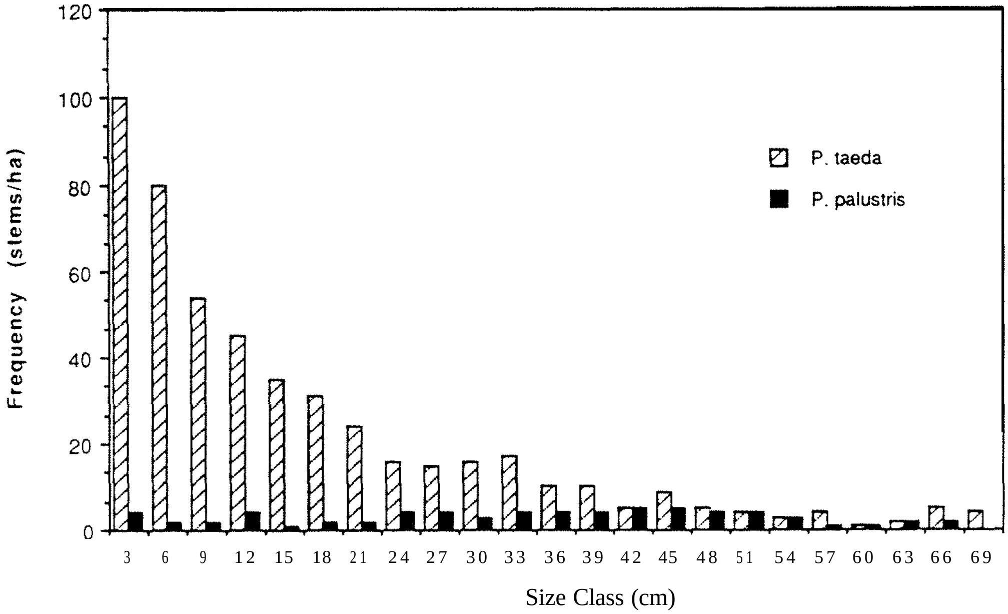

Figure 4.-Size-class distributions for loblolly pine (P. taeda) and longlcaf pine (P. palustris) for WS77

LITERATURE CITED

Alexander, M. 1977. Introduction to soil microbiology, 2nd ed. John Wiley and Sons, New York.

American Public Health Association. 1976. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, New York.

Bard, G.E. 1949. The mineral nutrient content of the annual parts of herbaceous species growing on three New York soils varying in limestone content. Ecology 30:384-389.

Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. pp. 112136. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., and Reiners, W.A., eds.Fire regimes and ecosystem properties. Forest Service General Technical Report WO-26.

Gagnon, D., LaFond, A., and Amiot, L.P. 1958. Mineral content of some forest plant leaves and of the humus layer as related to site quality. Canadian Journal of Botany 36:209-220.

Garren, K.H. 1943. Effects of fire on vegetation of the southeastern United States. The Botanical Review 9:617-654.

Garten, C.T. 1978. Multivariate perspectives on the ecology of plant mineral element composition. The American Naturalist 112:533-544.

Gilliam, F.S. 1983. Effects of fire on components of nutrient dynamics in a lower Coastal Plain flatwoods ecosystem. Ph.D. thesis. Duke University, Durham, N.C.

Gilliam, F.S. 1988. Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor Coastal Plain forest. Bulletin of the Torrey Botanical Club 115:265-271.

Gilliam, F.S. 1990. Ecosystem-level significance of acid forest soils. in press. In: Wright, R.J., Baligar, V.C., and Murrmann, P., eds. Utilization of acidic soils for crop production. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Gilliam, F.S. and Christensen, N.L. 1986. Herb-layer response to burning in pine flatwoods of the lower Coastal Plain of South Carolina. Bulletin of the Torrey Botanical Club 113:42-45.

Gilliam, F.S. and Richter, D.D. 1985. Increases in extractable ions in infertile Aquults caused by sample preparation. Soil Science Society of America Journal 49:1576-1578.

Gilliam, F.S. and Richter, D.D. 1988. Correlations between extractable Na, K, Mg, Ca, P and N from fresh and dried samples of two Aquults. Journal of Soil Science 39:209-214.

Grigal, D.F. and Ohmann, L.F. 1980. Seasonal changes in nutrient concentrations in forest herbs. Bulletin of the Torrey Botanical Club 107:47-50.

Hatchell, G.E. and Henderson, J.E. 1976. Moisture characteristics of some Coastal Plain soils on the Francis Marion National Forest. U. S. D. A. Forest Service Paper SE-150.

Isaac, R.A. and Kerber, J.D. 1971. Atomic absorption and flame photometry: Techniques and uses in soils, plant, and water analysis. pp. 17-37. In: Walsh, L.M., ed. Instrumental methods for analysis of soils and plant tissue. Soil Science Society of America, Madison, WI.

Jenny, H. 1980. The soil resource. Springer-Verlag, New York.

Lowther, J.R. 1980. Use of a single sulphuric acid-hydrogen peroxide digest for the analysis of Pinus radiata needles. Communications in Soil Science and Plant Analysis 11:175-188.

Mehlich, A. 1953. Determination of P, Ca, Mg, K, Na, and NH,. North Carolina Soil Test Division Mimeograph, Raleigh.

Peterson, D.L. and Rolfe, G.L. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. The American Midland Naturalist 107;325-339.

Platt, W.J., Evans, G.W., and Rathbun, S.L. 1988. The population dynamics of a long-lived conifer (Pinus palustris). The American Naturalist 131:491-525.

Radford, A.E., Ahles, H.E., and Bell, C.R. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill.

Reardon, J., Foreman, J.A., and Searcy, R.L. 1966. New reactants for the colorimetric determination of ammonia. Clinica and Chemica Acta 14:403-405.

Richter, D.D. 1980. Prescribed fire: effects on water quality and forest nutrient cycling in forested watersheds of the Santee Experimental Forest in South Carolina. Ph.D. thesis. Duke University, Durham, N.C.

Richter, D.D., Ralston, C.W., Harms, W.R., and Gilliam, F.S. 1984. Effects of prescribed tire on water quality at the Santee Experimental Watersheds in South Carolina. pp. 29-39. In: Water quality and environmental issues on southern forest lands. Proceedings 1984 Southern Regional Meeting of the National Council of the Paper Industry for Air and Stream Improvement. Atlanta, GA.

Richter, D.D., Ralston, C.W., and Harms, W.R. 1982 Prescribed tire: effects on water quality and forest nutrient cycling. Science 215:661-663.

Richter, D.D., Ralston, C.W., and Harms, W.R. 1983 Chemical composition and spatial variation of bulk precipitation at a Coastal Plain watershed in South Carolina. Water Resources Research 19: 134-140.

Schlesinger, W.H., Gray, J.T., and Gilliam, F.S. 1982. Atmospheric deposition processes and their importance as sources of nutrients in a chaparral ecosystem of southern California. Water Resources Research 18:623-629.

Siccama, T.G., Bormann, F.H., and Likens, G.E. 1970. The Hubbard Brook Ecosystem Study: productivity, nutrients, and phytosociology of the herbaceous layer. Ecological Monographs 40:389-402.

Thiessen, A.H. 1911. Precipitation for large areas. Monthly Weather Review 39:1082-1089.

Trewartha, G.T. 1954. Introduction to climate. McGraw-Hill, New York.

U. S. D. A. 1980. Soil survey of Berkely County, South Carolina. National Cooperative Soil Survey, Washington, D.C.

Wells, B.W. 1942. Ecological problems of the southeastern United States Coastal Plain. The Botanical Review 8:553-561.

Zar, J.H. 1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.

THE EFFECT OF A HIGH INTENSITY FIRE ON THE PATCH DYNAMICS OF VA MYCORRHIZAE IN PINYON-JUNIPER WOODLANDS

Carole Coe Klopatek, Carl Friese, Michael F. Allen, Leonard F. DeBano and Jeffrey M. Klopatek'

Abstract-Overall effects of fire on forest ecosystems are complex, ranging from reduction of aboveground biomass to impacts on soil microbial processes. This study reports on the short-term ecological effects of a high intensity fire on the vesicular-arbuscular (VA) mycorrhizae distribution, density and diversity in pinyon-juniper woodlands. In fall of 1989, 1 hectare of mature pinyon-juniper located near the Grand Canyon, Arizona, was intentionally burned using drip torches. Soil cores were taken from interspaces and beneath canopies of pinyon and juniper during the spring of 1989 and immediately prior to and 96 hours after burning the following fall. In the spring, there were no differences in VA mycorrhizal species richness under pinyon, juniper or interspaces. Glomus fasciculatum and G. aggregatum were the two most frequently observed species. Immediately before the bum, species richness was slightly lower than in spring for each of the three cover types. Following burning, G. fasciculatum, G. deserticola, and G. macrocarpum were the only remaining species in each of the three covet types. Seasonal differences in soil spore densities were found between spring and pre-burned conditions. Spore numbers were significantly lower in interspaces than under canopies. Post-bum spore numbers were significantly reduced under tree canopies (up to 88 percent loss) as compared with the interspaces (47 percent loss). Loss of mycorrhizae was negatively correlated with soil temperature and heating duration, which varied with the amount of litter and duff burned (under tree canopies) and subcanopy position.

INTRODUCTION

The importance of mycorrhizae in ecosystem function is well documented (Allen 1988; Mosse 1973; Menge and others 1978; Safir and others 1987). Without mycorrhizac many plants show a decreased growth rate or fail to develop beyond germination (Harley and Smith 1983; Mosse 1973; Powell and Bagyaraj 1984). Studies have shown that this symbiosis is fragile, and that mycorrhizal activity decreases with increasing levels of disturbance (Daft and Nicholson 1974; Habte 1989; Janos 1980; Jasper and others 1989; Klopatek and others 1988; Warner 1983; Williams and Allen 1984). For example, the frequency of vesicular-arbuscular (VA) mycorrhizal propagules decreases from a moderate disturbance such as livestock grazing (Bethlenfalvy and Dakessian 1984a; Reece and Bonham 1978) to a severe disturbance such as surface mining (Allen and Allen 1980; Gould and Liberta 1981; Zac and Parkinson 1982).

Klopatek and others (1979) estimated that the pinyon-juniper association is the third most expansive vegetation type in the United States. It covers approximately 32.5 million hectares in the western U.S. and 5.75 million hectares in Arizona (Arnold and others 1964). Pinyon-juniper woodlands are located between arid and semiarid mesic ecosystems. On the xeric end of the scale, juniper trees and desert shrubs coexist, while pinyon and ponderosa pine coexist on more mesic sites. Intermediate between these limits both pinyon pine and species of juniper exist together with interspace areas occupied by shrubs, grasses and other herbaceous cover. Why these trees exist in such diverse environments may be due to their mycorrhizal association. For example, it is known that many arid land shrub species are VA mycorrhizal, as are juniper trees, while all pine species are ectomycorrhizal.

Pinyon-juniper woodlands are managed for multiple use. As a result, both grazing (over 100 years West 1984) and prescribed burning (over 75 years USDA Forest Service) are perturbations that have occurred simultaneously in these woodlands for many years. Natural and prescribed fires impact the spatial mosaic patchwork of both VA mycorrhizae (juniper, interspace grass and shrub) (Klopatek and others 1988) and ectomycorrhizae in forest ecosystems (pine, spruce, and fir) (Mikola and others 1964; Schoenberger and Perry 1982). Until recently, little was known about the response of VA mycorrhizal symbionts to fire. Klopatek and others (1988) showed that after a simulated fire, VA mycorrhizal colonization was reduced when burning temperatures exceeded 90" C. Soil water availability at the time of burning also played an important role in VA mycorrhizal survival, with dry soils being more of a detriment than wet soils because of higher resultant temperatures. Gibson and Hetrick

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'Microbial Biologist, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Lab., Arizonia State University Campus, Tempe, AZ and Department of Microbiology, Arizona State University, Tempe, AZ; Research Assistant and Professor, respectively, Systems Ecology Research Group, San Diego Slate University, San Diego, CA; Supervisory Soil Scientist, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Lab., Arizonia State University Campus, Tempe, AZ; Associate Professor of Botany, Arizona State University, Tempe, AZ.

(1988) found significant reductions of three VA mycorrhizal species following a fire in the tall grass prairie of Kansas. Dhillion and others (1988) stated that colonization levels of VA mycorrhizal fungi in little bluestem roots were significantly reduced on burned sites when compared to unburned but, increased significantly after one growing season. Their results suggest that the response of VA mycorrhizal fungi to fire may be attributed to changes in the host plant rather than the direct effect of fire. Fire temperatures did not reach a level high enough to kill all the plants, thereby leaving a large residual VA mycorrhizal pool in the soil and in plant roots. In fact, they showed that fire actually stimulated plant growth, unlike tires in pinyon-juniper woodlands.

In previous work, we determined that fire had a negative impact on VA mycorrhizae by decreasing the number of propagules. We wanted to determine if these results were representative under field conditions. Thus, the objective of this study was to determine how fire effects VA mycorrhizae density, diversity and distribution under field conditions in the pinyon-juniper ecosystem. Results on the effects of fire on ectomycorrhizae are forthcoming.

MATERIALS AND METHODS

Site Description

The study area is located on the Coconino Plateau of the Colorado Plateau, adjacent to the Grand Canyon National Park on the Kaibab National Forest. Site elevations range from 1875 to 2075 meters. Soils are Lithic and Fluventic Ustochrepts having a sandy loam texture and belong to the Winona-Boysag association (Hendricks 198.5). Kaibab limestone, with intrusions of Moenkopi sandstone, are the dominant parent materials; slope is minimal, ranging from O-2 percent. The seasonal regime of cold, wet winters and hot summers with occasional thunderstorms in this region, results in this being the evolutionary center for pinyon-juniper development (Nielson 1987). Annual precipitation of 350 millimeters is bimodally distributed; approximately half occurs as intense thunderstorms from July to September, with the remainder coming as mild winter rains or snows from December to April. Soil moisture deficits exist from March through October. Temperatures are variable, ranging from -27 to +38° C with an average of 150 days between last and first frost. Permanent weather recording stations are located in Tusayan, Arizona, less than 20 kilometers from the study area.

The area is dominated by pinyon pine (Pinus edulis Engelm.) and Utah juniper (Juniperus osteosperma (Torr.) Little). Several species of grass [blue grama grass (Bouteloua gracilis (H.B.K.) Lag. ex Steud.), squirrel tail (Sitanion hvstrix (Nutt.) J.G. Smith), Stipa sp.] and shrub species [snakeweed (Guttierrezia sarothrae (Pursh) Britt and Rusby), rabbitbrush (Chrvthothamnus sp.), cliffrose (Cowania mexicana var. stansburiana (Torr.) Jepson)] dominate the interspaces.

Experimental Design

From the area described above, we chose approximately 1 hectare of mature pinyon-juniper (250 plus years old) as our study site. The site was divided into quadrants (4 subplots) in which the position and number of each pinyon, juniper, and interspace was mapped. Every tree was marked with brass tags bearing ID numbers. The site was fenced to exclude livestock grazing. On September 11, 1989, we burned the site using hand-held drip torches. All living, downed, and dead fuels were ignited. Burning was conducted by the Kaibab National Forest, Tusayan Ranger District with assistance of the National Park Service, Grand Canyon.

Soil samples were evaluated for VA mycorrhizal spores in the spring of 1989 and immediately before and 96 hours after the September bum. Spring samples were taken to assess seasonal variability. During each sampling period, soil cores were taken from the same three randomly selected pinyon and juniper and interspaces in each of the four quadrants. Soil cores were taken 96 hours after the bum (post-bum) because trees were still burning and smoldering. Soil cores were taken from the base of the tree, mid canopy and at the canopy edge to a depth of 10 centimeters. This yielded 18 cores per quadrant, totaling 72 tree cores (2 tree species X 3 trees per quadrant X 3 samples per tree X 4 quadrants = 72). Four additional soil cores were taken per quadrant from interspaces, for a total of 16 interspace samples. Cores were wrapped in polyurethane and refrigerated at 4” C until processed.

In the laboratory, each sample was sieved (2 millimeters) to remove rocks and allowed to air-dry. From this, 20-gram samples were taken to estimate spore numbers using differential centrifugation (Ianson and Allen 1986). Spores were placed in a petri dish with sterile distilled water and examined under a dissecting microscope at 40X. Spores were divided into live and dead. Viability was determined by placing spores on a microscope slide, those which exuded cytoplasm when crushed were considered viable. Species identification were determined with a compound microscope at 400-1000X. Spore numbers are reported as means with ± standard errors of the mean. Significant differences ($p < 0.05$) in spore numbers were isolated using Tukey’s honest significant difference measure. Percent loss of mycorrhizae was calculated by subtracting the difference between pre- and post-bum spore numbers and dividing it by the pre-bum spore number.

RESULTS AND DISCUSSION

Species Richness

Eight species of VA mycorrhizal fungi were recovered from the site (table 1). In spring (May 1989), there were no differences in species richness under pinyon, juniper, or interspaces (fig. 1). Glomus fasciculatum and G. aggregatum were the two most frequently observed species with G. macrocarpum being the least dominant. Pinyon pine, although ectomycorrhizal, has been reported to have numerous VA mycorrhizal propagules around its base (Klopatek and Klopatek 1986). This is likely due to: 1) aeolian deposition of spores, and 2) the intermixing of juniper roots with those of pinyon. Wind deposits sand particles under pinyon pine (Barth 1980; Klopatek 1987) and presumably deposits these large spores along with the sand. In addition, on a recent excavation, we found juniper roots intertwined with pine roots (Klopatek and Klopatek, unpublished). Thus, pinyon is an important repository for VA mycorrhizal propagules. This is in contrast to other pine dominated forests where no VA mycorrhizal spores are found (Kovacic and others 1984).

Table 1.--List of species from soils taken from under pinyon and juniper canopies and interspaces. No differences in species were found in either of the three cover types. Species are Listed in the order of relative abundance.

Glomus macrocarpum Tut & Tut
G. occultum (Walker)
G. mosseae (Nicol & Gerd) Gerd. & Trappe
Scutellospora calospora (Nicol. & Gerd.) Walker & Sanders
G. deserticula Trappe, Bloss & Menge
G. aggregatum Schenck & Smith
G. fasciculatum (Taxter sensu Gerd.) Gerd. & Trappe
Acautospora laevis Gerd. & Trappe

Species richness varied with season. Immediately before the fall burn, species richness dropped in each of the three cover types (fig. 1) compared with spring. Species richness was greatest in interspaces covered with grass, followed by pine and juniper soils, respectively. In post-burn samples, no differences in richness were found among the three cover types; but, species richness declined in all post-bum samples (fig. 1). G. fasiculatum, G. deserticula, and G. macrocarpum were the only species that survived the fire. These species are all thick walled as compared with the other five (table 1). In addition, they are commonly found in very arid, alkaline soils (Bethlenfalvay and others 1984; El-Giahmi and others 1976; Pfeiffer and Bloss 1980; Safir 1987) and, therefore, may be more resistant to extreme temperatures.

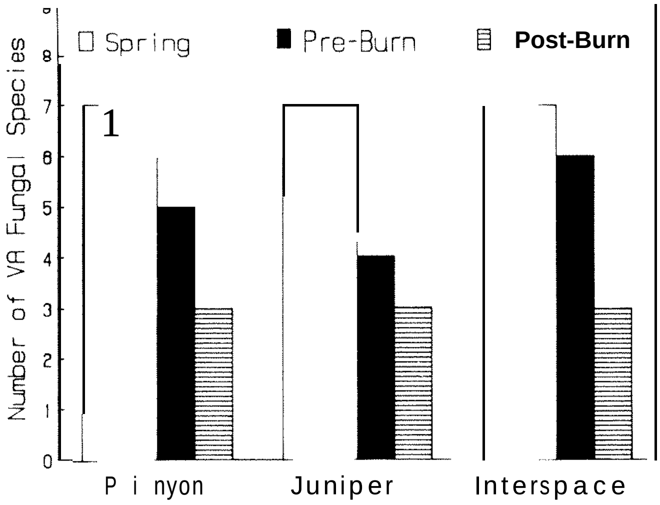

Figure 1.--Change in the number of VA mycorrhizal species in soils taken from beneath pinyon and juniper and interspaces due to change in season and effect of fire

Spore Densities

Spore density varied under pinyon, juniper, and interspaces during the spring and pre-bum samplings (fig. 2). Overall spore counts under pinyon were not significantly higher in the spring than in pre-bum samples. Significant differences existed ($p < 0.05$) between spring and pre-bum samples in juniper and interspace soils (fig. 2). This decrease between spring and pre-bum samples may be attributed to a large amount of germination and hyphal activity rather than spore production following the summer rains. There were statistical differences ($p < 0.05$) in spore numbers between juniper and pinyon soils in the spring sampling, and most samples were significantly greater ($p < 0.05$) than interspaces (fig. 2). In general, the pre-bum pattern of spore dispersal exhibited the highest proportion at the base of the trees and decreased outward.

Burning significantly ($p = < 0.05$) decrease the overall number of VA mycorrhizal spores in soils beneath pinyon and juniper canopies (up to 88 percent) and interspaces (up to 47 percent loss) (fig. 2). Following the bum, spore numbers under canopies ranged from a high of sixteen to a low of four per 20 grams of soil. There did not seem to be a pattern of spore distribution and subcanopy position. The substantial losses under canopies was probably due to the direct effects of the soil temperatures. The highest soil temperatures were reached under canopies (up to 315” C at 2 centimeter depth) compared with interspaces (up to 68” C at 2 centimeter depth). The large fuel load, including aboveground material, litter, and duff, in addition to a more complete combustion of these fuels, probably contributed to a more intense bum under the canopies. Smoldering duff and tree stumps maintained high temperatures for several days. Magnitude and duration

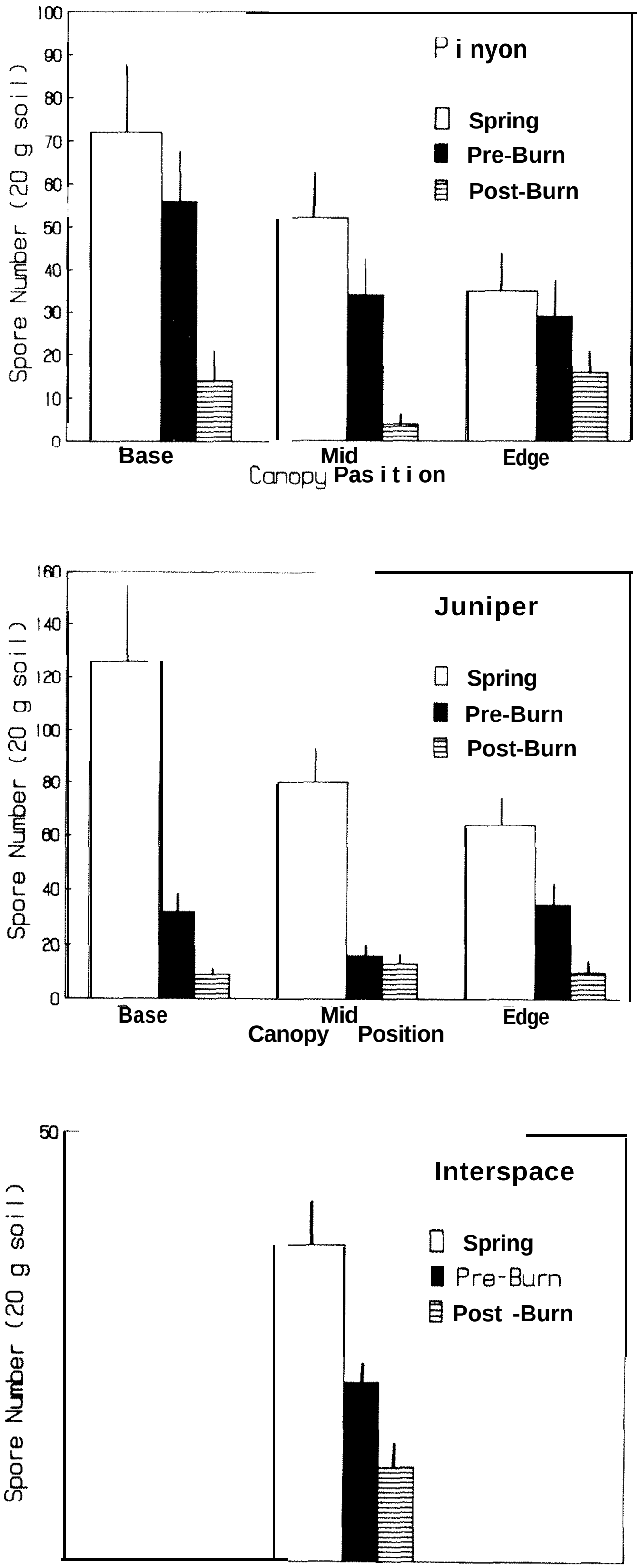

Figure 2.--Number of VA mycorrhizal spores per 20-gram soil sample taken from beneath pinyon and juniper canopies and interspaces. Samples were taken at three locations under tree canopies--base, mid and canopy edge and from grass covered interspaces

are the two principal factors causing heat injury to plants (Hare 1961) and are also likely to be deleterious to VA mycorrhizal fungi. Smoke resulting from burning of the trees may also have contributed to the loss in mycorrhizae as it has been shown to reduce other microbial activities (e.g., Li and others 1988).

Interspaces had little aboveground vegetation and litter and no duff, which resulted in an overall lower soil temperature. Klopatek and others (1988) showed interspaces were the least affected by a simulated bum compared with canopy microcosms. We observed that tire either swept through the interspaces or did not burn at all. Pruning of grasses does not adversely affect mycorrhizal colonization, but temporarily inhibits sporulation (Powell and Bagyaraj 1984). We anticipate that the burning of grasses will produce the same response. If grasses are killed, and roots are not severely damaged by the fire, we theorize that root pieces will serve as propagules. Tommerup and Abbot (1981) showed that colonized root pieces can remain viable propagules for extended periods in partially dried soils, but they lose viability once moisture levels increase, (Gould and Liberta 1981; Hall 1979) due to decomposition. Thus, the fire shifted the distribution of spores from under the canopies to the interspaces.

The time required for mycorrhizal populations to recover following tire in pinyon-juniper woodlands is unknown. Janos (1980), MacMahon (1987), and Allen and Allen (1988) suggest that mycorrhizal fungi are essential in ecosystem recovery, facilitating plant establishment by regulating nutrient flow from the soil to the plant. Thus, in order to understand and manage this ecosystem, it is necessary to understand mycorrhizal response to fire and how it affects patch dynamics that lead to a mosaic landscape pattern (i.e., from a canopy dominated mycorrhizal community to a interspace dominated mycorrhizal community). This “patch” pattern of disturbance is unlike a widespread disturbance, such as stripmining (Klopatek and Klopatek 1984). Thus, the natural mosaic configuration of canopy and interspace leads to a significant shift in the “patchwork dynamics” of mycorrhizal distribution following tire.

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LITERATURE CITED

Allen, E.B.; Allen, M.F. 1980. Natural reestablishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. Journal of Applied Ecology 17:139-147.

Allen, E.B; Allen, M.F. 1988. Facilitation of succession by the non-mycotrophic colonizer Salsola kali (Chenopdiaceae) on a harsh site. Effects of mycorrhizal fungi. American Journal Botany 75:257-266.

Allen, M.F. 1988. Re-establishment of VA mycorrhizas following severe disturbance: comparative patch dynamics of a shrub desert and a subalpine volcano. Proceedings of the Royal Society of Edinburgh 94B:63-71.

Arnold, J.F.; Jameson, D.; Reid, E. 1964. The pinyon-juniper type of Arizona: Effects of grazing, tire, and tree control. Prod. Res. Rep. 84. Washington, DC: U.S. Department of Agriculture. 28 p.

Barth, R.C. 1980. Influence of pinyon pine trees on soil chemical and physical properties. Soil Science Society of America 44:804-809.

Bethlenfalvay, G.J.; Dakessian, S. 1984a. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in Northern Nevada. Journal of Range Management 37(4):212-216.

Bethlenfalvay, G.J.; Dakessian, S.; Pacovsky, R.C. 1984. Mycorrhizae in a southern California desert: ecological implications. Canadian Journal of Botany 62:519-524.

Daft, M.J.; Nicolson, T.H. 1974. Vesicular-arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. New Phytologist 73:1129-1138.

Dhillion, S.S.; Anderson, R.C.; Liberta, A.E. 1988. Effect of fire on the ecology of little bluestem (Schizachvrium scoparium). Canadian Journal of Botany 66:706-713.

El-Giahmi, A.A.; Nicolson, T.H.; Daft, M.J. 1976. Endomycorrhizal fungi from Libyan soils. Transactions of the British Mycological Society 67: 164-169.

Gibson D.; Daniels Hettick, B.A. 1988. Topographic and fire effects on the composition and abundance of VA-mycorrhizal fungi in a tallgrass prairie. Mycologia 80:433-441.

Gould, A.S; Liberta, A.E. 1981. Effects of topsoil storage during surface mining on the viability of vesicular-arbuscular mycorrhiza. Mycologia 73:914-922.

Habte, M. 1989. Impact of simulated erosion on the abundance and activity of indigenous vesicular-arbuscular mycorrhizal endophytes in an oxisol. Biology and Fertility of Soils 7:164-167.

Hall, I.R. 1979. Soil pellets to introduce vesicular-arbuscular mycorrhizal fungi into soil. Soil Biology and Biochemistry 11:85-86.

Hare, R.C. 1961. Heat effects on living plants. Occasional Paper NO. 183. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 32 p.

Harley, J.L.; Smith, S.E. 1983. Mycorrhizal symbiosis. London: Academic Press Inc. 483 p.

Hendricks, D.M. 1985. Arizona Soils. Tucson, AZ: University of Arizona Press. 244 p. + map.

Ianson, D.C.; Allen, M.F. 1986. The effects of soil texture on extraction of vesicular-arbuscular mycorrhizal fungal spores from arid sites. Mycologia 78:164-168.

Janos, D. 1980. Mycorrhizal influence in tropical succession. Biotropica 12:56-64.

Jasper, D.A.; Abbot, L.K.; Robson, A.D. 1989. Soil disturbance reduces the infectivity of external hyphae of vesicular-arbuscular mycorrhizal fungi. New Phytologist 112:93-99.

Klopatek, C.C; Klopatek, J.M. 1984. Mycorrhizae: Effect on plant productivity in Great Basin coal-mine soils. Proceedings 6th North American Conference on Mycorrhizae, Bend, OR. p. 308.

Klopatek, C.C.; Klopatek, J.M. 1986. Mycorrhizae, microbes and nutrient cycling processes in pinon-juniper ecosystems. In: Proceedings Pinyon-Juniper Conference. Gen. Tech. Rep. Int-125. Ogden UT.: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. pp. 360-364.

Klopatek, C.C.; DeBano, L.F.; Klopatek, J.M. 1988. Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodlands. Plant and Soil 109:245-249.

Klopatek, J.M.; Olsen, R.J.; Emerson, C.J.; Jones, J.L. 1979. Land use conflicts with natural vegetation in the United States. Environmental Conservation 6:191-199.

Klopatek, J.M. 1987. Nitrogen mineralization and nitrification in mineral soils of pinyon-juniper ecosystems. Soil Science Society of America 51:453-457.

Kovacic, D.A; St. John, T.V.; Dyer, M.I. 1984. Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. Ecology 65: 1755-1759.

Li, S.W.; Fredrickson, J.K.; Ligotke, M.W.; Van Voris, P.; Rogers, J.E. 1988. Influence of smoke exposure on soil enzyme activities and nitrification. Biology and Fertility of Soils 6:341-346.

MacMahon, J.A. 1987. Disturbed lands and ecological theory: an essay about mutualistic associations. In: Restoration Ecology. London: Cambridge University Press. pp. 222-237.

Menge, J.A.; Johnson, E.L.; Platt, R.G. 1978. Mycorrhizal dependency of several citrus cultivars under three nutrient regimes. New Phytology 81:553-559.

Mikola, P.; Laiho, 0.; Erikainen, J.; Kuvaja, K. 1964. The effect of slashburning on the commencement of mycorrhizal associations. Acta Forestalia Fennica 77: 1- 11.

Mosse, B. 1973. Advances in the study of vesicular-arbuscular mycorrhizae. Annual Review of Phytopathology 11: 171-196.

Nielson, R.P. 1987. On the interface between current ecological studies and the paleobotany of pinyon-juniper woodlands. In: Proc. Piiyon-Juniper Conf. 13-16, Reno. NV. USDA Forest Service. Gen. Tech. Rep INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. pp. 93-98.

Pfeiffer, C.M.; Bloss, H.E. 1980. Vesicular-arbuscular mycorrhizal fungi on soybean in Arizona. Mycologia 72:1038-1040.

Powell, C.Ll.; Bagyaraj, D.J. 1984. VA mycorrhiza. Boca Raton, FL: CRC Press Inc. 234 p.

Reece, P.E.; Bonham, C.D. 1978. Frequency of endomycorrhizal infection in grazed and ungrazed blue grama plants. Journal of Range Management 31:149-151.

Safir, G.R. 1987. Ecophysiology of vesicular-arbuscular mycorrhizae. Boca Raton, Fl: CRC Press Inc. 224 p.

Schoenberger, M.N.; Perry, D.A. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas fir and western hemlock seedlings: a greenhouse bioassay. Canadian Journal of Forest Research 12:3433-353.

Tausch, R.J.; West, N.E. 1988. Differential establishment of pinyon and juniper following tire. The American Midland Naturalist 119:175-184.

Tommerup, I.C.; Abbott, L.K. 1981. Prolonged survival and viability of VA mycorrhizal hyphal after root death. Soil Biology and Biochemistry 13:431-433.

Tress, J.; Klopatek, J.M. 1987. The pinyon-juniper woodlands of northern Arizona: Successional dynamics. In: Proceedings Pinyon-Juniper Conference. Gen. Tech. Rep. Int-125. Ogden UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. pp. 80-85.

USDA Forest Service. 1981. Effects of fire on flora. In A stateof-knowledge review, National fire effects workshop. Gen. Tech. Rep. WO-16. Washington, DC: U.S. Department of Agriculture, Forest Service. pp 41-43.

Warner, A. 1983. Re-establishment of indigenous vesicular-arbuscular mycorrhizal fungi after topsoil storage. Plant and Soil 73:387-394.

West, N. 1984. Successional patterns and productivity potentials of pinyon-juniper ecosystems. In: National Research Council/National Academy of Science. 1984. Developing strategies for rangeland management. Boulder, CO: Westview Press.

Williams, S.E.; Allen, M.F. 1984. Proceedings: VA mycorrhizal and reclamation of arid and semiarid lands. Scientific Rep. No. SA1261. Laramie: University of Wyoming, Wyoming Agricultural Experiment Station,

Zac, J.C.; Parkinson, D. 1982. Initial vesicular-arbuscular mycorrhizae development of slender wheatgrass on two amended mine spoils. Canadian Journal of Botany 60:2241-2248.

FOREST SOIL CHARACTERISTICS FOLLOWING WILDFIRE IN THE SHENANDOAH NATIONAL PARK, VIRGINIA

David A. Groeschl[1], James E. Johnson, and David Wm. Smith”

Abstract-Forest floor and mineral soil samples were collected and analyzed to determine physical and chemical differences among three burn levels (high, low, and unburned) under a mixed pine forest one year after a mid-July, 1988 wildfire. Total forest floor thickness and weight were significantly different among all three burn levels. Low intensity surface fires consumed the surface Oi-Oe layer of the forest floor leaving the Oa layer relatively intact, whereas high intensity fires resulted in the complete destruction of the forest floor. Total carbon and nitrogen concentration and content were significantly higher in residual Oa material of low burn areas compared to unburned Oa material. Active acidity (pH) in the top 10 cm of mineral soil in high and low burn areas measured 4.6 and was significantly higher than unburned areas with a value of 4.3. Total carbon and nitrogen levels in the surface 10 cm of mineral soil were also higher in low burn areas whereas high burn areas were lower than unburned sites. Mineral soil inorganic nitrogen levels were significantly higher in both high and low burn areas compared to unburned areas, thereby providing a pulse of available nitrogen for plant uptake.

INTRODUCTION

Fire has and will continue to play an important role in affecting biotic and edaphic components of forest ecosystems. The Table Mountain pine (*Pinus pungens* Lamb.) - pitch pine (*Pinus rigida* Mill.) forest complex is typically considered a fire-adapted community. In fact, several authors (Sanders and Buckner 1988; Barden and Woods 1976; Zobel 1969) concluded that high intensity fires were necessary to ensure successful regeneration and establishment of Table Mountain pine by (1) opening serotinous cones (Table Mountain pine), (2) inducing basal sprouting (pitch pine), (3) destroying excessive litter and exposing the mineral soil, (4) eliminating dense understory vegetation, and (5) destroying allelopathic substances. However, little is known about the role and impact of variable intensity wildfire on forest floor and mineral soil characteristics upon which these species occur.

High elevation sites supporting mixed pine forests are generally moisture-limiting and typified by shallow, acidic rocky soils with minimal rooting volume and associated infertile conditions. Low intensity fires (prescribed and wildfire) may actually enhance soil fertility by increasing pH (Grier 1975; Metz and others 1961; Wells and others 1979), providing an influx of inorganic forms of nutrients and increasing solubility of these nutrients (Alban 1977; Metz et al 1961; Lewis 1974; Covington and Sacket 1986), and volatilizing compounds such as monoterpenes which are known to have inhibiting effects on bacteria populations responsible for ammonification and nitrification processes (White 1986a). Conversely, high intensity fires may result in a significant reduction of the total nutrient capital from the site resulting in the further reduction of already poor site quality conditions. However, these losses following high intensity fires may not be altogether detrimental, since Table Mountain pine is thought to have a low nutrient requirement which may naturally select and promote the maintenance of this species on xeric, poor quality sites.

Much work has been done on the effect of prescribed fires on soil properties, but these fires are generally of low intensity and results are stated as contrasts between burned and unburned. In contrast, variable intensity wildfires provide comparisons among several intensity levels; however, statistical analyses and inferences from results are limited due to non-random placement and inability to replicate treatments. Nonetheless, wildfires provide a unique study arena because of their natural occurrence and exhibition of several intensity levels. The objectives of our study are to determine forest floor and mineral soil physical and chemical properties following a variable intensity wildfire within a mixed pine forest and to discuss the possible importance of these impacts in relation to existing vegetation.

METHODS

Study Site

On July 11, 1988, the National Park Service (NPS) located a lightning-caused wildfire on Dove1 Mountain in the Shenandoah National Park and adjacent private lands. Dove1 Mountain is located approximately 6.5 km northeast of the town of Shenandoah in Page county, Virginia. The mid-July wildfire burned approximately 3.50 ha before being brought under control and declared extinguished on August 8, 1988.

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[1] Silviculture Forester, ITT Rayonier Inc., Forest Research Center, P.O. Box 819, Yulee, FL 32097.

‘Associate Professor-Extension Specialist, and Professor of Forestry, respectively, Department of Forestry, Cheatham Hall, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

The study area is located in the Blue Ridge Physiographic region and is underlain by the Erwin (Antietam) and Hampton Geologic Formations (Allen 1967). Soils are derived from granodiorite, arkosic sandstone, and greenstone and have not been classified into series but are typically shallow and skeletal, with numerous rock outcroppings. Elevations in the area range from 350 to 800 m and slope inclination ranges from 40 to 65 percent. Mixed pine forests consist prcdominatly of Table Mountain, pitch, and Virginia pine (Pinus virginiana Mill.).

Field Methods

Areas were selected within the burned and adjacent unburned forest so that conditions of uniform species composition, age, and density; slope position, aspect, elevation, and steepness; and soil characteristics were represented. Fire intensity or burn levels were not actually measured, however, this terminology is used to categorize and represent the level of overstory mortality that resulted following tire occurrence. High intensity bum levels represent greater than 75 percent overstory mortality of basal area and crown cover, whereas low intensity bum levels represent less than 25 percent overstory mortality. A combination of crown and surface fires resulted in high intensity bum sites whereas surface tires represented low intensity bum areas. All sampling occurred on backslope positions with southwest-facing slopes.

Forest floor and mineral soil sampling occurred simultaneously during the first full growing season following the fire. Three sites were located within each bum level for a total of 9 sites. At each site, six sampling points were randomly located for a total of 18 forest floor and composite mineral soil samples within each bum level. The forest floor was sampled with a 100-cm^2 template. At each sampling point, a knife was used to cut along the template border and the Oi-Oe layer was removed and bagged. The Oa layer was removed separately and also bagged. Mean depth of the Oi-Oe and Oa layers were determined within each tire intensity level. At each sampling point, three mineral soil samples were taken to a depth of 10 cm, and combined to form one composite sample. Bulk density samples were also taken to the 10-cm depth at each sampling point using the excavation method (Blake and Hartge 1986).

Lab Methods

Forest floor samples were oven-dried at 65°C for 48 hours, and rocks and other non-plant material were removed to determine weight of the Oi-Oe and Oa layers of the forest floor per unit area. Forest floor samples were sieved to remove the mineral soil fraction before being ground in a 2-mm Wiley mill. Ground samples were then remixed with the mineral soil fraction using a sample splitter. Total carbon was determined using a Leco™ high-temperature induction furnace (Nelson and Sommers 1982). Total nitrogen was digested using the micro-Kjeldahl method of Bremner and Mulvaney (1982), followed by analysis of the resultant extracts using a Technicon™ autoanalyzer.

Composite mineral soil samples were air-dried and sieved to separate coarse fragments. Active acidity, measured as pH, was determined using a 2:1 distilled water to soil ratio. Total nitrogen and carbon levels of the surface 10 cm of mineral soil were determined using the same procedures as those used for forest floor samples. Inorganic nitrogen was determined by extracting exchangeable NH_4-N, NO_3-N, and NO_2-N, using 2M KCl extractant, followed by analysis with a Technicon™ autoanalyzer.

Statistical Methods

Forest floor and mineral soil variables were subjected to analysis of variance for a completely randomized design followed by Tukey's multiple comparison procedure to determine significant differences at the 0.05 level among fire intensity levels (high, low, and unburned).

RESULTS AND DISCUSSION

Forest Floor Parameters

In forest ecosystems, the major portion of macro-nutrients are tied up in the surface organic matter. These nutrients are slowly released through the process of microbial-mediated decomposition and mineralization. Under normal oxidation conditions, organic matter provides a slow release, revolving fund of nutrients for plant uptake. Conversely, fire tends to rapidly release these nutrients either by volatilizing lower molecular weight gases (H_2O, and N) into the atmosphere or concentrating many basic cations in the residual ash.

Wildfire consumes the forest floor in direct proportion to the intensity of the fire. Mean depth of the Oi-Oe layer in unburned areas was 1.4 cm; however, this layer was totally absent in low bum areas the first year after the fire (fig. 1).

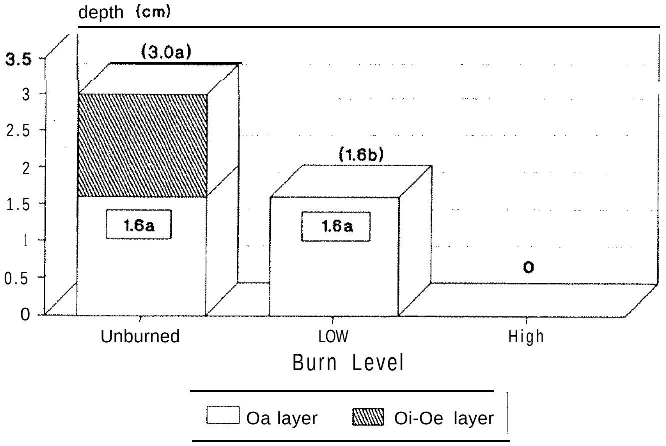

Figure 1 - Forest floor depth one year after fire occurrence. [Values in boxes represent comparisons among Oa layers while values in parentheses represent totals (Oi-Oe + Oa). Means followed by the same letter are not significantly different at the 0.05 level.]

Although the Oi-Oe layer was consumed following low intensity fires, the Oa layer was left relatively intact with a mean depth of 1.6 cm. Mean depth of the Oa layer in unburned areas was also 1.6 cm. Unlike low intensity surface fires, high intensity fires resulted in the complete destruction of the entire forest floor (Oi-Oe + Oa). Therefore, the remaining discussion of forest floor parameters will focus mainly on differences between low and unburned areas.

Similar to trends in depth, forest floor weight also changes in direct proportion to the intensity of the fire. Mean weight of the Oi-Oe layer for unburned sites averaged 24390 kg ha^{-1} while no weights were recorded for low burn areas due to the consumption of this layer during pyrolysis (fig. 2). Unlike the Oi-Oe layer, Oa layer weights were not different between unburned and low burn areas.

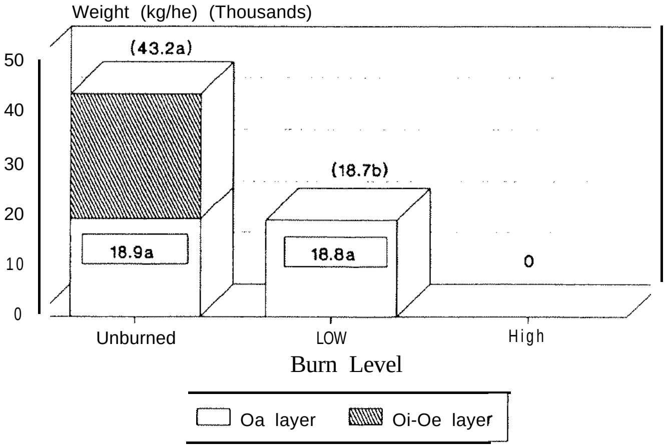

Figure 2 - Forest floor weight (kg ha^{-1}) one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

Total forest floor depth and weight, represented by combining the Oi-Oe and Oa values, was significantly less on burned areas due to the partial or complete destruction of forest floor material (figs. 1, 2). Assuming that high, low, and unburned areas had similar forest floor depths and weights prior to fire occurrence, low burn values would then represent a 47 percent reduction in depth and a 57 percent reduction in weight while high intensity burn areas represent a 100 percent reduction in depth and weight compared to unburned sites.

Reductions in forest floor depth and weight following burning have been well documented in the literature. Immediately after a periodic winter burn in the south, total forest floor weights were decreased from 26900 kg ha^{-1} to 19600 kg ha^{-1}. After 20 years of annual summer burns, the forest floor was reduced to 7800 kg ha^{-1}, whereas annual winter burns reduced the forest floor to 14600 kg ha^{-1} (Brender and Cooper 1968).

Several studies (Brender and Cooper 1968; Moehring and others 1966; Romancier 1960) have demonstrated that prescribed burning does not result in a significant loss of forest floor material. In fact, a single prescribed burn may remove only a small percentage of the total forest floor depth and weight. Results from this and other related studies indicate that reductions in forest floor material are directly related to fire intensity.

Total C concentration (%) and content (kg ha^{-1}) were significantly higher in the residual Oa material collected from low burn areas compared to unburned Oa material. Total C concentration of Oa material from low and unburned areas were 61.0 and 52.7 percent, respectively (fig. 3). Since post-fire Oa weights were similar for low and unburned areas, increases in total C concentration also resulted in greater C content (kg ha^{-1}) of the Oa layer on low burn sites. Overall, however, total C content for the entire forest floor was 50 percent lower on low burn areas, compared to unburned areas, due to the consumption of the overlying Oi-Oe layer.

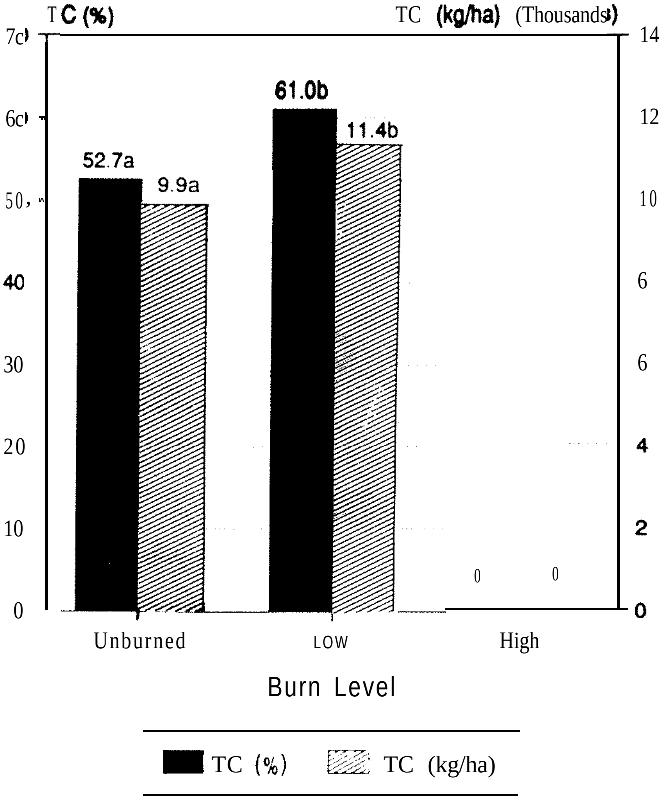

Figure 3 - Total carbon concentration (%) and content (kg ha^{-1}) of the Oa layer one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

The major elemental components of organic matter include N, 0, H, and C. During normal decay processes of organic matter, some C is converted to CO,, some is incorporated into microbial tissue while the remaining C is converted to more stable humus forms which are higher in total C concentration than the original organic matter (Stevenson 1986). Pyrolysis reactions tend to accelerate this process by volatilizing lighter atomic elements (N,O,H) while converting the original organic matter to more stable humus forms that contain a higher percentage of reduced, elemental C. Likewise, other basic cations (K,Ca,etc.) along with reduced, elemental C, are concentrated in the residual ash following fire. The reduction of C and the concentrating effect of pyrolysis reactions would explain the increase of total C noted in the Oa layer of low bum areas in this study. This reduced form of C does not supply a readily mineralizable source for microbial assimilation and may remain in the soil as fusain for many years (Soper 1919; Hansen 1943). Since C is a large chemical constituent of organic matter (approximately 58%), a loss of organic matter following tire will result in a reduction in C content from the site. The more intense the fires, the greater the consumption of the forest floor and subsequent C pool. Organic matter also serves as an important source of N, P, and S, which are also reduced following consumption of the forest floor.

Similar to C trends, total N concentration (ppm) and content (kg ha^{-1}) were also higher in the residual Oa material of low burn areas compared to unburned Oa material (fig. 4). An increase in total N following low intensity fires may be **due,** in part, to an increase in inorganic N in the Oa layer. Several authors (White and others 1973; Klemmedson and others 1962; Kovacic and others 1986) have found similar trends in inorganic N concentrations one year after prescribed fires. This increase may be attributed to incomplete combustion and volatilization of N with subsequent downward translocation and reprecipitation of N gases in cooler forest floor and mineral soil layers (Klemmendson and others 1962; Tangren and McMahon 1976; Wells 1971). Substantial amounts of NH4-N arc also produced chemically by soil heating and microbially after fire. Unlike NH_4-N, NO,-N is not produced during soil heating, but is formed during subsequent mineralization and nitritication processes. Additionally, White (1986a) found that potential N mineralization and nitrification increased in residual forest floor material following prescribed fires. Jones and Richards (1977) suggested that nitritication processes following tire may not **be** due to Nitrosomonas or Nitrobacter bacteria but to heterotrophic fungi. Increases in total N may also be correlated with an increase in total C and/or to an increase in N2-fixation following tire. N2-fixation may contribute 10 to 100 kg ha" of N annually (Stevenson 1986).

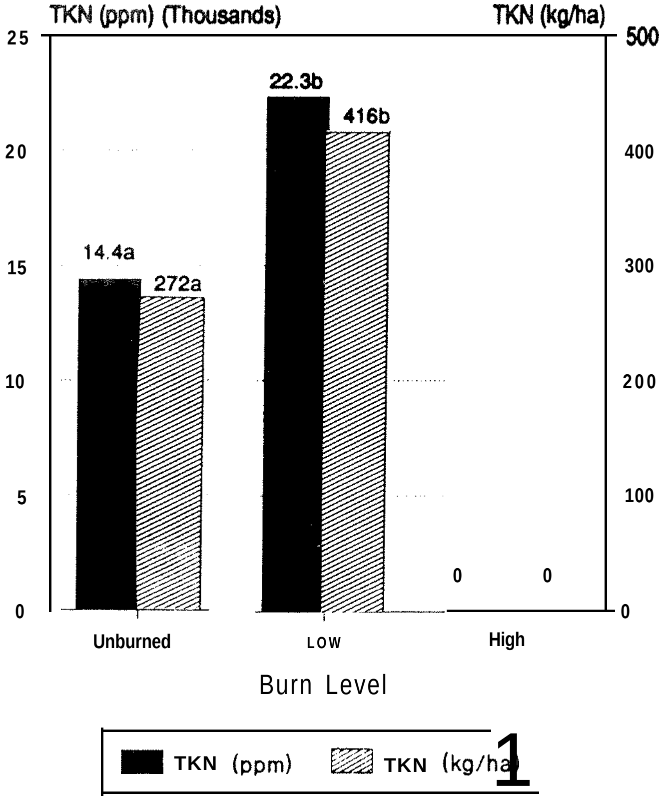

Figure 4 - Total nitrogen concentration (%) and content (kg ha.‘) of the Oa layer one year after tire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

Assuming homogeneity on burned and unburned sites prior to fire occurrence, combined forest floor (Oi-Oe + Oa) C and N values for low burn areas **would** represent a 50 and 28 percent reduction, respectively, compared to unburned values (figs. 5, 6). These reductions in total C and N content of the residual forest floor in low **bum areas is attributed to the** consumption of the overlying Oi-Oe layer during pyrolysis.

Generally, low intensity fires, as occurred on some areas in this study, may remove only the Oi-Oe layer, leaving the Oa layer relatively intact. This residual Oa layer serves to protect the underlying mineral soil from erosion and provides a more mineralizable source of nutrients (White 1986a). Conversely, high intensity tires may remove the entire forest floor, thereby exposing the mineral soil to the vagaries of weather and possibly reducing infiltration, water holding capacity, and other associated benefits attributable to the surface organic matter.

composition and crown heights. Within each component the stand structure and composition may be remarkably uniform (Dix and Swan 1971).

The fire regime consists of short to long interval crown tires and severe surface fires in combination. Stand replacement fires are the norm and surface fires alone are rare, occurring along the edges of crown fires where tire behavior was moderated. Ground fires can be persistent in deep organic soils.

Hazardous fire weather conditions are encouraged by lengthy summer days which result in long diurnal drying periods as well as by extended periods of low precipitation and humidity. In northern British Columbia very large lightning-caused fires have occurred decadally and reached 180,000 ha. Man-caused tires have sometimes surpassed this size during the past 50 years.

Heinselman (1981) summarized fire regimes for the boreal forest. Presettlement fire cycles ranged from 50 to 200 years for types shared by the Boreal White and Black Spruce Zone of northern British Columbia. Fire cycles there differ between forest types, but likely average 140 years.

Since most of the landscape in this zone is subject to fire, stand age class distribution data have been used to model fire cycles and the effects of tire suppression. For northwestern and northeastern British Columbia, fire cycles were 125 and 202 years respectively (Smith 1981). However, a regional fire cycle is a composite, with the components having their own shorter or longer cycles as a function of site type (Rowe 1983).

Although much evidence exists for aboriginal burning and an increased fire frequency due to the presence of European man in the boreal forest (Lutz 1959), specific references to northern British Columbia are rare. House (1909) told of a hunting expedition in northwestern British Columbia during which his native guide set several grass fires in order to approach a herd of caribou under the cover of smoke.

Lewis's (1982) native informants in northern Alberta described the use of prescribed tire for creating and maintaining meadows, manipulating riparian vegetation, clearing campsites and trails, removing windfalls, and creating firewood. It is likely that such practices were carried out in the boreal forest of neighboring British Columbia, influencing the fire regime there as well.

Lutz (1959) documented fires in the boreal forest caused by European man's escaped campfires as well as his deliberate tiring of the forest in order to create supplies of dry fuelwood, signal other parties, drive moose, and promote the growth of forage for domestic stock. Fire was also used to remove local forest cover, thus thawing the permafrost and permitting excavation for minerals (Dawson 1888).

Fire Effects and Succession

The natural role of fire in the boreal forest of North America has been described in detail (Foote 1983; Kay11 1968; Kelsall and others 1977; Lutz 1955; Rowe 1983; Rowe and Scotter 1973; Viereck and Schandelmeier 1980). With stand-replacing crown fires and tree species which are fire sensitive and usually killed by fire, forest regeneration depends on "on-site" or "off-site" adaptations.

On-site adaptations to fire include cone serotiny (lodgepole pine), semi-serotiny (black spruce), root suckering (trembling aspen), and root collar sprouting (paper birches). Species such as white spruce, tamarack, and subalpine fir require live survivors off-site but near enough to provide seed to the burned area. The hardwoods produce prolific amounts of light seed which, if carried by the wind to the burned site, may result in a post-fire hardwood component as well.

Lesser vegetation also possess post-fire reproductive strategies, such as sprouting from roots, rhizomes, and stems, or the production of many light wind-disseminated seeds (Rowe 1983). Some, such as high bush cranberry *(Viburnum edule*) and pink corydalis (*Corydalis sempervirens*) have seeds that germinate following stimulation by fire (Viereck and Schandelmeier 1980).

Natural regeneration of tree species after fires in the Boreal White and Black Spruce Zone is quite prompt; many forest stands show an age range of only 10 to 15 years, sometimes up to 20. A wave of tree establishment often takes place in the first 5 to 7 years. However, where initial restocking levels are low and seed source, seedbed, and vegetative competition conditions continue to be favorable, recruitment may continue for several decades (Parminter 1983).

Post-fire changes in floristic composition may be minor, with succession becoming an exercise in changing structure and species dominance. For instance, black spruce - sphagnum moss and black spruce - lodgepole pine types generally exhibit little change in composition as time since fire increases. Even though identifiable stages exist (Foote 1983), vegetation cycling by fire rather than orderly replacement of species through succession is common (Methven and others 1975; Viereck 1983).

In other situations, the proportion of the post-fire stand made up by early successional species, such as trembling aspen, the paper birches, and lodgepole pine, may increase over the pre-fire values for those species. Indeed, they may not have been present at all. Other species, such as white spruce, black spruce, and subalpine fir, will be less represented on a proportional basis until later in the life of the stand.

Although trembling aspen and lodgepole pine overtop white spruce during most of the stand's lifetime, the latter species survives and eventually replaces the former in the absence of fire. In most cases all three species become established simultaneously post-fire (Parminter 1983). A similar situation holds for lodgepole pine and black spruce, and lodgepole pine and subalpine fir mixes. Notably, if fire returns before the more shade-tolerant species (the spruces and subalpine fir) are sexually mature, the more fire-adapted early successional species (trembling aspen, paper birches, and lodgepole pine) will have the upper hand and dominate the post-fire site.

Resource Management Implications

Fire suppression costs in the Boreal White and Black Spruce Zone can be high, the annual area burned large, and the economic value of much of the timber resource relatively low. Therefore, fire effects and post-tire vegetation response are important when making decisions on appropriate wildfire suppression response (as well as in planning for prescribed burning).

Post-tire vegetation development depends on many factors such as the type of pre-fire vegetation present and its state of development; the season of fire occurrence; fire behavior and intensity; the depth of bum; fire size; the nature of the off-site vegetation; physical site characteristics; and post-fire environmental conditions. In spite of all of these variables, the most likely course of post-fire succession can be anticipated.

Post-fire vegetation succession models act as predictive tools to aid in resource management decision-making. After 17 cover types in the Boreal White and Black Spruce Zone were delineated following the approach of Hansen and others (1973), a modification of Kessell and Fischer's (1981) methodology was used to show the multiple pathways of post-fire succession. The possible post-fire outcomes, and the further development of the cover types with and without fire, have been detailed (Parminter 1983).

Considerable prescribed burning is carried out to enhance domestic range and wildlife habitat (primarily for large ungulates). Conversion of coniferous to mixedwood stands or of mixcdwood to shrub- and herb-dominated types occurs as prescribed burning shortens the fire frequency.

PONDEROSA PINE ZONE

This zone is found at lower elevations in some of the main valleys of the southern third of the central interior. It extends south into the Pacific Northwest states.

Climatically it is the driest, and in summer the warmest, biogeoclimatic zone in the province (Mitchell and Erickson 1983). It is classed as semi-arid continental. The summers are warm and the mean annual precipitation ranges from 200 to 300 mm. Moisture deficits occur during the growing season.

Ponderosa pine (*Pinus* ponderosa) is the predominant tree species, and often forms open park-like stands with an understory of bluebunch wheatgrass *(Agropyron spicatum)*. Douglas-fir and trembling aspen occur on moister sites, and western larch (*Larix occidentalis*) is rarer. Grasslands are mixed with the forest cover throughout the zone.

Fire History

Evidence of fire is found as charcoal layers in the soil, charred bark, and fire-scarred trees (primarily ponderosa pine and Douglas-fir). The fire regime most often consists of frequent light surface fires and, rarely, long interval crown fires. The role of tire is to maintain the stand, keeping the understory relatively open and the ground free of excessive woody fuel buildup (Agee 1990). The rarer crown fires in this type open up gaps within the stand which then fill in with a new age class of ponderosa pines.

Charcoal deposited in lake sediments from local and regional grassland and forest fires indicated a fire history going back 300 years or more in the southern part of the Ponderosa Pine Zone (Cawker 1983). Many fires have been lightning-caused. A proportion can be attributed to aboriginal prescribed burning, which Barrett and Amo (1982) and Gruel1 (1985) found to have increased fire frequency in ponderosa pine habitats of the interior western states.

Fire history studies in North America have revealed fire frequencies of about 6 to 15 years for the types of ponderosa pine stands found in British Columbia (Wright 1978; Wright and Bailey 1982). One of the earliest local investigations was that of Melrose (1923). In the southeastern portion of the province he dated 13 tire events between 1729 and 1908, for a fire frequency of 13.7 years.

Dorey (1979), working just above the Montana border, constructed a fire chronology based on 14 fire-scarred trees which indicated a history of surface fires between 1813 and 1940. The tire frequency works out to 6.3 years overall.

Cartwright's (1983) data show a fire frequency of 9 years for a mixed ponderosa pine - Douglas-fir forest near Kamloops, British Columbia. Low (1988) found values of 7.2 and 10.5 years for two areas in the same vicinity.

Fire Effects and Succession

Windfall, insect attacks, mortality, and frequent tire have historically maintained open ponderosa pine and mixed ponderosa pine - Douglas-fir stands (Wright 1978). Tree seedlings established after fire begin the development of an even-aged group. An uneven-aged forest results from this pattern.

Under a natural regime most of the understory grasses, forbs, and shrubs are maintained and enhanced by tire. Low severity tires favor resprouting, while germination from seed is favored after high severity fires (Saveland and Bunting 1988). However, mortality of fire-sensitive understory species, as well as conifers, does take place.

Fuel removal by grazing of domestic stock and fire suppression has significantly affected fire frequencies, either lengthening them substantially or removing the influence of tire altogether. Dorey (1979) found the fire frequency to have been 5.9 years prior to, and 9.6 years after 1911. No fires took place since 1940. Low (1988) found an area with a tire frequency of 10.5 years between 1672 and 1900 which had not experienced fire since 1901. Another with a tire frequency of 7.2 years between 1774 and 1933 had not had a fire since 1934.

Early accounts of the ponderosa pine forests described them as being fairly open and interspersed with large areas of grassland. Crown fires seldom occurred in these types (Whitford and Craig 1918). With tire exclusion, such stands become dense, many younger trees establish in the understory, and tree growth stagnates (Arno 1988). Total fuel loading becomes higher and the amount of ladder fuels increases dramatically, increasing the possibility of crown tires (Steele and others 1986). Douglas-fir often invades the lower canopy and becomes predominant, where before it had been absent or minor (Amo 1988; Dorey 1979). Understory vegetation becomes depleted due to the denser tree canopy.

Resource Management Implications

Historical sentiment against underbuming these ponderosa pine forests related to the death of young seedlings, loss of timber production, scarring of trees, and depletion of soil nutrients (Melrose 1923). The opinion of the Forest Branch was that a continued role for surface fires in these stands would be an economic misfortune (Forest Branch 1923).

The ecological consequences of the exclusion of fire from these stands have been recognized in the past two decades. Prescribed burning is now carried out in many ponderosa pine and mixed ponderosa pine - Douglas-fir forests to maintain and enhance domestic range and wildlife habitat. Other reasons include fuels reduction (especially in the urban/wildland interface zone) and visual resource management. Prescribed fire may be combined with mechanical treatments, such as spacing, thinning, pruning, or selection logging.

LITERATURE CITED

Agee, James K. 1981. Fire effects on Pacific northwest forests: flora, fuels, and fauna. In: Annual Meeting Proceedings, Northwest Forest Fire Council, November 23-24, 1981. Portland, Oregon. pp. 54-66.

Agee, James K. 1990. The historical role of fire in Pacific northwest forests. In: Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis, Oregon. pp. 25-38.

Annas, R.M. 1983. Boreal white and black spruce zone. In: Forestry Handbook for British Columbia, Fourth Edition. Forestry Undergraduate Society, University of British Columbia, Vancouver, B.C. pp. 254-258.

Amo, Stephen F. 1988. Fire ecology and its management implications in ponderosa pine forests. In: Ponderosa pine - the species and its management, symposium proceedings. September 29 - October 1, 1987, Spokane, Washington. Washington State University, Pullman, Washington. pp. 133-139.

Barrett, Stephen W. and S.F. Amo. 1982. Indian fires as an ecological influence in the northern Rockies. Journal of Forestry 80(10):647-651.

Beese, William J. 1986. Effects of prescribed burning on some coastal B.C. sites. In: Annual Meeting Proceedings, Northwest Fire Council, November 18-19, 1986. Olympia, Washington. pp. 1-14.

Benedict, R.E. 1915. Disposal of logging slash in British Columbia. In: Forest Protection in Canada 1913 - 1914. Committee on Forests, Commission of Conservation Canada. Ottawa, Ontario. pp. 101-121.

Cartwright, D. 1983. Evaluating the effects of prescribed burning on bighorn sheep. Unpub. B.S.F. Thesis, Faculty of Forestry, Univ. of British Columbia, Vancouver, B.C. 31 p. Appendices.

Cawker, K.B. 1983. Fire history and grassland vegetation change: three pollen diagrams from southern British Columbia. Canadian Journal of Botany 61(4):1126-l 139.

Cwynar, Les C. 1987. Fire and the forest history of the North Cascade Range. Ecology 68(4):791-802.

Curran, M.P. 1988. Slashbuming effects on tree growth and nutrient levels at Mission Tree Farm: project status. In: Degradation of Forested Land: "forest soils at risk." Proceedings of the 10th B.C. Soil Science Workshop, February 1986. Ministry of Forests, Land Management Report Number 56. Victoria, B.C. pp. 294-313.

Dawson, George M. 1888. Report on an exploration in the Yukon District, N.W.T. and adjacent northern portion of British Columbia, 1887. Geological & Natural History Survey of Canada. Dawson Bros., Montreal, Quebec. 277 p.

Dix, R.L. and J.M.A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Canadian Journal of Botany 49(5):657-676.

Dorey, Robin J. 1979. A fire history investigation and the effects of fire exclusion on a ponderosa pine forest in southeastern British Columbia. Unpub. B.S.F. Thesis, Faculty of Forestry, Univ. of British Columbia, Vancouver, B.C. viii + 56 p.

Eis, Slavoj. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. University of British Columbia, Faculty of Forestry Bulletin No. 4. Vancouver, B.C. 76 p.

Fahnestock, George R. and J.K. Agee. 1983. Biomass consumption and smoke production by prehistoric and modem forest fires in western Washington. Journal of Forestry 81(10):653-657.

Farley, A.L. 1979. Atlas of British Columbia - people, environment, and resource use. The University of British Columbia Press, Vancouver, B.C. 136 p.

Foote, M. Joan. 1983. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. USDA Forest Service Research Paper PNW-307. Portland, Oregon. 108 p.

Forest Branch. 1923. Report of the Forest Branch of the Department of Lands for the year ending December 31, 1922. King's Printer, Victoria, B.C. pp. L9-L10.

Franklin, Jerry F. and C.T. Dymess. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Portland, Oregon. 417 p.

Franklin, Jerry F. and R.H. Waring. 1979. Distinctive features of the northwestern coniferous forest: development, structure, and function. In: Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biology Colloquium. Oregon State University Press, Corvallis, Oregon. pp. 59-86.

Franklin, Jerry F., A. McKee, F.J. Swanson, J. Means, and A. Brown. 1979. Age structure analyses of old-growth Douglas-fir stands: data versus conventional wisdom. Bulletin of the Ecological Society of America 60(2):102.

Franklin, Jerry F., K. Cromack, Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW-118. Portland, Oregon. 48 p.

Franklin, Jerry F. and T.A. Spies. 1984. Characteristics of old-growth Douglas-fir forests. In: Proceedings of the 1983 Convention of the Society of American Foresters, October 16-20, 1983, Portland, Oregon. Society of American Foresters, Washington, D.C. pp. 328-334.

Gruell, George E. 1985. Indian fires in the interior west: a widespread influence. In: Proceedings - symposium and workshop on wilderness fire. USDA Forest Service General Technical Report INT-182. Ogden, Utah. pp. 68-74.

Hansen, Henry L., L.W. Krefting, and V. Kurmis. 1973. The forest of Isle Royale in relation to fire history and wildlife. University of Minnesota Agricultural Experiment Station Technical Bulletin 294, Forestry Series 13. Minneapolis, Minnesota. 43 p.

Haeusslcr, S., J. Pojar, B.M. Geisler, D. Yole, and R.M. Annas. 1984. A guide to the coastal western hemlock zone, northern drier maritime subzone (CWHf) in the Prince Rupert Forest Region, British Columbia. Ministry of Forests, Land Management Report Number 21. Victoria, B.C. 164 p.

Harris, Arland S. and W.A. Farr. 1974. The forest ecosystem of southeast Alaska - 7. forest ecology and timber management. USDA Forest Service General Technical Report PNW-25. Portland, Oregon. 109 p.

Heinselman, Miron L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In: Fire Regimes and Ecosystem Properties, Proceedings of the Conference, December 11-15, 1978, Honolulu, Hawaii. USDA Forest Service General Technical Report WO-26. Washington, D.C. pp. 7-57.

House, Edward J. 1909. A hunter's camp-fires. Harper and Bros., New York. 402 p.

Howe, C.D. 1915. The reproduction of commercial species in the southern coastal forests of British Columbia. In: Forest Protection in Canada 1913 1914. Committee on Forests, Commission of Conservation Canada. Ottawa, Ontario. pp. 212-230.

Judd, C.S. 1915. Douglas fir and fire. In: Proceedings of the Society of American Foresters 10(2):186-191.

Kayll, A.J. 1968. The role of fire in the boreal forest of Canada. Environment Canada, Forestry Service Information Report PS-X-7. Chalk River, Ontario. 15 p.

Kelsall, John P., E.S. Telfer, and T.D. Wright. 1977. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Fisheries and Environment Canada, Canadian Wildlife Service Occasional Paper Number 32. Ottawa, Ontario. 58 p.

Kessell, Stephen R. and W.C. Fischer. 1981. Predicting postfire plant succession for tire management planning. USDA Forest Service General Technical Report INT-94. Ogden, Utah. 19 p.

Klinka, K., R.N. Green, P.J. Courtin, and F.C. Nuszdorfer. 1984. Site diagnosis, tree species selection, and slashbuming guidelines for the Vancouver Forest Region. Ministry of Forests, Land Management Report Number 25. Victoria, B.C. 180 p.

Lewis, Henry T. 1982. A time for burning. University of Alberta, Boreal Institute for Northern Studies Occasional Publication No. 17. Edmonton, Alberta. 62 p.

Low, D.J. 1988. Effects of prescribed burning on non-target wildlife species associated with fire prone ecosystems in the southern interior of British Columbia. In: Wildlife and Range Prescribed Burning Workshop Proceedings, October 27-28, 1987, Richmond, B.C. Faculty of Forestry, Univ. of British Columbia, Vancouver, B.C. pp. 185-196.

Lutz, H.J. 1955. Ecological effects of forest fires in the interior of Alaska. USDA Technical Bulletin No. 1133 Washington, D.C. 121 p.

Lutz, Harold J. 1959. Aboriginal man and white man as historical causes of forest tires in the boreal forest, with particular reference to Alaska. Yale University School of Forestry Bulletin No. 65. Yale University, New Haven, Connecticut. 49 p.

Mathewes, Rolf W. 1973. A palynological study of postglacial vegetation changes in the University Research Forest, southwestern British Columbia. Canadian Journal of Botany 51(11):2085-2103.

Martin, Robert E., D.D. Robinson, and W.H. Schaeffer. 1976. Fire in the Pacific Northwest - perspectives and problems. In: Proceedings Annual Tall Timbers Fire Ecology Conference, Pacific Northwest, Number 15, October 16-17, 1974, Portland, Oregon. Tall Timbers Research Station, Tallahassee, Florida. pp. l-23.

Melrose, G.P. 1923. History written in trees. American Forests 29(355):414-415.

Methven, I.R., C.E. Van Wagner, and B.J. Stocks. 1975. The vegetation on four burned areas in northwestern Ontario. Environment Canada, Forestry Service Information Report PS-X-60. Chalk River, Ontario. 20 p.

Mitchell, W.R. and W.R. Erickson. 1983. Ponderosa pine bunchgrass zone. In: Forestry Handbook for British Columbia, Fourth Edition. Published by the Forestry Undergraduate Society, University of British Columbia, Vancouver, B.C. pp. 296-301.

Munger, Thornton T. 1940. The cycle from Douglas fir to hemlock. Ecology 21(4):451-459.

Parminter, John. 1983. Fire history and fire ecology in the Prince Rupert Forest Region. In: Prescribed Fire - Forest Soils Symposium Proceedings, March 2-3, 1982, Smithers, B.C. Ministry of Forests Land Management Report No. 16. Information Services Branch, Victoria, B.C. pp. l-35.

Peterson, L.D. 1989. Vegetation response to slashbuming: a 3-year progress report. Ministry of Environment and Ministry of Forests, Integrated Wildlife Intensive Forestry Research Report IWIFR-39. Victoria, B.C. 38 p.

Pojar, Jim. (editor) 1983. Forest ecology. In: Forestry Handbook for British Columbia, Fourth Edition. Published by the Forestry Undergraduate Society, University of British Columbia, Vancouver, B.C. pp. 221-247.

Pojar, J. and K. Klinka. 1983. Coastal western hemlock zone. In: Forestry Handbook for British Columbia, Fourth Edition. Published by the Forestry Undergraduate Society, University of British Columbia, Vancouver, B.C. pp. 268-272.

Pojar, J., K. Klinka, and D.V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. Forest Ecology and Management 22(1,2):119-154.

Rigg, George B. and C.T. Richardson. 1938. Profiles of some sphagnum bogs of the Pacific coast of North America. Ecology 19(3):408-434.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quatemary Research 3(3):444-464.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York. pp. 1351.54.

Saveland, James M. and S.C. Bunting. 1988. Fire effects in ponderosa pine forests. In: Ponderosa pine - the species and its management, symposium proceedings. September 29 - October 1, 1987, Spokane, Washington. Washington State University, Pullman, Washington. pp. 125131.

Schmidt, R.L. 1957. The silvics and plant geography of the genus *Abies* in the coastal forests of British Columbia. Department of Lands and Forests, British Columbia Forest Service Technical Publication T.46. Victoria, B.C. 31 p.

Schmidt, R.L. 1960. Factors controlling the distribution of Douglas fir in coastal British Columbia. Quarterly Journal of Forestry 54(2):156-160.

Schmidt, R.L. 1970. A history of pre-settlement fires on Vancouver Island as determined from Douglas-fir ages. In: Tree-ring Analysis with Special Reference to Northwest America. Proceedings of a Conference, February 19-20, 1970. University of British Columbia, Faculty of Forestry Bulletin No. 7. Vancouver, B.C. pp. 107-108.

Smith, J. Harry G. 1981. Fire cycles and management alternatives. In: Fire Regimes and Ecosystem Properties, Proceedings of the Conference, December 11-15, 1978, Honolulu, Hawaii. USDA Forest Service General Technical Report WO-26. Washington, D.C. pp. 511-531.

Spies, Thomas A. and J.F. Franklin. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal 8(3): 190-201.

Steele, Robert, S.F. Amo, and K. Geier-Hayes. 1986. Wildfire patterns change central Idaho's ponderosa pine - Douglas-fir forest. Western Journal of Applied Forestry 1(1):16-18.

Stewart, Glenn H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research 16(3):558-568.

Viereck, L.A. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. In: The role of fire in northern circumpolar ecosystems. John Wiley & Sons, New York. pp. 201-220.

Viereck, Leslie A. and L.A. Schandelmeier. 1980. Effects of tire in Alaska and adjacent Canada - a literature review. USDI Bureau of Land Management BLM-Alaska Technical Report 6. Anchorage, Alaska. 124 p.

Whitford, H.N. and R.D. Craig. 1918. Forests of British Columbia. Committee on Forests, Commission of Conservation Canada. Ottawa, Ontario. 390 p.

Wright, Henry A. 1978. The effect of fire on vegetation in ponderosa pine forests, a state-of-the art review. Texas Tech University Range and Wildlife Information Series Number 2, College of Agricultural Sciences Publication No. T-9-199. 21 p.

Wright, Henry A. and A.W. Bailey. 1982. Fire ecology - United States and southern Canada. John Wiley & Sons, New York. 501 p.

ANTHROPOGENIC FIRE AND TROPICAL DEFORESTATION: A LITERATURE PERSPECTIVE

Michael R. Wetzel and Philip N. Omi'

Abstract-Antbropogenic tire is an important agent of tropical destruction. Fire has been the primary tool of rural and technologically primitive people for managing and manipulating their natural environment. For more than a century observers and researchers have recorded and documented the process of deforestation by tire throughout the tropics. Using the cumulative written work of these investigators, we describe how human-caused fire in the tropics has contributed to deforestation. Human use of fire cannot be eliminated, nor is its elimination necessarily desireable; however, it must be managed. Education of tire users must form the core of any tire management program. Until an effective fire management policy can be implemented, anthropogenic tire will continue to contribute to tropical deforestation.

INTRODUCTION

Fire in nature is an awesome force. In human hands it has become our most powerful tool for altering the face of the earth (Sauer 1958). Today, as it has been since mankind first learned to use it, fire is the primary tool of rural and technologically primitive people for manipulating and managing their natural environment (Stewart 1956).

Unfortunately, tire has become one of the most important agents in the worldwide destruction of tropical forests, and 98 percent of tropical fires are anthropogenic, started by some intentional or unintentional human action (Batchclder 1967). Anthropogenic fire has been identified as the most serious threat to Venezuela's forests (Budowski 1951; Camero-Zamorra 1952). In India human-caused fire has been responsible for the loss of much of the subcontinent's forests (Troup 1926). On the Indonesian island of Java periodic, long-continued human firing of vegetation has been the greatest menace to its forests (Shuitemaker 1950 in Bartlett 1955). Through repeated burning the tropical forests around the world have been reduced in area and often replaced by savannas and grasslands (de la Rue 1958; Batchclder and Hirt 1966; Walter 1971).

For more than a century observers and researchers have recorded and documented tropical man's often careless and negligent use of fire. Using the cumulative written work of many of these scientists, we have put together a general scenario, based upon a myriad of specific cases, about how fire has contributed to forest destruction in the tropics.

Batchelder and Hirt (1966) wrote:

> . . because the number of interrelationships among fire, man, and [the] environment are nearly infinite; no one condition or set of conditions can be assumed to be dominant for all parts of the tropics.

We understand and heartily endorse this observation. As a result of the pantropical view we have taken, our generalizations are not necessarily appropriate to all tropical ecosystems, macrosites, and microsites. The information we are providing, while valid in general, must be checked against site specific conditions. Undoubtedly, tropical forest land managers and policy makers have a great and present need for extensive and intensive research about tire behavior and fire effects in their forests.

TROPICAL FOREST LOCATION

Tropical forests are located in lowland elevations -- generally below 1300 meters -- of the large, global belt around the equator, primarily between the Tropics of Cancer and Capricorn. Where tropical climatic conditions extend beyond the north and south tropical latitudes, so do the tropical forests. The forests are concentrated in Africa and the Americas with more than half of the closed forests located in South and Central America. The forests of the Amazon River drainage account for the bulk of the New World's closed forest. In contrast the vast majority of open tropical forests are located in Africa (See table 1).

TROPICAL DEFORESTATION

Estimates of tropical forest area range from 15 million to 19 million square kilometers -- approximately 42 percent of all tropical land and 13 percent of the earth's land surface. Closed forests -- those with a continuous canopy -- account for about 9 to 11 million square kilometers (UNESCO 1978). Deforestation rates for the closed forests are largely hypothetical and vary with the estimator and the definition of deforestation used. Stated loss rate figures run from 100,000 to 245,000 square kilometers per year (Myers 1981).

Geographically, the losses are pantropical. The pressure on the forests is greatest at the forest edge where they are most accessible. This edge can be a broad ecotonal belt or an abrupt boundary.

'Consulting Forester, Michael R. Wetzel & Co., Denmark, SC and Professor of Forest Fire Science, Colorado State University, Fort Collins, CO.

Table 1. Global Location of tropical forests by percent of total tropical forest area (U.S. Interagency Task force 1980).

Type of Forest (pct)	Location
All Tropical Forests (1.9 billion hectares)	
42 percent	South and Central America
37 percent	Africa
21 percent	Asia/Australia/Oceania
Closed Tropical Forests (1.1 billion hectares)	
50 percent	South and Central America
30 percent	Africa
20 percent	Asia/Australia/Oceania
Open Tropical Forests (0.8 billion hectares)	
64 percent	Africa, Asia, Australia, Central and South America

Primary deforestation activities are industrial logging, fuelwood gathering, and agricultural clearing. Of these three, destruction associated with the forest farmer is the most important; and the forest farmer's primary tool is fire(Nichols 1901; Budowski 1956; Dcnevan 1978). Some overlap in deforestation activities does exist. For example forest farmers often move into logged areas to establish their farm plots.

In using the term forest farmer we mean the traditional shifting agriculturalist as well as the modern "pioneer" farmer-settler. Development, greater rural population densities, and the demands of a market economy have in many places changed subsistence shifting agriculture so much that ecologically it is not much different than the farming practices of the pioneer settlers.

FLAMMABILITY OF TROPICAL FOREST TYPES

In the tropics the climatic regulators of vegetation type are the amount of rainfall during the wet season and the duration and intensity of the dry season (Walter 1971). Three general forest types are relevant to our look at anthropogenic fire and deforestation. In order of most rainfall and shortest dry season they are: the tropical rain forest, the semi-deciduous forest, and the deciduous forest (Mueller-Dombois 1981). Deciduous forests can be further divided into moist and dry forests (Walter 1973). The moist deciduous forests receive more rainfall than the dry deciduous forests and grow on soils with greater water-holding capacity. Rain, semi-deciduous, and moist deciduous forests are closed forest types. Dry deciduous forests are open types.

The three closed forest types are fire independent ecosystems (Vogl 1977). Successful natural ignitions are rarely sustained. Low tight levels on the floor of the closed forest during the growing periods prevent growth of significant amounts of herbaceous vegetation. High temperatures and moisture levels promote rapid decay of litterfall. Furthermore, low fuel loading and large fuel size, high moisture content, and wide fuel spacings, combined with the high ignition temperature typical of most tropical forest fuels, mitigate against prolonged, continuous combustion in the undisturbed closed forest (Batchelder and Hirt 1966; Trollope 1980). Open forests do have herbaceous and shrub understories because light penetrates to the forest floor. Once the undisturbed closed forest is cleared, though, xeric understory and overstory species become established on the site and at the forest edge. This secondary vegetation is more likely to sustain combustion if ignited. After fire has invaded the forest once, the forest remains in constant danger from human set fires (Spurway 1937; Aubreville 1947; Budowski 1966).

Flammability of Tropical Rain Forests

The tropical rain forest is evergreen or mostly evergreen. Though there is no true dry season, there can be a relatively dry period in this forest type. Even in such a "dry" period precipitation averages at least 100 millimeters per month. Mean annual temperature hovers around 24 degrees Celsius. Decomposition rates are rapid, so there is only a thin litter layer on the forest floor at any given time. Primarily due to its high moisture level, the undisturbed tropical rain forest is almost fireproof. Once the forest is opened, though, it becomes susceptible to burning. Dead and live vegetation in the opening and at the forest edge quickly dry upon exposure to the intense tropical sun, thus becoming more flammable. Under these circumstances the tropical rain forest will burn.

Flammability of Semi-deciduous and Deciduous Forests

The semi-deciduous and deciduous forests are seasonal forests because they exist in the alternating climates of wet summers and dry winters. The number of dry months varies from roughly three to six in the semi-deciduous forest, six to eight in the moist deciduous forest, and eight to ten in the dry deciduous forest (Walter 1971). Mean temperatures range between 20 and 28 degrees Celsius.

The alternating wet and dry seasons is conducive to fire occurrence. During the wet season there is substantial plant growth which cures in the dry season. The deciduous plants not only dry out, but also shed their leaves. Nevertheless, like the rain forest, the semi-deciduous forest ordinarily does not burn easily. If this forest is opened to the sun's insolation, however, its vegetation dries, becomes more flammable, and, therefore, more likely to burn if exposed to an ignition source.

The deciduous forest is more susceptible to burning in its unaltered state (Walter 1971, 1973). As the dry period grows longer and more severe, greater numbers of deciduous tree species and fewer evergreen species occupy the forest while total tree density decreases. The deciduous forest, especially the open forest, has greater fuel accumulations due to abundant litterfall and the curing of grasses and other low understory vegetation during the dry season. Exposed to the tropical heat, these fuels quickly dessicate. Under these circumstances there are sufficient fuels of small size, low moisture content, and close spatial arrangement to carry a surface fire when fire enters the forest. As the dry period grows longer and more intense, the potential fuels become more flammable and the fire danger is magnified.

The fuel complex and fire potential of tropical forests are altered by human activity that removes the vegetation, thus creating openings in the forests. After the initial clearing fuel loading increases in all size classes, scattered evenly over the site. After a variable period of exposure to solar heating these fuels dry sufficiently to burn. In the following years grasses and other herbaceous vegetation, as well as woody species, occupy the site as pioneers in secondary succession. This vegetation, adapted to drier, open environments, grows more or less evenly over the site and dries rapidly in the absence of precipitation. These early successional conditions provide a fuel complex that will burn without cutting and extended drying (Vogl 1969; Walter 1971). If disturbed forest sites are repeatedly burned, highly flammable, quickly regenerating grasses such as Imperata species rapidly dominate the site; creating an easily burned, self-replacing fuel complex.

THE PROCESS OF DEFORESTATION BY FIRE

Anthropogenic fire is concentrated in the open and ecotonal areas of the tropics where humans live and work. Annually, sometimes more often, and usually at the end of the dry season, residents set their fires. Generally, these are surface fires which are carried by ground litter and herbaceous and shrub vegetation. Fire intensities are usually low due to low available fuel loadings, high fuel moisture and relative humidity, and discontinuous fuel spacing. Fire fronts are typically shallow and narrow. Areas burned are normally small and patchy (Batchelder and Hirt 1966).

These fires pose two major problems important to deforestation. Foremost, with some exceptions, few people make any attempt to control their fires. They simply rely on the low flammability of surrounding green vegetation to contain the tires. This lack of concern about fire control is all too common throughout the tropics.

The second problem is a result of the first. Too many fires escape the intended burning area. Cook (1909) observed that fires were usually allowed to spread wherever fuels would carry them. As the population density of forest farmers increases, abandoned and productive agricultural plots remain in close proximity (Denevan 1978). Abandoned plots are frequently composed of xeric secondary vegetation that readily burns during the dry season. Fires intentionally set in the productive plots accidentally bum into the nearby abandoned plots. These escaped, uncontrolled, human set wildfires eventually spread into the adjoining forest. This scenario accounted for nearly 100,000 hectares of wildfires in Mexico's eastern Yucatan Peninsula during the summer of 1989 (National Fire Protection Association 1989; Garrett 1989).

The actual process of deforestation by fire has been described by several authors from Cook in 1921 to Mueller-Dombois in 1981. Fire originating in adjacent open areas burns to the forest border. Depending on the intensity of the fire, density of the vegetation at the forest edge, fuel loading, and forest moisture conditions, fire may or may not penetrate the forest. Under normal circumstances fire will not enter a rain forest, but fires can burn from several meters to 1 or 2 kilometers into the semi-deciduous and deciduous forests. Once at or within the forest edge, fire intensity lessens as available fuel decreases and relative humidity increases. Fire damage is usually minimal. Herbaceous growth, coppice stumps, low bushes, suckers, and seedlings are killed and varying amounts of duff and litter are removed by the tire. Saplings and some fire sensitive species may be killed. Also, larger trees may be scorched or scarred around the butt.

The killing of undergrowth and trees in the burned forest area opens more of the forest to direct sunlight. Grasses quickly establish and rapidly grow in the sunlit areas. In forests which adjoin annually burned savannas or which surround annually burned openings, the invading understory vegetation provides the fuel that will allow the next season's fires to spread farther into the forest. Furthermore, opening of the forest edge to greater sunlight alters the edge microclimate to a drier type which also may contribute to increased intensity of the next tire.

LONG-TERM EFFECTS OF UNCONTROLLED FIRE USE

The forest vegetation shields the soil and the site from the drying effects of the sun and wind. Repeated fires open forests and expose the forest soils by removing living vegetation and litter. Soil surface temperatures rise and relative humidity decreases in response to direct solar exposure. Addition of new organic matter is reduced. Given these conditions, the closed nutrient cycling system of the tropical forest is damaged. Movement of essential nutrients to the forest vegetation is interrupted (Richards 1952). Wind and solar insolation dessicate the exposed soil and contribute to increased evapotranspiration which further reduces soil moisture. Microorganism populations shrink as organic matter content causes reduced nitrogen fixation and nutrient mineralization. Soil impoverishment is the result (Camero-Zamorra 1952).

The combined effect of repeated firing, insolation, and torrential rains is a breakdown in soil structure. Under these forces the soil disaggregates and compacts (Pittier 1939; Jha and others 1980). Soil density increases and porosity decreases leading to reduced soil moisture holding capacity. In the oxisots, ultisols, inceptisols, and the red earths typical of the humid and seasonal tropics a hardpan may develop if exposed to repeated wetting and drying (de la Rue 1958; Donahue and others 1977). Once exposed to the elements, erosion of the fragile topsoil becomes a serious problem.

With progressive opening of the forest microclimate warms and dries, soil moisture and fertility decline, and less demanding woody and herbaceous plants adapted to drier conditions become established (Budowski 1956). Forest vegetation that survives the repeated fires or degraded site conditions lingers on singly or as relict groves and gallery forests (Batchelder and Hirt 1966). Forest regeneration that overcomes the poorer site conditions is either killed during regular burning or suppressed by the invading vegetation which is more fire-resistant (Innes 1971; Vogl 1977). Eventually, even the most fire-resistant woody species are eliminated. At this point the forest site is totally degraded and deforestation is complete. Continual tiring wilt prevent the return of forest growth to formerly forested sites.

MANAGEMENT OF ANTHROPOGENIC FIRE

The challenge is to halt haphazard fire use without prohibiting rational use of fire for legitimate agricultural and non-agricultural land management. However, since tire is the primary land clearing tool of most agriculturalists, implementation of a rational fire management program will be a difficult and sensitive task. Human use of fire can never be successfully eliminated, nor is its prohibition necessarily desirable. A fire management program, while serving to preserve and protect tropical forests and human welfare, must respect the basic rural cultural foundations on which burning rests. It must also allow for inevitable and unavoidable economic use of forests and grasslands.

Governments of countries with tropical forests have become more aware of the forest fire problems they face and of the need to protect their forest resources. We suggest that the first task in dealing with the tire problem should be the formulation of a national fire policy to provide a framework for further actions. Every nation has a unique fire situation, and each nation's tire policy should reflect that uniqueness. In every case, though, the all-important human dimensions of tire must be addressed. Human-caused fires arc preventable, but fire policy that threatens traditional land uses will ultimately fail.

To bring anthropogenic fire under control the affected people must understand and support management programs. Education is essential to impart understanding and to change the attitudes of fire users toward fire and the environment. Hand in hand with an educational effort, an agricultural or forestry extension program could be established to instruct users about the correct application of fire and its positive and negative effects on the land and its vegetation. The negligent and indifferent tire habits so common in the tropics must be reformed for a program of managed fire to be successful.

Education is a long-term solution to a pressing problem; nevertheless, the best of intentions, the finest policy statement, and the most modem science and technology will avail us little if the attitudes of fire users remain unaltered. Mr. Helmut Haufe, FAO Regional Forestry Officer in Latin America, stated that anthropogenic wildfires in too many cases are "due to the lack of a proper information and instruction system" (pers. comm. 1981). Mr. Haufe's statement is a significant endorsement for an extensive and vigorous fire education program.

Other actions that may help manage the anthropogenic fire problem are more appropriately considered under the headings of agricultural and rural development, but bear mentioning here. These actions include providing alternatives to traditional agricultural practices and incentives to take up the alternatives. The already mentioned extension programs could help develop and promote alternative methods and technologies. Land use, tax, rural development, and internal colonization policies can also be adjusted to reduce the motives for negligent and abusive fire use.

CONCLUSION

In 1967 Batchelder wrote that the "use of fire in the tropical world is no longer in a stage of 'ecological climax' wherein a stable, harmonious relationship to the environment exists." In fact over the past hundred, if not several hundred years, the careless and repeated use of fire has resulted in ecological disturbances which have steadily forced the retreat of tropical forests worldwide. Natural succession, which normally heals ecological wounds and returns ecosystems to their predisturbance states, has been halted by the frequent and often devastating nature of anthropogenic tire. Insofar as tropical forest regeneration is concerned, continuous anthropogenic fire disturbances are unnatural and, therefore, beyond the adaptive and recuperative powers of forest ecosystems. Repeated burning leads to replacement of the original vegetation by a series of seral communities more easily burned until a fire disclimax community is finally established.

In a paper delivered to the West Indian Agricultural Conference in 1901 Nichols called for an immediate end to uncontrolled burning in the tropics. Ninety years later a great variety of voices still echo his call. Since 1901 efforts to reduce the frequency and effects of anthropogenic fire in the tropics have failed. The burning continues. Effective fire management policies, that are strong on education must be developed and implemented. Without them increasing population, development, and colonization pressures within the tropical forest regions will assure the unabated cultural use of fire in its present destructive form.

LITERATURE CITED

Aubreville, A. M. 1947. The disappearance of the tropical forests of Africa. Unasylva 1:5-1 1.

Bartlett, H.H. 1955. Fire in relation to primitive agriculture and grazing in the tropics: annotated bibliography. Volume 1. University of Michigan Botanical Gardens, Ann Arbor.

Batcheider, R.B. 1967. Spatial and temporal patterns of fire in the tropical world. In: Proceedings of the Tall Timbers Fire Ecology Conference 6:171-190.

Batchelder, R. B. and Hirt, H. F. 1966. Fire in tropical forests and grasslands. United States Army Natick Laboratory Technical Report 67-47-ES.

Budowski, G. 1951. Los incendios forestales en Venezuela. Agricultor Venezolano 16(152): 24-28.

Budowski, G. 1956. Tropical savanna: a sequence of forest felling and repeated burnings. Turrialba 6:23-33.

Budowski, G. 1966. Fire in tropical American lowland areas In: Proceedings of the Tall Timbers Fire Ecology Conference 5:5-22.

Camero-Zamorra, J. 1952. Quemas e incendios forestales. Agricultor Venzolano 17(158): 39-43.

Cook, 0. F. 1909. Vegetation affected by agriculture in Central America. United States Department of Agriculture Bureau of Plant Industry, Number 145.

Cook, 0. F. 1921. Milpa agriculture, a primitive tropical system. In: Annual report of the Smithsonian Institution, pp. 307-326.

Denevan, W. W. 1978. The causes and consequences of shifting cultivation in relation to tropical forest survival. In: Brown, S., Lugo, A. E. and Liel, B. eds., The role of tropical forests on the world carbon cycle, pp. 140-156. United States Department of Energy.

Donahue, R. L., Shickline, J. C. and Robertson, L. S. 1977 Soils: an introduction to soils and plant growth. Prentice-Hall, Englewood Cliffs, New Jersey.

Garrett, W. E. 1989. La ruta maya. National Geographic 176:424-479.

Jha, M. N. Badola, K. C., and Pande, P. 1980. Soil changes due to podu cultivation in the state of Orrissa. In: Proceedings of the 2nd forestry conference, pp.2-7. Forest Research Institute and Colleges, Dehra Dun.

Innes, R. R. 1971. Fire in West African vegetation. In: Proceedings of the Tall Timbers Fire Ecology Conference 11:147-174.

Mueller-Dombois, D. 1981. Fire in tropical ecosystems. In: Proceedings of the conference- -fire regimes and ecosystem properties, pp. 137-176. United States Department of Agriculture Forest Service General Technical Report WO-26.

Myers, N. 1981. Conversion rates in tropical moist forests In: Mergcn, F., ed., Tropical forests - utilization and conservation, pp. 48-66. Yale University, School of Forestry and Environmental Studies, New Haven, Connecticut.

National Fire Protection Association 1989. Fires burn in Yucatan jungle. Wildland Fire Management Briefings 2(4):21.

Nichols, H.A.A. 1901. The harmfulness of bush fires in the West Indies. Indian Forester 27:384-390.

Pittier, H. 1939. Consideraciones acerca de la destruccion de los bosques e incendio de las sabanas. Boletin de la Sociedad Venezolano de Ciencias Naturales 3:291-302.

Richards, P. W. 19.52. The tropical rain forest. Cambridge University Press, Cambridge.

de la Rue, E. D. 1958. Man's influence on tropical vegetation. In: Proceedings of the Ninth Pacific Science Congress 20:81-93.

Sauer, C. 0. 1958. Man in the ecology of tropical America In: Proceedings of the Ninth Pacific Science Congress 20:104-1 10.

Spurway, B. J. 1937. Shifting cultivation in Sarawak. Malayan Forester 6:124-128.

Stewart, 0. C. 1956. Fire as the first great force employed by man. In: Thomas, W. L., ed., Man's role in changing the face of the earth, pp. 115-133. University of Chicago Press.

Trollope, W. S. W. 1980. Fire in savanna. In: De V. Booyscn, P., ed., Ecological effects of fire in South Africa. CSIR. Pretoria.

Troup, R. S. 1926. Problems of forest ecology in India. In: Tanslcy, A. G. and Chipp, T. F., ed., Aims and methods in the study of vegetation, pp. 283-313. White Friars Press, London.

UNESCO 1978. Tropical forest ecosystems: a state-of-knowledge report. Paris.

U. S. Interagency Task Force on Tropical Forests 1980. The world's tropical forests: a policy, strategy, and program for the United States. Department of State Publication 9117.

Vogl, R. J. 1969. The role of fire in the evolution of the Hawaiian flora and vegetation. In: Proceedings of the Tall Timbers Fire Ecology Conference 9:50-60.

Vogl, R. J. 1977. Fire: a destructive menace or a natural process? In: Cairns, J. and Dickson, K., eds., Recovery and management of damaged ecosystems, pp. 262-289. University of Virginia Press, Charlottesville.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Mueller-Dombois, D., trans., Burnett, J. H., ed. Van Nostrand Reinhold Company, New York.

Walter, H. 1973. Vegetation of the Earth in relation to climate and ecophysiological conditions. Wise, J., trans Springer-Verlag, New York.

WILDFIRE EN THE PALEOZOIC: PRELIMINARY RESULTS OF A CASE STUDY ON THE FIRE ECOLOGY OF A PENNSYLVANIAN FLOODPLAIN FOREST, JOGGINS, NOVA SCOTIA, CANADA

Nan Crystal Arens[1]

Abstract-Sediments of the Joggins Section, Cumberland Basin, western Nova Scotia accumulated in lowland forests approximately 300 million years ago. The 4,000-meter-thick sedimentary sequence includes channel and overbank sandstones interbedded with stacked immature paleosols developed in thick mudstone horizons. Fusain (charcoal) is common in all sedimentary facies present at Joggins. Fusain occurs as isolated macroscopic clasts and also as recognizable layers of clasts and particles within the mudstone/paleosol facies. These layers are interpreted as tire-event horizons. In one example, an ancient tree, rooted below a tire horizon, is preserved with its charred periderm intact. Palynological analysis shows that there is an increase in taxonomic diversity immediately following this fire. Although arborescent lycophytes remain dominant in the palynoflora, cordaitean and medullosan gymnosperms enter the postfire community. These groups decline later as prefire vegetation is reestablished. Numbers of fern-spore species increased following fire, although ferns did not become more abundant. Studies of fire-related floristic patterns preserved in the fossil record can test ecological generalizations and theory derived from present day ecosystems and may help ecologists understand the role of changing fire regimes in long term vegetational change.

INTRODUCTION

The classic image of Carboniferous lowland ecosystems is a static and steamy tropical wetland. Groves of arborcscent lycophytes with their understory of tree ferns and pteridosperms (seed-bearing plants with fern-like foliage) stand in ever-wet soils, while along the riverbanks clumps of sphenopsids flourish. Stutzer and Noé (1940) wrote: "It is difficult to believe that such a thing [wildfire] happened in view of the moist condition of the Carboniferous forests. Judging from the plant associations that grew there, tires could not have spread rapidly in a swamp forest.” However, Izlar (1984) reported that portions of the Okefenokee Swamp-Marsh Complex bum every 25 to 30 years, and that this fire regime maintains the floral composition and heterogeneity characteristic of the ecosystem. As our understanding of wetland ecosystem ecology develops, we are called to reevaluate our view that ancient swamp and floodplain ecosystems were static. We must reexamine the role of fire in these systems.

For this reason, I have begun a study of community dynamics and fire ecology in the Joggins Section (Middle Pennsylvanian) of western Nova Scotia, Canada. This paper reports on the initial study testing the feasibility of detailed ecological reconstruction of this ancient ecosystem. In this paper, I will: (1) show that ecological-scale resolution of the fossil record is possible in this stratigraphic section; (2) establish that wildfire was a significant factor in this ancient ecosystem; and (3) demonstrate that wildfire may have, in part, controlled the distribution of some floodplain plants.

GEOLOGIC SETTING

The Joggins section is located in the Cumberland depositional basin of western Nova Scotia, Canada (fig. 1). Approximately 4,000 meters of sediment are well exposed in a continuous cliff outcrop along the eastern shore of Chignecto Bay. The outcrop face is approximately perpendicular to strike; bedding dips range from 15” to 20” south. Sediments are Middle Pennsylvanian (approximately 305 m.y.b.p.), and have been biostratigraphically dated as latest Westphalian A through earliest Westphalian C using miospores (G. Dolby, unpublished data). Joggins sediments are well correlated with other terrestrial and marine deposits in the North American midcontinent, the Appalachians, and Europe (Phillips and others 1985).

The 4,000 meters of sediment exposed at Joggins record 2 to 5 million years of history (Harland and others 1989). The inferred rapid sedimentation rate suggests that decade-scale or finer stratigraphic resolution may be possible at Joggins. Such fine time-scale stratigraphic resolution is essential for the study of community dynamics and responses to disturbance in an ancient ecosystem. Without adequate time-stratigraphic resolution the record of ecological-scale processes will be obscured by the homogenizing effect of slow sedimentation.

The Joggins stratigraphic sequence consists of channel, levee, and overbank sandstones, floodplain mudstones, and thin coals probably attributable to floodplain ponds. Fluvial facies were deposited in an anastomosing river system that drained the Cobequid Highlands to the present-day southeast (Rust and others 1984). Thin, organic-rich lacustrine limestones also occur in the lower portions of the section. I have observed

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[1] Botanical Museum of Harvard University, 26 Oxford St., Cambridge, MA 02138.

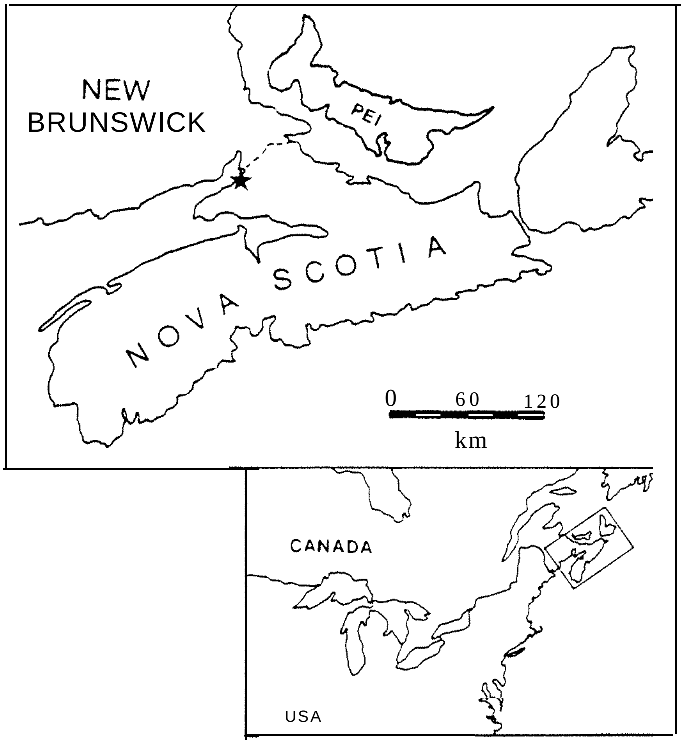

Figure 1.--Location of the Joggins Section area.

no evidence of marine facies or marine influence on terrestrial facies at Joggins. Within the Joggins Section sediments tend to redden and sandstones to coarsen up-section. Rust and others (1984) concluded that these trends indicated a tectonically mediated steepening of the alluvial plain, which lowered relative water table and increased the amount and grain-size of transported sediment.

For this study, the clastic floodplain mudstone/paleosol facies are of particular interest. Mudstone horizons vary from 1 to 20 meters in thickness and are interbedded with crevasse-splay and channel sands. In lower portions of the section, mudstones and paleosols constitute 70 to 80 percent of the stratigraphic section. Color of mudstones varies from gray-green to mottled to gray-red or red up section, corresponding to the inferred water table gradient. Despite this general trend, there is substantial color variation on a finer stratigraphic scale within the section. Mudstones are commonly very poorly-bedded to structureless with moderate to well-developed immature paleosols. Paleosols are characterized by root traces and localized root casts, siderite rhizoconcretions, and locally developed soil structures. Recognizable soil horizons are commonly absent or poorly developed; paleosols generally have uniform texture vertically. Upright trees are commonly preserved as partial sandstone molds within mudstone facies. These trunks may be partially filled or cast in mud, commonly with a rind of vitrinous coal, which is the preserved remains of the lycophyte tree's thick periderm.

Together, these observations suggest that floodplain mudstones were deposited in frequent (geologically speaking) flooding events that emplaced small amounts (centimeters) of fine-grained sediment, rather than in catastrophic events depositing tens or hundreds of centimeters of sediment. Under this depositional regime, clastic swamp trees would not be substantially disrupted by sedimentation events, but, continual redefinition of soil surface by sediment input would cause successive readjustment of soil profile and lead to the observed lack of well-developed horizons. This model fits well with observations of modem tropical rivers such as the Brahmaputra in India and Bangladesh (Coleman 1969) and the Orinoco in Venezuela (Armando Torres, 1991, personal communication).

During deposition of Joggins sediments, the Pennsylvanian Maritimes Basin was near-equatorial and had a tropical to subtropical climate (Rowley and others 1985, Galtier and others 1986). Ziegler and others (1981) reconstructed this region at about 15" north latitude and in a zone of Easterlies. Peat-forming ecosystems at Joggins and in the Springhill coal field to the east are interpreted as groundwater-influenced (rheotrophic), rather than raised, bog systems (Calder and others in press). Groundwater-fed systems occur in the East African rift, where availability of moisture varies seasonally (Cecil and others 1988) If rheotrophic bogs occurred in Nova Scotia during the Pennsylvanian, it is possible that they, too, formed under conditions of seasonally varying moisture availability. However, Cecil and others interpreted the Westphalian B as equitably and adequately wet, based on the relative abundance of ombotrophic versus rheotrophic bogs in the central Appalachians. Conversely, Phillips and Peppers (1984) interpret the Westphalian B as drier and more seasonal than the preceding and succeeding epochs based on swamps in the North American midcontinent. Rowley and others (1985) reconciled these interpretations by suggesting that an increasingly monsoonal climate coupled with the orographic effect of the developing Appalachian highlands to the southwest of the Canadian Maxitimes Basin created regionally different rainfall patterns across the Euramerican coal province. In the Maritimes Cumberland Basin, higher paleolatitude and the presence of highlands to the east could further intensify such a regionally seasonal climate.

The Joggins fluvial sandstones provide direct sedimentological evidence for fluctuating discharge that suggests seasonal rainfall. Multistoried sandstones, graded pebbly sandstones, scour tills, conformable mud drapes, and fan sheetflow in overbank deposits all point to variability in stream discharge, which is consistent with the monsoonal interpretation. However, it is impossible to determine from sedimentological evidence alone whether flood events occurred with seasonal or decade-scale frequency. By either interpretation, though, the ancient landscape at Joggins experienced periods when evapotranspiration exceeded precipitation, thus allowing fuels to dry sufficiently to permit wildfire. In this respect, the climate-induced fire regime may have been quite similar to that in the Okefenokee swamp (Izlar 1984) or the Orinoco floodplain.

EVIDENCE OF WILDFIRE ON THE JOGGINS FLOODPLAIN

The presence of tire in the Joggins ecosystem is inferred from the presence of fusain (charcoal) throughout Joggins sediments. Fusain occurs at Joggins in several sedimentary contexts. In coals, fusain occurs as discrete layers that are laterally continuous for meters on the scale of the outcrop. Within these horizons, fusain may occur as discrete, macroscopic clasts or in a mechanically ground, powdery form. Within the mudstonelpaleosol facies, fusain also occurs as clasts distributed in discrete, sharp-bounded horizons that can be traced laterally for meters along the exposed outcrop. Clasts occur in a matrix of finely-ground charred material with varying amounts of clay. Fusain clasts varying from a few millimeters to 50 centimeters (tig. 2 a-c) are also common in the sandstones and siltstones associated with channel facies. The largest fusinized logs show a perpendicular surface fracture pattern consistent with charring by fire. In the reddest sandstone facies, charred logs are common in mud drapes of channel fill and in point-bar deposits.

The origin of fusain and related materials described from coal macerals has been the subject of much debate between workers who favor a pyrolitic origin for this material and others who believe fusain is produced by some unknown slow oxidization process. Scott (1989) reviewed the evidence and arguments and concluded that most fusain found in the Paleozoic and Tertiary rock record is the direct result of surface burning of vegetation or other surficial organic material. Ting (1982) agreed: “Fusinite and semifusinite are derived primarily from woody tissues charred or partially charred during swamp fire. Once charred, the fusain progenitor--charcoal--becomes extremely stable and inert to any chemical and biochemical attack and is thus well preserved. Some coal beds may contain 20-25 percent fusinite, occurring in numerous fusain bands that suggest frequent swamp fires during peat accumulation.” Cope and Chaloner (1985) added that wildfire was an important ecological factor since the evolution of a land flora in the Silurian and Devonian. In accordance with these conclusions, I adopt the charcoal interpretation of fusain and will refer to fusain as fossil charcoal.

METHODS FOR POLLEN ANALYSIS

The samples analyzed were collected stratigraphically above and below a horizon of fusain clasts, mechanically disaggregated charcoal, and clay associated with the preserved stump of an ancient tree (fig. 2 d-e). The stump, which is located about 150 meters south of McCarren Creek (Rust and others 1984), is preserved in mudstonelpaleosol capped by an overbank sand body. The locality is in the lower portion of the section measured by Rust and others (1984) but is not noted in their published stratigraphic section, probably because cliff-face erosion had not yet exposed the stump at the time of their field work. When collections for this study were made (August, 1989), the stump was badly eroded, but periderm material preserved as fusain rather than vitrinite was clearly visible and the outline of the enlarged base of the tree was easily traceable to a well-defined and laterally continuous horizon of fossil charcoal.

Based on the abundance of centimeter-sized fusain clasts within the mudstone/paleosol facies, this horizon is interpreted as a fire event horizon that records a single wildfire in an ancient stand. This conclusion is based on analogy with studies of Recent sediments, which show that even in lakes, where in situ deposition is less likely than on the floodplain environment, peaks in charcoal abundance can be correlated with single fire events within the drainage basin and charcoal clast size can be related to transport distance (Clark 1988, 1990).

A mudstone sample from below the charcoal horizon sampled prefire vegetation. Stratigraphically successive samples were taken at l-centimeter intervals above the fusain layer. Samples were processed according to standard palynological technique (e.g. Traverse 1988). Rock was degraded in concentrated hydrofluoric acid; unwanted organic material was oxidized with HCl and bleach; clay was removed by heavy liquid separation with ZnCl. Strew slides were made with glycerin jelly. Each slide was scanned systematically and each palynomorph encountered was recorded by genus. Species-level diagnosis was made only for the most abundant spore genus, Lycospora, the spore of several arborescent lycophytes. In each sample, 400 palynomorphs were counted and taxa relative abundances were calculated. Following the count, each slide was scanned for additional rare forms. Relative abundance is plotted by stratigraphic position to yield standard pollen diagrams (figs. 3 and 4).

When interpreting a palynological analysis, one must keep in mind several caveats. First, differing quantities of pollen and spores are produced by different taxa. Wind pollinated plants, for example, produce prodigious amounts of pollen and spores while partially or wholly entomophilous plants will be relatively underrepresented in the dispersed pollen and spore record. This caveat is traditionally reconciled by admitting that palynomorph relative abundance cannot be translated directly into quantitative stand measures such as standing biomass or DBH. In the modem pollen record, differential spore production can be a significant confounding factor. However, entomophily was probably less important in the Carboniferous than among modem angiosperms. Consequently, one might expect pollen and spore relative abundance to be a better proxy for individual plant relative abundance in these ancient forests. It is also possible to develop conversion factors that will allow pollen and spore abundance to better approximate other measures of stand composition. This approach has been successfully applied to Pleistocene and Recent stands (Davis and Goodlett 1960).

Figure ‘L.--Physical evidence for fire in Joggins Section rocks. (a-b) Compressions of fusinized (burned) wood in fine-grained sandstone associated with a channel deposit, Spicer’s Cove. Note perpendicular fracture pattern characteristic of burned wood. (c) Charcoal fragments and impressions of unburned plant axes in channel sandstone. Arrows indicate charcoal fragments. (d-e) Tree cast with burned periderm. (d) Extensively eroded outline of tree stump showing outline of tree base extending to dark, charcoal-rich horizon (at hammer shank). Palynological samples taken one meter to the left of hammer position. (c) Close-up of burned trunk. Pen and arrow indicate fusinized material.

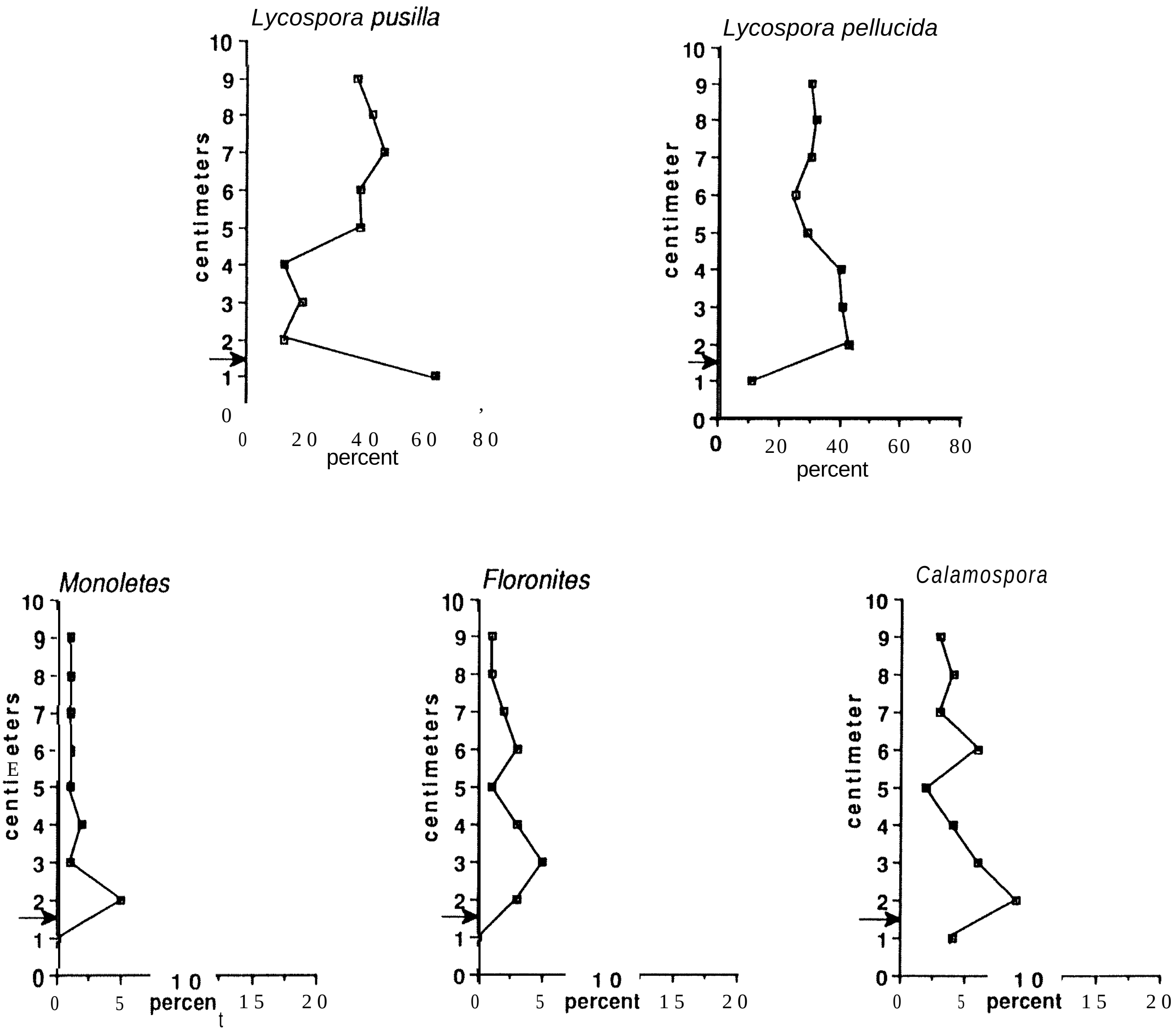

Figure 3.--Relative abundances of several palynomorph taxa. Arrows indicate stratigraphic position of fusain horizon.

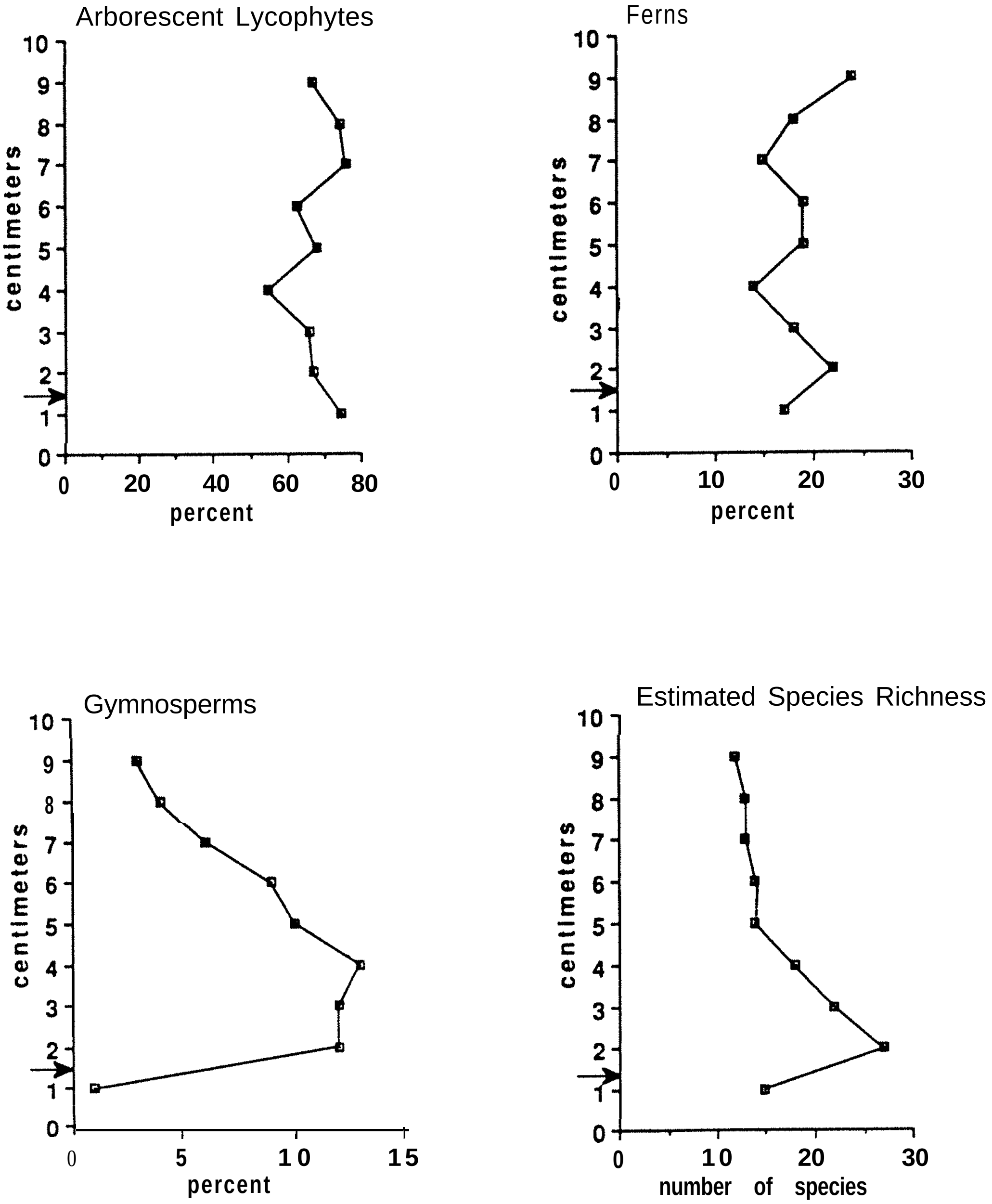

Figure 4.--Relative abundances of major plant groups and estimated species richness. Arrows indicate stratigraphic position of fusain horizon.

However, such conversions are only now being developed for the Carboniferous (Willard 1986). Future interpretation of these communities will incorporate this more quantitative approach to stand composition; however, that is beyond the scope of this preliminary study. Second, changes in pollen and spore abundances do not necessarily mean a change in stand composition. Some modern plants are stimulated to reproduce by disturbance, thus enriching their representation in the dispersed pollen and spore record. At this stage of the study, this influence cannot be discounted, but at the scale of stratigraphic resolution applied in this paper, pollen and spores are regarded as good indicators of standing vegetation (Davis and Goodlett 1960). Clearly, one must tailor questions asked of the pollen record to the time-stratigraphic, taxonomic, and quantitative resolution appropriate to the data.

RESULTS

The spore species *Lycospora pusilla*, produced by some arborescent lycophytes, was most abundant (63 percent) in the prefire vegetation (fig. 3). The other arborescent lycophyte spore present (*Lycospora pellucida*) represented only 10 percent of the palynoflora. *Lycospora* is produced by a number of species in the stem genus *Lepidophloios*. Other palynomorphs including *Calamospora*, the spore of the sphenopsid *Calamites*, and a complex of ferns made up approximately 10 and 15 percent of the palynoflora respectively. The pollen of gymnosperm taxa including *Monoletes*, the pollen of medullosan pteridosperms, and *Florinites*, pollen of the conifer relative Cordaites, were not present in the prefire palynoflora. A simple count of palynomorph taxa suggests that about 15 species were present. This estimate of species richness (fig. 4) is tentative and pending more complete taxonomic study of the palynoflora. Note also that, in some cases, a single spore and pollen taxon was produced by more than one megafossil taxon, thus underrepresenting species richness.

The sample collected stratigraphically immediately above the fire horizon shows several important changes in the palynoflora. Abundance of *Lycospora pusilla* declined dramatically from 63 to 13 percent. Conversely, *L. pellucida* increases from 11 to 43 percent. The increased relative abundance of *L. pellucida* is not entirely a relic of decline in abundance of *L. pusilla; L. pellucida* becomes absolutely more common in an average microscope field on slides of comparable palynomorph density. Fern spores and *Calamospora* become more common above the charcoal horizon. Medullosan and cordaitean gymnosperms also appear to enter the community following fire. The medullosan seed fern pollen, *Monoletes*, reaches its greatest abundance (6 percent) immediately above the fire horizon. Estimated species richness also reaches maximum (approximately 27 species) in the sample immediately above the fire horizon. This maximum includes several added rare or uncommon fern and herbaceous lycophyte taxa.

In stratigraphically successive samples above the fire horizon, several trends emerge. First, *L. pusilla* increases in relative abundance while *L. pellucida* declines until these taxa returned to approximately prefire levels. However, *L. pusilla* did not reclaim its prefire abundance within the sample interval. Likewise, *L. pellucida* declined in abundance throughout the sampling interval, but retained a higher postfire abundance (25 to 30 percent) throughout the sampling interval. In contrast with this gradual dominance exchange, *Monoletes* declined rapidly to a background abundance of 2 or 3 percent immediately after its abundance peak. *Florinites*, the pollen of cordaitean gymnosperms, increased in abundance more gradually to a maximum abundance in the second centimeter above the fossil charcoal horizon. Following this maximum, *Florinites* declined gradually to a background level similar to that of medullosan pollen. Species richness followed a similar trend of steady decline to the prefire level in the fourth centimeter above the fire horizon. This decline is driven mainly by the loss of the rare and uncommon fern and herbaceous lycophyte taxa that appear immediately above the fire horizon.

DISCUSSION

Rapid and relatively continuous (perhaps seasonal) sedimentation is a prerequisite for ecological-scale resolution of the fossil record. The Joggins Section appears to provide such conditions; however, absolute sedimentation rates are difficult or impossible to ascertain. Consequently, one must look to the vegetation for confirmation of time scale. If the Joggins strata can be interpreted at the ecological scale of resolution, one should be able to detect vegetation change stratigraphically above sedimentologically-inferred disturbances such as fires. Similarly, ecological resolution should show gradual reestablishment of plant abundances similar to those seen before the disturbance. Clearly, these predictions are realized in this case. Figure 4 shows that arborescent lycophytes suffer a 20-percent decline in abundance following fire. Note that arborescent lycophytes with small, wind-dispersed microspores are likely to be over-represented in the postfire palynoflora due to spores transported from nearby, unburned stands into the gap. The lycophyte decrease in postfire samples is largely counterbalanced by an increase in gymnosperms--initially by medullosan pteridosperms and subsequently by cordaiteans. Medullosans were characterized by large fronds displayed on an unbranched axis and minimal investment in low-density wood. Both of these features (minimal branching and low-density wood) are characteristic of modern colonizer trees in the tropics (Ashton 1978, Bazzaz and Pickett 1980, White 1983). Cordaiteans have a more substantial structural investment in greater volumes of dense wood. These structural observations support the conclusion that medullosans, with their “inexpensive” construction, filled the colonizer role in these ancient communities, with the more structurally “expensive” cordaiteans following in a mid-successional phase. Thus, the observed vegetation response, particularly the increase in gymnosperms, after fire establishes that ecological-scale changes are being observed; return to prefire abundances in stratigraphically subsequent samples reinforces the conclusion. These biological observations coupled with the inferred rapid sedimentation rate support an ecological-scale interpretation of the Joggins section. Thus, while I cannot conclude whether the sampled interval records decades or centuries in absolute time, the observed vegetation changes probably occurred within several generations of the plants involved--clearly an ecological-scale time frame.

If one accepts Scott’s (1989) conclusion that fusain in coals and clastic sediments records wildfire, then it is clear from the abundance of fusain in the Joggins sediments that fire was not only present but common in the Joggins swamp ecosystem. The influence of periodic tire on vegetation then becomes interesting. In a study of early Middle Carboniferous peat-forming mires, Phillips and others (1985) reported a correlation between an increased abundance of cordaitean gymnosperms and higher fusain percentages. In the upper "Pottsville" (Westphalian A/B corrclatives) coals of northeastern Tennessee and eastern Kentucky, Cordaites makes up 33 and 36.7 percent biovoiume in coal balls with 9 and 7.4 percent fusain respectively. In the same region, two correlative coals with lower cordaitean abundances (1.7 and 14.3 percent) contain lower proportions of fusain (0.8 and 2.6 percent respectively). A similar pattern was observed in the Upper Foot Seam, Lancashire, England, the Bouxharmont Seam in Belgium, and the Katharine Seam in the Ruhr, West Germany. Phillips and others (1985) conclude that this correlation reflects the cordaites' preference for drier habitats, which would be more prone to fire or other diagenetic oxidation.

The association of cordaitean gymnosperms with fusain is also observed in the Joggins fire horizon. In this case, however, detailed stratigraphic sampling shows that the cordaites were not simply growing in drier, tire-prone areas; rather, they were present in the community only after fire and could not maintain a significant presence without further disturbance. This suggests that fire (or disturbance in general) was an important factor in controlling the distribution of this taxon in the floodplain community.

A clear fusain/abundance relationship for ptcridosperms is not present in the data of Phillips and others (1985) from localities in the Euramerican Carboniferous. Medullosan pollen, Monoletes, is commonly not reported in standard palynological analysis because the large grains (100 to 200 micrometers) are eliminated from preparations by standard sieve techniques. Also, if the distribution of medullosan pteridosperms is patchy and ephemeral as hypothesized in this paper, its pollen might be easily missed in a grab-sampling regime. Consequently, absence of Monoletes from these reports (Phillips and others 1985) is not convincing evidence that pteridosperms were absent at those localities. At Joggins, however, the pollen of medullosan pteridosperms, like that of Cordaites, enters the community and has an abundance peak immediately above the fire horizon. Again, these data suggest that the distribution of Monoletes-producing pteridosperms was influenced by tire. Arens (manuscript in preparation) notes that some of the medullosan pteridosperms show morphologic and distributional characteristics consistent with their interpretation as colonizers of disturbed habitats, while others appear to have been understory plants. While colonizer and understory medullosans cannot be distinguished by their pollen, the restriction of medullosans to immediately above the charcoal horizon at Joggins supports the conclusion that some medullosans functioned as colonizing plants that required disturbance (in this case, fire) and were unable to maintain their presence (or at least to reproduce) on a site without subsequent disturbance. This conclusion can easily be reconciled with Phillips and others (1985); medullosan pteridosperms were an ecologically and taxonomically diverse group, and summary data that include taxa from both colonizer and understory medullosan guilds would obscure a correlation between medullosan ecotypes and fusain.

Pollen analysis across the fire horizon clearly shows that there is a vegetative response to disturbance. Two important trends emerge. First, the lycophytes--dominant taxa before the fire--suffer a major decline after fire, but gradually recover prefire dominance. Second, the lycophytes were replaced in the postfire community largely by gymnosperms, primarily pteridosperms and cordaiteans. However, these taxa apparently could not replace themselves on the site and eventually became locally extinct (Noble and Slatyer, 1980). Therefore, lycophytes and gymnosperms may also be filling different ecological guilds in the floodplain communities. The gymnosperms may represent key components of an early successional community that colonized habitat opened by tire; the lycophytes, then, constitute a later successional community that established in the shade of the colonizers and eventually succeeded to dominance in the area. Noble and Slatyer's (1980) model predicts that if fire occurs again during the gymnosperm stage of succession, mcdullosans and cordaiteans will continue to exist on the site. However, in the absence of tire (or some other disturbance), the gymnosperms will become locally extinct and lycophytes will reassert community dominance. This latter prediction was confirmed in this sequence. The ephemeral distribution of early successional gymnosperms, particularly pteridosperms, is supported by observations in many Pennsylvanian-age lowland environments (Phillips 1981).

Species richness trends associated with disturbed ecosystems are equivocal. In the tropical rain forests of Uganda (Eggeling 1947) and old fields of Nigeria (Jones 1956) species richness is low during the colonization stage, peaks in mid-succession, and declines in late succession. This is inconsistent with the diversity peak observed immediately after disturbance in the Joggins sequence. One possible interpretation is that the initial, low-diversity phase was too brief to be resolved or was not recorded in this sequence. However, in the Yellowstone National Park forest ecosystem (Dale Taylor, 1990, personal communication), the Australian grassland (Burrows, in preparation), and chaparral (Zedler 1977) species richness is greatest immediately following fire, as in the Joggins floodplain community. In these cases, species richness in enhanced by the presence of several codominant species and a variety of less common species, much as in the Joggins sequence. This pattern is promoted by microenvironmental variation generated by heterogeneity in the distribution of plant resources such as light, moisture, and nutrients in the disturbed site (Bazzaz and Sipe, 1987). Analyses of more Joggins fire horizons will undoubtedly clarify the pattern of species richness following disturbance on the ancient floodplain, and permit more definitive interpretation.

FUTURE WORK AT JOGGINS

The research described here represents the first stage of a larger study of the Joggins plant communities. Conclusions presented are, therefore, more accurately described as hypotheses to be tested. The Joggins record presents an opportunity to use fine-scale palynological analyses to interpret the effects of disturbance on ancient plant communities. With analysis of more stratigraphic sequences spanning charcoal horizons, one may ask: (1) Is there a generalizable trajectory of vegetation replacement following disturbance in the Middle Pennsylvanian moist floodplain forests? (2) Does a similar pattern occur in contemporaneous peat-forming ecosystems? (3) Does this observed pattern change with sedimentologically-inferred differences in soil moisture? (4) What trends in diversity are observed within and between successional guilds in clastic floodplains and in peat-forming mires? Such an approach, emphasizing dynamic patterns within communities over time scales of several plant generation, offers the opportunity to test ideas of community stability and coherence suggested for the Carboniferous (DiMichele and others 1985, Phillips and others 1985). It also offers a new and different system to test similar ideas derived from and argued about by ecologists studying modern plant communities.

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LITERATURE CITED

Ashton, P.S. 1978. Crown characteristics of tropical trees. In: P.B. Tomlinson and M.H. Zimmerman (eds.) Tropical Trees as Living Systems. Cambridge University Press, London, pp. 591-615.

Bazzaz, F.A. and S.T.A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. Annual Review of Ecological Systematics 11:287-310.

Bazzaz, F.A. and T.W. Sipe. 1987. Physiological ecology, disturbance, and ecosystems recovery. In: E.-D. Schulze and H. Zwölfer (eds.) Potentials and Limitations of Ecosystem Analysis. Ecological Studies 61, Springer-Verlag, Berlin, pp. 203-227.

Burrows, N.D. (in preparation) Aboriginal fire patterns in the western deserts of Australia.

Calder, J.H., M.R. Gibling and P.K. Mukhopadhyay (in press) Peat formation in a Westphalian B piedmont setting, Cumberland Basin Nova Scotia: implications for the interpretation of rheotrophic and raised paleomires.

Cecil, C.B., F.T. Dulong, J.C. Cobb, Supardi and P. Twinbull. 1988. Allogenic processes in the central Sumatra Basin--a modern analog for the origin of Lower Pennsylvanian coal-bearing strata in the eastern United States. In: M.H. Carter (ed.) U.S. Geological Survey Research on Energy Resources 1988 Abstracts with Programs. U.S. Geological Survey Circular 1025:8.

Clark, J.S. 1988. Stratigraphic charcoal analysis on petrographic thin sections: application to fire history in northwestern Minnesota. Quaternary Research 30:81-91.

Clark, J.S. 1990. Fire and climate change during the last 7.50 years in northwestern Minnesota. Ecological Monographs 60:135-159.

Coleman, J.M. 1969. Brahmaputra River: Channel processes and sedimentation. Sedimentary Geology 3:129-239.

Cope, M.J. and W.G. Chaloner. 1985. Wildfire: an interaction of biological and physiological processes. In: B.H. Tiffney (ed.) Geological Factors and the Evolution of Plants. Yale University Press, New Haven, pp. 257-277.

Davis, M.B. and J.C. Goodlett. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. Ecology 41:346-357.

DiMichele, W.A., T.L. Phillips and R.A. Peppers. 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. In: B.H. Tiffney (ed.) Geological Factors and the Evolution of Plants. Yale University Press, New Haven, pp. 223-256.

Eggeling, W.J. 1947. Observations on the ecology of the Budongo rain forest, Uganda. Journal of Ecology 34:20-87.

Galtier, J., T.L. Phillips and F. Chalot-Prat. 1986. Euramerican coal-swamp plants in mid-Carboniferous Morocco. Review of Palaeobotany and Palynology 49:93-98.

Harland, W.B., R.L. Armstrong, A.V. Cox, L.E. Graig, A.L. Smith and D.G. Smith. 1989. A Geologic Time Scale 1989. Cambridge University Press, Cambridge.

Izlar, R.L. 1984. Some comments on fire and climate in the Okefenokee Swamp-Marsh Complex. In: A.D. Cohen, D.J. Casagrande. M.J. Andrejko, and G.R. Best (eds.) The Okefenokee Swamp: It's Natural History, Geology, and Geochemistry. Wetland Surveys, Los Alamos, New Mexico.

Jones, E.W. 1956. Ecological studies on the rain forests of southern Nigeria, the plateau forest of the Okomu Forest Reserve. Journal of Ecology 44:83-117.

Noble, I.R. and R.O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Phillips, T.L. 1981. Stratigraphic occurrences and vegetational patterns of Pennsylvanian pteridosperms in Euramerican coal swamps. Review of Palaeobotany and Palynology 32:5-26.

Phillips, T.L. and R.A. Peppers. 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. International Journal of Coal Geology 3:205-255.

Phillips, T.L., R.A. Peppers and W.A. DiMichele. 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. International Journal of Coal Geology 5:43-109.

Rowley, D.B., A. Raymond, J. Totman Parrish, A.L. Lottes, C.R. Scotese and A.M. Ziegler. 1985. Carboniferous paleogeographic, phytogeographic and paleoclimatic reconstructions. International Journal of Coal Geology 5:7-42.

Rust, B.R., M.R. Gibling and A.S. Legun. 1984. Coal deposition in an anastomosing-fluvial system: the Pennsylvanian Cumberland Group south of Joggins, Nova Scotia, Canada. Special publication of the International Association of Sedimentologists 7:105-120.

Scott, A.C. 1989. Observations on the nature and origin of fusain. In: P.C. Lyons and B. Alpern (eds.) Peat and Coal: Origin, Facies and Depositional Models. International Journal of Coal Geology 12:443-473.

Stutzer, O. and A.C. Noé. 1940. Geology of Coal. Chicago Press, Chicago.

Ting, F.T.C. 1982. Coal macerals. In: R.A. Meyers (ed.) Coal Structure. Academic Press, New York, pp. 7-49.

Traverse, A. 1988. Paleopalynology. Unwin Hyman, Boston.

White, P.S. 1983. Horner's rules in eastern deciduous trees: allometry and its implication for the adaptive architecture of trees. Bulletin of the Torrey Botanical Club 110:203-212.

Willard, D.A. 1986. Comparison of megaspores, miospores, and coal balls in analysis of coal-swamp vegetation. American Journal of Botany 73:715.

Zedler, P.H. 1977. Life history attributes of plants and the fire cycle: a case study in chaparral dominated by Cupressus forbesii. Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems, USDA Forest Service General Technical Report WO-3:451-458.

Ziegler, A.M., R.K. Bambach, J.T. Parrish, S.F. Barrett, E.H. Gierlowski, W.C. Parker, A. Raymond and J.J. Sepkiski, Jr. 1981. Paleozoic biogeography and climatology. In: K.J. Niklas (ed.) Paleobotany, Paleoecology and Evolution. Praeger, New York, 2:231-266.

FIRE HISTORY AND FIRE ECOLOGY IN THE COSTA RICAN PARAMOS

Sally P. Horn[1]

Abstract-The high peaks of the Cordillera de Talamanca in southern Costa Rica extend above timberline and support bamboo- and shrub-dominated páramo vegetation. The charcoal stratigraphy of sediment cores from glacial lakes reveals that tires set by people or lightning have occurred in the highlands foe thousands of years. Historical sources and field evidence document numerous páramo tires since the mid-century. During the past 40 years, tire recurrence intervals at specific sites have ranged from 6 to about 30 years.

Patterns of postfire vegetation development support the initial floristics model of succession. The dominant bamboo (Chusquea [=Swallenochloa] subtessellata) resprouts vigorously following burning, as do associated ericaceous shrubs. Hypericum spp. suffer high mortality and recolonize by seed. Slow rates of growth and colonization by both woody and herbaceous species result in the persistence of bare patches of ground for a decade or more following burning.

INTRODUCTION

In a recent review of tropical alpine plant ecology, Smith and Young (1987) noted that fire is common on most tropical mountaintops. But the authors found few references on fire frequencies or fire history in tropical highlands, or on the impact of burning on vegetation, soil nutrients, and hydrology.

Since 1984 I have been working to fill this gap for the high mountains of southern Costa Rica. This paper summarizes the results of my research -- and that of U.S. and Costa Rican colleagues -- on fire history and tire ecology in the bamboo- and shrub-dominated piramos found above timberline in the Cordillera de Talamanca.

ENVIRONMENT AND VEGETATION

The uplifted granitic batholith that forms the backbone of the Cordillera de Talamanca is mantled by Tertiary volcanic and sedimentary rocks, which outcrop along with granodiorites and other intrusive rocks on the high peaks (Weyl 1957). About a dozen areas along the crest of the range reach above timberline, and support small to extensive stands of neotropical piramo vegetation (fig. 1). Many of these areas arc quite remote and remain poorly known botanically.

Ecological research has focused on the páramos surrounding Cerro Chirripo (3819 m), the highest peak in Costa Rica, and Cerro Buenavista (3491 m). Glaciers occupied the upper valleys of the Chirrip6 massif several times during the Pleistocene, leaving behind a picturesque ice-carved landscape dotted by some thirty glacial lakes. The extensive (> 5000 ha) Chirripo páramo is protected within Chirripd National Park, which was established in 1975. Access to this remote area is provided by rough trails that lead out of settlements on the lower foothills of the Cordillera de Talamanca.

The smaller (c. 1000 ha), unglaciated Buenavista plramo straddles the crest of the Cordillera de Talamanca along the Inter-American Highway route. There are no settlements within the piramo, but Cerro Buenavista is festooned with broadcasting towers, and jeep trails and electrical transmission line corridors crisscross the plramo. This area was the main route across the Cordillera de Talamanca even before the construction of the Inter-American highway in the 1940s, and the vegetation has long been affected by tree cutting, human-set fires, and grazing (Horn, 1989a). Janzen (1973a, 1983) believes that low forest, rather than plramo, covered the Buenavista peaks prior to extensive human disturbance.

In both physiognomy and floristics, the Talamancan piramos resemble the more extensive piramos of the northern Andes (Weber 1959), and most authorities consider them to mark the northern limit of piramo vegetation in the neotropics (Cuatrecasas 1979; Lauer 1981). The dwarf bamboo Chusquea (=Swallenochloa) subtessellata (Janzen 1983; Clark 1989; Horn 1989b) is a characteristic element within the páramos, forming monospecific stands in many areas (fig. 2). Woody dicots that grow intermixed with the bamboo include species in the Ericaceae, Hypericaceae, and Compositae families. A variety of herbaceous plants, many of Andean affinity, occur beneath the shrub canopy and in more open areas.

The oak Quercus costaricensis dominates the montane forests that are found just below timberline in the Buenavista and Chirripó highlands. The upper limit of oak forest ranges in elevation from about 3150 m to 3300 m. In some areas, oak forest 20-30 m high gives way to l-3 m high bamboo- and shrub-dominated páramo along an abrupt boundary; elsewhere

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[1] Assistant Professor, Department of Geography, and Faculty member, Graduate Program in Ecology, University of Tennessee, Knoxville, TN.

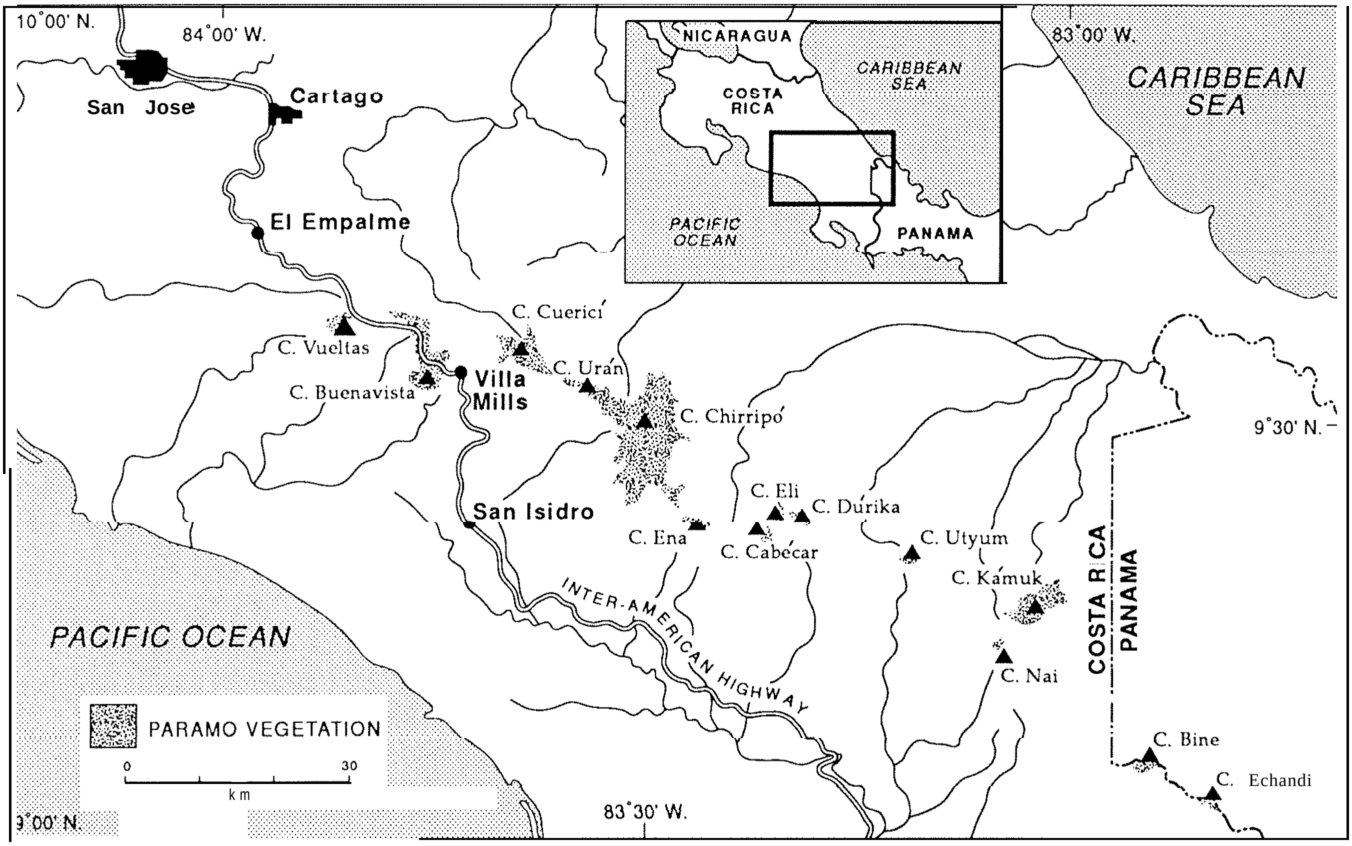

Figure 1. The piramos of the Cordillera de Talamanca, Costa Rica. The extent of páramo vegetation is based on Gómez (1986) and the 1:50,000 scale topographic maps published by the Instituto Geográfico Nacional.

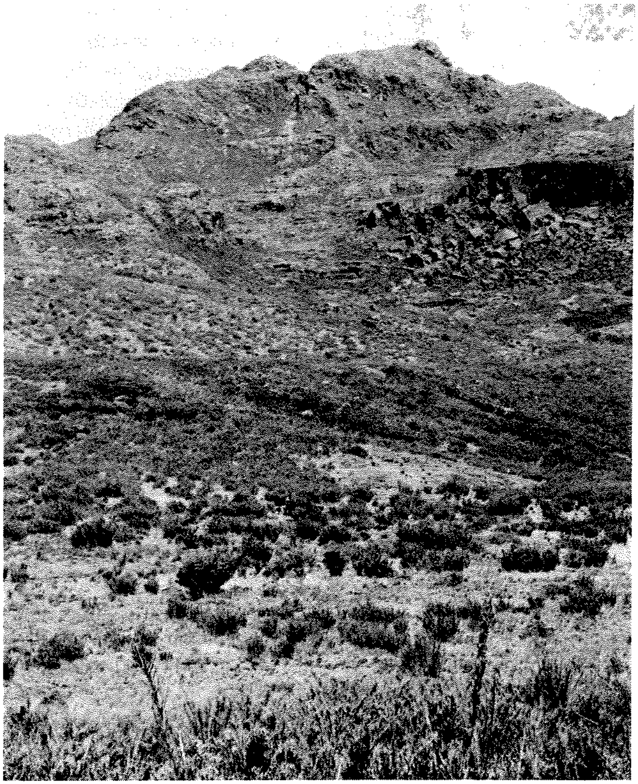

Figure 2. Nearly monospecific stand of the bamboo Chusquea subtessellata in the Valle de los Conejos in the Chirripó páramo.

the two communities are separated by broad transitional zones supporting large shrubs and small trees other than oak. Some of the trees and shrubs within these transitional zones also occur, in more stunted form, within the páramos of the high peaks.

Low annual temperatures and a highly seasonal precipitation regime characterize the climate of the Costa Rican páramos. Meteorological data from the Cerro Páramo station (3475 m) near Cerro Buenavista show a mean annual temperature during the period 1971-79 of 7.6” C (Instituto Costarricense de Electricidad, unpub. data). The warmest months, April and May, averaged only 1.4” C warmer than the coldest month, January.

Average annual precipitation during the period 1971-1984 at Cerro Páramo was just over 2500 mm. Typically only about 10% of the total precipitation falls during the dry season or “verano” that lasts from mid-December to late April. Frost is frequent in the piramos, and hail has been observed (Dohrenwend 1972), but there are no reliable reports of snowfall (Coen 1983).

Clouds and mist frequently bathe the páramos, and must contribute an appreciable (though as yet unmeasured) amount of moisture. High atmospheric humidity moderates the dry season, but for days or weeks during this period the condensation belt lies below timberline, resulting in clear, dry weather on the high peaks. Some perennial herbs die back at this time, and vegetation and litter quickly dry out, providing the fuel for fires.

Although burning is most widespread during the driest first 4 months of the year, a secondary rainfall minimum (the "veranillo") during mid-year may allow some burning. After a succession of several rainless days in July, 1981, experimental fires started in the Buenavista páramo ignited readily and burned quickly to their fuel breaks (G.B. Williamson, pers. comm. 1982).

RECENT FIRE HISTORY

All of the Costa Rican páramos are protected within national parks or reserves, but there are no written fire records for these management areas. Documentary evidence of burning consists of occasional references in the scientific and popular literature, and old photographs that reveal evidence of burning. Fires are often too small to be readily apparent on satellite imagery, and aerial photograph coverage of the páramos is limited.

However, the slow rate of organic matter decomposition in the continuously cool páramo environment (Janzen 1973b) results in the long persistence of field evidence of past fires. Fire-killed shrub stems are conspicuous throughout the páramos, even at sites that burned more than two decades earlier. Some shrubs preserve evidence of multiple fires (fig. 3), and annual growth rings in living and fire-killed stems provide information on fire recurrence intervals (Horn 1986; Williamson and others 1986).

Field evidence indicates that all of the larger páramos east of Cerro Utyum (Dúrika, Chirripó, Urán, Cuerici, Buenavista, Vueltas; fig. 1) have burned since the mid-century (Weston 1981). Human carelessness, arson, helicopter and plane crashes, and escaped agricultural fires are among the ignition sources for recent burns (Horn 1986). Although human activity can explain all recent fires, lightning could also have played a role. Costa Rica has one of the highest incidences of thunderstorms in the world (World Meteorological Organization 1953, 1956), and lightning has been observed striking both the forested slopes and treeless summit of Cerro Chirripó (Horn 1989c). Such strikes might occasionally ignite fires on the high Talamancan peaks, as they do on Mountain Pine Ridge, Belize (Kellman 1975).

Many areas within the Chirripó and Buenavista páramos have burned two or three times since 1950 (Horn 1986, 1989b, 1989c, 1990a). Fire recurrence intervals at specific sites have ranged from 6 to about 30 years. Given the slow rate of vegetation recovery within the páramos (see below), 6 years is probably close to the minimum fire recurrence interval possible. At least this many years of postfire growth is likely required to generate enough fuel to carry a second fire.

Figure 3. Resprouting shrub of *Vaccinium consanguineum* on Cerro Zacatales in the Buenavista páramo showing stems killed in two successive fires. The larger, central stem was killed in the penultimate fire at the site, after which the shrub resprouted, producing the smaller dead stems that were killed by the last fire at the site. Following the last fire the shrub again resprouted. Older (twice-burned) stems can be differentiated based on position, degree of charring, presence or absence of bark, and extent of decay, and annual growth rings in dead and living stems can be counted to estimate fire recurrence intervals. The visible length of the tape measure is 60 cm.

Recent fires in the Chirripó páramo have been much larger than fires in the Buenavista páramo. Páramo fires along the highway route have tended to burn out relatively quickly because they encountered insufficient fuel, fuel that was too moist, or a fire break created by a road or electrical transmission line corridor. The larger Chirripó páramo has provided an extensive and continuous fuel bed not interrupted by roads or other fire breaks, and fires, once started, have tended to spread over hundreds or thousands of hectares.

The post-1950 fire record in the Buenavista and Chirripo highlands suggests a link between fire and drought. Figure 4 graphs monthly precipitation in the driest month and the two consecutive driest months during the period 1952-1985 at Cerro Páramo (1971 onwards) and at the nearby Villa Mills station (3000 m) located just below timberline. I assume that these data reflect trends that would also have been evident at Cerro Chirripó, located 30 km to the east. The triangles denote known fire years in the Buenavista and Chirripo highlands, and in the intervening Cuerici paramo (fig. 1), with the size of the triangles indicating the total area above 3000 m elevation estimated to have burned in that year.

Not surprisingly, the largest high-elevation fires have tended to occur during the driest years. Between 1952 and 1985 there were 3 years in which the driest month (February or March) recorded less than 0.5 mm rainfall, and in each of those years a large (> 100 ha) fire occurred in the Chirripó paramo and surrounding montane forests. If rainfall records for 1952-1985 are indicative of long-term trends, the data suggest that extremely dry years conducive to widespread burning may be expected to occur about once a decade in the Chirripo and Buenavista páramos.

LONG-TERM FIRE HISTORY

Charcoal fragments in sediment cores from glacial lakes in the Chirripo highlands provide evidence of ancient fires in the Costa Rican páramos. A short (110 cm) sediment core recovered from Lago Chirripó (3520 m) in the Valle de los Lagos in 1985 preserved two distinct layers of macroscopic charcoal and an abundance of microscopic charcoal fragments (Horn 1989c). The charcoal particles appear to have been derived primarily from fires within the watershed of the lake and in adjacent areas of the Chirripo paramo. Charcoal concentrations varied with depth in the sediments, suggesting temporal variations in fire frequency (fig. 5). Although absolute fire frequencies cannot be determined from the charcoal data, variations in charcoal abundance may provide indications of relative fire frequencies. However, the relationship between fire history and sedimentary charcoal concentrations is complicated (Clark 1983), and factors unrelated to burning also may have affected the charcoal curve (Horn, 1989c).

Charcoal fragments were present in all of the samples from the Lago Chirripo sediment core, indicating that fires have affected the lake basin and surrounding areas since the sediments in the core began accumulating some 4000 years ago. A longer core raised from a glacial lake in an adjacent valley in 1989 (Horn 1990b, and in prep.) spans the last 10,000 years, and also contains charcoal, confirming and extending the short core record. In the Chirripo paramo fire is clearly not a disturbance factor introduced by modern human society; burning due to human action or lighting has occurred for thousands of years.

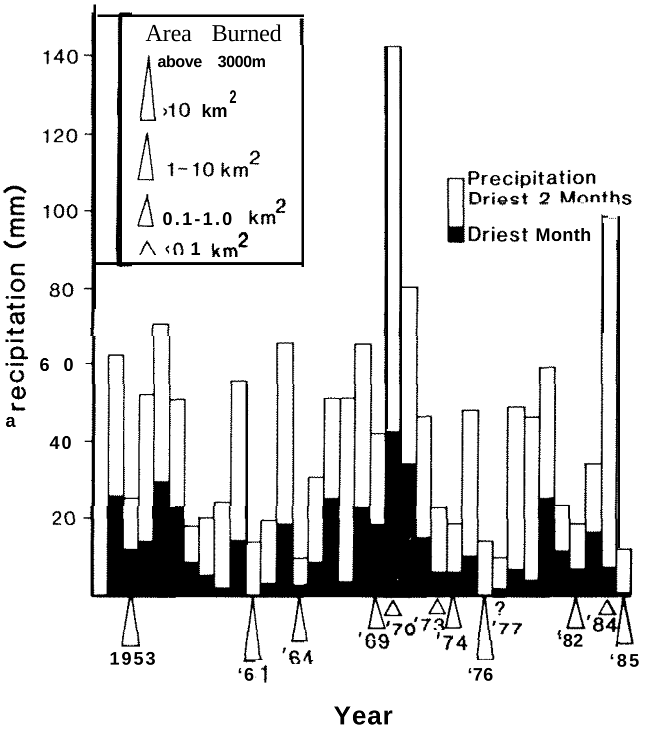

Figure 4. Dry season precipitation in the Buenavista highlands and the distribution of recent high elevation fires. Rainfall data are from the Cerro Páramo (1971 onwards) and Villa Mills stations (Instituto Costarricense de Electricidad unpub. data). The question mark in 1977 reflects uncertainty as to whether a forest fire that burned near Cerro Chirripó that year extended above 3000 m elevation.

THE IMPACT OF BURNING

Effects of Fire on Soils and Hydrology

Soils within the Costa Rican páramos are usually well-drained, rich in organic matter, and acidic, with pH values as low as 4.0 (Harris 1971). Soil samples collected by Leftwich (1973) within a recent burn area in the Buenavista páramo showed lower organic matter and C/N ratios, and higher exchangeable calcium and magnesium, than did samples from an adjacent unburned area. Field evidence of erosion has been noted on some burns, but soil loss following burning has not been quantified. No information is available on the hydrological impact of burning, though such studies would be of interest given the important watershed function of the páramos and surrounding montane forests.

Effects of Fire on Páramo Vegetation

Postfire vegetation dynamics in the Buenavista and Chirripo páramos have been examined by Janzen (1973b, 1983), Chaverri and others (1976, 1977, and in prep.), Williamson and others (1986) and Horn (1986, 1989b, 1990a). The slow rate of decomposition in the Costa Rican páramos has been an asset in these studies, as persistent fire killed stems can be identified and measured to provide information on the species composition and stature of the preburn woody vegetation.

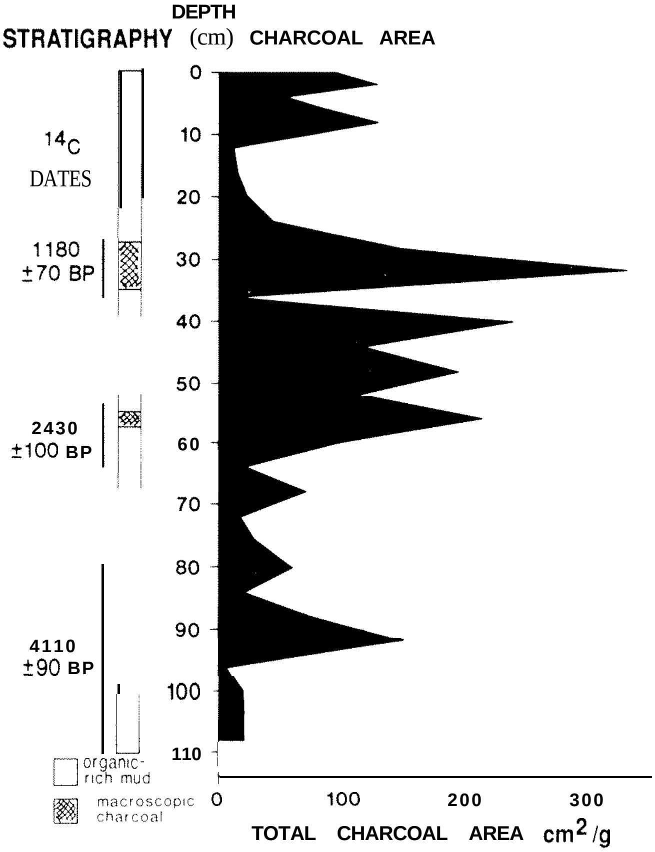

Figure 5. Diagram showing charcoal and sediment stratigraphy of a 110 cm core from Lago Chirripó.

Patterns of postfire vegetation recovery in the Costa Rican páramos support the initial floristics model of succession. The first species to colonize burned ground are the shrubs and herbs that comprise the mature vegetation. As appears to be the case in other tropical montane ecosystems (Smith and Young 1987), the Costa Rican páramos harbor no early successional specialists, and no invasion of plant species from outside communities takes place following disturbance.

Regeneration after and between tires is largely vegetative. Following fire, most woody plants and many herbs resprout vigorously, sometimes within just a few weeks of burning (Chaverri and others 1977). The bamboo Chusquea subtessellata and the ericaceous shrubs Vaccinium consanguineum and Pernettia coriacea show resprout rates of 90-100 percent following crown consumption and the death of aboveground stems (table 1). These vigorous sprouters rarely, if ever, establish seedlings, but may produce sprouts at new locations along widely diverging root and rhizome systems.

The common páramo shrub Hypericum irazuense supplements vegetative reproduction with seedling establishment. The species exhibited very low (4-14%) rates of basal resprouting at my study sites (table I), but Janzen (1973b) noted abundant suckering by H. irazuense (his H. caracasanum) following a fire on Cerro Asunción in the Buenavista páramo. Fire intensity and antecedent soil moisture conditions may be important controls of resprouting ability in this shrub.

For the narrow leaf congener Hypericum strictum all fires may be lethal; the species showed complete mortality at the Tower 65 site (table 1) and may be an obligate seeder.

Postfire seedling recruitment by Hypericum spp. and other shrubs and herbs relies largely on the influx of seeds from surrounding, unburned areas. The apparent lack of soil seed reserves (Horn 1989b) results in a very slow rate of seedling

Table 1. Percent basal resprouting by bamboo and shrubs following crown Loss at paramo burn sites[a].

	BURN SITE			
	Tower 65	Conejos	Zacatales	Sábila
Chusquea subtessellata	100	96		100
Vaccinium consanguineum	98	90	96	98
Pernettia coriacea	93		96	95
Escallonia poasana				57
Rapanea pittieri	25			15
Hypericum irazuense	4	6	12	14
Senecio firmipes	4			
Hypericum strictum	0			

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[a] Only data for species with sample sizes greater than twenty at individual burn sites are included. For sample sizes and details on study sites and methods, see Horn (1989b).

Table 2. Postfire height and percent height recovery of resprouting shrubs and bamboo at paramo burn sites[a].

	SITE AND YEARS SINCE LAST FIRE			
	Tower 65 1 yr	Conejos 9 yr	Zacatales 12 yr	Sábila ≥ 12 yr
Chusquea subtessellata	34 cm (18%)	103 cm (98%)	141 cm (113%)	191 cm (129%)
Vaccinium consanguineum	22 cm (26%)	76 cm (71%)	67 cm (87%)	103 cm (88%)
Pernettia coriacea	16 cm (24%)		46 cm (97%)	65 cm (79%)
Hypericum irazuense	20 cm (15%)	91 cm (64%)	65 cm (71%)	111 cm (70%)
Escallonia poasana	14 cm (17%)		96 cm (116%)	148 cm (171%)
Rapanea pittieri	19 cm (14%)		117 cm (78%)	172 cm (126%)

[a] Only the six most common woody species are listed. See Horn (1989b) for samples sizes and standard deviations, and details on sites and field methods. Percentage height recovery equals mean maximum postfire plant height divided by the mean maximum height of unbroken, prefire (burned) stems. The prefire stature of plants partly reflects the time intervals between the last and penultimate fires at the sites, which was ≥16 years at the Tower 65 site, 15 years at the Conejos site, ≥ 12 years at the Zacatales site, and ≥29 years at the Sábila site.

colonization and may delay significant seedling recruitment for several years following fire. Where potential seed sources are distant (as near the centers of large burns), recolonization by Hypericum irazuense and other fire-sensitive species may not occur until the rare individuals that resprouted following burning grow to maturity and begin seed production within the burn area.

Growth rates of seedlings and suckers are extremely slow (tables 2,3). The fastest growing woody species, the bamboo Chusquea subtessellata, requires about 8-10 years to regain its average prefire stature (Janzen 1983; table 3, this paper). Coupled with the slow pace of seedling colonization, the slow growth rates within the Costa Rican páramos result in the long persistence of gaps created by burning. Bare patches of ground from 0.1 m^2 to 0.5 m^2 or larger in size may persist for a decade or more following fires, particularly on large burns where seed influx is low.

The strong resprouting ability of most of the dominant woody species in the Costa Rican páramos minimizes compositional shifts following burning (Horn 1989b). If a site dominated by bamboo and ericaceous shrubs burns, postfire cover the first year, and for at least a decade afterwards, will be dominated by bamboo and ericaceous shrubs. Major shifts in woody species composition will be observed only at sites with a substantial cover of fire-sensitive shrubs. Herbaceous species may reach higher cover values on such burns, where greater shrub mortality results initially in less competition for space and other resources.

Based on observations at Cerro Zacatales in the Buenavista páramo, Williamson and others (1986) described a "fire cycle" in the Costa Rican páramos in which postburn cover is initially dominated by grasses and sedges, but reverts ultimately to shrub dominance if the site is kept free of fire for a sufficient period (perhaps 20 years). For reasons outlined above, such a cycle will be most evident where shrub mortality is very high, and where flowering plants are present nearby to reseed the burn site. When shrubs are closely spaced and suffer low mortality from fire, grasses and sedges may contribute little to postfire cover. Few graminoids or other herbs were present 3 years after a fire on Cerro Asunción (Janzen 1973b), a site characterized by high shrub survival and vigorous suckering. Greater herbaceous cover was observed 1 and 4 years after a fire at the nearby Tower 65 site, where 40% of the woody perennials (mostly Hypericum irazuense shrubs) died following crown loss. t even at this site, shrubs and bamboo dominated the initial postfire cover (Horn 1989b and unpub. data).

Graminoids, when abundant, will provide fine fuels that can support frequent fires. Williamson and others (1986) have suggested that when such fires occur at 5-10 year intervals

Table 3. Postfire stem diameters and percent diameter recovery for burned shrubs and bamboo at paramo burn sites[a].

	SITE AND YEARS SINCE LAST FIRE			
	Tower 65 1 yr	Conejos 9 yr	Zacatales 12 yr	Sábila ≥ 12 yr
Chusquea subtessellata	0.55 cm	0.73 cm	0.89 cm	1.20 cm
Vaccinium consanguineum	0.29 cm (13%)	1.98 cm (66%)	1.50 cm (70%)	2.13 cm (64%)
Pernettia coriacea	0.26 cm (26%)		0.68 cm (78%)	1.03 cm (63%)
Hypericum irazuense	0.16 cm (13%)	1.19 cm (58%)	0.86 cm (55%)	1.46 cm (60%)
Escallonia poasana			3.07 cm (125%)	3.52 cm (94%)
Rapanea pittieri	0.26 cm (15%)			2.92 cm (103%)

[a] Only the six most common woody species are listed. Sample sizes and standard deviations are listed in Horn (1986). Percentage diameter recovery equals mean maximum postfire stem diameter divided by the mean maximum prefire (burned) stem diameter. No data are available on prefire stem diameters of Chusquea subtessellata.

they may impede shrub recovery and facilitate the ultimate development of continuous grassland. Preliminary trials indicated that some shrubs may release allelopathic chemicals that inhibit the growth of grass and sedge seedlings and hence reduce the risk of fire (Williamson and others 1986).

CONCLUSION

Fire plays an important role in most of the world's shrublands (Christensen 1985), and the páramos of Costa Rica seem to be no exception. The low annual temperatures, high annual rainfall, and seasonal drought that characterize these tropical alpine habitats provide the fuel for periodic fires. Sedimentary charcoal evidence shows that fires have occurred in the Chirripó páramo for at least 10,000 years; fires due to human activity or lightning may be of similar antiquity in other páramo areas.

Postfire regeneration follows initial floristics and is principally vegetative for the major woody species, many of which resprout vigorously after fire. The ultimate origin of this resprouting ability is uncertain, but selection in the face of periodic fires may have reinforced the trait. Some shrubs rely on seedling recruitment to repopulate burned areas, but the lack of soil seed reserves gives the sprouters a strong advantage in the first few postfire years. Low rates of seed influx and slow growth following germination or sprouting result in exceedingly slow recovery rates; 10 years after burning, most shrubs will not have regained their prefire adult stature and bare patches of ground may still be conspicuous.

ACKNOWLEDGMENTS

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LITERATURE CITED

Chaverri, A.; Vaughan, C.; Poveda, L.J. 1976. Informe de la gira efectuada al macizo de Chirrip6 al raiz del fuego ocurrido en Marzo de 1976. Revista de Costa Rica 11:243-279.

Chaverri, A.; Vaughan, C.; Poveda, L.J. 1977. Datos iniciales sobre la fragilidad de un pdramo frente a los efectos de fuego (abstract). In: Wolda, H., ed. Resumenes recibido para el IV simposio internacional de ecología tropical, 1977 March 7-11, Panama, pp. 26-28.

Christensen, N.L. 1985. Shrubland fire regimes and their evolutionary consequencences. In: Pickett, S.T.A.; White, P.S., eds. The ecology of natural disturbance and patch dynamics, pp. 86-100. Orlando, FL: Academic Press.

Clark, R.L. 1983. Fire history from fossil charcoal in lake and swamp sediments. Ph.D. dissertation, University of Australia, Canberra. 189 p.

Clark, L.G. 1989. Systematics of Chusquca section Swallenochloa, section Verticillatae, section Serpentes, and section Longifolia (Poaceae: Bambusoideae). Systematic Botany Monographs 27:1-127.

Coen, E. 1983. Climate. In: Janzen, D.H., ed. Costa Rican natural history, pp. 35-46. Chicago: University of Chicago Press.

Cuatrecasas, J. 1979. Comparación fitogeográfica de páramos entre varias cordilleras. In: Salgado-Labouriau, M.L., ed., El medio ambiente pdramo, pp. 89-99. Mérida, Venezuela: Ediciones Centro de Estudios Avanzados.

Dohrenwend, R.E. 1972. The energetic role of the trade wind inversion in a tropical subalpine ecosystem. Ph.D. thesis, State University College of Forestry at Syracuse University. 298 p.

Gómez, L.D. 1986. Vegetación de Costa Rica. San Jose, Costa Rica: Editorial Universidad Estatal a Distancia. 327 p.

Harris, S.A. 1971. Podsol development on volcanic ash deposits in the Talamanca range, Costa Rica. In: Yaalon, D.H., ed. Paleopedology: origin, nature, and dating of paleosols, pp. 191-209. Jerusalem: international Society of Soil Science and Israel University Press.

Horn, S.P. 1986. Fire and páramo vegetation in the Cordillera de Talamanca, Costa Rica. Ph.D. dissertation, University of California, Berkeley. 146 p.

Horn, S.P. 1989a. The Inter-American highway and human disturbance of páramo vegetation in Costa Rica. Yearbook of the Conference of Latin Americanist Geographers 15: 13-22.

Horn, S.P. 1989b. Postfire vegetation dynamics in the Costa Rican páramos. Madroiio 36(2):93-114.

Horn, S.P. 1989c. Prehistoric fires in the Chirripó highlands of Costa Rica: sedimentary charcoal evidence. Revista de Biología Tropical 37(2):139-148.

Horn, S.P. 1990a. Vegetation recovery after the 1976 páramo fire in Chirripó National Park, Costa Rica. Revista de Biología Tropical (forthcoming).

Horn, S.P. 1990b. Timing of deglaciation in the Cordillera de Talamanca, Costa Rica. Climate Research 1:81-83.

Janzen, D.H. 1973a. Sweep samples of tropical foliage insects: descriptions of study sites, with data on species abundances and size distributions. Ecology 54(3):659-678.

Janzen, D.H. 1973b. Rate of regeneration after a tropical high elevation tire. Biotropica 5(2): 117-122.

Janzen, D.H. 1983. *Swallcnochloa subtessellata* (chusquea, batamba, matamba). In: Janzen, D.H., ed. Costa Rican natural history, pp. 330-331. Chicago: University of Chicago Press.

Kcllman, M. 1975. Evidence for Late Glacial age fire in a tropical montane savanna. Journal of Biogeography 2:57-63.

Laucr, W. 1981. Ecoclimatological conditions of the páramo belt in the tropical high mountains. Mountain Research and Development 1(3-4):209-221.

Leftwich, V. 1973. Soil characteristics at the various field sites in Costa Rica. In: Tropical biology: an ecological approach, Organization for Tropical Studies coursebook 73.2, pp. 598-602. Durham, NC: Organization for Tropical Studies.

Smith, A.P.; Young, T.P. 1987. Tropical alpine plant ecology. Annual Review of Ecology and Systematics 18:137-158.

Wcbcr, H. 1959. Los páramos de Costa Rica y su concatenación fitogeográfico con los andes suramericanos. San Jose, Costa Rica: Instituto Geográfico Nacional. 72 p.

Wcston, A.S. 1981. Páramos, cicnagas, and subpáramo forest in the eastern part of the Cordillera de Talamanca. Unpublished report prepared for the Tropical Science Center, San José, Costa Rica. 2.5 p.

Wcyl, R. 1957. Contribución a la geología de la Cordillera de Talamanca de Costa Rica (Centro America). San Jose, Costa Rica: Instituto Geográfico Nacional. 87 p.

Williamson, G.B.; Schatz, G.E.; Alavardo, A.; Redhead, C.S.; Stam, A.C.; Sterner, R.W. 1986. Effect of repeated fires on tropical páramo vegetation. Tropical Ecology 27:62-69.

World Meteorological Organization. 1953. World distribution of thunderstorm days. I. Tables. Geneva: World Meteorological Organization.

World Meteorological Organization. 1956. World distribution of thunderstorm days. II. Tables of marine data and world maps. Geneva: World Meteorological Organization.

A SURVEY OF ABORIGINAL FIRE PATTERNS IN THE WESTERN DESERT OF AUSTRALIA

N.D. Burrows and P.E.S. Christensen'

Abstract-Aborigines who occupied vast tracts of the Australian deserts used tire extensively for many purposes. The recent departure of Aborigines from traditional burning practices has coincided with an alarming decline in native mammal fauna. It has been postulated that the combined effects of a changed fire regime, predation by feral animals, and competition from feral herbivores has contributed to mammal decline in this otherwise pristine environment.

Black-and-white aerial photography, satellite imagery, and field observations have revealed that the size, distribution, frequency, and intensity of tires in a part of the Western Desert have changed dramatically over the last 36 years. In an area west of Lake Mackay the average tire size has increased from 34 hectares in 1953 to over 32 000 hectares in 1986. The small-grained mosaic of burnt patches of varying ages that existed during Aboriginal occupation of the land has been obliterated by large, intense and infrequent lightning-caused wildfires. Some evidence of a relationship between fire mosaic and the richness of flora and fauna was obtained during this survey.

INTRODUCTION

About one third of the Australian continent is classified as desert. In the State of Western Australia, the Great Victoria, Gibson, and Great Sandy Deserts occupy some 1.3 million square kilometres and collectively are commonly known as the Western Desert (Tonkinson 1978). Rainfall is low (annual average ranges from 150 to 250 millimetres), and unpredictable, and long periods of drought are common. Rainfall is mostly from cyclones and thunderstorms and surface water is only abundant for short periods following rain. Summers are hot and winters are cool. The Western Desert is well vegetated and surprisingly rich in wildlife. Highly flammable hummock grasslands, comprising species of *Triodia* and *Plectrachne* (spinifcx), dominate red sandy soils.

Aborigines first arrived on the Australian continent at least 50,000-60,000 years ago and occupied the deserts of the interior by at least 20,000 years ago (Mulvancy 197.5; Flood 1983). Aboriginal people showed remarkable resilience and resourcefulness to survive in a vast expanse of scattered food and water resources (Tonkinson 1978). They were highly mobile, were able to exploit a variety of resources in different areas at different times, and developed a detailed knowledge of the environment. Fossil evidence suggests climatic and cultural continuities lasting at least 10,000 years (Gould 1971), so there has been a long period of Aboriginal influence on the desert biota.

The Western Australian Department of Conservation and Land Management (CALM) manages about ten million hectares of desert conservation reserves which range in area from two hundred thousand hectares two million hectares. The management priority for these reserves is the conservation of native flora and fauna. However, in spite of the apparent pristine nature of these reserves and the lack of direct European impact, a sudden and alarming decline in native mammals has been reported (Bolton and Latz 1978; Burbidge 1985; Burbidge and others 1988; Burbidge and McKenzie 1989). Burbidge and Jenkins (1984) reported that about 33 percent of Western Australian desert mammmals are extinct or endangcrcd. They noted that this decline had occurred over the last 30 to 50 years. Burbidge and McKenzie (1989) have shown that all declines and extinctions have been restricted to native mammals with a mean adult body weight in the range from 35 grams to 5,500 grams (critical weight range). The desert conservation reserves arc relatively pristine and have not been directly modified or disturbed by European activities. Generally, recent extinctions of wildlife have been associated with habitat destruction or modification by humans (Burbidgc 1985).

Ngaanyatjarra Aborigines from the Warburton area of Western Australia believe that the "mitika", or burrowing bettong (*Bettongia lesueur*), had "gone to the sky because the country had not been cleaned up" (de Graaff 1976). "Clean up" is a term often used by Aborigines for burning the vegetation (Jones 1980). Kimbcr (1983) reported that Pintubi Aborigines believed that perhaps a "big bushfire" caused the disappearance of the golden bandicoot (*Isoodon auratus*). Scientists have proposed three main hypotheses to explain the decline and in some cases, extinction of desert mammals. Burbidgc and Johnson (1983) proposed that changes in fire regime, predation by feral animals, and competition from feral herbivores as the main factors, acting either independently or in combination, leading to mammal decline in the arid zone.

'Senior Research Scientist and Principal Senior Research Scientist, Department of Conservation and Land Management, 50 Hayman Rd, Como, Western Australia 6153.

Recent changes in the fire regime were a direct consequence of the exodus of Aboriginal people from the desert to settlements in missions, outstations and other communities (Gould 1971; de Graaf 1976; Latz and Griffin 1978; Kimber 1983; Saxon 1984). Latz and Griffin (1978) postulated that Aborigines created a stable ecosystem by "burning the country in a mosaic pattern". They claimed that mosaic burning reduced the extent and continuity of heavy fuels, and therefore reduced the occurrence of intense wildfires. They also stated that a second effect of mosaic burning was to create a range of "states" in the vegetation, from early postfire plant communities to old mature patches. They were of the opinion that such diversity of states would host a greater variety of plants and animals.

The extensive use of fire by desert Aborigines is well documented by early explorers (Warburton 1875; Carnegie 1898) and more recently by anthropologists and ecologists (Finlayson 1943; Jones 1969; Calaby 1971; Gould 1971; de Graaf 1976; Tonkinson 1978; Kimber 1983). Kimber (1983) observed that the Pintubi used fire in a skilful and controlled manner for many reasons, such as hunting, signalling, to "clean up" the country, for ceremonies, and for fun. He provides a general description of when fires were lit and the range in fire sizes. He also made some rough calculations of the proportion of country burnt and the approximate age since fire, based on information in the diaries of Davidson, who explored parts of the Tanami Desert in 1900. However, little quantitative information about the fire regime during traditional Aboriginal occupation of vast tracts of desert land is available.

Quantitative data on past and present fire regimes are of considerable interest to the Western Australian Department of Conservation and Land Management, which is engaged in a multidisciplinary study aimed at maintaining and improving the conservation status of desert ecosystems. As part of this project, experimental reintroductions of selected species of rare and endangered mammals to the Gibson Desert Nature Reserve will be attempted. Prior to reintroduction, prescribed fires will be used to recreate the kind of fire mosaic which is believed to have existed before the departure of Aborigines. Feral predators such as foxes and cats will also be controlled in the experiment.

The aim of this study is to define, as clearly as possible, the fire regime during the occupation of the Western Desert by Aborigines prior to European contact and to compare this with the present-day fire regime. In doing so, we could test the hypothesis of a recent and dramatically changed fire regime as proposed by Latz and Griffin (1978) and others. A knowledge of past fire regime would also greatly assist with the development of appropriate fire management strategies for desert conservation reserves.

We use Gill's (1981) definition of fire regime, which is the history of fire frequency, fire season (season in which fires burnt), fire intensity, and fire size.

METHODS

The departure of Aborigines from their desert homelands started with first European contact at the end of the nineteenth century. Amadio and Kimber (1988) present a summary of European exploration and contact with Aborigines of the northern portion of the Western Desert and also describe the movements of Aboriginal people away from their homelands and into European settlements. To reconstruct the fire regime, it was desirable to study fire on land from which Aboriginal people living a more-or-less traditional lifestyle, had most recently departed. We learnt that a very remote tract of land to the west of Lake Mackay in Western Australia was probably the last homeland utilized in a traditional manner by Pintubi people (Richard Kimber pers.comm.). The study site of some 54,000 hectares is on the eastern edge of the Great Sandy and Gibson Deserts and lies between longitudes 128°35'E and 128°50'E and latitudes 22°8'S and 22°18'S (Figure 1). The area is arid, with an average annual rainfall probably less than 225 mm (there are no meteorological stations nearby). Most of the rain falls in summer but both the amount and the seasonal distribution are highly variable. As a result of the arid climate and sandy soils, the vegetation consists mainly of hummock grasses (spinifex) and associated small shrubs, herbaceous plants and scattered low trees. The sand plain that covers most of the study area is crossed by

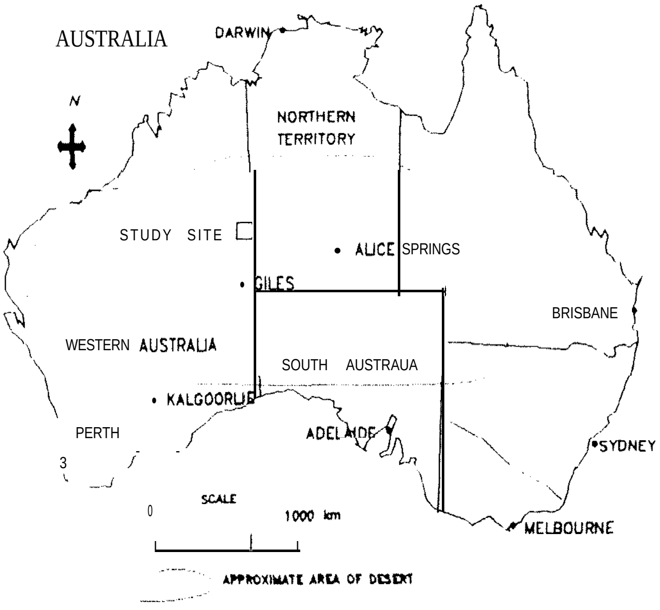

Figure I: Location of the study area in the Western Desert The approximate boundary of land classified as desert is shown.

longitudinal, stable dunes which trend east-west. There are numerous saltpans, salt lakes, and claypans scattered throughout the area. The largest salt lake is Lake Mackay, which has a total area of about 3,500 square kilometres (Blake 1977). The salt lakes, saltpans, and claypans are dry except after heavy rain.

The main exodus of Pintubi Aborigines from this area commenced in the early 1960s, with the last people coming into Kintore and Kiwirrikura communities in 1985 (Richard Kimber, pers. comm.).

We have used early black-and-white aerial photographs to help reconstruct the fire regime at the study site during Aboriginal occupation. This technique was supplemented by reviewing the literature and by talking with Pintubi and Pitjantjatjarra Aborigines to obtain information about their use of fire. The current fire regime, particularly size and distribution of burnt patches, was inferred from Landsat satellite imagery and by visiting the study site and surveying fire history. While in the field we also surveyed vascular plant and vertebrate animal abundance within areas of different age since the last fire.

Aerial Photographs and Landsat Imagery.

Details of aerial photography available for this area are presented in table 1. The earliest aerial photographic surveys were completed in 1953 by the Royal Australian Air Force as part of the Blue Streak rocket project during an era of extensive rocket development and testing in Australia. Fire scars showed clearly on both aerial photographs and Landsat imagery. Fire scars that appeared on the 19.53 photography were mapped onto a base map at a scale of 1:50,000.

Additional tire scars which appeared on successive photographs were mapped onto separate sheets, but at the same scale, to form a series of overlays. Landscape features such as salt lakes, claypans, saltpans, sand dunes, and major creeks and streams were also mapped. The area and perimeter of each tire scar for each time series was calculated using a computer-linked digitizing board. Initially, an attempt was made to accurately age tire scars based on tonal intensities of the scars indicated on the photographs. The different toning of the fire scars represented different stages of revegetation, or tire succession, with recently burnt areas showing up as very bright patches. This proved to be difficult and tire scars could only be rated as "very recent" (up to 5 years old), or "recent" (S-10 years old), based on the extent of re-vegetation. While older scars were barely discernible, no attempt was made to map scars that did not have clearly visible boundaries.

Field Survey of Biological Indicators

The second technique used to obtain details about past and present tire regimes and the fire environment of the study area was ground survey of biological indicators. Some 50 kilometres of line transect was surveyed by vehicle traverse in 1989 and visually discernible fire boundaries recorded. A fire boundary was defined as the boundary between two recognizable fuel ages or between vegetation burnt at different times. Within each fuel age encountered, the time since the last tire was estimated by counting "annual" growth rings from tree stem cross- sections. Because of the uncertainty of the period between growth rings, accurate aging of tire scars was not possible. Based on ring counts from areas of known fire history, stem analysis enabled the time since fire to be estimated to within ±11 percent of actual time. Measures of vegetation cover and height were also useful for estimating the age of vegetation. In some instances, the aerial photographs were used to estimate time since last fire. Circular plots of 100 metres radius were established in each fuel age and the number and abundance of plant species recorded. A list of animals utilizing each fuel age was compiled by searching for burrows, diggings, scats, and tracks. The Pintubi and Pitjantjatjarra guides who accompanied us, skillfully identified signs of animal activity and provided us with the Aboriginal names for the animals.

RESULTS

Aerial Photographs

There has been a dramatic change in the mean and median size of burnt patches in the period from 1953 to 1986. From table 1, it can be seen that the area recently burnt (up to 10 years prior to photography) has increased from 23.6 percent of the study area in 1953, to almost 60 percent by 1986. Also, the mean size of tires has increased almost 1,000 fold

Table 1. Number, area, and perimeter statistics for burnt patches clearly visible on black-and-white aerial photography and on Landsat satellite imagery of a 53,483 ha study in the Western Desert, Western Australia.

Year	Number of burnt patches	Burnt patch size (ha)				Total burnt (ha)	Total perimeter (km)
		Maximum	Mean	Mode	Median		
1953	372	1,744	34	2	6	12,643	1,198
1973	27	13,534	845	5	197	22,800	412
1977	3	30,618	10,584	-	•	31,752	293
1988	1	32,184	•	•	•	32,184	272

over the same period. Habitat boundary, which is the total fire perimeter within the study site and is a measure of the boundary between vegetation of different ages since fire, has decreased from 1,198 kilometres in 1953 to 272 kilometres in 1986. This indicates a substantial reduction in the diversity of fire ages or states of postfire succession within the landscape.

A visual inspection of the fire scars mapped for each time of photography revealed a number of obvious patterns. In 1953, when groups of Pintubi Aborigines were living on the land, there were some 372 individual, recent fire scars visible on the aerial photographs (see fig. 2). Many of these concentrated around major salt lakes, claypans, and saltpans. While it is not possible to determine the ignition source of all fires, many scars showed the classic shape of having been lit by a person dragging a firestick in a straight line. Many of the fires burnt between the sparsely vegetated sand dune crests. By 1973, some 11 years after Aborigines began to leave the land, the small-grained mosaic of burnt patches that existed in 1953, had begun to be erased and to be replaced by large tracts of recently burnt country and large tracts long unburnt. The ignition source of these fires may have been lightning or the few Aboriginal people who remained in the area. This temporal trend of increasing fire size and increasing pyric homogeneity has continued until the present day, and there now exists vast tracts of country burnt at the same time by a single fire or multiple lightning strikes. There are also vast areas which have not been burnt for in excess of 30 years. This pattern is repeated across the Western and Central Deserts (Griffin and Allan 1985).

Figure 2. The patchwork of fire scars is clearly evident on early (1953) black-and-white aerial photographs. Most fires were lit by Pintubi Aborigines who occupied the desert at the time of photography.

The frequency distribution by size class of fire scars is shown in figure 3 for 1953 and 1973 photography. By 1977 and 1986, most of the study area had been burnt by only a few fires lit at about the same time

A useful measure of the size and distribution of burnt and unburnt patches is the ratio of variance to mean patch size (Peilou 1977). A random distribution produces a ratio of near 1. A uniform or over dispersed distribution results in a ratio greater than 1 while a clumped or contiguous distribution yields a value much less than 1. In 1953, the patchiness ratio of both burnt and unburnt areas was 0.62 to 0.72, or close to 1, indicating a random distribution of patches (figure 4). The mean length of continuous burnt vegetation had increased from 467 metres in 1953 to 2,570 meters in 1986 and the variance ratio had reduced to 0.43, indicating a clumped distribution of patch size and a significant increase in mosaic grain size (Peilou 1977). Line transects across photographs of a portion of the study area to reveal a spectrum of recently burnt (< 10 years) and long unburnt vegetation are also useful for quantifying burn mosaics. This "substitute pattern" of alternating black and white stripes is a representation of the varying grain size of the two phase mosaic (Peilou, 1978). These patterns are presented in figure 5 for the 1953 photography and 1986 satellite imagery.

Field Survey of Biological Indicators

An example of the results of a vehicle traverse along a line transect showing the ages of vegetation since the last fire and the total number of animal species recorded from observations of tracks, diggings, and scats is shown in figure 6. The traverse was conducted in 1989. While most of the vegetation, was about 6 years old at the time of the traverse, there were small patches of older vegetation which had escaped the most recent fire. Often, these patches were found on the leeward side of natural fire barriers such as sand dune

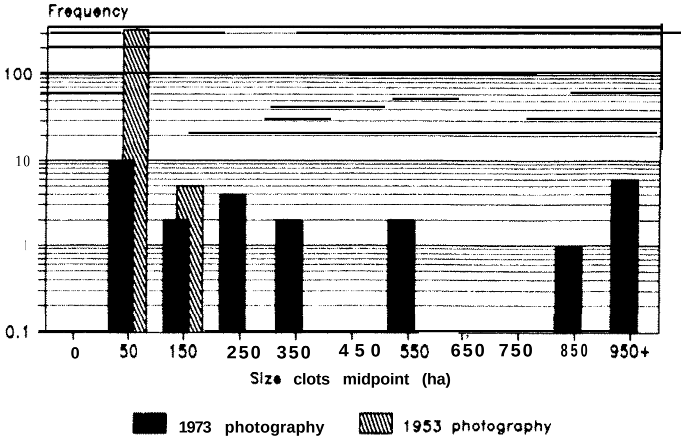

Figure 3. Frequency distribution of size classes of recent fire scars evident on 1953 and 1973 black-and-white aerial photographs of a part of the Western Desert.

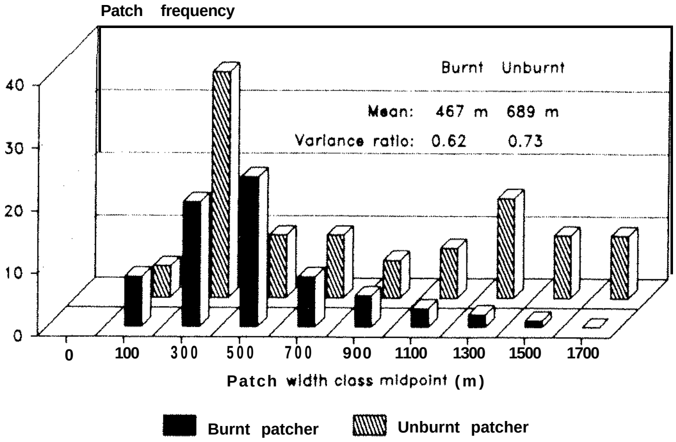

Figure 4. Percentage frequency distribution by size classes of the width of recently burnt (< 10 years) and long-unburnt patches of desert vegetation measured along transects across 1953 black-and-white aerial photographs.

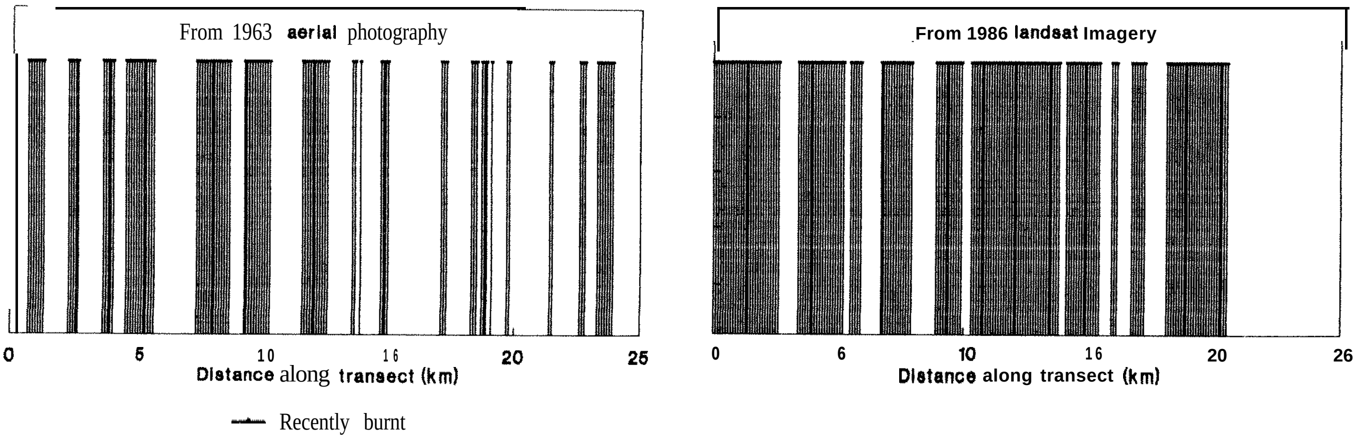

Figure 5. Substitute patterns for two two-phase mosaics (recently burnt and long-unburnt vegetation) of the Western Desert study area from 1953 aerial photography and 1986 satellite imagery.

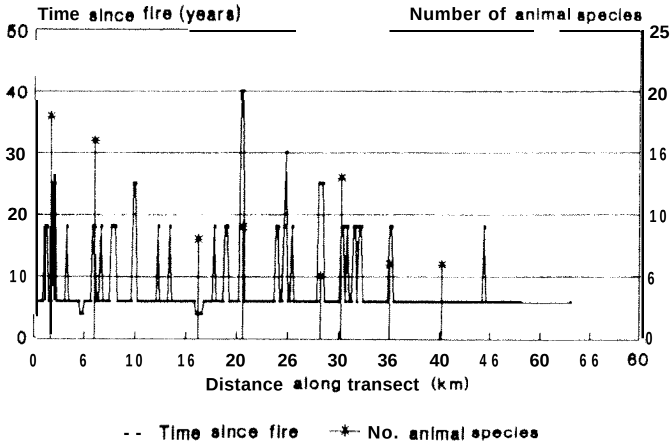

Figure 6. Age of vegetation (time since tire) along a transect across desert vegetation in 1989. Also shown are numbers of animal species estimated from diggings, scats, and tracks at points along the transect.

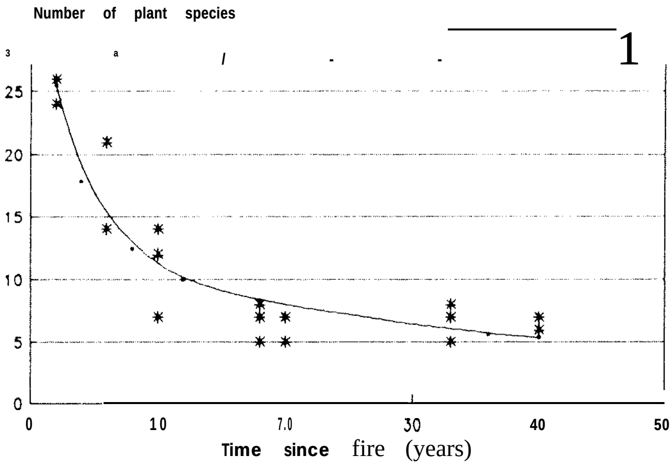

Figure 7. Numbers of plant species within a loo-meter-radius plot with time since last fire in desert vegetation near Lake Mackay, Western Australia.

crests, salt lakes, and claypans. Generally, long unburnt patches were small (200-400 m across). The oldest patch of vegetation was 40 ± 4 years. Animal species numbers, based on the survey technique used here, were highest in areas where there was a mosaic of 6- and 18-year-old vegetation. Where vegetation age was predominantly 6 years or less, or in one case where it was 40 years old, species numbers were low.

Plant species diversity decreased with increasing time since tire (fig. 7). Older vegetation was dominated by large, senescent rings of spinifex (*Triodia* species), whereas recently burnt patches contained a range of herbaceous plants as well as woody shrubs and spinifex. Many woody shrubs had resproutcd from lignotuber or regenerated from soil-stored seed following tire.

DISCUSSION

Fire size

There has been a dramatic and sudden increase in the mean and median size of burnt patches in the study area, coinciding with the departure of Pintubi Aborigines. The average size of a burnt patch has increased from 34 hectares in 1953 to 32,184 hectares in 1986 (table 1). During Aboriginal occupation of this land, there existed a tine- grained mosaic of burnt patches across the landscape as a result of Aboriginal burning and natural lightning tires. The Pintubi and Pitjantjatjarra men who guided us around the study area, found old, long-unburnt spinifcx as aesthetically displeasing and continually fired the spinifex as we travelled across the desert.

Kimber (1983) suggests that Aborigines had a good deal of control over fire, using wind, humidity and natural fire barriers such as claypans and sand dunes to control the size and intensity of tires. Our observations of the concentration of tire scars around resource-rich areas such as rockholes, creeks, claypans, and salt lakes is consistent with observations made by Kimber (1983). The fire regime around these resource rich landscape units may not be typical of areas less utilized by Aborigines. Partitioning and utilization of the landscape by Aborigines requires further investigation.

The abundance of small fire scars (< 10 hectares) visible on the 1953 aerial photography suggests either fires were lit under mild conditions and burnt at a low intensity or extensive tracts of heavy fuel sufficient to sustain large and intense fires did not exist. Many generations of Aborigines frequently burning off the land would result in a situation of discontinuous, patchy fuels, ranging from recently burnt to long-unburnt patches. However, when the human ignition source was removed from the desert, the fuels gradually accumulated over large, continuous tracts of land. Lightning strikes in summer have resulted in the massive and intense wildfires observed today. The grain size of the two-phase mosaic (recently burnt and long-unburnt) has increased over the last 36 years, as shown in figures 4 and 5.

Time of Year of Fires

Kimber (1983) believes that most burning by Aborigines was done in August to October and immediately prior to rains in December to February. Occasionally, large tires caused either by Aborigines or by lightning, burnt during the hot, dry, windy summer months. In the area studied here, it would not have been possible for a fire to become very large in 1953, as the fuels were discontinuous as a result of patch burning and natural fire barriers. Kimber suggests that the time of year for burning is not as important to Aboriginal people as the opportunity to bum. de Graaf (1976) observed that Aboriginal fires in the desert were lit all year round and not seasonally.

Both de Graaf (1976) and Kimber (1983) reported that certain areas of the desert were not burnt by Aborigines because Aborigines did not visit these places for religious reasons, or feared that fire would destroy sacred objects. The season of burning was, however, very important in the monsoon forest regions of the Northern Territory (Jones 1980; Haynes 1985) and to Wadjuk Aborigines in the south-west of Western Australia (Hallam 1975).

Today the main ignition source in the remote deserts is lightning. Thunderstorms are common over the summer months and large, lightning-caused wildfires have been reported (Griffin and others 1983).

The benefits to Aborigines by way of increased food resources as a result of firing the spinifex were evident during this study. Recently burnt country supported a diverse range of herbs and animals, particularly reptiles, whereas long-unburnt vegetation was generally less diverse in flora and fauna. However, we were unable to show any strong correlations between time since fire (fuel age) and total animal species numbers, although there was a trend between the spatial diversity of fuel age and animal numbers (fig. 6). Animal species numbers were based on visual observations of tracks, diggings, and scats, thus limiting the extent to which the data can be interpreted. More detailed studies of animal activity in relation to the temporal and spatial diversity of fuel age are needed. Postfire succession in spinifex communities has been described by Burbidge (1943) and Suijdendorp (1981). All authors report an increased level of plant diversity soon after fire. The range of fire-adaptive traits expressed by desert vegetation has also been reported by these authors.

As noted, there has been a significant change in fire regimes in recent times, and there is at least limited scientific evidence to suggest that this has contributed to the decline in mammal fauna. This change may have further predisposed mammals to predation by introduced predators. It is reasonable to accept the importance of temporal and spatial diversity within a landscape on resource levels and habitat opportunities (Latz and Griffin 1978, Pielou 1977). Saxon (1984) stated that “when large areas of a single landscape type are subjected to large uniform disturbances, they threaten the survival of wildlife species which depend on irregular boundaries of natural fire patterns to provide a fine grained mosaic of resources”. Bolton and Latz (1978) have shown that a range of post-fire successional stages is important habitat for the western hare-wallaby (*Largorchestes hirsutus*). Burbidge and Pearson (1989) explain the lack of rufous hare-wallabies *(Largorchestes hirsutus)* in the Great Sandy Deserts as being due to the lack of frequency of small-scale burns and to high fox numbers.

It is somewhat ironic that modern mammal extinctions in the Australian deserts are in part due to the changed fire regime that resulted from the departure of Aborigines and consequent lack of Aboriginal burning. Tindale (1959), Merrilees (1968), and Jones (1968) have all concluded that extensive burning by Aborigines contributed to the extinction of the Pleistocene mega-fauna. Today, it is likely that the large, intense wildfires which occur throughout the deserts arc placing extreme stress on some plant and animal communities (Griffin 1981). These intense fires are damaging vast areas of fire-sensitive vegetation such as marble gum (*Eucalyptus gongliocarpa),* desert oak *(Alocasuarina decaisneana*), and mulga *(Acacia anuera)* (Start 1986). There is sufficient evidence of the disadvantages of the current wildfire regime on the conservation status of desert reserves to warrant the development and implementation of managed fire regimes that mimic those in place during Aboriginal occupation of the land.

Today, aircraft are being used in parts of some Western Australian desert conservation reserves to set patch burns under carefully defined conditions to create a mosaic effect of burnt and unburnt patches across the landscape (Burrows and Thomson 1990). This study, together with detailed fire ecology studies currently in progress, will provide a basis for determining the frequency of fire and the size and distribution of burnt patches.

When the habitat has been rehabilitated through the prescribed use of fire and introduced predators controlled, then there will be an opportunity for translocating rare and endangered mammals to parts of their former range.

CONCLUSION

Black-and-white aerial photographs, Landsat imagery, and field observations have revealed that the size and intensity of fires in a part of the Western Desert west of Lake Mackay have increased dramatically over the last 36 years or so. This increase is attributed to the departure of Aboriginal people from the area during the 1960s. Aborigines used fire extensively for a multitude of reasons, resulting in a small-grained mosaic of burnt patches of different ages across the landscape. Such landscape diversity maximised resources available to Aborigines and to desert animals. Today, in the absence of frequent burning by Aborigines, fuels have accumulated over vast areas and when these fuels are ignited by lightning under hot, dry, windy summer conditions, large and intense wildfires sweep across the desert. This changed fire regime appears to have resulted in a lower diversity of animals and plants.

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LITERATURE CITED

Amadio, N.; Kimber, R. 1988. Wildbird Dreaming: Aboriginal Art from the Central Deserts of Australia. Melbourne, Australia: Greenhouse Publications. 112 pp.

Blake, D.H. 1977. Explanatory notes on the Webb geological sheet. Bureau of Mineral Resources, Geology and Geophysics. Canberra: Australian Government Publishing Service. 19 pp.

Bolton, B.L.; Latz, P.K. 1978. The Western Hare-wallaby *Lagorchestes hirsutus* (Gould) (Macropodictae) in the Tanami Desert. Australian Wildlife Research 5: 285-293.

Burbidgc, N.T. 1943. Ecological succession observed during regeneration of *Triodia pungens* R. Br. after burning. Journal of the Royal Society of Western Australia 28: 149-156.

Burbidge, A.A. 1985. Fire and mammals in Hummock grasslands of the arid zone. pp. 91-94. In: Ford, J. ed. Fire Ecology and Management In Ecosystems of Western Australia. Proceedings of a Symposium. Western Australian Institue of Technology Campus, May 1985. Perth. Western Australia.

Burbidge, A.A. and Jenkins, R.W.G. (1984). Endangered vertebrates of Australia and its island territories. Australian National Parks and Wildlife Service, Canberra. 25 pp.

Burbidge, A.A.; Johnson, K.A. 1983. Rufous Harc-wallaby *Largorchestes hirsutus*. pp. 99-100. In: Strahan, R. ed. The Australian Museum Complete Book of Australian Mammals. Sydney: Angus and Robertson Publishers.

Burbidge, A.A.; Johnson, K.A.; Fuller, P.J.; Southgate, R.I. 1988. Aboriginal knowledge of mammals of the central deserts of Australia. Australian Wildlife Research 15: 9-39.

Burbidge, A.A.; McKenzie, N.L. 1989. Patterns in the decline of Western Australia's vertebrate fauna: Causes and conservation implications. Biological Conservation 50: 143-198.

Burbidge, A.A.; Pearson, D.J. 1989. A search for the Rufous hare-wallaby in the Great Sandy and Little Sandy Deserts, Western Australia, with notes on other mammals. Department of Conservation and Land Management, Western Australia, Technical Report No. 23. 9 pp.

Burrows, N.D. ; Thomson, C. 1990. Desert Dreaming. Department of Conservation and Land Management, Western Australia, Landscope 5 (2): 10-16.

Calaby, J.H. 1971. Man, fauna and climate in Aboriginal Australia. pp. 80-93. In: Mulvaney, D.J.; Golson, J. eds. Aboriginal Man and Environment In Australia. Canberra: Australian National University Press.

Carnegie, D. 1898. Spinifex and Sand. 1973 edition. Blackburn: Penguin Colonial Facsimiles, Penguin Books. pp. 4.54.

de Graaf, M. 1976. Aboriginal use of tire. pp. 14-20. In: Fox, R.E. ed. Report on the use of Fire in National Parks and Reserves. Darwin: Department of the Northern Territory.

Finlayson, H.H. 1943. The Red Centre. Sydney: Angus and Robertson Ltd. pp. 343.

Flood, J. (1983). Archeology of the Drcamtime. Collins Publishers, Sydney.

Gill, A.M. 1981. Adaptive responses of Australian vascular plant species to fires. pp. 243-272. In: Gill, A.M.; Groves, R.H.; Noble, I.R. eds. Fire and the Australian Biota. Canberra: The Australian Academy of Science Publishers.

Gould, R.A. 1971. Use and effects of fire among the Western Desert Aborigines of Australia. Mankind 8(1): 14-24.

Griffin, G.F. 1981. The role of fire in arid lands. pp. 96-101. In: Stanburg, P.J. cd. Bushtires: Their Effect on Australian Life and Landscape. Sydney: Macleay Museum, University of Sydney Press.

Griffin, G.E.; Allan, G. 1985. Fire and the management of Aboriginal owned land. pp. 46-52. In: Proceedings of the Application of Science and Technology to Aboriginal Development in Central Australia: Workshop. Alice Springs.

Hallam, S.J. 1975. Fire and Hearth: A Study of Aboriginal Usage and European Usurpation in south-western Australia. Canberra: Australian Institute of Aboriginal Studies. 221 pp.

Haynes, C.D. 1985. The pattern and ecology of munwag; traditional Aboriginal fire regimes in north-central Arnhemland. Proceedings of the Ecological Society of Australia 13: 203-214.

Jones, R. 1969. Fire-stick farming. Australian Natural History 16: 224-228.

Jones, R. 1980. Cleaning the country: The Gidjingali and their Amhemland Environment. Broken Hill Proprietary Co. BHP Journal 1:10-15.

Kimber, R. (1983). Black lightning: Aborigines and fire in Central Australia and the Wesem Desert. Archaeology in Oceania 18:38-45.

Latz, P.K.; Griffin, G.F. 1978. Changes in Aboriginal land management in relation to fire and to food. pp. 77-85. In: Hetzel, B.S.; Frith, H.J. eds. The Nutrition of Aborigines in Relation to the Ecosystem of Central Australia. Melbourne: CSIRO.

Merrilccs, D. 1968. Man the destroyer; late Quaternary changes in the Australian marsupial fauna. Journal of Royal Society of Western Australia. 51(1): l-24.

Mulvaney, D.J. 1975. The Pre-History of Australia. Revised edition. Baltimore: Penguin Books. 346 pp.

Pielou, E.C. 1977. Mathematical Ecology. New York: Wiley-Interscience Publishers. 268 pp.

Suijdendorp, H. 1981. Responses of the hummock grasslands of northwestern Australia to fire. pp. 417-424. In: Gill, A.M.; Groves, R.H.; Noble, I.R. eds. Fire and the Australian Biota. Canberra: Australian Academy of Science Publishers.

Saxon, E.C. 1984. Introduction to patch-burning. pp. 5-6. In: Saxon, E.C. ed. Anticipating the Inevitable: A Patch-Bum Strategy for Fire Management at Uluru (Ayers Rock - Mt. Olga) National Park. Melbourne: CSIRO.

Start, A.N. 1986. Status and management of mulga in the Pilbara region of Western Australia. pp. 136-139. In: Sattler, P.J.S. ed. The Mulga Lands. The Royal Society, Queensland.

Tindale, N.B. 1959. Ecology of primitive Aboriginal man in Australia. pp. 36-51. In: Keast, J.A.; Crockcr, R.L.; Christian, C.S. eds. Biogeography and Ecology in Australia. Monographiae Biology. 8. The Hague: W. Junk.

Tonkinson, R. 1978. The Mardudjara Aborigines: Living The Dream In Australia's Desert. New York: Holt, Rinehart and Winston Publishers. 149 pp.

Warburton, P.E. 1875. Journey Across The Western Interior of Australia. Perth: Fascimile edition 1981, Hesperion Press. 307 pp.

INDIAN USE OF FIRE AND LAND CLEARANCE IN THE SOUTHERN APPALACHIANS

Michael S. DeVivo[1]

Abstract-The myth of an unbroken primeval forest, extending across eastern North America at the dawn of European settlement, has been perpetuated in the writings of both laymen and scholars throughout the present century. Accounts of sixteenth, seventeenth, and eighteenth century explorers, however, document vast amounts of cleared land held by aboriginal inhabitants, who likely populated the continent in much higher numbers than have been traditionally accepted. Fire was the principal tool used by the Indians to clear vegetation. Despite frequent historical reference to the Indian use of fire and the documentation of Indian old fields, the role of fire has been largely underplayed. Fire was implemented for forest management, driving game, and preparing land for agriculture. This paper examines the impact of tire and related anthropogenic disturbances on the southern Appalachian landscape before white settlement.

INTRODUCTION

Man's role as an agent of landscape change has long been a theme of research in historical geography (Newcomb 1969). However, the influence of eastern North America's aboriginal inhabitants on the physical environment before European settlement has not been studied adequately. This paper offers an overview of anthropogenic disturbances in the southern Appalachians during an era of aboriginal habitation, with especial reference to population, fire, land use, and land clearance.

ACCOUNTS BY EARLY EUROPEAN EXPLORERS

Permanent European settlement of the eastern United States did not occur until more than a century after the Columbus landfall in 1492, despite explorers' ventures along the coast, and subsequently into the interior of the continent, in pursuit of geographic knowledge during the sixteenth century (Brown 1948). Journals often contain comments as to the apparent presence or absence of forest, but other landscape traits were documented as well, such as aboriginal population and land use. In any event, the early explorers have provided documentation that refutes the popular notion of an unbroken virgin forest extending across eastern North America. Of particular significance were the travels of Giovanni Verrazano in 1524, Jacques Cartier a decade later, and Samuel de Champlain in the early 1600s (Sauer 1971, 1980), but their accounts depict extensive areas of cleared land prior to European settlement only along the Atlantic coast and adjacent navigable waterways. Very few reports documenting conditions of the southeastern interior were provided by explorers. Narratives of the expedition led by Hemando de Soto between the years 1538 and 1543, however, offer illustrations of extensive maize fields, canebrakes, and open land on the southeastern coastal plain and in the southern mountains (Boume 1904; Hakluyt 1611; Rostlund 1957; U.S. 1939).

ABORIGINAL POPULATION AND DEPOPULATION

Supplementing explorers' accounts is a body of literature in which students have sought to determine the pre-contact aboriginal population of the Americas. These studies suggest that the aboriginal population of the southern Appalachians was much greater than heretofore accepted, and that it declined rapidly, largely because of disease transmitted by the Europeans following the Columbus landfall in 1492. Furthermore, aboriginal inhabitants were numerous enough and sufficiently advanced to significantly alter the region's vegetation.

Humans have occupied the southern Appalachians for over 12,000 years (Dickens 1976; Frizzell 1987). It is widely accepted that the Cherokees occupied the region at least since the protohistoric period; their settlement core was restricted to western North Carolina, east Tennessee, north Georgia, and northwestern South Carolina, but claimed lands extending north to West Virginia and Kentucky (Dickens 1987; Frizzell 1987; Goodwin 1977). Mooney estimated the Cherokee population at no more than 22,000, a figure accepted and advanced by Kroeber (Denevan 1976; Goodwin 1977; Kroeber 1939; Swanton 1946).

Denevan, however, has indicated that the "authority of Kroeber has impeded serious consideration of North American aboriginal populations" and that "it is time for a reconsideration" (Denevan 1976). Unfortunately, one of the principal problems in estimating North American aboriginal populations, especially in the southeastern interior, is the lack of historical evidence. Historical documentation regarding Indian populations is more widely available for Latin American regions than for Anglo-America, largely because the former have a longer history of direct European contact and settlement. Because "estimates of aboriginal American populations have yielded a picture of small scale preconquest human population in the Western Hemisphere" (Dobyns 1966; Denevan 1976), anthropologist Henry Dobyns has proposed the use of depopulation ratios for calculating pre-Columbian

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[1] Assistant Professor of Geography and History, Oregon Institute of Technology, Klamath Falls, OR.

populations. His estimates contrast rather sharply with Kroeber's; for example, Kroeber estimated a hemispheric total of 8.40 million, whereas Dobyns estimates 90.04-l 12.55 million (Denevan 1976), and Geographer Michael Williams has noted:

> There is the strong possibility that in the late fifteenth century the Western Hemisphere may have had a greater total population than western Europe. The implications of these figures for forest disturbance and destruction are enormous (Williams 1989).

Today, Kroeber's estimates are considered much too low (Denevan 1976), and Dobyns' method offers an alternative, probably more realistic estimate. Dobyns' scheme employs a depopulation ratio, that is "the ratio of degree of decline from the time of contact to the population nadir" (Denevan 1976). Dobyns determined the depopulation ratios for aboriginal tribes and regions for which relatively reliable information is available and derived an average of 20: 1 (a population decline of 95%). Borah further supports high figures; he estimated pre-contact New World native population at about 100 million, which suggests a depopulation ratio of up to 25:1 (Borah 1964; Denevan 1976; Dobyns 1966).

The application of depopulation ratios is a viable means of estimating the pre-contact aboriginal population of the southern Appalachians. Archaeological evidence and travel accounts indicate rapid population decline during the sixteenth century, and the southeastern interior was not subject to exploration, description and interpretation, and settlement by Europeans until long after contact had been made on the East and Gulf coasts, as well as in the Southwest (Denevan 1976).

Figures of 7,400-10,000 are assumed to be rather reliable estimates for the Cherokees' nadir population during the early to mid-eighteenth century (Goodwin 1977), and application of a 20:1 or 25:1 depopulation ratio indicates that the pre-contact population would have been between 150,000 and 250,000. The difference between these estimates and Kroeber's estimate of 22,000 is highly significant. A quarter of a million inhabitants would have had a larger impact on the region's physical landscape than a comparatively scant population of 22,000 people. Obviously, the likelihood of extensive forest clearance would have been much greater.

The aboriginal inhabitants had been important components in the region's ecosystem. When disease, a major perturbation, decreased their numbers or eliminated them from some areas entirely, a major ecological change took place. Geographer Erhard Rostlund (1960) determined that buffalo (Bison *bison*) had not entered the Southeast by A.D. 1500, but migrated into the region after the middle of the sixteenth century, extending their habitat to the Atlantic and Gulf coasts. Historian Alfred Crosby suggests that the dramatic decrease in numbers of Amerindians opened up an econiche for the buffalo.

> Something had kept these animals out of the expanses of parklike clearings in the forest that periodic Amerindian use of fire and hoe had created. That something declined or disappeared after 1540. That something was, in all likelihood, the Amerindians themselves, who naturally would have killed the buffalo for food and to protect their crops (Crosby 1986).

ABORIGINAL SETTLEMENT FEATURES AND THE USE OF FIRE

Topography was probably the determining factor in the distribution of Indian settlements (Dickens 1976). Virtually all sites occurred along relatively extensive floodplains. A nucleated village of two or three acres appears to have been the predominant type of settlement, although sites could have been as small as a quarter of an acre, or as large as six acres (Dickens 1976). Villages ranged in size from a few houses to perhaps as many as fifty houses surrounded by log palisades. Large areas *of* bottomland adjacent to the villages were probably maintained for agricultural activity (Dickens 1976). Fire was the principal tool used by Indians to clear vegetation. Despite frequent historical reference to fire, and the documentation of "Indian old fields," Indian use of fire in North America has been greatly underestimated (Brown 1948; Day 1953; Gersmehl 1970; Goodwin 1977; Johannessen and others 1971; Martin 1973a, 1973b; Maxwell 1910; Thompson and Smith 1970). Fire was useful in driving game and opening the forest "to increase visibility, improve forage, expose the mast, and help keep down the weeds" (Gersmehl 1970). In the Great Smoky Mountains, fires were set at frequent intervals to encourage the growth of certain plant species, such as blueberries *(Vaccinium vacillans)*, which were useful for human consumption as well as wildlife habitat (Lindsay 1976).

The Cherokees, perhaps inadvertently, used fire for forest management. Plants having relatively little value, such as white pine, hemlock, birch, maple, and weeds were burned in order to encourage the growth of more valuable species. The Indians also burned the areas surrounding their villages to prevent catastrophic fires (Goodwin 1977).

Eastern Woodland Indians set fire periodically to bum accumulated litter and undergrowth and to encourage grassland (Thompson and Smith 1970). Periodic fire was especially important for the maintenance of prairies and canebrakes. Sondley has documented the existence of expansive grassland communities in the Asheville Basin at the dawn of white settlement.

> Most of the lands on and near the French Broad River ... were in prairies.... At the mouths of the smaller streams in that region tributary to the French Broad River were large canebrakes extending for miles up those tributaries (Sondley 1930).

Ralph Hughes determined that under continuous protection from fire, cane stands "lose vigor, thin out and die" (1966). Moreover, canebrake deterioration can be prevented with periodic fire. Thus, because canebrakes were present in the Asheville Basin at the onset of pioneer settlement and because their maintenance requires frequent fire, it seems likely that the Cherokees set fire to the Asheville Basin at regular intervals in order to clear the land of brush and trees. Following pioneer settlement, a combination of fire suppression (or a decrease in burning), uncontrolled grazing, and cultivation of floodplains was probably responsible for the decline of the extensive canebrakes.

Perhaps the most widespread use of fire by the Indians was in the preparation of land for agriculture. After undergrowth was burned, larger trees were killed by girdling. Planting began when sunlight passed through the dead branches; maize, beans, and squash were usually planted in the same field (Brown 1948). Maize (Zea *mays*) was the most important staple in the Indians' diet, and may have been cultivated as early as 100 B.C. It was planted extensively on the floodplains of major streams and rivers. Corn was harvested in the late summer and early fall and was often processed into several different items. These most often included various flours and cakes such as succotash, samp, hominy, hoecake, and ash-cake. Corn was also a principal ingredient in soups and stews. Beans (*Phaseolus*), probably introduced at a bout 800 A.D., were next in importance as a cultivated crop, (Yamell 1976) and were usually planted alongside corn. In fact, cornstalks were often used as beanpoles. The use of beans and corn in combination implied "complementation" in the natives' diet and as a result provided high nutrition. Squashes (*Cucurbitacae*) including pumpkins, gourds, and summer crookneck, were also an important staple. Certain squash varieties had been cultivated as early as 2300 B.C. The Cherokees planted squashes beside beans and maize. The sunflower (*Helianthus annus*) was probably domesticated during the second or third millennium B.C. (Yamell 1976) and had a multitude of uses. For example, its seeds yielded an edible table oil and flour that could be made into bread (Goodwin 1977).

Some wild edibles, such as spinach-like pigweed (*Amaranthus*) and goosefoot *(Chenopodiutn albutn),* grew along wet ditches and streams. Blackberries (*Rubus argutus*), raspberries (*Rubus odoratus*), and blueberries *(Vacciniutn vacillans*) were used. Nut-bearing trees provided the Indians with acorns, chestnuts, and walnuts, and sap from some trees provided sweetening agents such as maple syrup. Because Indians were strongly dependent on food from "wild" vegetation, some authorities believe that the Indians themselves were responsible for the wide distribution of certain trees, such a mockemut hickory (*Carya cordiformis*) and black walnut (*Juglans nigra*) (Goodwin 1977; Maxwell 1910).

The Cherokees obtained a number of fruits through contact with the Europeans in the sixteenth, seventeenth, and eighteenth centuries. These introduced fruits included watermelon (*Citrullus vulgaris*), peach (*Prunus persica*), apple (*Malus pumila*), and pear (*Pyrus communis*). Orchards were generally confined to moist, sandy soils at elevations below 3,000 feet; however, isolated stands of apple trees are at elevations up to 5,000 feet.

The Indians undoubtedly depended heavily on wild plants and animals for food, and they nurtured some forestland as a source of such foods. They also cleared large areas of settlements to provide fuelwood, and cleared extensive areas for agriculture.

Accounts of travelers document the abundance of cultivated fields and expansive grasslands throughout the Cherokee country. De Soto, in 1540, marched for a day through cultivated fields in southwestern North Carolina; subsequent explorers include De Luna in 1559-l-561, Pardo in 1566-1568, Batt in 1667, Lederer in 1670, Needham and Arthur in 1673, Cuming in 1730, and Timberlake in 1762 (Boume 1904; Hudson and others 1985; Hudson 1987; Sondley 1977; Williams 1927, 1928). Perhaps Bartram's account of his travels of 1775 are the most informative. The botanist reported extensive open prairies and fields of corn along the Little Tennessee River Valley (Harper 1958).

Virtually all permanent native settlements were limited to the floodplains of major streams and rivers for good reason. Their economy was based principally on agriculture, and it was impractical, if not impossible, to farm on steeply sloping terrain or at high elevations where erosion and microclimatic conditions were unfavorable. In southwestern North Carolina, the 3,000-foot contour follows the boundary between lands that are relatively suitable for agriculture and those that are not; the same is likely true for much of the southern Appalachians. Slopes are typically gentle below 3,000 feet and are typically much steeper at higher elevations.

Indians used fire to clear land for agriculture, and it is likely that some fires burned larger areas than intended. On shallow soils serotinous needleleaf conifers tended to dominate following a bum. On deep soils and open slopes hardwoods persisted or invaded after a fire. Deep-soiled, sheltered mesic sites were probably less susceptible to burning.

Rostlund suggested that in the pre-contact southeastern United States, the aboriginal inhabitants' burning of vegetation resulted in maximum land clearance. After their depopulation and the concomitant reduction in frequent burning, the area of cleared land decreased and the proportion of forestland increased (Rostlund 1957). Silvical characteristics of some forested areas in the southern Appalachians seem to support

Rostlund's hypothesis. For example, in the contemporary Joyce Kilmer Memorial Forest in southwestern North Carolina, a high proportion of old-growth yellow-poplar dominates some mesic sites. Yellow-poplar is an aggressive pioneer species on fertile sites following drastic disturbance (McCracken 1978), and in examining the forest, Lorimer has determined that "disturbances as far back as 1550 are almost certainly indicated by substantial numbers of the intolerant tulip tree in corresponding age classes" (Lorimer 1980). Possibly a fifteenth- to sixteenth-century Indian settlement that was located at sites now dominated by yellow-poplar (*Liriodendron tulipfera*) was a source of major disturbance. Perhaps after the European introduction and the subsequent diffusion of epidemic disease during the mid-fifteenth century, the settlement was largely depopulated, and pioneer species, such as yellow-poplar, invaded previously cleared areas.

CONCLUSION

The ability of aboriginal inhabitants to clear forest has often been grossly underestimated. In fact, anthropogenic perturbations over the last one or two millennia have accounted for much of the Southeast's forest composition, which is dominated by disturbance-initiated species (Buckner 1989). In the southern Appalachians, the Indians' livelihood depended on the use of fire to clear land and on the cultivation of crops along the floodplains of major rivers and their tributaries. Before contact with Europeans, the Cherokees and their ancestors probably cleared all bottomland in the region at one time or another. Moreover, the Cherokees' pre-Columbian ancestors may at one time have been numerous enough to clear all land below the 3,000-foot contour.

LITERATURE CITED

Borah, W. 1964. America as model: The demographic impact of European expansion upon the non-European world, 35th Congreso Intemacional de Americanistas, Mexico: Actas y Memorias 3:379-387.

Boume, E.G., ed. 1904. Narratives of the Career of Hemando de Soto. New York: Allerton Book Co.

Brown, R.H. 1948. Historical Geography of the United States. New York: Harcourt, Brace & World, Inc.

Buckner, E.R. 1989. Evolution of forest types in the Southeast. In Proceedings of Pine-Hardwood Mixtures: A Symposium on Management and Ecology of the Type, ed. T.A. Waldrop, pp. 27-33. Asheville, North Carolina: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Crosby, A.W. 1986. Ecological Imperialism: The Biological Expansion of Europe, 900-1900. New York: Cambridge University Press.

Day, G.M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34:329-346.

Denevan, W.M. 1976. The Native Population of the Americas in 1492. Madison: University of Wisconsin Press,

Dickens, R.S. 1976. Cherokee Prehistory. Knoxville: University of Tennessee Press.

Dobyns, H.F. 1966. Estimating aboriginal American population, an appraisal of techniques with a new hemispheric estimate. Current Anthropology 7:385-416.

Frizzell, G.E. 1987. The Native American experience. In The History of Jackson County, ed. M.R. Williams, pp. 33-66. Sylva, North Carolina: Jackson County Historical Association.

Gersmehl, P.J. 1970. Factors leading to mountaintop grazing in the southern Appalachians. Southeastern Geographer 10(1):67-72.

Goodwin, G.C. 1977. Cherokees in Transition: A Study of Changing Culture and Environment Prior to 1775. Chicago: University of Chicago Department of Geography Research Paper No. 18 1.

Hakluyt, R., transl. 1611. The Discovery and Conquest of Terra Florida by Don Ferdinando De Soto and Six Hundred Spaniards His Followers. New York: originally published by the Hakluyt Society, London, reprinted by Burt Franklin.

Harper, F. 1958. The Travels of William Bartram: Naturalist's Edition. New Haven: Yale University Press.

Hudson, C. 1987. Juan Pardo's excursion beyond Chiaha. Tennessee Anthropologist 12(1):74-87.

Hudson, C.; Smith, M.; Hally, D.; Polhemus, R.; and DePratter, C. 1985. Coosa: A chiefdom in the sixteenth-century southeastern United States. American Antiquity 50(4):723-737.

Hughes, R.H. 1966. Fire ecology of canebrakes. Proceedings, Tall Timbers Fire Ecology Conference: 149-158.

Johannessen, C.L.; Davenport, W.A.; Millet, A.; and McWilliams, S. 1971. The vegetation of the Willamette Valley. Annals of the Association of American Geographers 61(2):286-302.

Kroeber, A.L. 1939. Cultural and natural areas of native North America. University of California Publications in American Archaeology and Ethnology 38: l-242.

Lindsay, M. 1976. History of the grassy balds in Great Smoky Mountains National Park. U.S. Department of Interior National Park Service Research/Resource Management Report No. 4.

Lorimer, C.C. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61(5):1169-1184.

Martin, C. 1973a. Fire and forest structure in the aboriginal eastern forest. Indian Historian 6(3):23-26.

Martin, C. 1973b. Fire and forest structure in the aboriginal eastern forest. Indian Historian 6(4):38-42,54.

Maxwell, H. 1910. The use and abuse of forests by the Virginia Indians. William and Mary College Quarterly Historical Magazine 19(2):73-103.

McCracken, W.H. 1978. Comparison of Forest Cover Prior to and Following Disturbance in Two Areas of the Great Smoky Mountains National Park. Unpublished M.S. Thesis, University of Tennessee, Knoxville.

Newcomb, R.M. 1969. Twelve working approaches to historical geography. Association of Pacific Coast Geographers Yearbook 31:27-50.

Rostlund, E. 1957. The myth of a natural prairie belt in Alabama: An interpretation of historical records. Annals of the Association of American Geographers 47(4):392-411.

Sauer, C.O. 1971. Sixteenth Century North America. Berkeley: University of California.

Sauer, C.O. 1980. Seventeenth Century North America. Berkeley: Turtle Island.

Sondley, F.A. 1930. Asheville and Buncombe County. Asheville: The Citizen Co.

Swanton, J.R. 1946. The Indians of the Southeastern United States. Smithsonian Institution Bureau of American Ethnology Bulletin 137.

Thompson, D.Q. and Smith, R.H. 1970. The forest primeval in the Northeast - a great myth? Proceedings, Tall Timbers Fire Ecology Conference 10:255-265.

U.S. Final Report of the U.S. DeSoto Expedition. 1939. 76th Congress, 1st Session, House Doc. 71, 17.

Williams, M. 1989. Americans and Their Forests: A Historical Geography. Cambridge: Cambridge University Press.

Williams, S.C. 1927. Lieut. Henry Timberlake's Memoirs 1756-1765. Johnson City, Tennessee: Watauga Press.

Williams, S.C. 1928. Early Travels in the Tennessee Country 1540-1800. Johnson City, Tennessee: Watauga Press.

Yamell, R.A. 1976. Early plant husbandry in eastern North America. In Cultural Change and Continuity, Essays in Honor of James Bennett Griffin, ed. C.E. Cleland, pp. 265273. New York: Academic Press.

SPECIAL SESSION: THE YELLOWSTONE FIRES

BARK BEETLE-FIRE ASSOCIATIONS IN THE GREATER YELLOWSTONE AREA

Gene D. Amman[1]

Abstract-The large forest fires in and around Yellowstone National Park in 1988 bring up many ecological questions, including the role of bark beetles. Bark beetles may contribute to fuel buildup over the years preceding a fire, resulting in stand replacement fires. Fire is important to the survival of seral tree species and bark beetles that reproduce in them. Without fire, seral species are ultimately replaced by climax species. Following fire, bark- and wood-boring beetles respond to fire-injured trees. Because of synchrony of the fires and life cycles of the beetles, beetle infestation in 1988 was not observed in fire-injured trees. However, endemic populations of beetles, upon emergence in 1989, infested large numbers of fire-injured trees. Of the trees examined in each species, 28 to 6.5 percent were infested by bark beetles: Pinus contorta (28 percent) by Ips pini; Pseudotsuga menziesii (32 percent) by Dendroctonus pseudotsupae; Picea engelmannii (65 percent) by Dendroctonus rufipennis; and Abies lasiocarpa (35 percent) by Buprestidae and Cerambycidae. Most trees infested by bark beetles had 50 percent or more of their basal circumference killed by fire. Bark beetle populations probably will increase in the remaining fire-injured trees.

INTRODUCTION

Insects and diseases are important in modifying the age structure and species composition of many forests. Their activities contribute to accumulation of dead fuels that make large-scale fires possible--resulting in new stands of the host tree. The stands are then temporarily free of attack (Kilgore 1986). The mosaics of different-aged stands created as the result of fires assure survival of both trees and insects that infest them. However, fire is more important to the survival of some ecosystems than others. Following fires, injured trees are susceptible to infestation by bark beetles. Subsequent buildup of bark beetle populations can result in killing of uninjured trees.

In this paper I will discuss bark beetle ecology (1) as it may contribute to fuel buildup and fire intensity and (2) as it relates to fire-injured trees in the aftermath of forest fires. Lodgepole pine (Pinus contorta Douglas), the most prevalent tree species in the Greater Yellowstone Area (GYA) and one that we know the most about with respect to bark beetle-tree interactions, will be discussed more fully than other species.

BARK BEETLES AS CONTRIBUTORS TO FUEL BUILDUP

Pfister and Daubenmire (1975) recognized four basic successional roles for lodgepole pine: minor seral, dominant seral, persistent, and climax. Large areas of lodgepole pine in the GYA have almost no spruce-fir component. Despain (1983) concludes these are essentially self-perpetuating climax lodgepole pine stands that often exceed 300 to 400 years of age, with no evidence of fire since establishment.

Mountain pine beetle (MPB) infestation characteristics differ by lodgepole pine successional roles. In stands where lodgepole pine is seral and stands have been depleted by beetle infestations, lodgepole will be replaced by the more shade-tolerant species in the absence of fire. These shade-tolerant species consist primarily of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) at the lower elevations and subalpine fir (Abies lasiocarpa [Hook.] Nutt.) and Engelmann spruce (Picea engelmannii Parry) at the higher elevations. Starting with the stand generated by fire, lodgepole pine grows rapidly and occupies the dominant position in the stand. Fir and spruce seedlings also become established in the stand but grow more slowly than lodgepole pine.

Once the lodgepole reach susceptible size, MPB infestations kill 30 to over 90 percent of trees 12.7 cm and larger diameter at breast height (Cole and Amman 1980; McGregor and others 1987). After each infestation, both residual lodgepole pine and the shade-tolerant species increase their growth (Roe and Amman 1970). Infestations are repeated as the residual lodgepole pines reach size and phloem thickness conducive to beetle infestation and survival (Amman 1977). This cycle is repeated at 20- to 40-year intervals, depending upon growth of the trees (Roe and Amman 1970). Although size and phloem thickness are the variables necessary for beetle epidemics to occur, some authors (e.g., Berryman 1978) believe trees must be weakened before MPB can infest them. However, this has not been demonstrated, and will require detailed studies of beetle populations progressing from low level into the early phases of an epidemic (Schmitz 1988). Fuel levels and fire hazard continue to increase with each beetle infestation (Brown 1975; Flint 1924; Gibson 1943; Roe and Amman 1970) until lodgepole pine is

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[1] Principal Entomologist and Project Leader, Mountain Pine Beetle Population Dynamics Research Work Unit, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Ogden, UT.

eliminated from the stand, or until a fire occurs that kills most trees (including thick-barked, fire-resistant species), and the stand regenerates to lodgepole pine.

Where lodgepole pine is persistent or climax (Pfister and Daubenmire 1975), the association of lodgepole pine and mountain pine beetle is somewhat different. In these cases, the forest consists of lodgepole pine of different sizes and ages, ranging from seedlings to a few overmature trees. In these forests, MPB infests and kills many of the pines as trees reach large size. Openings created in the stand, as a result of the larger trees being killed, are seeded by lodgepole pine. The cycle is then repeated as other lodgepole pines reach sizes and phloem thicknesses conducive to increases in beetle populations (Amman 1977).

Amman (1977) hypothesized that periodic MPB infestations continue the multi-aged nature of the stands. A mosaic of small clumps of different ages and sizes may occur. The overall effect is likely to be more chronic infestation by the beetle because of the more constant source of food. Beetle infestations in such forests may result in the death of fewer trees per hectare during each infestation than would occur in even-aged stands (caused by stand replacement fires) and in those stands where lodgepole pine is seral. Fires in uneven-aged persistent and climax lodgepole pine forests should not be as hot as fires where widespread epidemics of beetles have occurred because smaller, more continuous deposits of fuel are added to the forest floor under chronic beetle infestations. Thus, with lighter accumulations of fuel, fires tend to eliminate or weaken some of the trees but do not cause total elimination and complete regeneration of the stand. An example is the situation described by Gara and others (198.5) in south-central Oregon, where lodgepole pine forms an edaphic climax. Here, fires are slow moving, and the heat of smoldering logs scorches roots and sides of trees. Later these injured trees are invaded by fungi that work their way up the roots into the trunks. Subsequently, mountain pine beetles are attracted to and kill these trees. As the dead trees rot and fall over, the stage is set for another fire.

Most fires that occur in lodgepole pine are either slow and smoldering or are rapidly moving, intense crown fires (Lotan and others 1985). High-intensity fires tend to favor lodgepole pine over such species as Douglas-fir (Kilgore 1986) and would likely occur following epidemic beetle infestations. Brown (1975) states that the major vegetation pattern found in lodgepole pine today was caused by stand replacement fires, although many uneven-aged lodgepole pine stands result from lower intensity surface fires.

In south-central Oregon, Stuart and others (1989) have related lodgepole pine regeneration pulses to mountain pine beetle and fire disturbances. They observed that (1) stands that experienced periodic MPB epidemics accompanied by a fire had an even-aged structure; (2) stands that had periodic MPB epidemics and no fire had a storied, bimodal size structure; and (3) stands that experienced mortality by low level MPB populations, with or without low intensity fire, had multi-aged structure.

Romme and others (1986) examined the effects of beetle outbreaks on primary productivity in forests dominated by lodgepole pine in northwestern Wyoming. They concluded that the mountain pine beetle does not regulate primary productivity. Even though MPB has drastic effects upon stands (considering the forest landscape comprises a mosaic of stands in various stages of succession), annual productivity for the landscape is relatively constant despite continual fluctuations of individual stands. The sudden and massive death of a large proportion of the biomass leads to only a brief drop in primary productivity and to a more equitable distribution of biomass and resources. Therefore, the primary function of large MPB infestations and the death of large numbers of lodgepole pine appears to be survival of host and beetle by creating large amounts of fuel for fire that, when ignited, eliminate competing vegetation and regenerates lodgepole pine (Amman 1977; Roe and Amman 1970; Romme and others 1986).

The mosaic of stands of different ages created by the action of MPB and fire is ideal for MPB survival. Because stands are coming into sizes conducive to continual MPB infestation and survival, a continual supply of food is provided. However, an ideal mosaic for MPB probably did not occur following the 1988 GYA fires because fire behavior was influenced more by drought and wind than by fuels. Virtually all forest age and fuel categories burned (Christensen and others 1989).

Romme and Despain (1989) state that the mosaic created by the 1988 fires will be more homogeneous than the mosaic created by fires in the early 1700's, and few ecological consequences will be incurred because succession is slow. One consequence is likely to be a major MPB infestation in 80 to 120 years because at this age many lodgepole pine stands sustain their first beetle outbreak, again creating a large amount of dead fuel in a relatively short period, setting the stage for another stand replacement fire (Roe and Amman 1970). The timing of MPB infestations, when lodgepole pine are mature in seral stands, not only assures large amounts of fuel from the dead trees for a stand replacement fire but also adequate seed to regenerate the stand (Peterman 1978). Peterman suggests the ecological role of MPB could be to decrease the probability of lodgepole stands, with a high degree of serotiny, producing stagnant stands of offspring. By preventing the stand from getting too old, much less seed would be available. Such a mechanism could have evolutionary significance to lodgepole pine because stagnant stands do not reproduce well, and the stand following the stagnant stand could be outcompeted by climax tree species. Peterman further points out that prevention of stagnant stands would be advantageous to MPB because the beetle does not reproduce well in small, stagnant trees.

The contribution of dead fuel buildup, a result of the 391 000 ha infestation of MPB in Yellowstone National Park that was still active in 1982 (Gibson and Oakes 1987), to behavior of the 1988 fires was masked by the extreme fire conditions (Christensen and others 1989). Studies of small fires in portions of Yellowstone not involved in the 1988 tires probably would elucidate interactions of MPB infestations, dead fuel buildup, and fires. A relationship similar to MPB, lodgepole pine, and fire has been proposed for southern pine beetle (SPB) (D. frontalis Zimmermann) and pines in the Southern United States. There, pines are replaced by hardwood tree species in the absence of fire (Schowalter and others 1981). Therefore, survival of SPB and its host in natural stands is dependent upon frequent fires.

Bark beetles infesting climax tree species would not have the same need for a close relationship with forest fires as those infesting seral species. The spruce beetle (SB) (D. rufipennis [Kirby]) and the Douglas-fir beetle (DFB) (D. pseudotsugae) usually kill small groups of trees. However, occasionally they also cause heavy mortality, favoring large trees over vast areas, after building up in windthrown trees. For example, SB killed millions of Engelmann spruce in Colorado between 1939 and 1951 (Massey and Wygant 1954) and white spruce (P. glauca [Moench] Voss) in Alaska between 1960 and 1973 (Baker and Kemperman 1974). Schmid and Hinds (1974) describe the scenario in spruce-fir stands in the central Rocky Mountains following spruce beetle infestations. Following a spruce-beetle outbreak, the percentage of subalpine fir in the stand increases, with fir dominating the stand. As fir reach 125 to 175 years of age, they begin to die, with the bark beetle Dryocoetes confusus Swaine being one of the mortality factors. Young spruce and fir increase their growth as overstory fir die. The less shade-tolerant spruce is then favored over fir as the original canopy fir are killed. Spruce becomes dominant as it outlives fir and gains greater size. Eventually, the cycle is repeated. Spruce beetle generally live in moist forests where fires are less frequent and intense because of moist, sparse fuels (Amo 1976). Small fires in the spruce-fir type would expose mineral soil and probably favor establishment of spruce.

The Douglas-fir beetle seldom creates widespread destruction in the Rocky Mountains, generally killing groups of dense mature Douglas-fir (Fumiss and Orr 1978). These groups are usually widely separated, and the space created by death of some overstory trees usually regenerates to Douglas-fir.

These observations suggest coadaptive or coevolutionary relationships between bark beetles and their host trees, and the importance of fire in maintaining these relationships for seral tree species.

BARK BEETLE/FIRE-INJURED TREE ASSOCIATIONS

Following the 1988 GYA fires, large numbers of trees girdled or partially girdled by heat remained at the bum perimeter and are providing infestation opportunity to bark beetles. Beetles may increase to large numbers and infest uninjured trees after most of the fire-injured trees are killed.

The bark beetle situation in the GYA at the time of the. 1988 fires shows that the species were at low population levels, except the DFB. The massive infestations of MPB that covered over 391 000 ha in Yellowstone Park in 1982 had declined to only 125 ha by 1986 (Gibson and Oakes 1987) and to no infested trees in 1987 (Gibson and Oakes 1988). In 1988, insect detection flights over the park were not made because of fire fighting efforts and smoke (Gibson and Oakes 1989). However, on the nearby Bridger-Teton National Forest, MPB infestation had declined from 1,296 ha in 1987 to 364 ha in 1988 (Knapp and others 1988).

Although no survey estimates are available for other bark beetle species in Yellowstone Park, surveys of adjacent areas showed only the DFB was increasing, whereas spruce beetle infestation was light (Knapp and others 1988) and pine engraver (Ips pini Say) populations had declined (Gibson and Oakes 1989).

The small populations of bark beetles in the GYA at the time of the 1988 fires, coupled with timing of the fires in relation to life cycles of bark and wood infesting beetles, resulted in few fire-injured trees being infested in 1988. The SB, DFB, and pine engraver all emerge to infest new material in the spring, prior to occurrence of the fires. The MPB emerges in late July and early August, but few were in the GYA.

Studies were started in 1989 to determine bark beetle infestation of fire-injured trees and potential buildup of beetle populations. Observations were made in three areas: (1) near the Madison River, approximately halfway between Madison Junction and West Yellowstone (the North Fork fire); (2) along the John D. Rockefeller, Jr., Memorial Parkway, south of Yellowstone's South Gate (the Huck fire); and (3) in the Ditch Creek area of the Bridger-Teton National Forest (Hunter fire). In each area, variable plots (10 basal area factor) were established: area 1, three plots; area 2, nine plots; and area 3, seven plots. All trees in the plots were numbered so that survival of individual trees can be followed for several years. Survival of scorched trees can be predicted from volume of crown scorch (Ryan and others 1988). Peterson and Arbaugh (1986) found crown scorch and basal scorch were best predictors for lodgepole pine survival, and crown scorch and insect attack were most important as predictors of survival of Douglas-fir. However, the researchers did not identify the insects. I used the percentage of basal circumference in which the cambium was killed, rather than relating infestation to crown scorch, because of the high sensitivity of lodgepole and spruce to even light ground fire. Some bark was removed from trees infested by insects so that insects could be identified. Because our plots were mostly at low elevations (2 050 to 2 400 m), trees consisted mostly of lodgepole pine and Douglas-fir. The limited nature of our observations preclude their use for making predictions of bark beetle activity beyond our plots. Greater coverage of the burned area is planned in 1990.

Lodgepole Pine

Lodgepole pine is the most abundant tree in the samples. Overall, 28 percent of the trees were infested by the pine engraver (*Ips pini* Say) (table 1). infested, only one had not been scorched by tire. All others had 50 percent or more basal girdling (phloem killed by tire). Most commonly, trees infested by the pine engraver had 100 percent basal girdling (table 2). Many of these trees showed little evidence of scorch and looked healthy except for boring frass made by the beetles. Upon closer inspection, however, the trees were completely girdled at the base by a light ground tire. Geiszler and others (1984) also found most lodgepole pine infested by pine engraver were moderately to heavily injured following a tire in Oregon.

It is not surprising that a large number of trees were infested by pine engraver because they are able to reproduce in wind-broken material (including large branches) and in decadent trees near death (Sartwell and others 1971). There always seems to be plenty of such material available. Consequently, the engraver is almost always present in substantial numbers, although not necessarily causing noticeable tree mortality.

Only one tree containing MPB was observed (Hunter tire on the Bridger-Teton National Forest) and it was not on a plot. Observations over the years suggest that MPB is not strongly attracted to fire-scorched trees, so few trees would be infested even if a large population had been present in the GYA. The MPB seldom breeds in trees injured or killed by tire in numbers sufficient to cause an increase in the population. Hopkins (1905) found no MPB in fire-injured ponderosa pine in the Manitou Park area of Colorado. However, he did observe several secondary species, including the red turpentine beetle (*D. valens* Lec.). sequent publication concerning insect damage in the National Parks, Hopkins (1912) stated that forest tires contribute, to a limited extent, to the multiplication of certain species that breed in tire-scorched trees, but as a rule forest fires kill more beetles

Table I.--Number of trees examined and the percentage infested by bark- and wood-boring beetles for plots located in three fires in the Greater Yellowstone Area, 1989

Tree species	Fire							
	North Fork		Huck		Hunter		ALL fires	
	No.	Pct	No.	Pct	No.	Pct	No.	Pct
Lodgepole pine	0	0	67	24	58	33	125	28
Douglas-fir	34	18	25	52	4	25	63	32
Engelmann spruce	0	0	2	50	15	67	17	65
Subalpine fir	0	0	9	33	8	38		35
All species	34	18	103	31	85	38	2::	32

Table 2.--Number and percentage of trees infested by bark- and wood-boring beetles in different fire-injury categories, Greater Yellowstone Area, 1989

Tree species	Percentage of basal circumference killed by fire									
	0		1-25		26-50		51-75		76-100	
	No.	Pct	No.	Pct	No.	Pct	No.	Pct	No.	Pct
Lodgepole pine	21	5	4	0	15	0	12	25	73	41
Douglas-fir	10	28	3	0	IO	30	11	36	22	41
Engelmann spruce	0	0	1	0	0	0	0	0	16	69
Subalpine fir		0	0	0	0	0	0	0	17	31
All species	38	16	8	0	25	12	23	30	128	43

than they protect (by protect, he probably meant provide breeding habitat). Swaine (1918), referring to Canadian conditions, wrote that ground fires that injure and kill large numbers of trees may provide material for rapid development of bark beetles. He thought this was particularly true if tires occur year after year in neighboring localities. Apparently the proximity of fires would allow beetles to continue to build up their populations for several consecutive years. Blackman (1931), working on the Kaibab National Forest in northern Arizona, found MPB did not prefer fire-scorched trees. He thought the scorched phlocm did not offer favorable conditions for beetle offspring. The MPB has fairly limited requirements of phloem thickness and moisture in order to reproduce (Amman and Cole 1983).

In agreement with most observations in the Rocky Mountains that MPB are not attracted to fire-scorched trees, Geiszler and others (1984) observed MPB mostly in trees uninjured or lightly injured by fire, in direct contrast to pine engraver in moderate to heavily injured trees. Rust (1933) reported fire-injured ponderosa pine were infested by MPB the first year following a fire in northern Idaho; however, the infestation declined the next year.

The wood borers, both Buprestidae and Cerambycidae, were found occasionally in fire-injured lodgepole.

Douglas-fir

Douglas-fir was the second most common tree found on the plots. Of the trees examined, 32 percent were infested by insects, mostly DFB and a few wood borer larvae of Buprestidae and Cerambycidae (table 1). Most infested Douglas-fir had 50 percent or more girdling by fire (table 2). Some Douglas-firs that had needles and limbs completely burned were infested by DFB in the base where the bark was thick enough to protect the phloem from complete incineration or from drying so excessively that beetles would not construct egg galleries in it. Phloem in such trees was completely brown, and larvae probably will not complete development in such trees.

Fumiss (1965) studied the susceptibility of tire-injured Douglas-fir to bark beetle attack after a large tire in southern Idaho. He found 70 percent of the trees were infested by DFB 1 year after the fire. And even small or lightly burned trees attracted the beetles. He found incidence of attack increased with tree size and severity of crown and cambium injury by tire. However, infestation decreased sharply with outright tree killing by tire. Although beetles established brood in 88 percent of the trees, offspring numbers were small because of pitch invasion of the galleries and sour sap condition.

Fumiss (1965) did not report on DFB infestation in fire-scorched Douglas-fir beyond the first postfire year. However, following the Tillamook fire of 1933 in the coastal range of Oregon, DFB buildup in fire-injured Douglas-fir occurred. Beetles then killed large numbers of uninjured trees in 1935 and 1936, but the infestation soon subsided (Fumiss 1941). Fumiss thought beetles were able to increase because frequent fires in the Tillamook area provided large numbers of injured trees in which the beetles could reproduce.

Connaughton (1936) observed that delayed mortality of fire-injured Douglas-fir was mostly caused by insects (probably DFB) and fire damage to roots. He found Douglas-fir had a thick layer of duff around the trunk that burned slowly, heating the soil and badly injuring the roots. The evidence for root injury did not show up until a year or two after the fire in west-central Idaho.

Engehnann Spruce

Engelmann spruce constituted a small part of our tree sample, with only 17 trees examined. Spruce beetle infested 65 percent of the trees (table 1), and these were usually the larger diameter trees. Of the spruce, only those with 75 percent or greater basal girdling were infested (table 2). Some spruce burned similarly to Douglas-fir described by Connaughton (1936). Duff around the base resulted in a slow burning tire that often burned off the roots or so weakened them that the trees were easily blown over by wind. Windthrown trees with unscorched trunks created an ideal habitat for the SB, which shows a strong preference for windthrown trees (Massey and Wygant 1954; Schmid and Hinds 1974). Large numbers of spruce beetle larvae occurred in the spruce, as well as some larvae of Buprestidae and Cerambycidae.

Subalpine fir

Wood borers (Buprestidae and Cerambycidae) infested 35 percent of the 17 subalpine fir in the sample (table 1). All of the fir suffered 100 percent basal girdling. The bark was badly burned and not conducive to bark beetle infestation (table 2).

Whitebark Fine

Whitebark pine (P. albacaulis Engelm.), which is generally found at high elevations in GYA, did not occur in any of our plots. MPB infestations during the past 20 years caused considerable whitebark mortality (Bartos and Gibson 1990), but the number of infested trees was low at the time of the 1988 fires. Although MPB is not strongly attracted to fire-scorched lodgepole and ponderosa pines in the Rocky Mountains, Craighead and others (1931) state that it prefers weakened and tire-scorched western white pine (P. monticola Dougl.), one of the five-needle pines. Therefore, MPB may be more attracted to fire-injured five-needle pines, whitebark and limber (P. flexilis James), than to lodgepole pine.

CONCLUSIONS

Of the bark beetles in the GYA, MPB plays a significant role in converting live fuels to dead fuels in a relatively short period. This behavior probably promotes hot stand replacement fires that assure survival of lodgepole pine and, hence, survival of MPB. Fire is not as important in the ecology of bark beetles infesting climax tree species.

Although a limited number of fire-injured trees were sampled in the GYA, almost one-third were infested by bark beetles. Therefore, numbers of infested trees in the sampled areas likely will increase because of the remaining large numbers of fire-injured trees.

LITERATURE CITED

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. In: Mattson, W.J., cd. The role of arthropods in forest ecosystems: Proceedings of the 15th International Congress of Entomology, 1976 August 19-27; Washington, DC. New York: Springer-Verlag: 3-18.

Amman, G.D.; Cole, W.E. 1983. Mountain pine beetle dynamics in lodgepole pine forests. Part 2: Population dynamics. Gen. Tech. Rep. INT-145. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 59 pp.

Amo, S.F. 1976. The historical role of tire on the Bitterroot National Forest. Res. Pap. INT-187. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 29 pp.

Baker, B.H.; Kemperman, J.A. 1974. Spruce beetle effects on a white spruce stand in Alaska. Journal of Forestry. 72: 423-425.

Bartos, D.L.; Gibson, K.E. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. In: Whitebark pine ecosystems: ecology and management of a high-mountain resource. Symposium proceedings; 1989 March 29-31; Bozeman, MT. Gen. Tech. Rep. INT-270. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 171-178.

Bcrryman, A.A. 1978. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest pest management. In: Berryman, A.A.; Amman, G.D.; Stark, R.W., eds. Theory and practice of mountain pine beetle management in lodgepole pine forests. Symposium proceedings; 1978 April 2.5-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 98-105.

Blackman, M.W. 1931. The Black Hills beetle. Tech. Pub. 36. Syracuse, NY: Syracuse University, New York State College of Forestry. 77 pp.

Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forests. In: Baumgartner, D.M., ed. Management of lodgepole pine ecosystems. Symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University Cooperative Extension Service: 429-456.

Christensen, N.L.; Agee, J.K.; Brussard, P.F.; Hughes, J.; Knight, D.H.; Minshall, G.W.; Peck, J.M.; Pyne, S.J.; Swanson, F.J.; Thomas, J.W.; Wells, S.; Williams, S.E.; Wright, H.A. 1989. Interpreting the Yellowstone tires of 1988: ecosystem responses and management implications. BioScience. 39: 678-685.

Cole, W.E.; Amman, G.D. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: Course of an infestation. Gen. Tech. Rep. INT-89; Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 56 pp.

Connaughton, CA. 1936. Fire damage in the ponderosa pine type in Idaho. Journal of Forestry. 34: 46-51.

Craighead, F.C.; Miller, J.M.; Evenden, J.C.; Keen, R.P. 1931. Control work against bark beetles in western forests and an appraisal of its results. Journal of Forestry. 29: 1001-1018.

Despain, D.G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology. 64: 23 l-234.

Flint, H.R. 1924. Various aspects of the insect problem in the lodgepole pine region. U.S. Department of Agriculture, Forest Service D-l Applied Forestry Notes. 54. 4 pp.

Fumiss, M.M. 1965. Susceptibility of fire-injured Douglas-fir to bark beetle attack in southern Idaho. Journal of Forestry. 63: 8-11.

Fumiss, M.M.; Orr, P.W. 1978. Douglas-fir beetle. Forest Insect and Disease Leaflet 5. Washington, DC: U.S. Department of Agriculture, Forest Service. 4 pp.

Fumiss, R.L. 1941. Fire and insects in the Douglas-fir region. Fire Control Notes. 5: 21 l-213.

Gara, R.I.; Littke, W. R.; Agee, J .K.; Geiszler, D.R.; Stuart, J.D.; Driver, C.H. 1985. Influence of fires, fungi and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. In: Baumgartner, D.M.; Krebill, R.G.; Arnott, J.T.; Weetman, C.F., eds. Lodgepole pine: the species and its management. Symposium proceedings; 1984 May 8-10; Spokane, WA. 1984 May 14-16; Vancouver, BC. Pullman, WA: Washington State University Cooperative Extension Service: 153-162.

Geiszler, D.R.; Gara, R.I.; Littke, W.R. 1984. Bark beetle infestations of lodgepole pine following a fire in south central Oregon. Zeitschrift fur angewandte Entomologie. 98: 389-394.

Gibson, A.L. 1943. Status and effect of a mountain pine beetle infestation on lodgepole pine stands. Unpublished Office Rep. Coeur d'Alene, ID: U.S. Department of Agriculture, Forest Insect Lab. 34 pp.

Gibson, K.E.; Oakes, R.D. 1987. Mountain pine beetle status report, Northern Region, 1986. Forest Pest Mgmt. Rep. 87-7. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 17 pp. plus maps.

Gibson, K.E.; Oakes, R.D. 1988. Bark beetle conditions, Northern Region, 1987. Forest Pest Mgmt. Rep. 88-4. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 21 pp. plus maps.

Gibson, K.E.; Oakes, R.D. 1989. Bark beetle conditions, Northern Region, 1988. Forest Pest Mgmt. Rep. 89-7. Missoula, MT: I1.S. Department of Agriculture, Forest Service, Northern Region. 20 pp. plus maps.

Hopkins, A.D. 1905. The Black Hills beetle. Bull. 56. Washington, DC: U.S. Department of Agriculture, Bureau of Entomology. 24 pp.

Hopkins, A.D. 1912. Insect damage to standing timber in the National Parks. Circ. 143. Washington, DC: U.S. Department of Agriculture, Bureau of Entomology. 10 pp.

Kilgore, B.M. 1986. The role of fire in wilderness: a state-of-knowledge review. In: Lucas, R.C. National wilderness research conference: issues, state-of-knowledge, future directions. Symposium proceedings; 1985 July 23-26; Fort Collins, CO: 70-103.

Knapp, A.; Weatherby, J.; Hoffman, J.; Kalve, V.; LaMadeleine, L. 1988. Forest insect and disease conditions, Intermountain Region, 1988. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region, State and Private Forestry, Forest Pest Management. 31 pp.

Lotan, J.E.; Brown, J.K.; Ncuenschwander, L.F. 1985. Role of tire in lodgepole pine forests. In: Baumgartner, D.M.; Krebill, R.G.; Arnott, J.T.; Weetman, G.F., eds. Lodgepole pine: the species and its management. Symposium proceedings; 1984 May 8-10; Spokane, WA. 1984 May 14-16; Vancouver, BC. Pullman, WA: Washington State University Cooperative Extension Service: 133-152.

Massey, C.L.; Wygant, N.D. 1954. Biology and control of the Engelmann spruce beetle in Colorado. Circ. 944. Washington, DC: U.S. Department of Agriculture, Forest Service. 35 pp.

McGregor, M.D.; Amman, G.D.; Schmitz, R.F.; Oakes, R.D. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Canadian Journal of Forest Research. 17: 1234-1239.

Peterman, R.M. 1978. The ecological role of mountain pine beetle in lodgepole pine forests. In: Berryman, A.A.; Amman, G.D.; Stark, R.W., eds. Theory and practice of mountain pine beetle management in lodgepole pine forests. Symposium proceedings; 1978 April 25-27; Pullman, WA. Moscow, ID: University of Idaho, Forest, Wildlife and Range Experiment Station: 16-26.

Peterson, D.L.; Arbaugh, M.J. 1986. Postfire survival in Douglas-fir and lodgepole pine: comparing the effects of crown and bole damage. Canadian Journal of Forest Research. 16: 1175-1179.

Pfister, R.D.; Daubenmire, R. 1975. Ecology of lodgepole pine, Pinus contorta Dougl. In: Baumgartner, D.M., ed. Management of lodgepole pine ecosystems. Symposium proceedings; 1973 October 9-11; Pullman, WA. Pullman, WA: Washington State University Cooperative Extension Service: 27-46.

Roe, A.L.; Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. Res. Pap. INT-71. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 23 pp.

Romme, W.H.; Despain, D.G. 1989. The long history of tire in the Greater Yellowstone Ecosystem. Western Wildlands. 15: 10-17.

Romme, W.H.; Knight, D.H.; Yavitt, J.B. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? American Naturalist 127: 484-494.

Rust, H.J. 1933. Final report on the study of the relation of fire injury to bark beetle attack in ponderosa pine (Tubb's Hill Bum). Coeur d'Alene, ID: U.S. Department of Agriculture, Bureau of Entomology, Forest Insect Field Station. 22 pp.

Ryan, K.C.; Peterson, D.L.; Reinhardt, E.D. 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Science. 34: 190-199.

Sartwell, C.; Schmitz, R.F.; Buckhom, W.J. 1971. Pine engraver, *Ips pini*, in the Western States. Forest Pest Leaflet 122. U.S. Department of Agriculture, Forest Service. 5 pp.

Schmid, J.M.; Hinds, T.E. 1974. Development of spruce-fir stands following spruce beetle outbreaks. Res. Pap. RM-131. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 16 pp.

Schmitz, R.F. 1988. Understanding scolytid problems in lodgepole pine forests: the need for an integrated approach. In: Payne, T.L.; Saarenmaa, H., eds. Integrated control of scolytid bark beetles. Proceedings, IUFRO Working Party and 17th International Congress of Entomology symposium; 1988 July 4; Vancouver, BC. Blacksburg, VA: Virginia Polytechnic Institute and State University: 23 l-245.

Schowalter, T.D.; Coulson, R.N.; Crossley, D.A., Jr. 1981. The role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. Environmental Entomology. 10: 821-825.

Stuart, J.D.; Agee, J.K.; Gara, R.I. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Canadian Journal of Forest Research. 19: 1096-1104.

Swaine, J.M. 1918. Canadian bark-beetles, Part 2. Bull. 14. Canada Department of Agriculture, Entomology Branch. 143 pp.

levels of confidence by comparing our model determinations with patterns that have occurred over the past 5-10 years and with current building permit issuance and opinion surveys. We will select the most descriptive model and refine it as needed.

How do we take advantage of the 1990 Census?

Although we are making headway with non-census data, the 1990 census data, when they become available in 1992 or 1993, promise to create a "desktop computer revolution." Along with benchmark demographic data, the census includes a survey of housing and housing units. For our purposes the census of housing will be very important because it describes the location and demographic characteristics of the people living in each housing unit. It also details ownership, condition, and value of the property (Kirchner and Thomas 1989).

The 1990 census data will be available on four census computer "summary tape files" (STFs):

- STF-1 and STF-2 will contain data on household type, race, sex, age, marital status, and detailed information on the residence obtained from the "short" census questionnaire sent to every home in the country. This information for the first time will provide good resolution in rural areas and will be traceable to the equivalent of a city block.

- STF-3 and STF-4 will contain the same basic data as the first two summary files, plus the information from the "long" census questionnaire. The long form will be answered by a 17 percent sample of households. This form will contain demographic information that fire planners may need, including income, educational background, migration, language, type and place of employment and housing information such as availability of a telephone.

In fact, this high level of resolution has created somewhat of a problem to the Census Bureau in maintainig confidentiality. In rural areas it might be possible to identify the source of some data--the income of a single ranch family for example--and the Bureau has had to incorporate methods to screen out such informalion.

One objective of our analysis will be to determine whether the detailed 17 percent survey will give us all of the demographic information we need in very sparsely populated areas, or whether we will still have to depend to some degree on other sources such as building permits and assessors' records. Much of our research will be aimed at correlating information that we can obtain from census records with factors that cause people to move into the interface area.

Micro Computers and Laser Discs

Although the 1990 census data will be available in several forms from hard copy reports to computer tapes, the most exciting improvement for computer-wise foresters will be that the information will eventually be available on laser read-only memory compact discs known as CD-ROMs, reflecting a decade of changing computer technology. By putting census data on laser discs, the Census Bureau will make great quantities of information available to the individual with a good personal computer and the computer capability to use the information. Compact discs have enormous potential because each 4-5/8-inch disc can store as much information as three computer tapes or 1,500 floppy disks. An expensive mainframe computer is not required to process information contained on a compact disc. However, one problem may be "data overkill." There is likely to be so much information that determining what information to use and how to use it efficiently will be difficult.

With the addition of a laser disc reader--available to almost every forestry or fire msnagement headquarters office for less than $1000--a microcomputer can become a desktop information system capable of printing STFs on demand.

However, despite the obvious advantages of compact discs, the Census Bureau is not releasing them as the basic medium for distributing 1990 census data because as yet, there is no standardization in disc technology. Until there is standardization as well as user-friendly software, much computer skill will be needed to use this new technology. To help users get started, the Census Bureau is making three CD-ROMS-Test Discs 1 and 2, and the 1985 American Housing Survey--available now. The discs sell for $125 each and can be ordered from the Bureau's Customer Service Office.

TIGER Files

A recent innovation, that may prove very valuable for model development and testing and for understanding wildland urban interface population dynamics, is the automated mapping system known as TIGER (Topologically Integrated Geographic Encoding and Referencing). This system has enabled the Census Bureau, working with the U.S. Geological

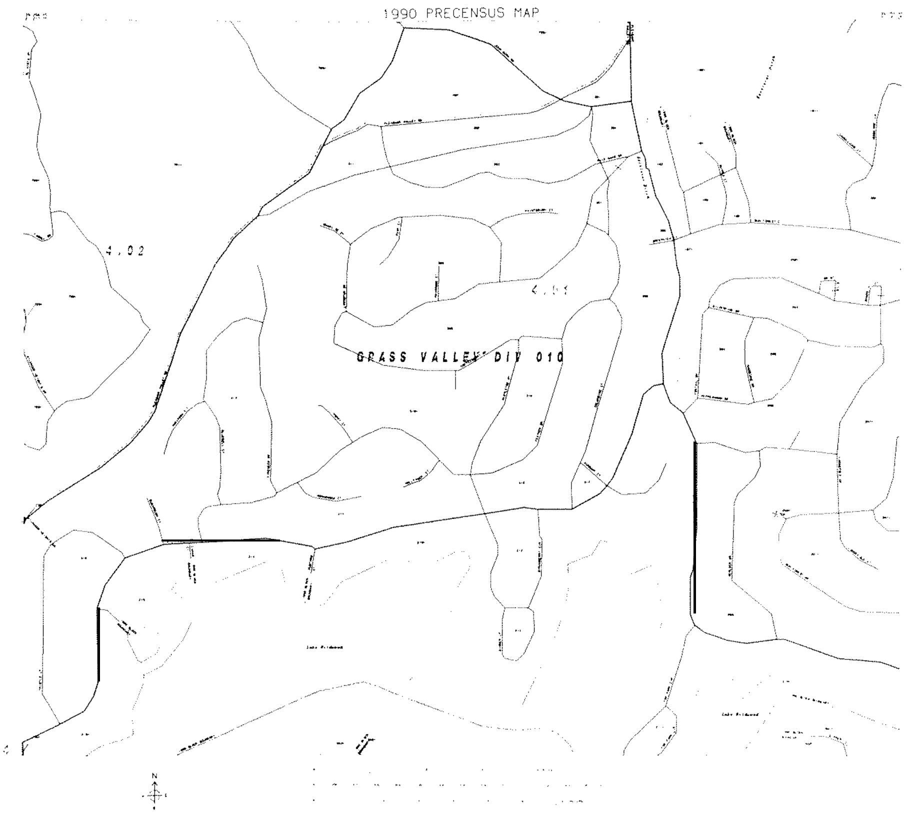

Figure 3--Section of preliminary map printed from the TIGER files. Map scale is about 4 inches to the mile. For many locations TIGER is capable of generating the most detailed and up-to-date maps available.

Survey, to develop computerized maps covering the entire United States (U.S. Department of Commerce 1985). TIGER is essentially a digital street map of the country (Fig. 3). The TIGER process uses geographical information system (GIS) technology that translates the intersection of boundaries of one type of information--census related information, for example--with information from another geographic feature.

The Bureau's preliminary plans envision TIGER boundary files for counties, census tracts, block numbering areas, and county subdivision. The road systems are so complete that forestry agencies should take a good look at them from the standpoint of updating their own transportation systems. The TIGER files currently are available only on magnetic tape, but the Bureau is looking at the possibility of releasing TIGER on CD-ROM as well.

As of now, TIGER files contain only geographical information--individual streets and other features digitally coded by latitude and longitude. They will not contain any 1990 census data. Several software companies are planning to combine the TIGER files with 1990 census data on compact discs.

Geographical Information System Technology

Desktop demographic systems become even more powerful when linked to geocoding and mapping software--geographical information systems (GIS). GIS technology and the proposed census data systems are virtually made for each other. Geographical information systems analysis can overlay many features about an area's population and urban development with data about the physical characteristics of the area (Thompson 1989). A GIS also provides a set of tools necessary to model and understand the flow of people, resources and commodities into and through the interface--essentially a depiction of the infrastructure.

CONCLUSION

The ability to assign a latitude and longitude to in-house records will be a fast effective link between census information and our wildland urban hazard reduction and fire prevention efforts. GIS technology will allow land and fire managers to superimpose population forecasts and trends, fire behavior factors, and even past fire occurrence records, enabling projections of fire problems years before they actually occur.

Although this paper has been oriented to the wildland urban interface fire problem, the potential for demographic research is much greater. The dynamics of populations and their attitude toward wildlands and their management affect all phases of forestry. We expect that many of the concepts and models that we are developing will apply equally to other forestry problems from wildlife management to watershed management.

LITERATURE CITED

Befort, W.A., A.E. Luloff, and M. Morrone. 1988. Rural land use and demographic change in a rapidly urbanizing environment. Landscape and Urban Planning, 16: 345356.

Bradshaw, T. K. 1987. The intrusion of human population into forest and rangelands of California. In: Proceedings of the Symposium on Wildland Fire 2000. April 27-30, 1987, South Lake Tahoe, California. Gen. Tech. Rep. PSW-101. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 15-21.

California Department of Forestry and Fire Protection. 1988. California's forest and range lands: growing conflict over changing uses. Forest and Rangeland Resources Assessment Program Report. Sacramento, CA. 347 p.

Davis, J. B. 1990. The wildland urban interface: paradise or battleground. Jour. of Forestry, Jan. 1990

Herbers, J. 1986. The new heartland. Times Books. Random House Inc., New York. 228 p.

Irwin, R. L. 1987. Local planning considerations for the wildland-structural intermix in the year 2000. P. 38-46. in Proc. Wildland Fire 2000. South Lake Tahoe, Calif., USDA For. Serv. Gen. Tech. Rep. PSW-101.

Irwin, R. L. 1988. What are we waiting for? In: Fire Safe California: Survival by Design. March 23,1988, California State University, Pomona; Pomona, CA. California Department of Forestry and Fire Protection, Sacramento, CA.

Kirchner, Russell J. and Richard K. Thomas. 1989. Desktop decisions. American Demographics. 11(8): pp 34-37.

Lindhult, Mark S., Julius Fabos, Pam Brown, and Nancy Price. 1988. Using geographic information to assess conflicts between agriculture and development. Landscape and Urban Planning 16: 333-343.

Long, Michael C. 1983. Understanding census data. Western Economics Research Co. Sherman Oaks, CA. 72 p.

Phillips, Clinton B. 1983. Instructions for zoning fire hazard severity in state responsibility areas in California. California Department of Forestry and Fire Protection. Sacramento, CA. 85 p.

Rice, Carol L. 1987. What will the western wildlands be like in the year 2000? future perfect or future imperfect. In: Proceedings of the Symposium on Wildland Fire 2000. April 27-30, 1987, South Lake Tahoe, California. Gen. Tech. Rep. PSW-101. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 26-31

Sweeney, Joan. 1979. Sierra lure--urban dropouts bring urban problems. Los Angeles Times. March 25.

Thompson, Boyce. 1989. Maps with brains. Governing 3(3): 40-46.

U.S. Department of Commerce, 1985. Tiger tales. Bureau of the Census. Washington DC. 48 p.

CLIMATE, FIRE, AND LATE QUATERNARY VEGETATION CHANGE IN THE CENTRAL SIERRA NEVADA

Eric G. Edlund and Roger Byrne[1]

Abstract-Fossil charcoal provides a record of significant changes in the importance of tire in the Central Sierra Nevada over the past 15,000 years. Changes in fire regime appear to be related to regional shifts in climate. During the late Pleistocene (ca. 12.5—10 ka), minimal sedimentary charcoal influx is correlated with fossil pollen and macrofossil indicators of a moist climate, probably with deeper spring snowpack than the present. In the early Holocene (10—7 ka), macrofossils indicate a shift from white and lodgepole pines to more xeric ponderosa pine-dominated forest. Charcoal influx climbs rapidly to maximum values in this zone, in conjunction with increases in fir, oak, and dwarf mistletoe pollen, along with bracken fern spores. Charcoal declines to modem values between about 7-3 ka, by which time the modem mixed conifer forest became established.

Changes in the abundance of bracken, dwarf mistletoe, oak and ponderosa pine can he strongly correlated with charcoal influx. The late-Pleistocene interval of minimum charcoal influx is a period in which dense forest surrounded the lake, indicating that fire frequency was not directly a function of fuel availability. Increasing summer drought in the early Holocene made tire an important factor in vegetation change. The zone of rapid increase in charcoal abundance, beginning 10,000 years ago, is associated with abrupt changes in vegetation, including the first appearance of ponderosa pines and firs following deglaciation.

INTRODUCTION

Concern over the potential impacts of climate change on natural ecosystems has demonstrated a need for long-term studies of vegetation-climate-fire relationships. Recent workers (Overpcck and others 1990; Clark 1988a) have suggested that prolonged warm-dry climatic intervals may lead to increases in fire frequency and intensity. The relationship is not a linear one, however; a shift to a warmer, drier climate could eventually reduce fire intensities as a function of decreased biomass available for burning.

The composition of forests in the Sierra Nevada has been strongly influenced by fire. Before twentieth-century fire suppression, fire frequencies in mixed conifer forests averaged about 7-10 years (Wagener 1961; Kilgore 1973). Studies of Sierran ponderosa (Weaver 1968), red fir, and sequoia-mixed conifer forests (Kilgore 1973) have demonstrated the extent to which the dominant montane tree species are adapted to periodic fire. The role of fire in higher elevation forests, where mountain hemlock and lodgepole pine dominate today, is less clearly understood (Rundcl and others 1988). Before the twentieth century, natural fires in the Sierra Nevada are believed to have been of generally mild intensity and limited extent.

Computer modelling of forest responses to climate change (Overpcck and others 1990) has indicated that an increase in the rate of ecological disturbance accompanying potential CO_2-induced climatic changes would produce greater changes in stand composition than would climate changes alone. Such impacts are of concern in modern forest management, particularly since paleoecological work has tied fire to climate changes on time scales of hundreds of years or less. Working on lake sediments from northwestern Minnesota, Clark (1988a) found high charcoal abundance from 1400-1600 A.D., a period of warm, dry climate in the area. Fire frequency during this interval is estimated at 44 years, compared to 85-90 years during the subsequent "Little Ice Age" of the 17th—19th centuries.

The role of climate in determining fire regimes may have been even more important during the major climatic shifts which have occurred over thousands of years since the last major ice age. Good evidence for a relationship between climate and fire frequency has been uncovered in midwestem North America. Early work by Waddington (1969) documented an increase in charcoal influx at Rutz Lake, Minnesota from 8—4,000 years ago, corresponding to a shift from oak to prairie vegetation. In southern Wisconsin, Winkler and others (1986) recorded increased charcoal 6,500—3,500 yr. B.P., at a time of lowered lake levels and a shift from mixed mesophytic forest to oak savanna.

Palcoccological work in the Sierra Nevada provides a chronology of postglacial climate change inferred from shifts in vegetation (see fig. 1 for locations discussed below). Late Pleistocene pollen and macrofossil records show evidence of colder, drier conditions, with sagebrush (*Artemisia*) and juniper important components of the vegetation (Adam 1967; Batchelder 1980; Cole 1983; Davis and others 1985; Davis and Moratto 1988). At some sites, pine and fir forests developed between 12,500—10,000 years ago, probably responding to soil development and a wetter climate. In the

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[1] Department of Geography, University of California, Berkeley, CA **94720.**

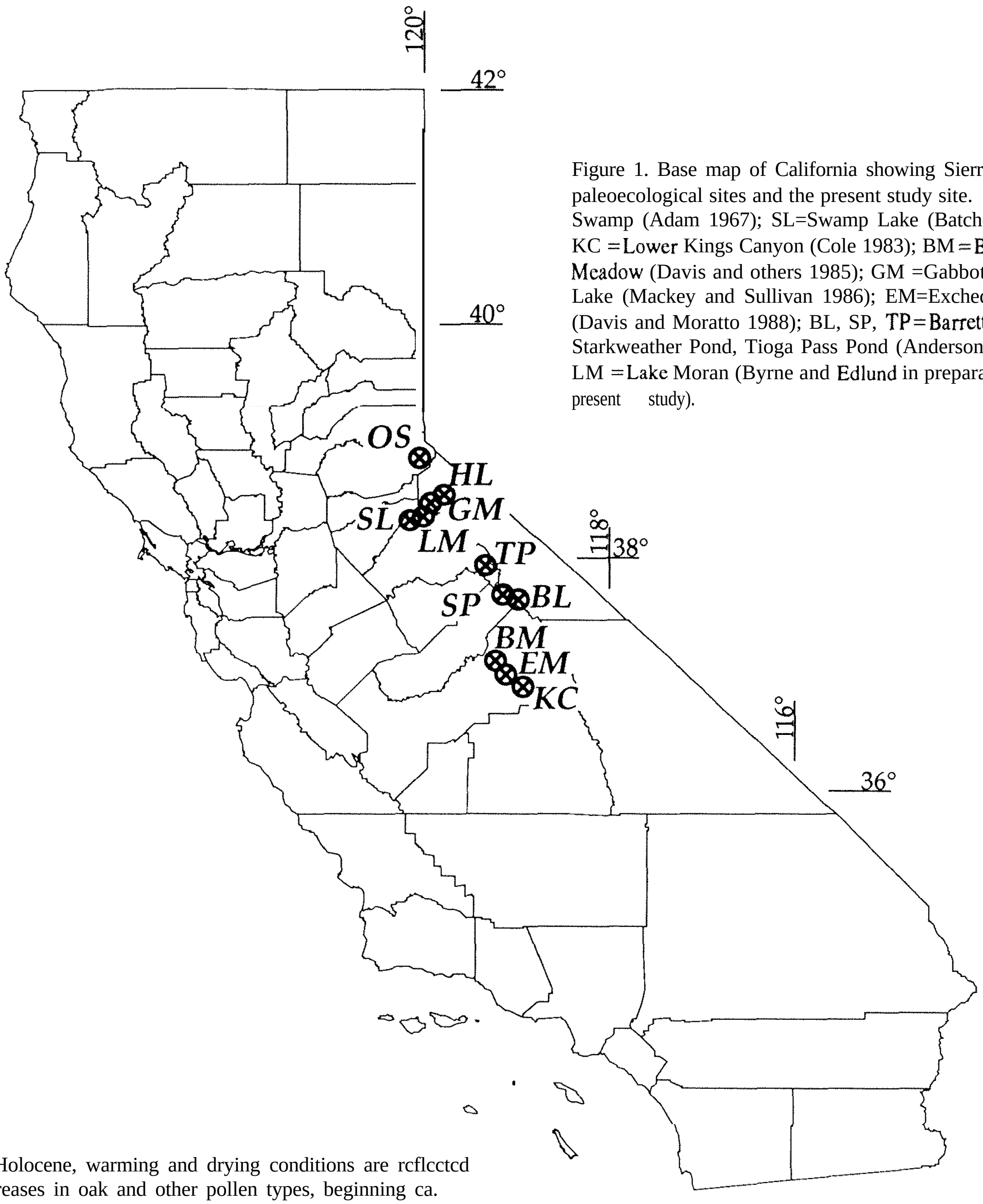

Figure 1. Base map of California showing Sierran paleoecological sites and the present study site. OS =Osgood Swamp (Adam 1967); SL=Swamp Lake (Batchelder 1980); KC =Lower Kings Canyon (Cole 1983); BM=Balsam Meadow (Davis and others 1985); GM =Gabbot Meadow Lake (Mackey and Sullivan 1986); EM=Exchequer Meadow (Davis and Moratto 1988); BL, SP, TP=Barrett Lake, Starkweather Pond, Tioga Pass Pond (Anderson 1990); LM =Lake Moran (Byrne and Edlund in preparation, and present study).

early Holocene, warming and drying conditions are reflected in increases in oak and other pollen types, beginning ca. 10—9,000 yr. B.P., and lasting until at least 6,500—5,000 yr B.P. (Mackey and Sullivan 1986; Byrne 1988; Davis and Moratto 1988; Anderson 1990). High elevation sites record increased effective precipitation beginning about 6,000 yr. B.P. (Anderson 1990). At some of the lower lake sites, warm-climate indicators persist until ca. 4,000—3,000 yr. B.P., when fir increased in response to the onset of Neoglacial cooling (Adam 1967).

The early Holocene xerothermic interval has been widely recognized in western North America. Mathewes (1985) summarized work in British Columbia documenting xerothermic conditions 1 0—7,000 yr. B.P., following an interval of cool moist climate in the late Pleistocene (12-10 ka). He argued that douglas-fir, alder, and bracken fern, which reach maximum levels in pollen records over this interval, are fire-adapted species which responded to increased tire frequency along with climatic warming.

In the Sierra Nevada, the existing evidence for changes in the role of fire during postglacial time is quite limited. At Exchequer Meadow (Davis and Moratto 1988), sedimentary charcoal reaches maximum abundance in deposits dated approximately 8,000—4,000 yr. B.P. At nearby Balsam Meadow (Davis and others 1985), macroscopic charcoal appears only after ca. 7,000 yr. B.P.

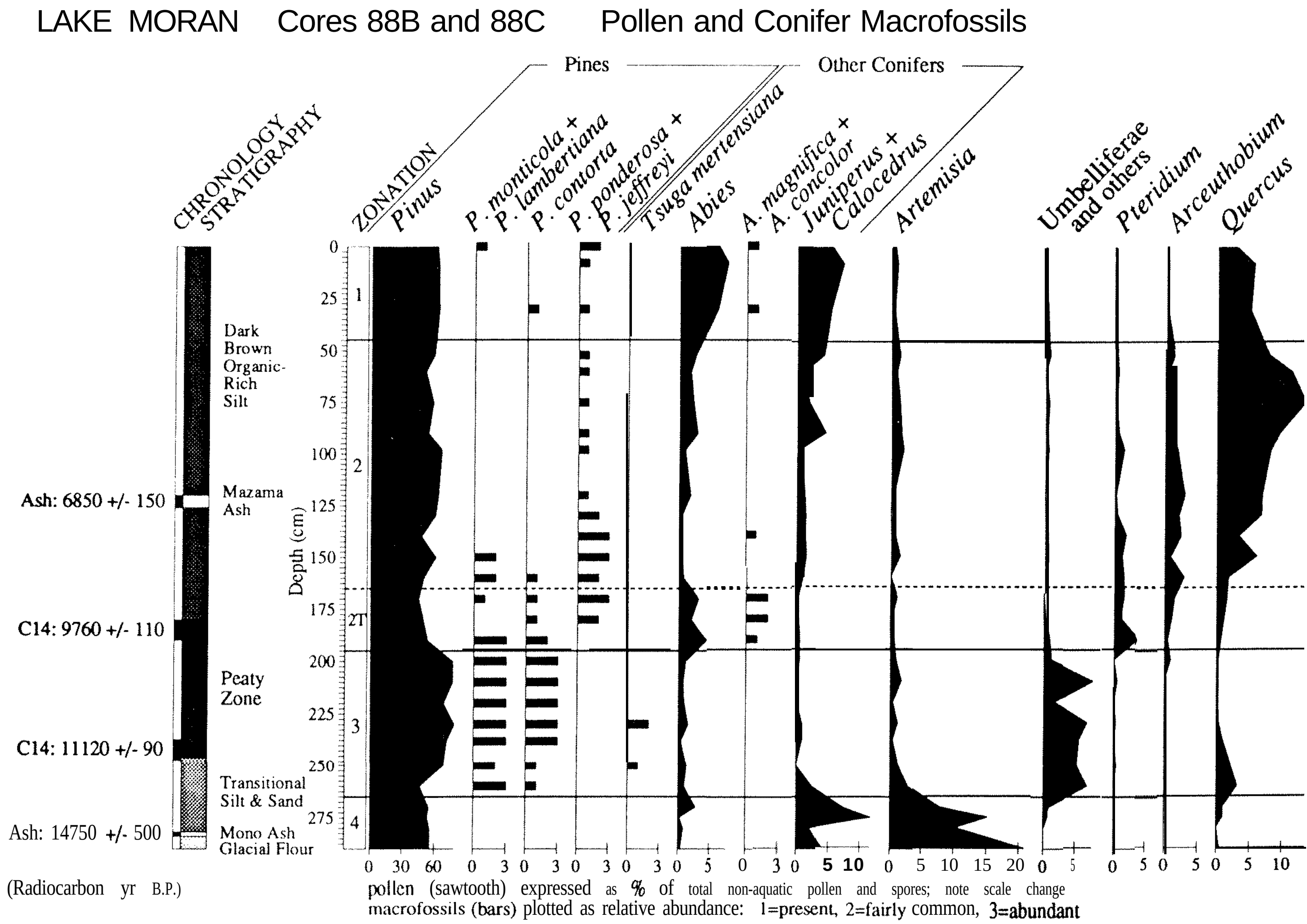

Figure 2. Selected pollen and macrofossils from Moran cores 88B and C. Sawtoothed pollen curves, labeled with genus or family name, indicate abundance as a percentage of total non-aquatic pollen grains and spores counted. Macrofossil bars, labeled by species, indicate relative abundance (see text). Zonation is by the authors. Radiocarbon dates were obtained from Beta Analytic, and volcanic ash layers were identified by Andrei Sama-Wojcicki, U.S.G.S.

METHODS

The lake sediment samples analyzed for this project were taken in October, 1988, using a standard Livingstone piston corer with 2" diameter barrel. Two cores, 88B and C, were taken within 2 meters of one another, and correlated by depth and stratigraphy. Cores were transported intact to the U.C. Berkeley Pollen Lab. Core B was used for macrofossil analysis, while core C was subsampled at 10-20cm intervals for pollen and microscopic charcoal analysis. ^{14}C dates were obtained on two ten-centimeter segments of core 88C. Two volcanic ash layers present in the cores were identified by Andrei Sama-Wojcicki at the United States Geological Survey in Menlo Park.

Extraction and preparation of pollen samples followed standard procedures as described by Faegri and Iversen (1975). Each pollen and charcoal sample underwent the same preparation, in order to eliminate differential effects of chemical treatments on the samples (Clark 1984). Pollen concentrations were calculated based on the ratios of *Lycopodium* control grains counted at each level. The curves of taxon abundance in Figure 2 are plotted as percentage of total non-aquatic pollen and spores counted; a total of at least 300 grains was identified at each level in the core. The diagrams were compiled using CALPALYN (Bauer and Orvis 1990).

Core 88B was sampled in measured segments of 5 or 10cm. Macrofossil sampling was based on standard procedures described by Birks (1980). Identification of pine needles was accomplished by comparing external morphology and thin sections with reference material and with Harlow's (1947) photographic key. For each sample, we calculated the total length of needle remains of each taxon. For Figure 2, length values were classified on a scale from 1, "present," with only one or two fragments per sample, to 3, "abundant," with total needle length exceeding 200mm per sample.

Microscopic charcoal was analyzed using 400x magnification and an ocular grid with squares 19.8 pm on a side. All charcoal fragments larger than one-half of a grid square were assigned to the appropriate size class, and the total area of charcoal was calculated. Calculated charcoal concentration

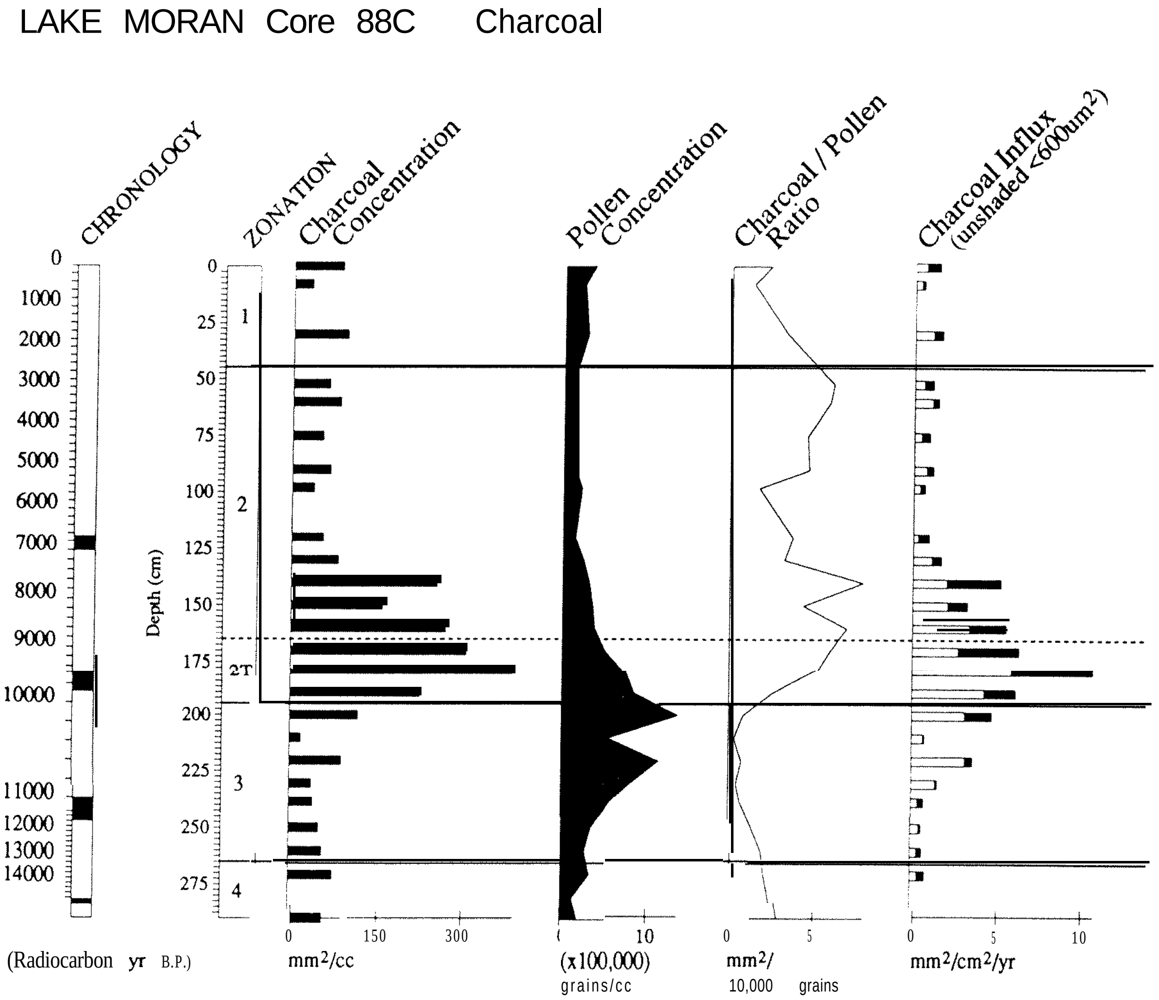

Figure 3. Charcoal and pollen indices for Moran core 88C. Sample depths and zonation are the same as in Figure 2 Calculated charcoal influx is divided into the share of fragments smaller (unshaded) and larger than $600\mu m^2$.

and influx to the lakebed are based on the ratio of counted charcoal to counted *Lycopodium* control spores (fig. 3). Sedimentation is estimated at a linear rate between radiocarbon and ash dates. Influx is not estimated for the glacial flour sample below the lowest tephra date. To control for variation in charcoal influx due to sedimentation processes, the ratio of charcoal to pollen was calculated for each sample (Cwynar 1978).

Charcoal Taphonomy

Questions of interpretation of sedimentary charcoal have been discussed in detail by Patterson and others (1987) and Clark (198817). Charcoal in lake sediments ranges in size from tine dust, ≤ 2 micrometers in diameter, to macroscopic fragments centimeters in length. Like dust, small particles may travel long distances once entrained. Charcoal may reach high altitudes in the convective plume which rises from a fire. More intense tires produce higher plumes, resulting in longer-distance transport of all size classes of charcoal. The smallest sizes of charcoal may reflect a subcontinental source (Clark 1988b). As a result, even lakes in areas of 20th century tire suppression contain high levels of charcoal in recent sediments (e.g., Lake of the Clouds, MN, Swain 1973). Conversely, local tires, recorded as fire scars on trees, may go unrepresented in lake sediments if the plume convects most charcoal beyond the lake basin (Patterson and others 1987).

Lakes with small watersheds can accurately record local fires (Anderson and others 1986). Lake Moran is a small lake with no inlet stream, and a drainage basin of about 12 hectares. In this setting, it may be expected that larger microscopic charcoal fragments in the lake sediments originated from nearby fires, while the smallest fragments record events within a larger region. Figure 3 breaks microscopic charcoal influx into small fragments, $<600\mu m^2$ in area, and larger pieces, which ranged up to $>14{,}500\mu m^2$. We assume that the fires which produced the larger charcoal fragments probably occurred within 5-10 km of the lake (cf. Clark 1988b).

VEGETATION HISTORY AND THE RECORD OF FIRES AT LAKE MORAN

The Mono Craters and Mazama ash layers and radiocarbon dates provide a chronology for the Lake Moran sediments. The lake was exposed by ice retreat some 15,000 years ago This represents an early date for Tioga (late-Wisconsin) deglaciation in the Sierra Nevada, confirming Batchelder's (1980) report from nearby Swamp Lake.

The earliest pollen assemblages (zone 4 on figure 2) reveal an open vegetation of sagebrush (*Artemisia*), juniper, and pines. This environment must have been effectively drier than the present study area, perhaps similar in appearance to higher subalpine environments today. No identifiable macrofossils are present in these sediments. Sedimentation rates were slow following the initial formation of the basin, and the calculated annual charcoal influxes are among the lowest in the core. Some large charcoal fragments ($> 2500\ \mu m^2$ in area.) are present, but it is uncertain whether these fragments blew into the lake from nearby fires, or were simply redeposited by the melting of the nearby glacier.

In late-Pleistocene zone 3, spanning ca. 12,500—10,000 yr. B.P., pine needles and high percentages of pine pollen indicate the establishment of a closed-canopy forest throughout much of the area (Figure 2). This forest signal is accompanied by increases in taxa normally associated with meadows, including members of the Umbelliferae, Liliaceae, Onagraceae, Malvaceae, and Ranunculaceae. (These taxa are grouped as "Umbelliferae and others" in Figure 2). The presence of mountain hemlock (*Tsuga mertensiana*), white pines (*Pinus monticola* and *P. lambertiana),* and lodgepole pine *(P. contorta* ssp. murrayana) indicate a moister climate than that found in the Sierra Nevada today. The meadow taxa may have become established on sites too wet for tree growth. During this time, deep snowpacks may have persisted late into the summer, damping the effects of California's summer drought season. Charcoal concentration is generally lower in this interval than anywhere else in the core (Figure 3). The ratio of charcoal to pollen is consistently low, and larger charcoal fragments ($> 600 \mu m^2$) are virtually absent. The evidence suggests that fires rarely burned the dense forest which surrounded the lake.

The Pleistocene/Holocene transition (subzone 2T) is marked by rapid increases in all measures of charcoal abundance (Figure 3). Charcoal concentration and influx reach maximum values here, at levels 5-10 times greater than in modern or late-Pleistocene sediments. Lodgepole and white pines were beginning to be replaced by yellow pines *(P. ponderosa* and/or *P. jeffreyi*) (Figure 2). During this transitional period, persisting less than 1000 years, firs (both *Abies magnifica* and *A. concolor)* became important constituents of the Moran forest.

The pollen record for zone 2 (Figure 2) shows a small relative decrease in pines, with increases in oaks and bracken fern (*Pteridium*). The evidence reveals a more open forest, with warmer summers allowing an increase in the relative importance of oaks. Dwarf mistletoe *(Arceuthobium)* pollen increases in this interval, perhaps indicating that conifers were under increasing ecological stress. Charcoal influx remains high until ca. 7,000 yr. B.P., dropping off to near-modem levels just above the Mazama ash layer (Figure 3).

Interestingly, both the charcoal/pollen ratio curve and the oak percentage curve (fig. 2) show continued high values through the middle Holocene (7,000—3,000 yr. B.P.). Since there is no evidence for changes in the lake's sedimentation regime, we rely on the consistently low charcoal influx values to infer a decrease in the intensity of fires during this interval, compared to the early Holocene; however, the oak, bracken and sagebrush suggest that the forest remained drier and more open than it is today. By 3,000 yr. B.P., Neoglacial cooling and/or increasing moisture allowed fir, lodgepole, and sugar pine to reoccupy the lake margin. Fire has remained less important than it was in the early Holocene, although modem charcoal influx exceeds late-Pleistocene minimum values.

The important implication of the high charcoal values is that the early Holocene was a period of more extensive and more intense fires than either the late Pleistocene or the late Holocene. Indeed, it seems likely that an increase in the importance of fire was the mechanism by which the changing postglacial climate produced dramatic shifts in vegetation. The source of the early Holocene charcoal may well have been the dense late-Pleistocene forest, which began to bum under a more xeric climatic regime.

Temporal changes in several pollen and macrofossil types show a strong correlation with the charcoal signal. Bracken is highly correlated with total charcoal influx, as is fir to a somewhat lesser extent. The latter relationship is puzzling but important; fir is not normally considered a fire-adapted species, particularly compared to its associates in the Sicrran montane forest. Red fir *(Abies magnifica*), the first species to appear in the macrofossil record, may have been able to effectively colonize fire-cleared patches, or it may have become established on soil fertilized by increased nutrient cycling under more frequent fires. In zone 2, increases in ponderosa pine, oak and dwarf mistletoe lag behind charcoal influx, but generally the curves for these taxa parallel the changes in the charcoal/pollen ratio. Umbelliferae and Cupressaceae pollen are negatively correlated with charcoal, as are lodgepole (*Pinus contorta*) and white pines *(P. lambertiana* and *P. monticola).*

CONCLUSIONS

Our results suggest that Sierran fire regimes have changed as a function of climate. In the Sierra Nevada, fire frequency and intensity are controlled by California's strongly seasonal precipitation regime. Today, summer drought makes fires increasingly likely in September and October, before the first winter rains. The Lake Moran record shows that from 12,000 to 10,000 years ago, summer drought was less pronounced than today, probably as a result of late-spring snowstorms and/or snowpack persisting into the summer. At that time, warm summers coupled with more abundant moisture led to the development of a dense mixed conifer forest, comprising several species which no longer grow together in the Sierra Nevada. Fire was less important as an ecological factor in this late-Pleistocene forest than in the Holocene.

At 10,000 yr. B.P., in association with a rapid increase in fossil charcoal influx, the local vegetation changed abruptly. Red fir and ponderosa pine first appeared at this time. Conversely, western white pine disappeared from the site, and lodgepole and sugar pine began a more gradual decline. Bracken fern became much more important about 10,000 years ago, while oak and dwarf mistletoe pollen increased more gradually, reaching maximum pollen percentages between 9,000–3,000 yr. B.P. We infer rapid environmental changes beginning at the end of the Pleistocene. The Lake Moran record demonstrates the importance of fire as a determinant of vegetation during this climatically significant period.

LITERATURE CITED

Adam, D.P. (1967). Late-Pleistocene and recent palynology in the Sierra Nevsda, California. In Cushing, E.J. and H.E.Wright, Jr., eds., Quaternary Paleoecology, pp. 275-301. New Haven: Yale University Press.

Anderson, R.S. (1990). Holocene forest development and paleoclimates within the central Sierra Nevada, California. Journal of Ecology (in press).

Anderson, R.S., R.B.Davis, N.G.Miller, and R.Stuckenrath (1986). History of late- and post-glacial vegetation and disturbance around Upper South Branch Pond, northern Maine. Canadian Journal of Botany 64: 1977-1986.

Batchelder, G.L. (1980). A late Wisconsin and early Holocene lacustrine stratigraphy and pollen record from the west slope of the Sierra Nevada, California. American Quaternary Association, 6th Biennial Meeting, Program and Abstracts, p. 13.

Bauer, R.L. and K.H.Orvis (1989). CALPALYN Pollen Diagram Program. University of California, Berkeley Pollen Lab.

Birks, H.H. (1980). Plant macrofossils in Quaternary lake sediments. Archiv für Hydrobiologie Beihefte: Ergebnisse der Limnologie 1.5: 1-60.

Byrne, R. (1988). Late-Quaternary climate and vegetation change in the central Sierra Nevada of California. 73rd Annual Ecological Society of America Meeting, Programs and Abstracts, p. 89.

Clark, J.S. (1988a). Effect of climate change on fire regimes in northwestern Minnesota. Nature 334: 233-23.5.

Clark, J.S. (1988b). Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling. Quaternary Research 30: 67-80.

Clark, R.L. (1984). Effects on Charcoal of Pollen Preparation Procedures. Pollen et Spores 26: 559-576.

Cole, K. (1983). Late-Pleistocene vegetation of Kings Canyon, Sierra Nevada, California. Quaternary Research 19: 117-129.

Cwynar, L. (1978). Recent history of fire and vegetation from laminated sediment of Greenleaf Lake, Algonquin Park, Ontario. Canadian Journal of Botany 56: 10-21.

Davis, O.K., R.S.Anderson, P.L.Fall, M.K.O'Rourke, and R.S.Thompson (1985). Palynological evidence for early Holocene aridity in the southern Sierra Nevada, California. Quaternary Research 24: 322-332.

Davis, O.K. and M.J.Moratto (1988). Evidence for a warm dry early Holocene in the western Sierra Nevada of California. Madroño 35: 132-149.

Faegri, K. and J.Iversen (1975). Textbook of pollen analysis, Third Edition. New York: Hafner Press.

Harlow, W.M. (1947). The identification of the pines of the United States, native and introduced, by needle structure. New York State College of Forestry Technical Publication 32.

Kilgore, B.M. (1973). The ecological role of fire in Sierran conifer forests: its application to national park management. Quaternary Research 3: 496-S 13.

Mackey, E.M. and D.G.Sullivan (1986). A 10,000 year palynological and stratigraphic record from Gabbot Lake, Alpine County, California. American Quaternary Association, 9th Biennial Meeting, Programs and Abstracts, p. 95.

Mathewes, R.W. (1985). Paleobotanical evidence for climatic change in southern British Columbia during late-glacial and Holocene time. Syllogeus 55: 397-422.

Overpeck, J.T., D.Rind, and R.Goldberg (1990). Climate-induced changes in forest disturbance and vegetation. Nature 343: 51-53.

Patterson, W.A., K.J.Edwards, and D.J.Maguire (1987) Microscopic charcoal as a fossil indicator of fire. Quatemary Science Reviews 6: 3-23.

Rundel, P.W., D.J.Parsons, and D.T.Gordon (1988). Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In Barbour, M.J. and J. Major, eds., Terrestrial Vegetation of California (2nd edition), pp. 559-599. California Native Plant Society, Special Publication 9.

Swain, A.M. (1973). A history of fire and vegetation in northeastern Minnesota as recorded in lake sediments. Quaternary Research 3: 383-396.

Waddington, J.C.B. (1969). A stratigraphic record of the pollen influx to a lake in the Big Woods of Minnesota. Geological Society of America Special Paper 123: 263-283.

Wagener, W.W. (1961). Past fire incidence in Sierra Nevada forests. Journal of Forestry 59: 739-748.

Weaver, H. (1968). Fire and its relationship to ponderosa pine. Proceedings Tall Timbers Fire Ecology Conference 7: 127-149.

Winkler, M.G., A.M.Swain, and J.E.Kutzbach (1986). Middle Holocene dry period in the northern Midwestern United States: lake levels and pollen stratigraphy. Quatemary Research 25: 235250.

FIRE-HERBICIDE SYSTEMS FOR MANIPULATING JUNIPER

D.M. Engle and J.F. Stritzke[1]

Abstract-Fire exclusion results in extensive encroachment of tire-intolerant junipers, specifically eastern redcedar (Juniperus_virginiana) and ashe juniper (J. ashei) into tallgrass prairies and other grasslands and hardwood forests of the central U.S. Control of both juniper species is possible with tire because they do not sprout from roots and so they are killed by intense fires that scorch the crown. However, low-intensity tires on sites with dense stands of junipers do not scorch crowns of larger juniper trees. One objective of our studies was to determine the effect of various paraquat treatments on juniper foliage water content, a primary factor affecting flammability of juniper crowns. A second objective was to determine if paraquat pretreatment would increase crown scorch from broadcast tires in tallgrass prairie. We evaluated leaf water content of eastern redcedar treated individually with two rates (0.3 or 1.1 kg/ha) of paraquat, in two carriers (water, oil-in-water emulsion), and at two volumes (47 or 188 I/ha) of carrier. The oil-in-water emulsion carrier reduced leaf water content more consistently than the other carriers, so we used the oil-in-water emulsion carrier in a study of paraquat applied aerially in early August. Rate ranged from 0.3 to 3.4 kg/ha and included two volumes (47 or 94 I/ha). All aerial applications of paraquat reduced juniper leaf water content to 50 percent or less three weeks after treatment compared to 100 percent water in untreated junipers. Leaf water content in the late summer dry season will normally decline to about 80 percent, a level too moist for ignition of juniper foliage. Combining paraquat with burning almost doubled the crown scorch of large trees over either treatment alone and increased kill of large trees to more than 50 percent compared to no trees killed with the burning-only or paraquat-only treatments.

INTRODUCTION

Tallgrass prairie and other grasslands of North American are regarded as tire-tolerant systems which evolved with fire as a part of the natural disturbance regime (Anderson 1982). Protection from fire results in extensive encroachment of tire-intolerant woody species, including eastern redcedar and ashe juniper into tallgrass prairies as well as into other grasslands and hardwood forests of the central U.S. (Arend 1950; Bragg and Hulbert 1976; Wright 1978). Juniper encroachment into these ecosystems has increased exponentially in recent years, modifying the physiognomy of these ecosystems and reducing their value as rangelands (Wright and Bailey 1980; Snook 1985).

Tallgrass prairies that become dominated by juniper are similar to other ecosystems that were previously grasslands or savannahs but now have successional processes driven by woody vegetation. Upon reaching a transitional threshold promoted by reduced tire frequency and intensity, new successional processes prevent reversion to grassland from overstory dominance by woody species, and fire is no longer an effective agent in reversing succession to grassland (Archer 1989; Bryant and others 1983; Walker and others 1981). Drastic anthropogenic modification (i.e., herbicides or mechanical manipulation) of the woody vegetation is necessary to convert the plant community to dominance by herbaceous plants (Archer 1989; Engle 1987).

Fire kills both species of juniper if tine fuel loading is sufficient to produce an intense fire that completely scorches the crown because neither species sprouts from roots or stems after topkill (Owensby and others 1973; Wink and Wright 1973). However, tree mortality decreases as tree size increases so fire intensity must increase to scorch the crown of taller trees (Bryant and others 1983; Dalrymple 1969; Engle and others 1988). Fire intensity and tree mortality are reduced further in dense stands of large trees because junipers reduce the production of tine fuel so that tires in these stands are of low intensity or perhaps fires fail to carry at all (Bryant and others 1983; Engle and others 1987).

Junipers are often controlled mechanically or by herbicides, but mechanical and herbicide methods of juniper control are generally either too expensive or are ineffective on large trees (Scifres 1980; Stritzke 1985). Small trees can be controlled individually with some soil-applied herbicides and paraquat applied in hot weather can result in considerable damage to trees (Engle and others 1988). Integration of several brush control treatments into a single set of treatments, i.e., integrated brush management, is one way to deal effectively with brush (Scifres 1980). Paraquat applied to individual trees in the summer has increased juniper crown damage from broadcast bums the following spring with light fine fuel loading (Engle and others 1988). A combination of broadcast application of paraquat followed by a prescribed burn has been suggested as an integrated method to control severe infestations of juniper (Engle and others 1988). We

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[1] Professors of Range Science and Weed Science, respectively, Oklahoma State University, Stillwater, OK.

conducted two studies, each with a separate objective: 1) to determine the effect of various paraquat treatments on juniper foliage water content, a primary factor affecting flammability of juniper crowns (Bunting and others 1983), and 2) to determine if aerial application of paraquat will reduce foliage water content and increase crown scorch from broadcast fires in tallgrass prairie.

METHODS

Study 1 was conducted on two sites approximately 15 km southwest of Stillwater, OK on the Oklahoma Agricultural Experiment Station's Agronomy Research Range. Shallow prairie was the primary range site of one location and red clay prairie was the primary range site of the other location. About 2800 kg/ha of tine fuel are produced on both sites in a normal year. Herbaceous understory was dominated by tallgrasses and eastern redcedar canopy cover was less than 5 percent.

Paraquat was foliar applied to individual eastern redcedar trees on August 17-18, 1988 with a compressed-air hand sprayer using a T-3 conejet nozzle to simulate aerial application. Treatments were in a factorial arrangement of paraquat (0.3 or 1.1 kg/ha), carrier (water or oil-in-water emulsion), and volume of carrier (47 or 188 l/ha). The design was completely randomized with ten replications on each of two sites located approximately 5 km apart. Eastern redcedar foliage was sampled at weekly intervals (August 24, September 1, and September 8) following treatment, weighed in the field, and dried in a forced-air oven to determine foliage water content, which is expressed on the basis of dry weight.

Study 2 was conducted in Johnston County, OK, approximately 30 km northeast of Ardmore, OK. The study area is located on a loamy prairie range site normally producing about 3900 kg/ha of forage in the absence of juniper interference. Ashe juniper, with canopy cover of approximately 25 percent, was the overstory woody dominant. The understory was a mixture of tallgrasses and midgrasses. Paraquat was applied aerially in the oil-in-water emulsion carrier to ashe juniper on August 9, 1989. Herbicide treatments included no herbicide treatment and paraquat applied at rates ranging from 0.3 to 3.4 kg/ha. Paraquat rate treatments were nested within two volumes (47 or 94 l/ha) of the carrier. Plots were 0.1 ha (30 X 30 m). The design was a randomized complete block with four blocks. Foliage was sampled three weeks after paraquat treatment, weighed in the field, and dried in a forced-air oven to determine foliage water content, which is expressed on the basis of dry weight.

Two blocks were burned with a headfire on September 1, 1989. At the time of the bum, air temperature was 38°C, relative humidity was 40%, average wind velocity was 8 km/h, and tine fuel loading within the juniper stand was visually estimated at 1500 kg/ha. Crown damage to trees and tree kill were determined in all treatment plots two months after the bum. Visual estimates of crown damage and tree kill were conducted on three size classes based on tree height: small (0.8 to 1.5 m), medium (1.5 to 2.5 m), and large (2.5 to 5.0 m).

We subjected the data from both studies to analysis of variance. Leaf water data from study 1 and study 2 were analyzed as repeated measures in time (Winer 1971). Means were separated by LSD subject to a protected F-test at the 95% probability level as suggested by Carmer and others (1989).

RESULTS

Study 1

Study site interacted ($P < 0.0001$) with treatment and sampling date so data from each study site were analyzed separately. No treatment effects were significant one week after paraquat application, but by two weeks after treatment, paraquat rate interacted with both carrier and volume of carrier ($P < 0.0224$ and $P < 0.0182$, respectively) at Site 2 (fig. 1). Water content of foliage with all treatments increased the second week after treatment, which we attributed to a change in available soil water in response to 20 millimeters of precipitation on August 28 between the first and second week after treatment. By the third week after treatment, leaf water had dropped drastically in trees in all treatments, with some below 50 percent leaf water. Paraquat treatment rate, volume, and carrier interacted at study Site 1 and 2 on the third week after treatment ($P < 0.0163$ and $P < 0.0002$, respectively). Foliage water content was lower in trees treated with the 1.1 kg/ha rate of paraquat and results were more consistent with the oil-in-water carrier (fig. 1).

Study 2

Leaf water content did not differ ($P > 0.1288$) between the two volumes of carrier on either sampling date so we averaged the rate data over the two volumes. Leaf water content was less in foliage of treated trees than in untreated trees two weeks after paraquat treatment and declined to 50 percent or less by three weeks after treatment with all rates of paraquat ($P < 0.0001$) (fig. 2). Although increasing rate of paraquat was not additive, all rates of paraquat desiccated ashe juniper foliage to the extent necessary to increase flammability by three weeks after treatment (Bunting and others 1983). Although juniper leaf water was higher in 1989 than in normal years (Engle and others 1988), leaf water content in the late summer dry season will normally decline only to about 80 percent, a level too moist for ignition of juniper foliage.

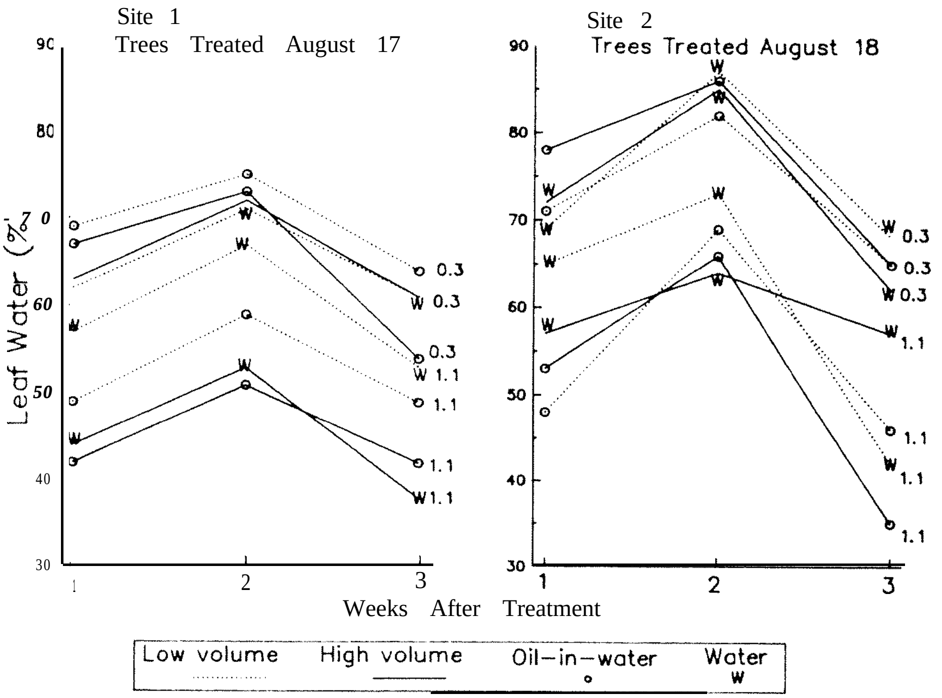

Figure 1 .- Leaf water (%) after paraquat application at Site 1 and Site 2. Paraquat rate (0.3 or 1.1) is in kg/ha. Low volume of carrier is 47 l/ha and high volume is 188 I/ha. Values are means of 10 trees. $LSD_{0.05}=13$ at Site 1 and $LSD_{0.05}=22$ at Site 2 on week 3. Foliage of untreated trees was 80% water at both study sites on September 8.

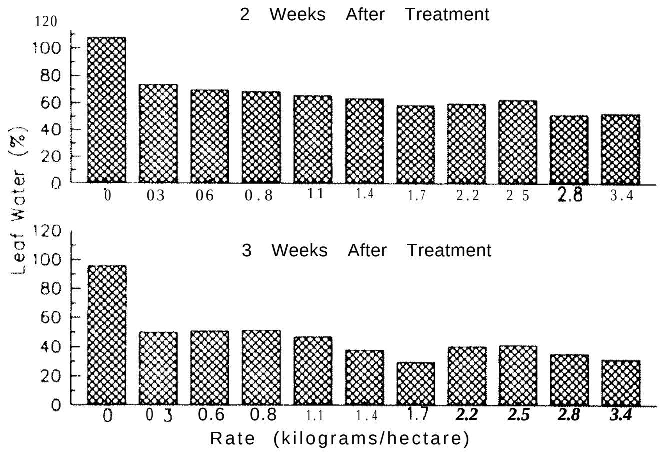

Figure 2.- Leaf water (%) two weeks and three weeks after paraquat was aerially applied on August 9, 1989. Valued are means of 8 trees, averaged over volume of carrier ($LSD_{0.05}=10$ on week 2 and $LSD_{0.05}=11$ on week 3).

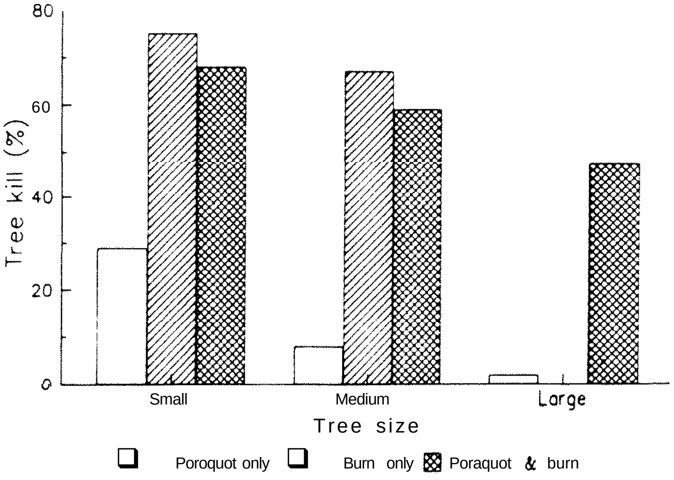

Figure 3.- Crown damage (%) two months after burning. Values for paraquat only treatments are averaged over rate. Treatments were not different ($P>0.0604$) for small and medium trees, but treatments were different ($P<0.0319$) for large trees ($LSD_{0.05}=27$).

Figure 4.- Tree kill (%) two months after burning. Values for paraquat only treatments are averaged over rate. Treatments were not different ($P>0.3031$) for small trees, but treatments were different ($P < 0.0392$) for medium and large trees ($LSD_{0.05}=48$ and 31, respectively).

The amount of crown damage to trees was not affected by either carrier volume or paraquat rate within the paraquat plus burn treatment for any size of tree ($P>0.1247$). However, crown damage and tree kill of medium and large trees differed ($P < 0.0604$) among the three treatments (paraquat only, burn only, or paraquat plus bum) (fig. 3 and 4). Crown damage to trees from tire alone and paraquat alone was similar to the results of previous studies (Engle and others 1987). The effects of paraquat and fire on large trees were approximately additive in respect to crown damage which exceeded 80 percent in the paraquat plus bum treatment plots (fig. 3). Paraquat and burning appear to have a synergistic effect in killing large trees in that almost no trees were killed by the single treatment of either paraquat or burning but half of large trees were killed by combining the two treatments (fig. 4).

DISCUSSION

Paraquat applied in hot weather by hand to individual trees (study 1) or applied aerially in a broadcast spray (study 2) was effective in reducing juniper foliage water content to below the critical point of 60 percent water (Bryant and others 1983; Bunting and others 1983; H.A. Wright, pers. comm.). Desiccation of juniper foliage by paraquat applied aerially almost doubled the crown scorch and increased the kill of large trees from 0 to 50 percent. The results of this study are in agreement with previous work in which desiccation of juniper foliage by treating individual trees with paraquat compensated partially for light tine fuel loading in cool-season fires the spring after summer paraquat application (Engle and others 1988).

We believe it is possible to use paraquat as a desiccant to promote crown fires in closed-canopied stands of juniper. Previous attempts to ignite crown fires have been unsuccessful in dense stands of ashe juniper in Texas (Bryant and others 1983) and in pinyon (Pinus edulis) and juniper woodlands in Nevada (Bruner and Klebenow 1979) possibly because of high foliage water content, gaps in the tree canopy, and cool fire-weather conditions. Bryant and others (1983) evaluated igniting windrows of recently dozed ashe juniper to produce an intense fue with flames in contact with standing trees to produce a crown fire in dense stands of ashe juniper, but no sustained crown fire resulted. However, six standing trees were killed for every dozed tree by the windrow fire thereby reducing the overall cost of mechanical treatment of the juniper stand. Bruner and Klebenow (1979) were unable to obtain crown tires in closed stands (i.e., no understory) of pinyon-juniper and concluded that crown tires are possible only when burned under hazardous conditions.

Our research indicates an integrated approach using paraquat and fue can be used to reduce overstories of large junipers for restoring tallgrass prairie dominated by junipers. Further research is needed to determine if crown fires can be ignited from paraquat-desiccated strips in dense stands of junipers using aerial ignition with a helitorch.

ACKNOWLEDGMENTS

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LITERATURE CITED

Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: An end paper. p. 297-308 In: Estes, J.R., R.J. Tyrl, and J.N. Brunken. Grasses and Grasslands. Systematics and Ecology. University of Oklahoma Press. Norman.

Arend, J.L. 1950. Influence of fire and soil on distribution of eastern rcdcedar in the Ozarks. Journal of Forestry 48:129-130.

Archer, S. 1989. Have southern Texas savannahs been converted to woodlands in recent history? The American Naturalist 134:545-561.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29: 19-24.

Bryant, F.C., G.K. Launchbaugh, and B.H. Koerth. 1983. Controlling mature ashe juniper in Texas with crown fires. Journal of Range Management 36:165-168.

Bruner, A.D. and D.A. Klebenow. 1979. Predicting success of prescribed fires in pinyon-juniper woodland in Nevada. U.S. Forest Service. Intermountain Forest and Range Experiment Station Research Paper INT-219.

Bunting, S.C., H.A. Wright, and W.H. Wallace. 1983. Seasonal variation in the ignition time of redberry juniper in west Texas. Journal of Range Management 36:169-171.

Carmer, S.G., W.E. Nyquist, and W.M. Walker. 1989. Least significant differences for combined analyses of experiments with two- and three-factor treatment designs. Agronomy Journal 81:665-672.

Dalrymple, R.L. 1969. Prescribed grass burning for ashe juniper control. Progress Report from Noble Foundation, Inc., Ardmore, OK.

Engle, D.M. 1987. The Cross Timbers Experimental Range--tomorrow's research today. In: Rollins, D., ed. Brush Management in the Cross Timbers Proceedings. Cooperative Extension Service. Oklahoma State University. Stillwater. Circular E-862.

Engle, D.M., J.F. Stritzke, and P.L. Claypool. 1987. Effect of paraquat plus prescribed burning on eastern rcdcedar (Juniperus virginiana). Weed Technology 2:172-174.

Engle, D.M., J.F. Stritzke, and P.L. Claypool. 1988. Herbage standing crop around eastern redccdar trees. Journal of Range Management 40:237-239.

Owensby, C.E., K.R. Blan, B.J. Easton, and O.G. Russ. 1973. Evaluation of eastern redccdar infestations in the northern Flint Hills. Journal of Range Management 26:256-260.

Scifres, C.J. 1980. Brush management: Principles and practices for Texas and the southwest. Texas A&M University Press, College Station. 360 pp.

Snook, E.C. 1985. Distribution of eastern redcedar on Oklahoma rangelands. p. 45-52 In: R.W. Wittwer and D.M. Engle (eds.) Proceedings of the Eastern Redcedar in Oklahoma Conference. Cooperative Extension Service, Division of Agriculture. Oklahoma State University E-849.

Stritzke, J.F. 1985. Chemical and mechanical control of eastern redcedar. pp. 61-69. In: Wittwer, R.W. and D.M. Engle, eds. Proceedings of the Eastern Redcedar in Oklahoma Conference. Cooperative Extension Service, Division of Agriculture. Oklahoma State University. E-849.

Walker, B.H., D. Ludwig, C.S. Holling, and R.M. Peterman. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology 69:473-498.

Winer, B.J. 1971. Statistical principles in experimental design. McGraw-Hill. New York.

Wink, R.L. and H.A. Wright. 1973. Effects of fire on an ashe juniper community. Journal of Range Management 26:326-329.

Wright, H.A. 1978. Use of fire to manage grasslands of the Great Plains: Central and Southern Great Plains. pp. 694-696. In: Hyder, D.N., ed. Proceeding of the First International Rangelands Congress.

Wright, H.A. and A.W. Bailey. 1980. Fire ecology and prescribed burning in the Great Plains--A research review. U.S. Department of Agriculture. Forest Service. Intermountain Forest and Range Experiment Station. General Technical Report INT-77.

ELASTICITIES ASSIST TARGETING OF ARSON PREVENTION PROGRAMS

R.A. Kluender and L.C. Thompson”

Abstract-Elasticities (percentage change in one factor divided by percentage change in another factor) were calculated to demonstrate the effect that reducing the number of arson fires in Arkansas counties had on area burned. Elasticities are employed by economists and managers to determine which factors yield the greatest returns per unit of effort expended. Hypothetical reductions in area burned and average wildfire size were determined by randomly decreasing arson wildfires. Results showed that as arson rates increased above 50 percent, disproportionately greater reductions in area burned accrued from reducing arson. Accordingly, counties with high elasticities for area burned should be the first targets for arson reduction campaigns. Elasticities for average tire size showed weak responsiveness to arson reductions. When the primary objective of a prevention program is reducing area burned, elasticities for area burned can provide another tool for wildfire prevention specialists to use in appraising where scarce resources can be best utilized.

INTRODUCTION

Achieving effective wildfire prevention and suppression programs requires proper analysis of available data and correct interpretation of results, which supports the generation and implementation of effective policy. Because of the tremendous task of acquiring, entering and extracting meaning from wildfire data, detailed analysis is commonly not performed. Instead, management targets (typically calculated statistics) or goals are used to gauge the yearly progression of control programs. Generally, these management targets are presented in a standardized form (as an example, on a “per thousand protected hectares” basis) because they provide a quick gauge across county and regional boundaries and can be used across state boundaries to weigh the success of innovative programs.

In Arkansas, state lands protected from wildfire by the Arkansas Forestry Commission (AFC) include all privately owned forest and pasture lands but not areas within incorporated town and city borders, row-crop lands, federal ownerships (such as national forest lands) and other public ownerships. The Associate State Forester for Protection in Arkansas has set four wildfire management targets for county and state level programs. They are: 1) less than 1.5 hectares per thousand protected hectares (TPH) burned per year; 2) not more than 0.37 tires per TPH per year; 3) an average fire size less than 4 hectares and; 4) less than 40 percent arson fires. The most important of these goals is the first, to keep burned area as low as possible. Counties below any particular target are considered within compliance relative to their wildfire prevention or suppression goals.

Factors such as weather, attitudes and prevention and suppression efforts all play a part in determining the final yearly toll to wildfires. However, increasing rates of arson (Arkansas Forestry Commission 1984-1989) have aroused concern. These trends were first reported by Kluender et al. (1988, 1989). Perhaps the most important findings of these studies were that local residents caused 70 percent of the arson tires and that arson tires had an average size twice that of other causes (8.4 vs. 4.2 hectares). Additionally, these studies indicated that while general state-wide trends were important, they did not provide the detailed information required to formulate county-level fire prevention and suppression plans. Preferably, prevention and suppression programs should be designed for local conditions to better target problems and reduce wildfire losses. Kluender et al. (1990) subsequently looked at county-level wildfire patterns and found considerable variability among Arkansas’ 75 counties for arson rates and area burned. The data showed that of the 35 counties that exceeded the AFC target of 40 percent arson rate, 27 counties also exceeded the target for area burned; and, of the 39 counties that exceeded the target for area burned, 28 counties also exceeded the target for arson rate. Of the 48 counties that exceeded either target, 28 counties simultaneously exceeded both targets. So, the link between higher arson rates and higher area burned is well established among counties.

Wise management dictates that limited budget dollars be disbursed in the most effective way. Frequently, in wildfire prevention campaigns, managers may wonder whether money is being spent in the right place or on the right program. Numerous appraisal methods have been used by various agencies from time to time. Benefit-cost ratios express some measured benefit against the cost of obtaining it. Measures of cost to protect a known “value at risk” adopt an actuarial approach to the same problem. These measures, however, are static, cross-sectional statements of expected benefit for given expenditure. A more sophisticated concept is the use of elasticities to identify the percentage change of a dependent variable (like hectares burned) for a percentage change in an

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‘Associate Professor Forest Economics and Associate Professor Forest Protection, Department of Forest Resources, Arkansas Agricultural Experiment Station, Monticello, AR 71655.

independent variable (like arson rate); thus, elasticities measure responsiveness to change. Elasticities are used by economists and policy makers to show how much change in a given factor to expect for a given change in a driving or causal variable (Pindyck and Rubinfeld 1981). Generally, those independent variables that produce the greatest changes in the dependent variable (highest elasticities) are the best choices for policy manipulation.

Two factors point to the need to reduce the total number of arson tires in the South. First, arson is, in most southern states, the greatest single cause of wildfires (USDA Forest Service 1984). Second, arson fires tend to be larger than those from other causes. This paper demonstrates the use of elasticities as a measure of responsiveness to arson prevention based on hypothetical reductions in total area burned and average tire size. Our objective was to describe a tool that wildfire managers might use to help them select targets for arson prevention programs.

METHODS

We acquired the records of all reported wildtires on lands protected by the Arkansas Forestry Commission (AFC) for the period January 1983 through December 1988 (Arkansas Forestry Commission unpublished data). These data included records developed from Individual Fire Reports (AFC Form 2410.1) filled out by suppression personnel immediately after a fire was investigated. Variables chosen for inclusion in this study were year, county, cause (for example, arson or debris burning) and hectares burned per tire. The data set included reports of 16,047 fires. A second data set was obtained from the AFC that contained total hectares and protected ares per county. The data sets were sorted by county and merged. The number of tires per TPH, area burned per year per TPH, average fire size, and percentage arson tires for each county were calculated.

Because we (and the AFC) were interested in evaluating the effects of reducing arson fires in counties with high arson rates (by AFC definition, high includes those that exceeded the AFC management target of 40 percent arson rate), counties with an arson rate greater than 40 percent were retained in the analysis. Thirty-five of Arkansas' 75 counties (47 percent) remained in the active data set.

To simulate an effective prevention program that reduced arson rate to the AFC target, individual arson fires were randomly eliminated from each county data set until arson fires comprised 40 percent or less of the total fires. After randomly reducing arson fires to 40 percent, average tire size, area burned per TPH and number of tires per TPH were recalculated for each county. Elasticities for area burned per TPH (E_{AREA}), and average fire size (E_{AVSIZE}) were calculated for each county. For example, elasticity of area burned was calculated by:

$$E_{AREA} = \frac{(\Delta AREA\ /\ AREA)}{(\Delta ARSON\ /\ ARSON)}$$

Where:

ΔAREA = Change in ares burned after reducing arson rate
AREA = Area burned before reducing arson rate
PARSON = Change in percentage arson fires
ARSON = Percentage arson tires before reducing arson rate.

Elasticity of average fire size was calculated in a similar manner.

Three replicates of the random reductions in arson fires for each county were created and the calculations for E_{AREA} and E_{AVSIZE} performed for each county in each replicate. An ANOVA was performed on the E_{AREA} and E_{AVSIZE} data sets to determine if differences existed between replicates. To establish relationships, E_{AREA} and E_{AVSIZE} were regressed against the percentage of arson fires in each county before the reduction to 40 percent. Regression analysis was also used to ascertain what contribution the pre-reduction arson rate and average tire size of each county made to E_{AREA}

A standard statistical package, SPSS (Norusis, 1988), was used to perform the initial data analysis and data sorting. The Quattro Pro spreadsheet (Borland International 1989) was used to calculate the elasticities, and SYSTAT (Wilkinson 1988) was used in the final comparison of pre- and post-reduction conditions and in the regression analysis. Statistical significance was accepted at the $\alpha = 0.05$ level.

RESULTS AND DISCUSSION

The ANOVA showed no differences among the replicates for either E_{AREA} ($F_{2,102} = 0.085$, $p = 0.919$) or E_{AVSIZE} ($F_{2,102} = 0.050$, $p = 0.951$). Therefore, we used the mean value for each county's elasticities in all further analyses.

Elasticities for area burned per TPH (E_{AREA}) with respect to arson rate were greater than 1 .O (unity elasticity) for 23 of 35 counties; these counties were considered responsive to reductions in arson fires (Figure 1). When this elasticity was regressed against arson rate the linear function was:

$$E_{AREA} = 0.388 + 0.013 \times \text{ARSON RATE}.$$

Both the constant and the slope were different from zero. While considerable variation was present in the data, general trends were obvious. The slope shows that the higher the initial level of arson fires, the greater will be the response of area burned to reductions in arson levels. Additionally, the best-fit line ($R^2 = 0.435$) rose above unitary elasticity at an arson rate of 49 percent. Accordingly, we reason that area burned per TPH would typically be responsive to changes when the arson rate in a county exceeds 49 percent, or 50 percent in round numbers.

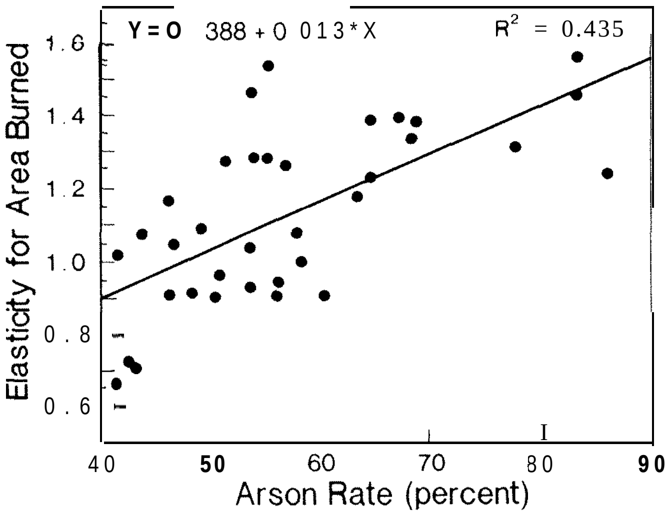

Figure 1. Elasticity for wildfire area burned compared with arson rate for 36 of 75 counties in Arkansas that exceeded the wildfire management target of 40 percent arson.

Elasticities for average fire size (E_{AVSIZE}) with respect to arson rate were all below unity and, hence, considered unresponsive. Although average fire size decreased when arson fires were eliminated, the reduction was relatively small when expressed as a percentage. Hence, E_{AVSIZE} was typically low. When this elasticity was regressed against arson rate neither the constant nor the slope were different from zero.

Finally, we regressed the elasticities of area burned as a dependent variable against arson rate and average fire size. The response surface was a quadratic function:

$$E_{AREA} = 0.187 + 0.014 \times \text{ARSON RATE} + 0.019 \times \text{AVERAGE FIRE SIZE} + 0.001 \times (\text{ARSON RATE})(\text{AVERAGE SIZE}).$$

However, only arson rate was different from zero; this surface had an R^2 of 0.549. Therefore, we conclude that arson rate alone, which had an R^2 of 0.435, is the best predictor for estimating E_{AREA}.

This analysis establishes that when the primary objective of a prevention program is reducing area burned, a good tool for choosing targets for the prevention program is the elasticity for area burned. For best results, ordinal ranking of counties should logically proceed from those with the highest to lowest elasticities. The best choice among counties with equal elasticities should be made by selecting the county with the largest average fire size.

We have shown that for Arkansas counties with high arson rates, disproportionately greater reductions in area burned can be expected when the number of arson fires is decreased. This is important because keeping burned area as low as possible is the most important goal of the AFC. Calculating and using elasticities for area burned will aid the efficient targeting of monies and other efforts for arson prevention programs. In areas where arson is not the primary cause of wildfires, perhaps other causes could be investigated in a similar manner.

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LITERATURE CITED

Arkansas Forestry Commission. 1984-1989. Annual fire reports: size and cause statistics for the years 1983 through 1988. Department of Commerce, Little Rock, AR (mimeo). 12 pp each.

Borland International. 1989. QUATTRO PRO User's Guide. Borland International, Inc. Scotts Valley, CA. 709 pp.

Kluender, R. A., L. C. Thompson and G. W. Callahan. 1988. Analysis of wildfire occurrence in southeastern Arkansas, 1984-1987. Proceedings Arkansas Academy of Science. 42:41-44.

Kluender, R. A., L. C. Thompson, R. J. McFarland and D. M. Steigerwald. 1989. Arkansas' incendiary wildfire record: 1983-1987. Proceedings Arkansas Academy of Science. 43:49-51.

Kluender, R. A., L. C. Thompson, R. J. McFarland and D. M. Steigerwald. 1990. An analysis of Arkansas' wildfire record by county, 1983-1988. Arkansas Agricultural Experiment Station Bulletin 925. Fayetteville, AR. 18 pp.

Norusis, M. J. 1988. SPSS/PC +, Statistical package for the social sciences, IBM/PC version. SPSS, Inc. Chicago, IL. 1500 pp.

Pindyck, R. S. and D. L. Rubinfeld. 1981. Econometric models and economic forecasts. McGraw-Hill. New York, NY. 630 pp.

USDA Forest Service. 1984. 1982 Wildfue statistics. U.S. Department of Agriculture, Forest Service Publication 82-D-2. Washington, DC. 49 pp.

Wilkinson, L. 1988. SYSTAT: The system for statistics. SYSTAT, Inc. Evanston, IL. 820 pp.

LONG-TERM IMPACTS OF FIRE ON COASTAL PLAIN PINE SOILS

William H. McKee, Jr.'

Abstract-Repeated burning of pine forests over long periods may have pronounced effects on the maintenance of soil fertility and soil development. Analyses of soils from four long-term prescribed burning studies in the Atlantic and Gulf Coastal Plain indicate that burning has had no effect on the total carbon and nitrogen level in the surface mineral soil. Winter burning increased the retention of nitrogen in the mineral soil over time. Changes in the carbon/nitrogen ratio in the forest floor with burning suggest that at least part of the increase in nitrogen in the mineral soil was due to pyrolysis of the litter. Available phosphorus was consistently increased in the surface 5 cm of soil by prescribed burning; however, the effect is less apparent on total phosphorus reflecting the low mobility of the nutrient. Concentrations of exchangeable bases in the surface soil increased with the frequency of burning. It is postulated that without burning, immobilization of calcium in the forest floor can lead in time to a magnesium:calcium imbalance and alteration of the soil formation processes.

INTRODUCTION

A concern about repeated burning is that it may reduce the "tilth" and productivity of soils in the long-term. Studying long-term effects of fire in the South is difficult, however, because burning has been part of the ecology of most fire sites there. Fire affects soil properties but measuring the cumulative effects on soil development takes many years and many fires. Data from some long-term burning studies in the Southeastern Coastal Plain offer clues about how fire influences soil forming processes.

Soil properties have been monitored in a number of Coastal Plain prescribed burning studies (McKee 1982, Ralston and others 1982, and McKee and Lewis 1983). In this paper I have combined the findings and updated the measurements for four major studies to develop indications of how burning may alter soil chemical properties and influence soil development.

MATERIALS AND METHODS

Study Areas

The four prescribed burning studies represent a wide range of soil textures, drainage classes, topographic positions, and understory vegetation. Brief descriptions of the four areas are as follows:

Alabama. This study is near Brewton, Alabama, on the upper Coastal Plain. Soils are classed as coarse loamy siliceous thermic (Typic Paleudults), complexed with fine loamy siliceous thermic (Typic Paleudults), loamy siliceous thermic (Grossarenic Paleudults) and loamy skeletal siliceous thermic (Typic Hapludults). Overstory vegetation consists of 60- to 70-year-old longleaf pine (Pinus palustris Mill.). Site index (age 50) ranges from 19 to 24 m, and undcrstory vegetation consists of grasses, forbs, and small woody sprouts.

Treatments are replicated eight times on 0.16-ha plots. Treatments examined here are an un-bum control and biennial winter burning. The study was initiated in 1970, and plots had been burned five times when data reported here were gathered. The last bum was applied about four months before sampling.

Florida. This study is on the Coastal Plain flatwoods in north central Florida. Soil on the study area is classed as sandy siliceous thermic (Aeric Haplaquods) with an organic pan between 46 and 61 cm deep. The overstory vegetation contains mixed, naturally seeded longleaf and slash (P. elliottii Engelm. var. elliottii) pines 60 to 70 years old. Site index (age 50) for the study area is 20 m, and average basal area is approximately 15.3 m^2 ha.

Treatments are replicated six times in a randomized block design on 0.81-ha plots. Treatments consist of an un-bum control, winter bum every four years, and annual winter burning. The annual winter bum was not imposed until six years after initiation of the study; at the time of sampling there had been 14 annual bums.

Georgia. The study is on a nearly level Coastal Plain site in south central Georgia. The site is poorly to somewhat poorly drained. Soils are loamy siliceous thermic (Arenic Paleaquults) covering about 2/3 of the site, loamy siliceous thermic (Arenic Plinthoquic Paleudults), tine loamy siliceous thermic (Plenthic Fraquidults), and loamy siliceous thermic (Arenic Paleaquults). Overstory trees arc longleaf and slash pines from 25 to 30 years old.

Plots consist of pastures of about 19.7 ha on which grazing is also observed. Treatments consist of no burning, triennial winter burning, biennial winter burning, and annual winter burning. Treatments have been in force for 40 years except for a 10-year period 25 years previously when the stand was regenerated.

'Soil Scientist, USDA Forest Service, Southeastern Forest Experiment Station, Charleston, SC.

development. With moisture conditions and parent materials he was observing, the end results would probably be a spodosol without tire and no spodic horizon with fire. Specific reports of such effects of tire on soil formation have not be published. It appears that the natural evolutionary pattern of soil development caused by water-soluble carbon, as observed by Herbauts (1980), can be moderated by burning. This conclusion is based on lysimeter studies on soils under forest cover where the degree of soil weathering was found to relate to the amount of soluble carbon moving through the profile. Nutrients moving from ash material after burning are alkaline (Raison and McGarity 1978), at least until the ash has dissolved and moved into the mineral soil. To some degree, burning destroys the substrate and either consumes or volatilizes organic acids produced in the forest floor. Such a change is assumed to be roughly proportional to the reduction of organic matter in the tire. The water-soluble carbon may be in a humic and fluvic acid (De Kimpe and Mattel 1976), in carbonic acid (McColl 1971), or in other soluble organic acids. Observations of Binkley (1986) on a site similar to that reported for on the South Carolina site in this report found that burning may convey resistance to soil acidification from atmospheric deposition or other sources by reducing pools of acid in the forest soils. Where sulfur dioxide from burning fossil fuels significantly acidifies precipitation, the resulting sulfuric acid is a much larger factor than carbonic acid (Cronan and others 1978). The acid radicals react with the soil to form salts with alkali, alkali earth, and amorphic metals that move through the soil horizons in the process of soil development.

Yaalon and Yaron (1966) indicate that any man-caused activity such as adding fertilizer or changing the pH will change the metapedogenetic processes that retard podsolization; the rate of change depends upon the intensity of treatments. Bidwell and Hole (1965) also discuss human practices as dominant factors in altering soil formation by controlling organic matter buildup. Thus, burning pine sites on the Coastal Plain tends to maintain soils in a less developed state and probably in a better tilth. Historically, such has been the case for much of the Coastal Plain, where tire maintains the pine ecosystem.

Phosphorus fractions in the surface mineral soil. Phosphorus was fractioned into various chemical forms in the surface 5 to 8 cm to determine the effect of prescribed burning on the disposition of phosphorus and its availability for plant uptake.

The amount of available phosphorus in the soil was slightly higher on burned than on control plots on all four study sites, but the differences were significant only on the South Carolina site (Table 2). On the Alabama site, phosphorus levels were 0.1 to 0.2 mg kg^{-1} higher on burned plots.

TABLE 2. Distribution of soil phosphorus in available, mineral and organic forms for the surface sample layer of soil on four sites.

Sampled sites burn treatment	Phosphorus Fractions			
	Available	Mineral	Organic	Total
		kg ha'		
Alabama (0-8 cm)				
No Burn	2.3	11.6	20.18	31.78
Biennial winter	2.4	12.0	23.3A	35.3A
Florida (0-8 cm)				
No Burn	7.1	15.4	18.0	33.4B
Periodic uinter	9.5	19.0	21.6	40.6A
Annual winter	10.5	19.3	21.2	40.5A
Georgia (0-8 cm)				
No Burn	2.4			
Periodic uinter	3.2			
Periodic summer	3.3			
Annual winter	2.7			
South Carolina (0-5 cm)				
No Burn	3.6B	25.9	52.1	78.0
Periodic uinter	4.5AB	27.5	45.8	73.3
Periodic summer	5.0AB	24.9	53.0	77.9
Annual winter	5.4A	29.9	56.4	86.3
Annual summer	4.1AB	27.6	51.6	79.2

Within columns and sites, values for chemical fractions followed by the same letter do not differ significantly at the 0.05 level. Available phosphorus represents both organic mineral fractions and is not used in computing the total phosphorus.

Annual and Periodic bums increased available phosphorus by 2.5 to 3.4 mg kg-’ in the O-8 cm depth on the Florida site. Available phosphorus ranged from 2.4 to 3.3 mg g^{-1} and increased with burning on the Georgia site.

Burning effect on individual mineral phosphorus fractions were relatively small and in most cases did not alter individual fractions, hence, the water soluble, aluminum and iron fractions are reported as mineral phosphorus. In general, the mineral phosphorus levels tended to increase with intensity of burning except on the South Carolina site where no trend was apparent. Changes in the available form of phosphorus or the magnitude of these changes do not appear to relate well to the phosphorus present in the mineral or organic forms.

Organic phosphorus accounted for 50 to 69 percent of total phosphorus in the surface 5 to 8 cm of soil on the three sites where measurements were taken. On the Alabama site, burning increased organic phosphorus by 16 percent or 3.2 mg kg^{-1}. On other sites, an apparent increase in organic phosphorus of 3 to 5 mg kg^{-1} was noted, but the increase was not significant. The amount of organic phosphorus was positively related to total phosphorus extracted from soils on these sites, accounting for 86 to 94 percent of the variation in total phosphorus.

Burning significantly increased total phosphorus (sum of the mineral and organic fractions extracted from sandy sites by 4 to 7 mg kg-‘. There is no apparent difference between the annual and periodic burning on the Florida site. Burning also tended to increase total phosphorus on the heavier soils of the South Carolina site, but the response was not significant. The large proportion of the total phosphorus in the organic form in soil indicates the need to investigate this form of the nutrient and to increase its availability to higher plants. Daughtrey and others (1973) found the release of organic phosphorus from a Coastal Plain soil was completely dependent on the activity of soil micro-organisms in decomposing organic matter. Nutrient release with burning would accelerate the breakdown of organic matter and release of organic phosphorus to the soil solution. Accumulation of organic matter and organic phosphorus is partly the result of small organic particles being washed from the forest floor into the soil.

Forest Floor Properties

Organic content. Prescribed burning predictably lowered the total weight and nutrient content of the forest floor on all four sites (Table 3). Across the range of sites, the unburned control plots contained from 13 to 59 T ha^{-1} of organic matter. Annual and biennial burning reduced the weight of organic matter in the forest floor by 39 to 44 percent on the

Table 3.--Average ueights of forest floor components after burning treatments on four study sites.

Site and burn treatment	Organic content	N	P	Ca	Mg	C:N Ratio
	ha^{-1} x 1000	- - - - - - - - - kg ha^{-1}	- - - - - - - - -			
site #1						
No burn	13.86A	226A	8.7~	67.2A	9.3A	30:1
Biennial burn	5.448	27B	3.1B	29.28	3.5B	100:1
Site #2						
No Burn	29.16A	131A	24.7A	115.0A	21.0A	111:1
Periodic winter	9.52A	378	6.78	40.06	11.0B	128:1
Annual Winter	4.54C	7B	3.08	19.08	6.0B	324:1
Site #3						
No burn	59.5	494	16.5~	83A	23.0A	60:1
Triennial burning	12.4	81	3.2B	21B	3.68	77:1
Biennial burning	7.48	56	2.20	15B	2.6B	66:1
Annual burning	17.16	100	4.2B	278	5.18	85:1
Site #4						
No burn	26.27A	408A	17.4	12.0A	19.0A	32:1
Periodic winter	18.468	3008	12.16	91.06	19.0A	31:1
Periodic summer	17.56B	277B	10.68	77.06	16.0AB	32:1
Annual Winter	10.48C	156C	7.28	52.0C	11.0BC	33:1
Annual summer	10.05C	129C	7.1B	48.0C	6.0C	39:1

Uithin columns and sites, values followed by the same Letter do not differ significantly at the 0.05 level. Where no Letters are shown, no significant differences are present.

Alabama site. Periodic burning on the Florida and South Carolina sites reduced the weight of the forest floor by 33 and 70 percent respectively. The forest floor reduction was 71 to 87 percent with burning on the Georgia site. Season of burning did not significantly affect the reduction total organic content.

Organic content of the forest floor on control plots is approximately the same for the South Carolina site as repotted 10 years earlier (Wells 1971). On these plots the forest floor contained 18.57, 26.88, and 26.27 T ha^{-1} after 10, 20, and 30 years of measurements (Metz and others 1961; Wells 1971). Thus, in terms of weight, the forest floor reached an equilibrium between 10 and 20 years after initiating the study, when the pine trees were about 45 years old. At 30 years, the forest floor contained 18 to 39 percent mineral material (determined by dry ashing the combined L, F, and H layer samples).

Wells and Jorgensen (1975) found that forest floor biomass reaches its peak in loblolly plantations at about age 30 in Piedmont stands. The sites in this study had considerably older trees, which produced less needles, but greater production of litter by hardwoods and herbs probably compensated for lower needle production.

Nitrogen. Nitrogen content in the forest floor decreased by as much as 95 percent with annual tires and 72 percent with biennial fires. Part of this nitrogen loss was from leaching water-soluble components and fine particulates from the forest floor into the soil. The forest floor of periodically burned plots had nitrogen losses ranging from 26 to 32 percent on the South Carolina site which had not been burned for five years at sampling, to a 72 percent loss on the Florida site which had been burned the previous year. Wells (1971) observed that the periodic burning on the South Carolina site 10 years earlier resulted in a nitrogen loss of about 112 kg ha^{-1} by volatilization. The 408 kg ha^{-1} of nitrogen in the forest floor on the control plots appear to represent an "equilibrium" value for this nutrient under the conditions imposed by the stand and the climate (Wells and Jorgensen 1975). Values on control plots on the other sites probably also represent near-equilibrium levels. Of interest are the nearly equal amounts of organic matter on the control plots of the Florida and South Carolina sites but about a four-fold greater amount of nitrogen on the South Carolina site than on the Florida site. The amounts of nitrogen in the forest floor probably reflect species and site conditions specific to each location.

The C:N ratio is a major determinant of availability of nitrogen and potential decomposition of the forest floor. The ratio of carbon to nitrogen widened by 1- to 3-fold on the Alabama and Florida sites following annual or biennial fires. On the South Carolina site much smaller increases (5 to 20 percent) occurred after annual bums, and no increases occurred after periodic bums. An exact C:N ratio is difficult to obtain because much of the organic matter is charred after burning. The magnitude of observed change, however, reflects an apparent nitrogen mobilization that cannot be explained by degree of carbon reduction. A number of rams fell on all the burned plots between burning and sampling. Comparison of forest floor values on the South Carolina site after 20 years shows a similar trend.

Heyward and Bamette (1934) observed that the L layer had a C:N ratio 2 to 3 times as wide as that of the F layer. Wells and Jorgensen (1975) observed a similar relationship for loblolly pine plantations in the Piedmont, where the C:N ratio of litter narrowed over time. Because it is primarily the L layer that is consumed by fire, it is surprising that burning results in a wider C:N ratio. Apparently, low-intensity tires have a "mobilizing effect" on nitrogen in the F layer, which may in part account for the increased nitrogen concentration in the upper 5 to 8 cm of mineral soil. Nitrogen relationships are supported by findings of Klemmedson and others (1962), who showed that burning accelerated nitrogen movement into the mineral soil. Light burning in ponderosa pine (*P. ponderosa* Dougl. ex Laws.) stands caused movement of 12.4 kg ha^{-1} nitrogen per year into the surface 2.5 cm of mineral soil. Wells and others (1979) summarized a number of investigations which indicate that appreciable mobilization of nitrogen as well as volatilization of the forest floor occurs after burning.

Phosphorus. Biennial or annual burning reduced the amount of phosphorus in the forest floor by 42 to 88 percent on all four sites. Periodic burning resulted in a 39 to 73 percent decrease in phosphorus in the forest floor. The season of periodic or annual burning did not affect phosphorus loss, and there was no significant difference between annual and periodic fires.

Calcium. Annual or biennial burning reduced calcium in the forest floor by 50 to 92 percent. Periodic burning resulted in a 28 to 39 percent reduction on the South Carolina site. Season of burning had no effect on changes in calcium content of this site. Thus, prescribed burning accelerated the rate of calcium return to mineral soil. This movement probably results from cations moving in the soil solution, but ash conduction may also be a factor. Wells and Jorgensen (1975) indicate that without burning, calcium loss from the forest floor is slow compared to potassium or magnesium loss and that after eight years appreciable quantities of the nutrient remain in the forest floor from a given year's deposition. Quantitatively, 50 percent of the magnesium from a given year's accumulated litter is lost from the forest floor in less than one year, while three years are required to obtain this degree of calcium mineralization (Jorgensen and others 1980).

Magnesium. Amounts of magnesium in the forest floor were approximately 1/4 to 1/10 those of calcium. The mobilization of magnesium with burning appears to be similar to that of calcium; and 43 to 71 percent magnesium was lost from the forest floor with biennial or annual burning. Periodic burning on the Florida site reduced magnesium by 52 percent. The period between burns and the season of burning did not significantly affect magnesium losses from the forest floor on the South Carolina site. Based on values reported by Wells and Jorgensen (1975) for loblolly pine in the Piedmont, the forest floor on these sites contains about 1/2 to 1/3 as much magnesium as in the tree biomass, and the nutrient would be expected to move out of the floor faster than calcium.

Forest Floor Mineral Relationships

To understand the quantitative relationships of the forest floor and increased nutrient concentration, the total contents are presented together for the surface 10 to 16 cm of mineral soil and forest floor.

Organic Matter. Burning reduced the organic matter content of the forest floor but not of the mineral soil. In fact, burning may have actually increased organic matter content of the mineral soil for the Alabama and Florida site but the increase was not statistically significant (Fig. 1). The result was a rather small loss of total carbon from the system due to burning part of the forest floor. The study sites in Florida and South Carolina, which have poor drainage, appear to have higher organic content in the mineral soil than those of Alabama and Georgia.

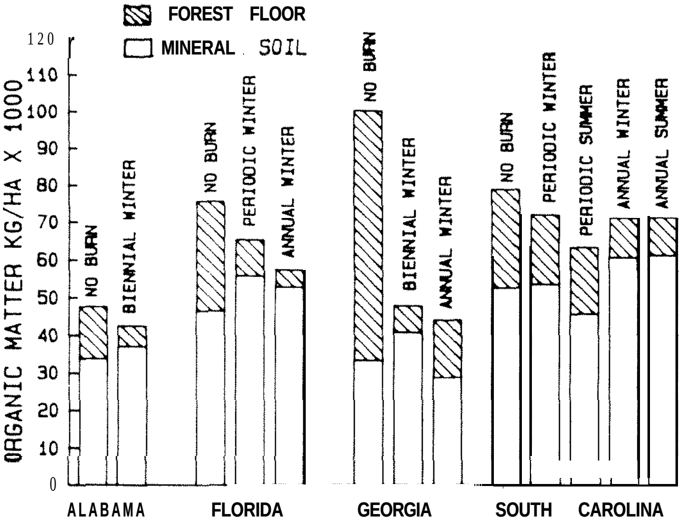

Figure 1. Organic matter content in the forest floor and soil after prescribed burning of coastal plain pine stands.

Nitrogen. On the sandy Alabama, Florida, and Georgia sites, burning caused a slight increase in nitrogen in the mineral soil despite a marked loss of forest floor weight after 8 to 40 years (Fig. 2).

Soil at the South Carolina site had been sampled after 10 years (Metz and others 1961), 20 years (Wells 1971), and 30 years (McKee 1982). Over 20 years between sample collection, total nitrogen changed little on the unburned control. After those treatments, there was a 20-year increase of 34 to 42 kg/ha--a four percent change for the periodic winter burn. The periodic summer burn (burned every seven years) resulted in a 128-kg nitrogen loss. The annual winter burn increased total nitrogen by 137 kg/ha. The striking effect was a 363-kg loss due to annual summer burn. Since both summer burns resulted in total nitrogen losses, summer burning apparently has a detrimental effect on the amount of nitrogen remaining in the surface mineral soil, while winter burning increases nitrogen. The exact cause is difficult to explain but may be related to a lack of nitrogen-fixing legumes that invade these treatment sites after summer burns.

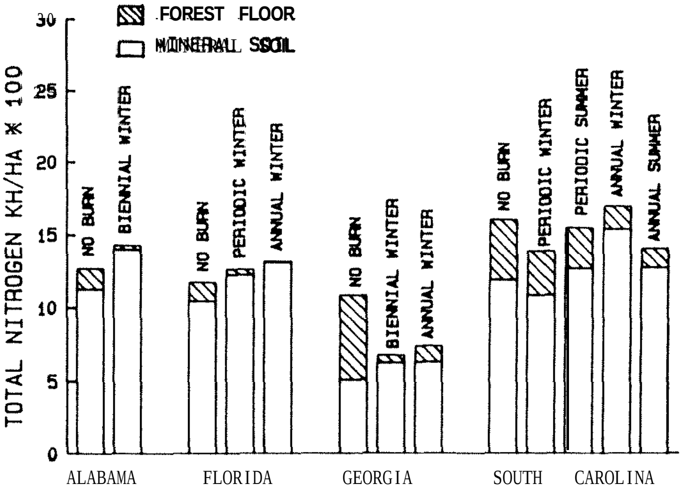

Figure 2. Nitrogen content in the forest floor and mineral soil after prescribed burning of coastal plain pine stands.

Phosphorus. Without burning, appreciable quantities of phosphorus were tied up in the forest floor on all four study sites (4 to 24 kg/ha) (Fig. 3). The amount of phosphorus in the mineral soil is difficult to relate to that of the forest floor. Available phosphorus was apparently increased by burning, but the quantities found did not relate well to frequency of burning. A standard chemical test suitable for all sites is difficult to select because numerous chemical forms of phosphorus are present. Available phosphorus levels appear to be slightly more responsive to treatments and are represented on all four sites.

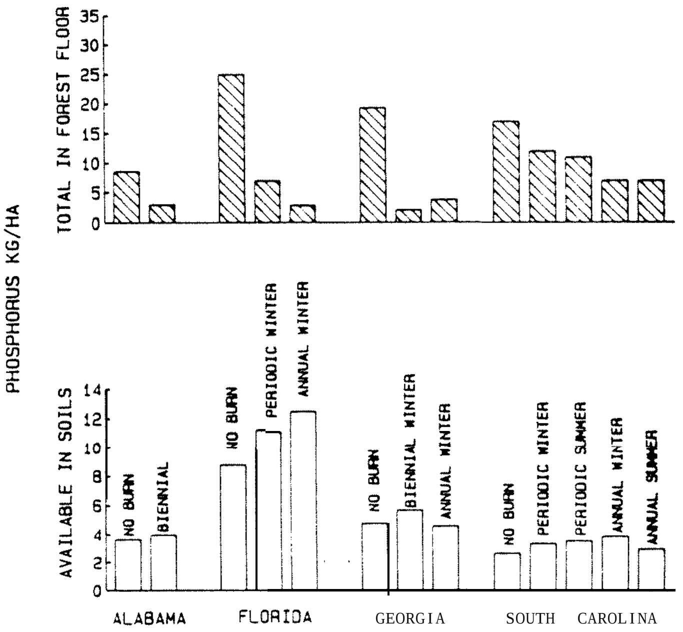

Figure 3. Phosphorus content of the forest floor and available phosphorus content in the mineral soil after prescribed burning of coastal plain pine stands.

Calcium. All the effects of burning on calcium appear to take place in the forest floor and the top 10 or 16 cm of mineral soil (Fig. 4). Without burning, 16 to 61 percent of the calcium present was in the forest floor. With burning, only 4 to 16 percent of the calcium was in there. The remainder was in the surface soil layers. These changes in calcium distribution logically account for the pH increase in the mineral soil associated with burning, and indicate a long-term effect on soil acidity. The amount of calcium in the forest floor decreased proportionally to the frequency of the burning on the Florida and South Carolina site. Earlier calcium observation on the South Carolina site, (Wells 1971) showed similar results, indicating little change in the calcium status of this site in the last 10 years.

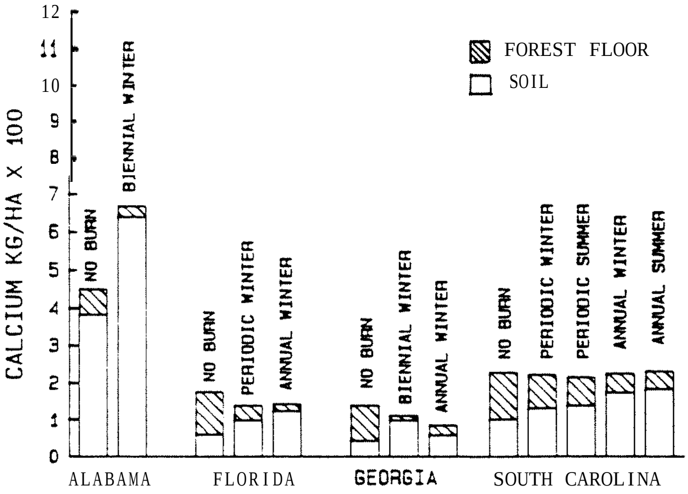

Figure 4. Calcium content in the forest floor and exchangeable calcium content in the soil after prescribed burning of coastal plain pine stands.

CONCLUSIONS

The most striking result of this analysis is the similarity of burning effects on soil properties despite obvious soil differences and probable differences in burning techniques, which were reported to be either low-temperature flank fires, or backfires.

Organic matter consistently builds up faster in mineral soil on burned areas, and burning only reduces total nitrogen in the forest floor. On unburned plots, 6 to 11 percent of the nitrogen was in the forest floor. Over the range of study sites, annual burning reduced total nitrogen in the forest floor to 12 to 32 percent of the unburned levels, but burning did not appear to reduce total nitrogen in the mineral soil after up to 30 years of treatment. However, a balance sheet for the studies requires nitrogen data for the vegetation which may be causing an increase in soil nitrogen.

The consistent increase in available phosphorus in mineral soil caused by prescribed burning, may be one of the most beneficial effects of the treatment. No consistent pattern was found for burning effects on phosphorus fractions. The nature of compounds formed apparently represents specific pH conditions and mineral components in the soil. However, in all cases burning obviously accelerated mineralization.

The cation response was quite similar for all sites. The soil depth used appeared to represent complete cycling of calcium. Trends indicate that the unburned forest immobilizes a large proportion of the calcium altering the nutrient balance of the soil in some cases. Magnesium and calcium responded similarly to burning treatments, but their ratios indicate that magnesium recycles faster or at least accumulates in mineral soil in the absence of burning.

It is apparent that burning alters soil formation and long-term productivity over time. Evidence suggests that burning may improve soil by retarding soil development and, probably, formation of spodic layers in the profile. Proof of this observation would probably require five to six pine rotations to compare soil development with and without tire.

LITERATURE CITED

Bidwell, O. W.; Hole, F. D. 1965. Man as a factor of soil formation. Soil Science 99:65-72.

Binkley, D. 1986. Soil acidity in loblolly pine stands with interval burning. Soil Science Society of America Journal 50:1590-1594.

Bray, R. H.; Kurtz, L. T. 1945. Determination of total organic and available phosphorus in soils. Soil Science 59:39-45.

Buol, S. W.; Hole, F. D.; McCraken, R. J. 1973. Soil genesis and classification. Ames, IA: Iowa State University Press. 360 pp.

Chang, S. C.; Jackson, M. L. 1957. Fractionation of soil phosphorus. Soil Science 84:133-144.

Cronan, C. S.; Reynolds, R. C. Jr.; Lang, G. E. 1978. Forest floor leaching contributions from mineral organic and carbonic acids in New Hampshire subalpine forests. Science 200:209-311.

Daughtrey, Z. W.; Gilliam, J. W.; Kamprath, E. J. 1973. Phosphorus supply characteristics of acid organic soils as measured by desorption and mineralization. Soil Science 115:18-24.

De Kimpe, C. R.; Martel, Y. A. 1976. Effects of vegetation on the distribution of carbon, iron and aluminum in the B horizons of Northern Appalachian spodosols. Soil Science Society of America Journal 40:77-80.

Herbauts, J. 1980. Direct evidence of water-soluble organic matter leaching in brown earth and slightly podzolized soil. Plant and Soils 54:317-321.

Heyward, F. 1937. The effect of frequent fires on profile development of longleaf pine forest soils. Journal of Forestry 35:23-27.

Heyward, F.; Bamett, R. M. 1934. Effect of frequent fires on chemical composition of forest soils in the longleaf pine region. Bulletin 265. Gainesville, Fl: University of Florida Agricultural Experiment Station. 39 pp.

Jackson, M. L. 1958. Soil chemical analysis. Englewood Cliffs, NJ: Prentice- Hall, Inc. 498 pp.

Jorgensen, J. R.; Well, C. G.; Metz, L. J. 1980. Nutrient changes in decomposing loblolly pine forest floor. Soil Science Society of America Journal 44:1307-1314.

Klemmedson, J. 0.; Schultz, A. M.; Jenny, H.; Biswell, H. H. 1962. Effect of prescribed burning of forest litter on total soil nitrogen. Soil Science Society of America Proceedings 26:200-202.

Lyle, E. S.; Adams, F. 1971. Effect of available soil calcium on taproot elongation of loblolly pine (Pinus taeda L.) seedlings. Soil Science Society of America Proceedings 35:800-805.

McColl, J. G. 1972. Dynamics of ion transport during moisture flow from a Douglas-fir forest floor. Soil Science Society of America Proceedings 36:668-674.

McKee, W. H., Jr. 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites. U. S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. Res. Pap. SE-234. 23 pp.

McKee, W. H., Jr.; Lewis, C. E. 1983. Influence of burning and grazing on soil nutrient properties and tree growth on a Georgia Coastal Plain site after 40 years. Pages 79-86. In: Proceedings of the Second Biennial Southern Silvicultural Research Conference, Asheville, NC. U. S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. Gen. Tech. Rep. SE-24.

Metz, L. J.; Lotti, T.; Klawitter, R. A. 1961. Some effects of prescribed burning on Coastal Plain forest soil. Asheville, NC: U. S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. Res. Pap. SE-133. 10 pp.

Nelson, D. W.; Sommers, L. E. 1973. Determination of total nitrogen in plant material. Agronomy Journal 65: 109-l 12.

Olsen, S. R.; Dean, L. A. 1965. Phosphorus. In: Black, C. A., ed. Methods of soil analysis. Agronomy 9:1035-1049.

Raison, R. J.; McGarity, J. W. 1978. Effect of plant ash on nitrogen fertilizer transformations and ammonia volatilization. Soil Science of America Journal 42: 140-143.

Ralston, C. W.; McKee, W. H., Jr.; Langdon, 0. G.; and Harms, W. R. 1982. Prescribed burning: uses and effects. Pages 154-162. In: Proceedings of the Symposium on The Loblolly Pine Ecosystem (East Region). North Carolina School of Forestry, Raleigh, NC.

Wells, C. G. 1971. Effects of prescribed burning on soil chemical properties and nutrient availability. Pages 86-99. In: Prescribed burning symposium proceedings. Asheville, NC: U. S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Wells, C. G.: Campbell, R. E.; DeBano, L. F.; et al. 1979. Effects of fire on soil. Washington, DC: U. S. Department of Agriculture, Forest Service. General Technical Report WO-7.

Wells, C. G.; Jorgensen, J. R. 1975. Nutrient cycling in loblolly pine plantations. Pages 137-158. In: Bemier, B.; Winget, C. H., eds. Forest soils and forest land management. Quebec, Canada: Les Presses de l'Universite' Laval.

Yaalon, D. H; Yaron, B. 1966. Framework for man-made soil changes: an outline of metapedogenesis. Soil Science 102:272-277.

FIRES, FORESTS, AND TRIBES IN THE NORTHERN PHILIPPINES: CULTURAL AND ECOLOGICAL PERSPECTIVES

Sharon Codamon-Quitzon[1]

Abstract-The study was exploratory. The researcher utilized participant observation, case study, and interview-discussion methods to gather data. Purposive stratified multi-stage sampling guided initial selection of 103 respondents in 3 groups: kaingineros, school teachers, and government officials. The study is an attempt to explain forest burning from the perspective of the tire-setter. It is the first of a series of investigations that interpret forest burning as a lifeway of a people who inhibit a rugged environment and who possess a unique socio-cultural temperament. Specifically, research focused upon the forest fire-setting behavior of the Ifugao, an ethnic tribe in the Cordilleras, a mountain range in Northern Philippines. This paper reports impacts of so&-culturally sanctioned indigenous forest burning practices the local economy, ecology, and society. Central to the issue of forest burning is the highly institutionalized Ifugao practice of muyung, or inherited private ownership of forests. Muyung greatly complicates governmental efforts to promote forest tire control, sound forest management, and sustainable forest development in Ifugao.

INTRODUCTION

Fire accounts for one-third of the damage done to the Philippines' critical watershed and forest lands. The problem continues to be addressed largely as a technical one, and forest management continues to be forestry-oriented following inception of the Social Forestry Program in the DENR. (The Philippine SFP, which was launched in 1982, is a radical departure from traditional programs, which put the forest before its occupants. Creation of the SFP is a mute admission that the conventional methods used to conserve and protect the forest have not succeeded.) Ifugao, now legally recognized as the Cordillcra Autonomous Region, was chosen for study because it had the highest rate of forest fires in the Northern Philippines and because its supposedly civic-minded and law-abiding people continue to bum forests despite the region's long history of Spanish and American religious endeavor and continuing government administration.

The study was designed to:

- document relevant demographic, economic, and social attributes of selected kaindinero respondents involved in forest burning practices in the area of study;
- determine level and type of knowledge (awareness), assessment (perception), and predisposition (attitudes) toward forests, forest fires, and forestry policies (including the presence and role of the local forestry agency in forest fire prevention and management),
- determine the existence and nature of beliefs relevant to forests and forest burning activities among the natives in the area;
- determine the role of revenge as a factor in forest burning;
- identify socio-cultural learning experiences that influence, reinforce, and institutionalize the practice of forest burning among the same; and
- review approaches adopted by the local forestry agency to prevention of forest fires.

LITERATURE REVIEW

Cruz (1985a, b) asserts that the fight against forest fire in the country is hampered by certain institutional and external problems compounded by public apathy toward forest protection due to the misconception that fire is the sole responsibility of the BFD. Misra (1983) described forest fire types, causes, uses, and prevention but did not focus on the personality of the fire-setter. Atabay (1978) and Binua (1978) argued for forest tire research to support forest protection, reforestation, and grassland management. Rabanal (1973) believes that the problem reflects a lack of knowledge on the part of those who regularly bum forests, who use fire to prepare land for planting and who do not fully understand the consequences of burning. Researcher like Duldulao, and others (n.d.) and Strasser (1970) stress the socio-economic angle, arguing that forest conservation consciousness cannot be instilled among those involved in the destructive activity unless they are given an alternative way of earning their living. Social and cultural characteristics of people living near or within fire-prone forest areas, and attitudes of those people regarding forest burning, local forestry agencies, and their representatives, were identified by Bertrand and others (1965) as factors relevant to the potential success of fire prevention programs. Forest fire has been attributed to plain ignorance of fire prevention practices, irresponsibility, carelessness, and grudges against forestry personnel.

METHODS

Place of Study

The study was conducted in the barangays of Bokiawan and Hucab in the municipality of Kiangan (1975 population

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[1] Senior Science Research Specialist, Ecosystems Research and Development Bureau, College, Laguna, Philippines.

15,985; area 443.3 km'), and in the barangays of Panopdopan and Nayon in the municipality of Lamut (1975 population 9,516; area 104.5 km'). These sites were selected based on greatest fire incidence, kaigin activity, concentration of forested area, food or eating habits, sustainability and availability of land, weather conditions and facilities affecting agriculture as principal mean of livelihood.

Research Design

Upland farmers or kainginero (shifting cultivators), who are termed munhabals in the Ifugao vernacular, served as the primary source of data; teachers and government officials served as secondary sources. The kaingineros were covered by complete enumeration, which yielded 60 respondents. The teachers and government officials group were criteria-selected using purposive stratified and multi-stage sampling. The Bureau of Public Schools (BPS) Form as of October 1978 and the Sangguniang Panlalawigan, Sangguniang Bayan, Barangay Council, and local BFD personnel were the sampling frames. Twenty respondents (10 from each municipality) from each group made up the sample. There were a total of 103 respondents (60 kaingineros, 20 teachers, 20 government officials, 2 municipal mayors and 1 BFD district officer--the last 3 treated as special case studies).

Collection of Data

Interview Method. Semi-structured interviews, mostly without the schedule on hand, were generally conducted inside offices, school premises, business establishment, and residential buildings in Bokiawan, Bolog, Ambabag, Baynihan, Baguinge, Cawayan, and Poblacion for Kiangan and in Panopdopan, Lawig, Nayon, Payawan, Mabatobato, Pieza, Bunog, Magullon, and Poblacion for Lamut. The term "forest tire" was sometimes used in place of "forest burning behavior" to make it easier for the kringineros to grasp the concept.

Interviews were sometimes recorded on tape, particularly "huddled types" when one interviewee suddenly became several as wives, children, and other members of the household also sought attention. The recorder was introduced as a radio set to prevent selfconsciousness. Inquiry was directed primarily to the head of family, who was informed beforehand of the object of research. For the secondary sources, the average interview time took 1 hour and 40 minutes. Most of these were approached during their "break" periods and were not briefed as to the purpose of the interview.

Participant Observation or Case Study Method. "Live-in" observations were made during waking hours and upon return of the kaingineros from their kaingins in the evenings. Interviews were conducted in the morning before the subjects set out, when they invariably spend some time huddled together outside their huts as if awaiting the sunrise. Some return at noon in order to have an early start on the next day's work or because the kaingins are located some distance from the dwellings. The interviewers also observed the baki performed by the different households, and these occasions also presented opportunities for casual and natural talks with the natives. The babiis is an Ifugao native ceremony or rite performed to invoke the favorable intervention of spirits of dead ancestors and gods or deities on the occasion of sickness in the family or in token of thanksgiving for favors received. The last day was spent in the kaingins for a first-hand view of the situation.

FINDINGS AND DISCUSSION

The case of the kaingineros is highlighted in this report.

Socio-Economic Attributes

Rokiawan. The study centered upon the activities of an all native, almost 50-percent unconverted and non-formally educated majority in the sitios of Bunog and Kayapa. Farming is the main occupation, with almost 50 percent professing ownership of payo (ricefield), habal (kaingin), muyung, and animals? Per-family income is not computed. Most families are engaged in wood-carving business. Elementary school children earn an average of P21 .00 per week by carving pieces of spoon and fork figurines, while older children earn an average of P87.50 per week, In Bunog, all heads of families depend on sales of coffee for their monthly income. The average quantity brought by each family to the town proper is to 5 gantas of coffee valued at P40.00 at P1.00 per chupa. Another source of money or cash income is the littuco (rattan fruit) which is harvested during September, October, and November and yields an average income of P250.00 at P25 per container. If they were to sell their palay, their income would be barely sufficient for daily needs. The owners of ricefields plant the traditional variety of palay and harvest only once a year. The yield is usually reserved for family consumption or for emergency barter in the adjacent or nearby barangays of Mungayang and Bayninan. Camote (sweet potato) harvested from the kaingins is the staple food. For those who own ricefields, rice is eaten alternately with camote.

Hucab. The study was centered in Hoba, where the kaingin system is the chief occupation. Camote is the main staple. The respondents also own pigs, chickens, and ducks. Cash income is derived from the sale of bananas and coffee grown in backyard gardens or in small orchards leased from other individuals (who are not necessarily Ayangans). Unlike the other native respondents, the residents of Hucab do not own forests.

Nayon. The live primary subjects were predominately male, married, educated, but unconverted kaingineros of Binoblayan. All admit having a habal or patch of unirrigated agricultural land, but not all possess a payo and a muyung. The sale of bananas provides each family with an average weekly income of P24.00. Three to 400 pieces of unripe bananas are sold at an average of P6.00 per hundred. Camote and corn are sold for about P20.00 per kerosene can.

Rice is harvested only once a year. The cash value of the palay harvested by a kainginero family averages P200.00 per year.

Panopdopan. The respondents have their own hospital, an elementary school building, and business establishments. Their characteristics are not basically different from those of residents of the other barangays studied. Those who were first to settle in the area are better off economically than those who came later. Panopdopan's forests were originally a public or communal forest site of the mother municipality of Kiangan. The residents of Panopdopan established ownership of these forests through the simple expediency of declaring them for taxation purposes and by claim of continuous and peaceful occupation. The privilege of developing these forests into ricefields or banana or coffee plantations has been exploited to the hilt. Residents leave their private forests well enough alone.

Cognitive Attributes

The findings about the kaingineros are generally applicable to all the groups studied. All kaingineros profess non-awareness of any government-promulgated law regulating kaingin. They believe that common law dictates that kaingins, are made in "open areas" regarded as "public land," and not on forests owned by private individuals. They do not understand why they should be prohibited from burning or utilizing fire as a tool in their kaingin practice. Forests are viewed primarily as private properties. The owner of a muyung is thought to be in the best position to care for it properly and manage it as a source of lumber, fuel, and the water that irrigates his ricefield. All claim that no one from the FNB had ever visited their areas. Non-observance of laws against burning accordingly stems in part from non-enforcement by the government. The local people are scarcely aware of the presence of a local forestry service, and find it very difficult to conceive that the muyung could ever be placed under state control. All agree that public lands should be distributed to the landless, who can develop these as sources of stable and adequate income and livelihood. All endorse stricter regulation and control of the activities of loggers and wood carvers in Ifugao, who are held responsible for the wanton destruction of the public forests.

Beliefs Relevant to Forests and Forest Burning Activities

Two pervasive beliefs are relevant. The first has to do with forest ownership and seems to provide the key to the burning behavior. The natives know that the government has legal right over the forest, but they believe that the right belongs to the people who own the forests. Some natives explained that the government owned the public forests. The second belief relates to tires in the muyung. The natives do not regard these as forest fires but merely as a routine activity or tool for preparing the kaingin portion of the forest land for planting. The munhabal sets fire to what a non-native would consider as forest when there is no known claimant to the area and when customary law defines the area as public land primarily for kaingin. Burning preparatory to planting is indispensably customary.

Socio-Cultural Learning Experiences That Influence, Reinforce and Institutionalize the Practice

The native who lives in a more remote area learns to eat camote morning, noon, and evening, or, if he is luckier then the other kids in the neighborhood, camote alternated with rice. Camote is planted mainly in the family kaingin. Cleaning of rice fields starts in January, and rice planting is completed by March. The ricefields are then temporarily abandoned while the natives prepare their kaingins, which are usually located some distance away from the ricefields. Cutting down of vegetation starts by April. The grasses and trees are left to dry for at least a month, then the natives go back to bum them. Burning commences by May. Mongo is planted as soon as burning is completed, and camote is planted August after the mongo is harvested. The camote crop is harvested 5 months later. The habal is then left idle until April, when the grasses are cut, dried, and burned preparatory to planting activities. The process is repeated year in and year out unless, the place is totally abandoned in favor of another occupant. There is no room for idleness. Those who do not own any habal or payo earn their livelihood by helping clean and prepare rice fields for planting in consideration of wages in money, or by cultivating and planting someone else's ricefield in return for half of the harvest. The culture is highly animistic. The native believes in a supreme being whom he calls Maknongan, in a hierarchy of lesser deities, and in ancestral spirits (anito). When a baki is performed for a particular purpose, sacrificial animals are butchered and offered to the spirits. The number and kind of animals sacrificed depend upon the financial capacity of the family requesting the baki. The raising of animals is thus required by religious customs, and kaingins must be cultivated to provide food for the livestock.

Observing forest tires on mountainsides, especially during the night, is pani-o (taboo). Those who observe such tires accidentally are cautioned to keep the matter strictly to themselves. This taboo enables a public forest fie-setter in Ifugao to go about his way unchallenged.

Revenge as a Factor in Forest Burning

Envy, anger, or hatred were seen as motives for burning in only a few cases. Respondents suggested that laborers employed by the local BFD office in its nursery and plantation set reforestation projects on fire to get even for being laid off, for delayed payment of wages, or simply to ensure their period of employment. There were insinuations that the local forestry office was in cahoots with its laborers in perpetuating tires, especially in the reforestation plantations, to justify its continuing budgetary allocation for forest fire protection.

Approaches Adopted by the Local Forestry Agency to Prevention of Forest Fires

- Constant forest guard patrol in fire-prone areas before and during the dry season.
- Intensification of forestry information drives.
- Constant dialogue with local leaders on forest conservation projects and programs.

Interestingly, the respondents interviewed in connection with this study declared non-awareness of these activities allegedly undertaken by the local BFD agency.

RECOMMENDATIONS

We recommend allocation of adequate funds for an intensive and extensive census to determine the number of people involved in kaingin-making throughout the country. The census should determine (a) the circumstances and factors that support kaingin-making, (b) the nature and extent of forest destruction resulting from tire and other causes, (c) local beliefs, customs, and practices pertaining to forests, their ownership, purpose, use, etc. in relation to government-promulgated forestry laws, rules, and regulations. The findings of the should be used to guide the repeal or amendment of existing forestry laws, which should be made compatible with local beliefs, customs, and practices.

We recommend allocation under title in favor of landless families solely dependent upon kaingin-making for survival of all available forest lands claimed under current ownership by reason of inheritance or succession or by actual, continuous, and peaceful possession for a period of more than 15 years provided that the recipients, their heirs, or their successors-in-interest shall not alienate their allocations or interests therein within 30 years from the date of allocation of title and, provided further, that no title of ownership shall be granted except after the lapse of 5 years from the date of allocation and upon proof of occupation, development, and improvement of his allocation particularly in tree planting of whatsoever kind suitable in the area. In the allocation of such forest lands, first priority should be given to the natives and second priority to local residents.

We recommend reorganization of the BFD, particularly on the district level. Personnel should be dedicated, competent, and active. Employment preference should be given to qualified applicants who are natives or residents of the districts served.

We recommend that adequate funds be allocated so that FEB offices throughout the country can regularly conduct information drives, and so that special educational efforts can be made in areas notorious for forest destruction.

The theoretical framework presented in this report should also receive further consideration. Some hypotheses worth testing are as follows:

- There is no relationship between level of education and level of information or knowledge about the destructive nature of forest fires.
- There is no relationship between level of information about the destructive nature of tires and forest burning behavior.
- There is no relationship between perception of the local forestry agency's role and forest burning behavior.
- There is no relationship between beliefs held about forest ownership and forest burning behavior.
- The indigenous institutions of the lfugaos that may be related to forest burning should receive further consideration and study.
- Camineros, or road maintainers employed by the government, members of the local police force, out-of-school youths, and others should be officially consulted as respondents in studies of this nature; they can be sources of pertinent and valuable information.

LITERATURE CITED

Atabay, Remilio C. 1978. Fire for grassland management. Canopy 4(4).

Bertrand, A.L., Jones, A.R., Taylor, M.L. 1965. Some human factors in woods burning: a study of change in beliefs of the residents of a National Forest in Louisiana. Bull. 601. Louisiana State University, Agricultural and Mechanical College, Experiment Station.

Binua, Tomas M. 1978. Forest fire research to protect our forest and save reforestation efforts Canopy 4(4).

Cruz, Marisa. 1985a. Will summer be forever a threat to our forests? Bagong Sibol April.

Cruz, Marisa. 1985b. Forest protection Bagong Sibol April.

Duldulao, A.C. Depositario, W.C. Olivar, J.D. [n.d.] An integrated project for kaingin control in the Philippines: a new approach to forest conservation, [A research proposal submitted to the Philippine Council for Agriculture and Resources Research Development, College, Laguna].

Misra, C.M. 1973. Forest fire: kind, causes, control and tool Canopy 9(7):5.

Rabanal, V.T. 1973. Forest destruction: a hindrance to national progress. Conservation Circular 9(6).

Strasser, R.C. 1970. Solution to forest fires and kaingin--making naval stores, Philippine Forests 12.

SMOKE MANAGEMENT: ARE RIGHTS INCLUDED WITH THE RESPONSIBILITY TO USE FIRE IN MANAGING PUBLIC LANDS?

Dean A. Shinn[1]

In the southeastern United States, the native biota of many natural ecosystems are adapted to periodic burning. It is generally believed that in Florida at the time of European intervention, these ecosystems were sustained as fire climax communities by relatively frequent fires, resulting both from natural and from cultural causes.

The preservation and where necessary the restoration of the aboriginal structure and function of biotic communities occurring on State Parklands is central to the mission of the Florida Park Service. In pursuit of this mission, park managers throughout the State have been charged with the responsibility of using fire and prescribed burning techniques to manage Florida's State Parks.

One might suppose that a public responsibility to use fire in this way would be accompanied by certain rights to produce and dispense smoke from the areas being burned. The premise of this paper is that such rights should naturally emerge from that public charge. However, Florida Statutes and the contingencies that they govern are not yet viewed in such a way that the practical circumstances associated with public land management can be administered form this point of view. In fact, potential liabilities, rather than rights, are among the most prominent aspects of the public responsibility to use fire as a tool in modern management of commonwealth resources.

In Florida, many state parks are small and are defined by boundaries that are uneven and often broken by parcels of adjacent private land. Many parks contain private inholdings wholly within their boundaries. Many are also situated in highly urbanized areas and are bordered, even surrounded, by high-value commercial and residential development. Very few of Florida's state parklands are located away from major roadways. In the Florida Panhandle, large areas are occupied by military installations, and many other areas are traversed by military and commercial flight paths. In addition, a relatively high proportion both of the seasonal and of the year-round population is composed of elderly people, many of whom have respiratory problems.

As a result, the heat, smoke, and ashes emitted from prescribed fires are likely to affect people and property beyond state park boundaries. Because developed areas potentially affected by prescribed fires are so close to parklands, and in many places are a major component of a park's external environment, the weather conditions under which fire can be safely used in parks are seriously constrained. In many places, burn prescriptions can be written to accommodate only winds of a very specific speed and direction. Along the Panhandle Gulf Coast, many State parklands can be burned under prescription only after a winter cold front has passed. Under such circumstances, the wind blows rather predictably from the north for a relatively reliable period of time. This situation restricts the range of options open to park managers in their use of fire to restore and preserve Florida's original natural ecosystems.

It must be emphasized here that land managers employed by the Florida Park Service are well aware of the legitimate and compelling hazards associated with the smoke emitted from prescribed fires. They have been and will continue to be diligent in planning fire management activities to avoid traffic hazards along major transportation corridors and to protect public health.

Certain other problems, such as ash falling into nearby swimming pools, soot soiling laundry hung on clothes lines, or simply the unusual smell of burning vegetation, are also associated with the smoke and ash produced by prescribed fires. These problems can be characterized as nuisances rather than as genuine dangers or health hazards, however.

These problems should be addressed first by establishing open, good-faith communications between park personnel and local citizens. A conscientious public relations effort should be an integral feature of each park's fire management program. The park's neighbors need to be informed about the benefits of responsible fire management procedures and advised of the fire planning process prior to prescribed burning activities being undertaken. Adoption of seriously constrained prescribed fire management procedures as a means of avoiding inconvenience, rather than genuine hazard, would be ill-advised and would likely not achieve anticipated long-range ecological objectives. Thorough, good-faith public relations efforts should be undertaken early in every prescribed fire and smoke management program.

Of course, even the best efforts to inform the public and to solicit the cooperation of all who might be affected may not be entirely successful. Some among a park's neighbors simply may not be reached or may not be persuaded to cooperate. Litigation may result.

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[1] District Ecologist, Division of Recreation and Parks, Florida Department of Natural Resources.

This being the case, the author sought to determine if a line of legal reasoning could be set forth to advance the notion that a set of legal rights to produce and dispense smoke should be acknowledged as being implicit to the public responsibility to use fire as a resource management tool on public lands. However, the existing case law in Florida does not specifically address this issue. Certain judicial decisions and findings that can be grouped under legal classifications such as "nuisances," "negligence," "environmental rights and remedies," and "explosion and fire" pertain to this subject only in a very general sense. It is unlikely that a cogent legal argument in support of "smoke rights" could be derived from the existing case law. Indeed, the time invested in attempting to do so might be ill-spent in the absence of a test case well suited to the development of such an argument. However, it is not likely that the Florida Park Service would wish to promote circumstances under which suitable legal reasoning could be developed through litigation. Therefore, other means of establishing "smoke rights" were investigated -- means that would also serve. to support the assertion of such rights, should a judicial defense of this concept become necessary.

Three options were examined: easements, land use plans, and original legislation.

Easements: Establishment of buffer zones around State parklands through the institution of conservation easements or other special land use agreements with owners of adjacent private lands can be used to codify mutual acceptance of specific fire and smoke management practices. This approach is most practical and most likely to be successful if undertaken while private lands surrounding parklands remain open and undeveloped. After residential or commercial development occurs, ownership -- and therefore decision-making authority -- is likely to be dissipated among many separate private interests. To achieve agreement concerning prescribed burning and smoke management contingencies with one, or with only a few, adjacent ranchers and timbermen can be a rather straightforward matter. On the other hand, reaching agreement among all potentially affected parties in an expanding area of mixed residential, commercial, and industrial land uses would be a much more ambitious undertaking. Therefore, conservation easements that acknowledge specific fire and smoke management rights and responsibilities should be established as early as possible in a region's development cycle. They should stipulate the conditions under which such rights and responsibilities can be exercised without risk of legal constraint and should attach in perpetuity to the land, with provision for conveyance with the deed to each succeeding owner,

Land Use Plans: In Florida: comprehensive growth management planning at the local level has been mandated by state law (Chapter 163, Part II, Florida Statutes), and a local land use planning process has been established by administrative rule (Chapter 9J-5, Florida Administrative Code). In this way, each county and municipal government in Florida has been charged with the responsibility to develop and to implement a comprehensive land use and growth management plan. This planning process can be used to establish an explicit public acknowledgement of the need to use prescribed fire as a land management tool and of the implicit consequence of dispersing smoke from the areas burned. Local planning documents are fitting legal instruments in which to codify this public acknowledgement of "smoke rights" in association with established fire management responsibilities.

However, the local planning process is a long and open-ended procedure. Its results can vary widely from one county to another and also among the municipalities within a single county. Within certain general state-wide parameters established by rule and within certain basic standards set by each county, the specific provisions incorporated into any particular plan can be either favorable or very unfavorable with respect to fire management on public lands. The quality and strength of provisions addressing fire and smoke management on parklands as finally adopted in a plan depend largely on the commitment and tenacity of local park staff and of sympathetic citizens. The propriety of fire as an appropriate tool in modem land use management should be introduced early and should be re-enforced at ever stage of the planning process. Because land use planning is a cyclic and reverberative process, specific achievements can be rather transitory. Involvement at the local level must be thorough and continuing.

Legislation: The Florida legislature is now debating enactment of the "Florida Prescribed Burning Act." (After this paper was presented, the Legislature enacted this initiative as Chapter 590.026, Florida Statures.) This document states that prescribed burning contributes to public safety 1) by reducing fuels and the risk of wildfires; 2) by helping to maintain biotic diversity and the ecological integrity of native communities; and 3) by facilitating the revegetation, restoration, reforestation, and enhancement of public and private lands. The bill also authorizes public education and technical training programs, where appropriate, in order to assure general acceptance and proper use of fire as a land management tool. It then declares that prescribed burning, when properly authorized, is in the public interest and does not constitute a public or private nuisance. Most important with respect to smoke management, the bill finds that prescribed burning is a property right of the landowner and that the owner or his agent, when conducting an authorized bum, is not to be held liable for damage or injury resulting from fire or smoke, unless negligence is proven.

This bill introduces into legal debate the prospect of establishing certain smoke rights in association with an acknowledgement of related prescribed burning and fire management responsibilities. Unfortunately, language in the bill that is pertinent to the concept of "smoke rights" is rather nebulous. It does not provide clear and precise guidance concerning assertions of negligence, especially where drifting or wind-driven smoke and ash are concerned. However, this draft legislation establishes a useful context for continuing public examination of the rights of land managers relative to fire and smoke management.

SUMMARY

Are smoke rights included with the responsibility to use fire in managing public lands? The premise of this paper is that certain rights to produce and disperse of smoke from lands subject to prescribed burning should be implicitly associated with the public responsibility to use fire as a land management tool.

The existing case law will not explicitly support such an assertion through legal argumentation, while public agencies are not inclined to promote litigation for the purpose of establishing favorable case law.

However, three alternatives exist for establishing such rights, or at least for developing legitimate public acknowledgement of the concept of such rights. To be practical and reasonably effective, easements specifying smoke rights should be instituted early in a region's development history. Local land use planning processes can be used to develop explicit public acknowledgement of contingencies associated with the use of tire as a land management tool, but involvement at the local level must be both consistent and persistent. In Florida, legislation specifically addressing fire and smoke management as a property right has been drafted (and was enacted as of October 1, 1990.) This latter alternative is a particularly straightforward approach. In each case, however, clear and direct communication with the public concerning the role of prescribed burning and smoke management in public land management is necessary.

LITERATURE CITED

Chapter 163, Part II, Florida Statutes: Intergovernmental Programs, County and Municipal Planning and Land Development Regulation.

Chapter 9J-5, Florida Administrative Code: Local Government Comprehensive Planning Regulations.

Chapter 590.026, Florida Statutes: Florida Prescribed Burning Act.

SPATIAL DYNAMIC FIRE BEHAVIOR SIMULATION AS AN AID TO FOREST PLANNING AND MANAGEMENT

Maria J. Vasconcelos and José M. C. Pereira'

Abstract-Mediterranean shrub communities dominate fire-prone landscapes in many parts of Portugal. It is feared that streamside anti-erosion buffers of natural shrub vegetation represent a fire hazard to plantations of eucalyptus and other trees. The FIREMAP system, which can simulate tire behavior in spatially nonuniform environments, was used to assess the extent to which tire buffers can become main vectors of fire spread in Portuguese landscapes. FIREMAP predicted that tire will spread across landscapes consisting of Eucalyptus sp. plantations and streamside borders of natural Mediterranean vegetation much more rapidly than across landscapes consisting of Eucalyptus plantations and streamborders of planted Quercus sp.

INTRODUCTION

About 70 percent of Portugal's land area is unsuitable for agriculture. It has been suggested that these areas should be the subject of reafforestation programs (Grupo Coordenador do Projecto Florestal 1986). Forests cover only about 36 percent of the country, so there is much room for this kind of initiatives, such as the ones recently attempted with support from organizations such as the World Bank and the European Economic Community.

Due to climatic and socio-economic factors, wildfires arc a major threat to Portuguese forests. An average area of 42 000 ha burned yearly from 1973 through 1985 and in 1989 about 54 000 ha of forests were destroyed by wildfires.

A recent trend in Portuguese forestry is the rapid expansion of plantations of exotic species for short rotation biomass production, for use by the paper and pulp industries. The environmental impacts of those plantations have been a topic of heated debate, and legislation was issued regulating soil preparation and plantation and silvicultural practices, with special emphasis on minimizing soil erosion, hydrological disturbances, and loss of biological diversity.

The legislation that regulates these plantations requires that natural vegetation be left along stream channels for erosion protection. The widths required depend on particular situations but are generally between 20 and 60 m. Consequently, the majority of the projects generate a striped landscape where buffers of constant width indiscriminately marginate stream channels.

In this paper we investigate the possibility that where natural vegetation consists of Mediterranean-type shrubs, this landscape structure may contribute to improved fire propagation by creating paths of faster spreading fire that make otherwise unavailable fuels more likely to bum. In fact, these shrub communities bum intensely and contribute to more effective preheating of the less easily ignited fuels in the neighboring plantation forest, thus setting the stage for larger, more intense fires.

The objective of this work was to use a PC-based spatial analysis system that simulates the spread of fire in a spatially nonuniform landscape in discrete time steps (the FIREMAP system) to assess the extent to which anti-erosion buffers along streams can become the main vector of fire propagation, or on the other hand, work as barriers to the spreading tire.

We simulated structurally simple landscapes, not only to facilitate interpretation of the results, but primarily because this corresponds to the actual spatial structure of Eucalyptus plantations.

FIREMAP

This fire spread simulation system, designed at the University of Arizona (Vasconcelos 1988), estimates fire characteristics in spatially nonuniform environments, and displays areas burned on maps. FIREMAP consists of the integration of the DIRECT module from the BEHAVE system (Andrews 1986) with a raster-based geographic information system, the Map Analysis Package -MAP- (Tomlin 1986), and allows distributed predictions of fire characteristics and simulation of fire spread.

In this framework, nonuniform fuels, weather, and topography data arc encoded, stored, and manipulated on thematic maps, where the field is represented as cells of a grid corresponding to uniform parcels of land. Because the homogeneity assumptions are met, Rothermel's model can be used within each unit.

The dynamic process of a spreading fire is simulated through the use of the distance functions of MAP. Distance functions deal with the measurement of weighted distances, allowing

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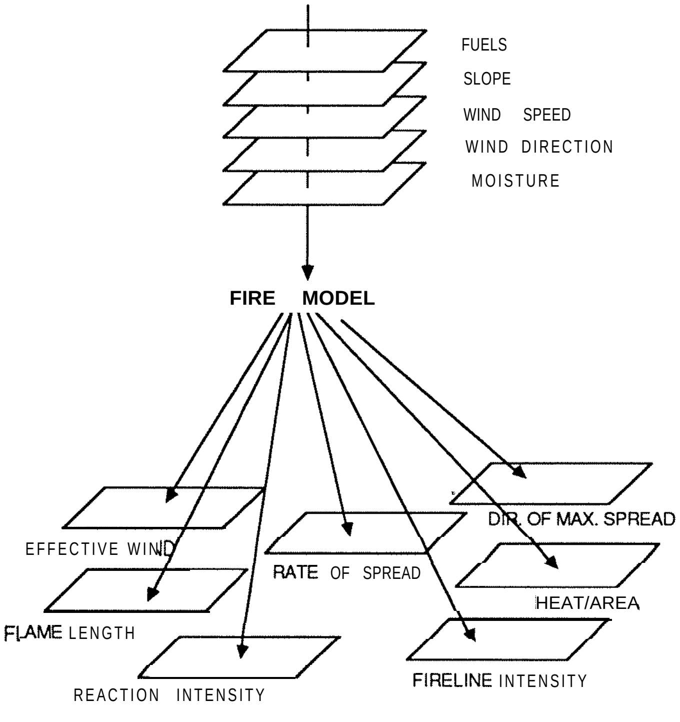
'Forester, Centro Nacional de Informação Geográfica, Rua Braancamp, 82 1 QD, 1200 LISBOA, Portugal; Assistant Professor, Departamento de Engenharia Florestal, ISA, Universidade Técnica de Lisboa, Tapada da Ajuda 1399 LISBOA CODEX, Portugal.

simulation of movement on a previously computed surface of "frictions". These are defined as the rate at which the fire spreads from one cell to its neighbors given the direction of the prevalent wind. The rates of spread overlay utilized depends upon weather conditions, and a new rates of spread overlay has to be utilized whenever there is a change in the weather. This is done by stopping the simulation at the end of a time step and proceeding with the spread process on a new rates of spread overlay that was calculated according to the new weather conditions.

Figure 1 illustrates how tire characteristics are computed for each cell of the data base and set of constant meteorological conditions, based on input overlays generated within MAP. These input overlays are created from the topography, vegetation, and weather data using the standard arithmetic and reclassification capabilities of MAP and the tables presented in Rothermel (1983).



APPLICATION

We ran four simulations to test fire sensitivity of four possible forest landscapes corresponding to four management alternatives for Eucalyptus sp. stands in a Mediterranean-type region. The simulations are for a 1.5 hour bum, in three 30-minute time steps, with a likely early summer weather scenario, which is summarized in table 1.

Table 1.--Weather conditions

	Temperature		Relative humidity	Wind	
	Dry	Wet		Speed[a]	Direction
	- Degrees F -		- Percent -	- Mph -	
First step	82	52	15	12	S
Second & third steps	84	51	12	12	S

[a] wind speed at midflame height

Some comments may be appropriate regarding the temporal and spatial scales we used. Under a normal weather scenario, it seems reasonable to assume constancy of temperature and relative humidity during 30 minute intervals. Wiidspeed and wind direction probably vary significantly at a liner time scale, and Fischer and Hardy (1972) indicate that the standard time for averaging windspeed is 10 minutes. However, Rothermel's model was designed to predict fue behavior under relatively uniform weather conditions (Rothermel, 1983), and although considerable weather changes in a 24-hour period should be expected, projection times of 2 to 4 hours, under constant meteorology are reasonable (Andrews 1986). A more sophisticated treatment of the interactions between wind, terrain, and fire behavior will probably require expansion of the FIREMAP system to include a surface windflow model such as KRISSY (Fosberg and Sestak 1986).

Spatial resolution of the database is considered appropriate since it satisfies what we believe to be the two most important considerations. On the one hand, cell size is small enough to capture all essential landscape features and overall structure. On the other hand, the cells are large enough in comparison to average flame front depths to ensure that steady state spread conditions are almost always present (Catchpole et al. 1989).

The Digital Data Base

The digital cartographic data base corresponds to a 2280 ha area of undulating terrain. Altitudes range from 200 m to 600 m with aspect predominantly to the east, northeast, and southwest on steeper slopes. The scale is 1:12,000 and there are 75 rows by 76 columns with a cell size of approximately 0.4 ha (1 acre). The data base consists of the following information layers: TOPOGRAPHY, STREAM CHANNELS, an LANDSCAPE1, 2, 3, and 4.

The landscape maps correspond to different management alternatives for vegetation buffers along ephemeral streams in Eucalyptus plantations. LANDSCAPE1 represents a landscape of continuous Eucalyptus stands without any kind of stream buffering. LANDSCAPE2 and LANDSCAPE3 represent soil conservation alternatives favored by Portuguese environmental legislation regarding fast-growing plantation forests. In landscapes 2 and 3, natural vegetation is retained as stream side buffer strips of predetermined minimum width. Different stages of shrub development are considered in landscapes 2 and 3. Landscape 2 represents the case of having medium height evergreen sclerophyllous shrubs along the streams and landscape 3 the case of tall and dense stands of the same shrub types. In the fourth vegetation alternative (LANDSCAPE4) a more balanced and diverse landscape is considered with wider strips of deciduous Ouercus sp. planted along stream banks. Figure 2 shows the stream channel pattern.

Simulation

Four sets of input maps for the fire model were generated as explained above. The FUELS overlays were created by reclassifying the vegetation types to one of the 13 standard fuel models (Anderson 1982) based on a correspondence presented in Barreto (1985). Barreto classifies most of the vegetation cover types found in Portuguese landscapes as the models included in the mentioned set of 13 models.
The correspondence we used for this particular case is as follows:

Eucalyptus sp. stands- fuel model 5
Medium evergreen sclerophyllous shrub stands- fuel model 6
Tall, dense evergreen sclerophyllous shrub stands-
fuel model 4
Deciduous oak stands- fuel model 9

FIREMAP generates maps with the expected tire characteristics for the 4 landscape alternatives in the 3 time steps and then simulates the spread of tire, with a given source point, for the alternatives considered. Maps of the expected flame lengths at each database cell are also provided.

RESULTS

The maps displaying the predicted areas burned and respective expected flame lengths are shown in figures 3 and 4. Table 2 shows the number of burned cells for each time step and landscape and Table 3 the number of cells in each flame length class for each of the 4 simulation scenarios.

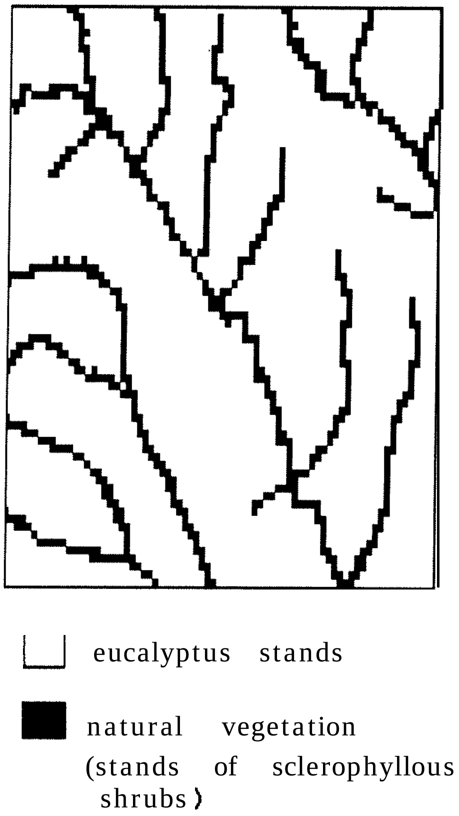


Figure 2.--The stream channels.

Table 2.--Cells burned

	1st step	2nd step	3rd step
	Number		
Simulation 1	66 (26.4)[a]	81 (32.4)	48 (19.2)
Simulation 2	91 (36.4)	102 (40.8)	82 (32.8)
Simulation 3	154 (61.6)	117 (46.8)	124 (49.6)
Simulation 4	38 (15.2)	20 (8.0)	31 (12.4)

[a] area burned, in hectares

Table 3.--Expected flame Lengths

	0 - 4 feet	4 - 8 feet	8 - 11 feet	>11 feet
	Number of cells			
Simulation 1	4	153	38	
Simulation 2	4	216	55	
Simulation 3	6	218	87	84
Simulation 4	16	64	9	

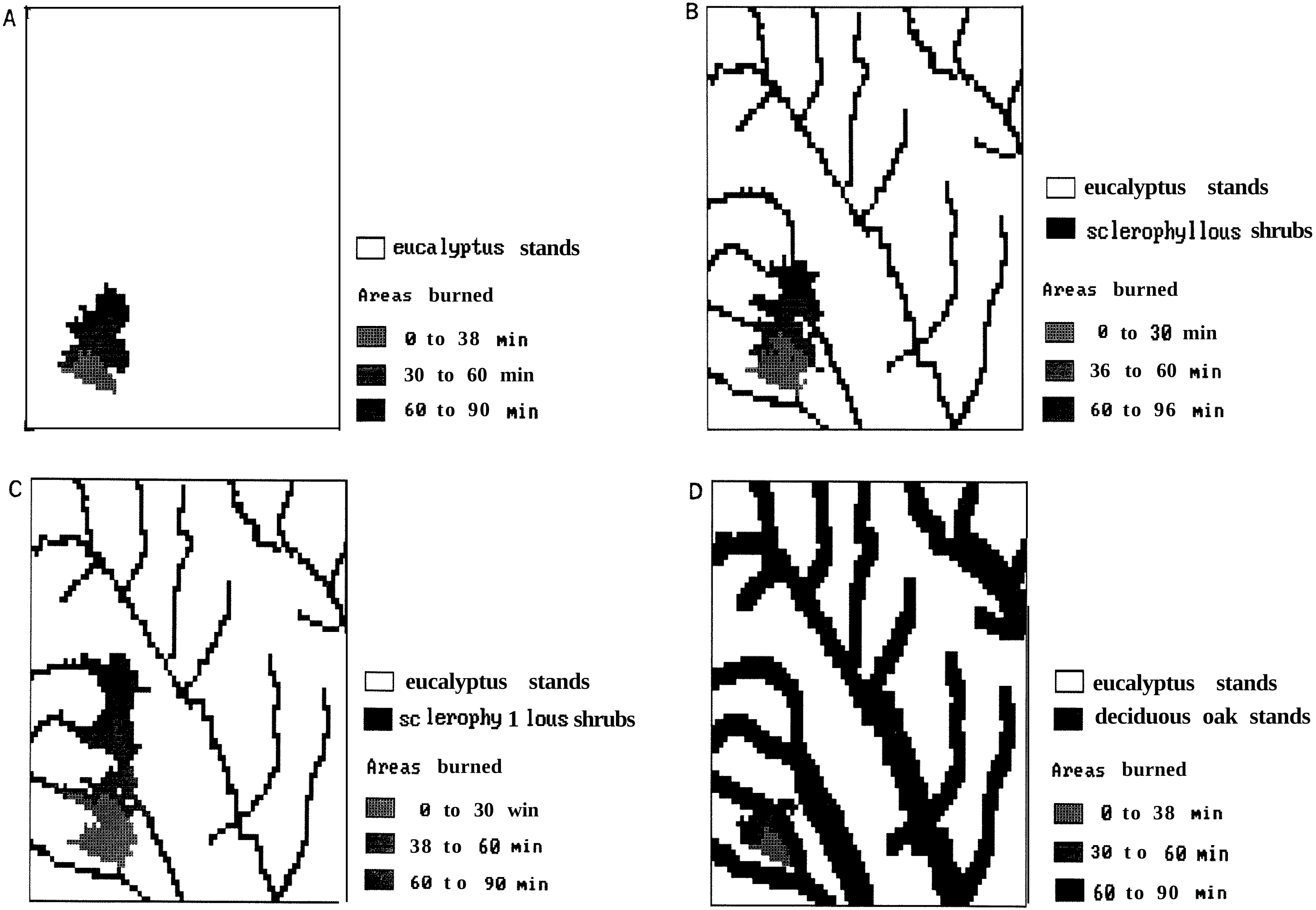


Figure 3.--Areas predicted to burn: (a) simulation 1, (b) simulation 2, (c) simulation 3, and (d) simulation 4

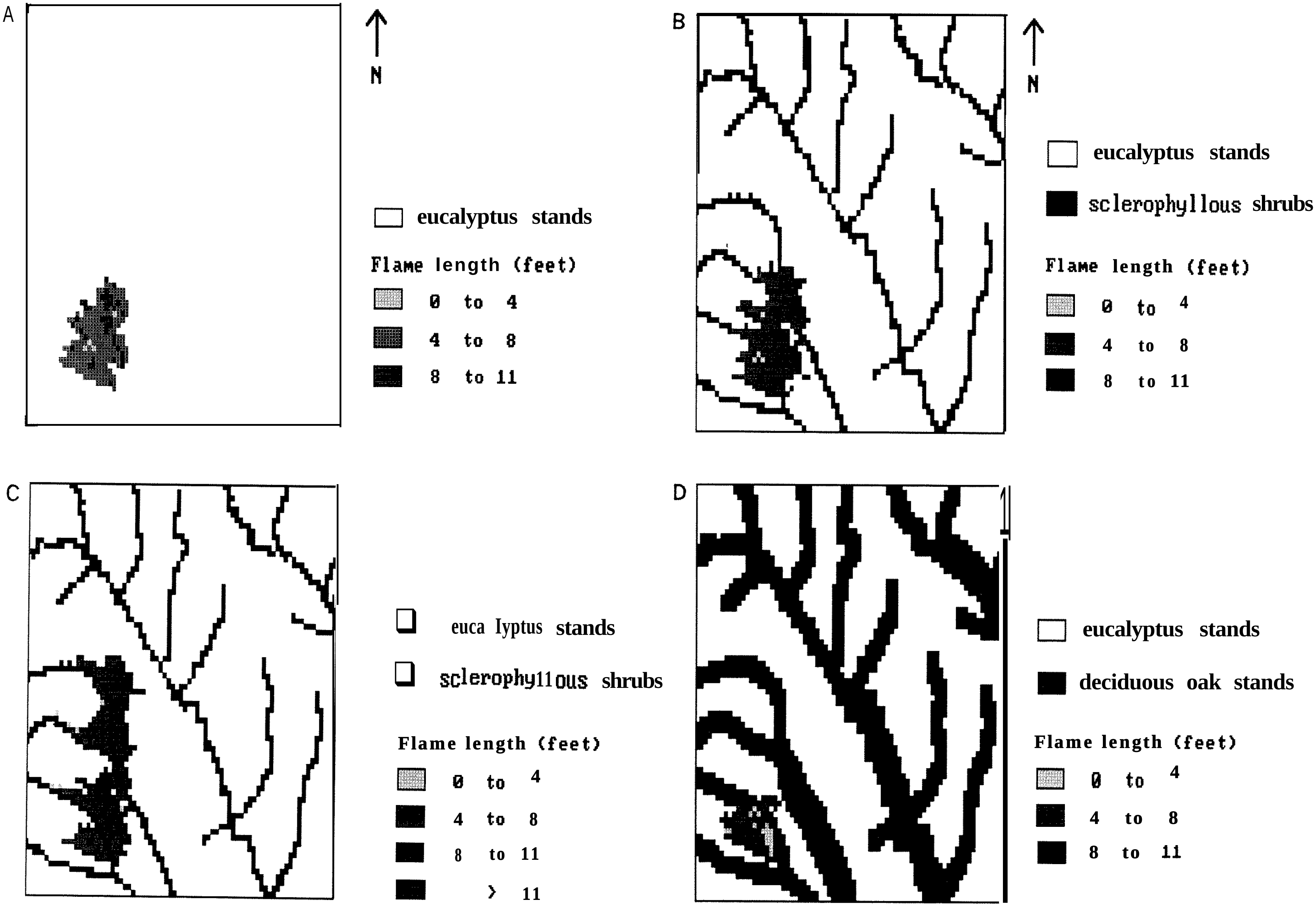


Figure 4.--Expected flame lengths: (a) simulation 1, (b) simulation 2, (c) simulation 3, and (d) simulation 4.

DISCUSSION AND CONCLUSIONS

The results above indicate that under the simulation conditions, natural vegetation left along stream banks may actually contribute to increased fire problems. In fact, there was an increase of 41 and 102 percent of predicted burned area on the second and third alternatives (shrub stands along stream banks) relative to the first alternative (Eucalyptus sp. only)

The simulation outputs suggest that the striped patterns generate preferential paths for tire, creating spreading conditions that lead to higher perimeter-to-area ratios of the burning area, thus improving propagation chances by increasing the length of contact with unburned fuels. On the other hand, the deciduous oak stands have lower rates of spread and create zones of "higher friction" that retard propagation of fire to the Eucalyptus stands. There was a decrease of 46 percent of predicted burned area for this alternative when compared with the first alternative. Given the importance of convective heat transfer in deep fuelbeds such as those represented by shrub formations, a worst case scenario involving higher windspeeds would probably emphasize even more the rapid spread of fire along the stream buffers.

Landscape planning in areas of intensively managed plantation forests is a problem involving multiple, potentially conflicting objectives. Conflicts arise not only between economic production and environmental protection, but also between different ecological concerns. In the present case study, FIREMAP was used to emphasize one such conflict, between erosion protection and fire hazard, in a way that provides information about fire characteristics in a surrogate laboratory mode. These quantitative data can be integrated with other economic and environmental information to support cost-benefit or multiobjective decision analyses of forest management alternatives.

ACKNOWLEDGMENTS

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LITERATURE CITED

Anderson, Hal E. 1982. Aids to determining fuel models for estimating fire behavior. Genera1 Technical Report INT-122. Odgen, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Andrews, Patricia L. 1986. BEHAVE: Fire behavior prediction and fuel modeling system - BURN subsystem, part1. USDA Forest Service, General Technical Report, INT-194, Intermountain Forest and Range Experiment Station.

Barreto, Luís S. 1985. Predição expedita do comportamento de fogos florestais (Adaptação de Rothermel, 1983). INIC, CEF.

Catchpole, E.A., T.J. Hatton and W.R. Catchpole. 1989. Fire spread through nonhomogeneous fuel modelled as a Markov process. Ecological Modelling, vol. 48, pp. 101-112.

Fisher, William C. and Charles E. Hardy. 1972. Fire weather observers' handbook. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, 152 pp.

Fosberg, Michael A. and Michael L. Sestak 1986. KRISSY: user's guide to modeling three-dimensional wind flow in complex terrain. USDA Forest Service. Pacific Southwest Forest and Range Experiment Station. General Technical Report PSW-92.

Grupo Coordenador do Projecto Florestal 1986. Programa de desenvolvimento florestal, Fase II do Projecto florestal. Ministério da Agricultura, Pescas e Alimentação. Gabinete do Ministro.

Rothermel, Richard C. 1983. How to predict the spread and intensity of forest fires. USDA Forest Service, General Technical Report, INT-143, Intermountain Forest and Range Experiment Station.

Tomlin, C. Dana 1986. The IBM personal computer version of the Map Analysis Package. GSD/IBM AcIS Project, Report No. LCGSA-85-16 Laboratory for Computer graphics and Spatial Analysis. Graduate School of Design, Harvard University.

Vasconcelos, Maria J. 1988. Simulation of fire Behavior with a geographic information system. Unpublished Master's Thesis. University of Arizona 1988.

LIST OF AUTHORS