FIRE ECOLOGY

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

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Abstract-The purpose of this review is to synthesize a long-term body of research dealing with fire 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 1-1 1 years were consistently dominated (70-90 percent cover) by Andropogon gerardii. With this increasing interval between fires other dominant warn-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 Thelise Cercist and fUlmus. Gallery forests on Konza Prairie dramatically increased from the time of European settlement (18.50) to present; this has been attributed to decreased tire frequency and intensity in the region. With continued fire 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. n 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 fire 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 fire 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 fire 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.

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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 Quercus 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.

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 (Andropogon gerardii) and other tall warm-season grasses (e.g., Andropogon scoparius, Sorghastrum nutans, and Panicum virgatum). Species along with a number of forbs, e.g. Solidago missouriensis and Vernonia 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. scoparius, S. nutans and other warm-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. Community 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 community 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	a.7 + 2.0b	7.8 + 1.7b
Salvia azurea	burned	*a	14.1 + 5.0b
	unburned	*a	1.1 + 0.3c
Ambrosia silostacha	burned	2.8 + 1.1a	2.5 + 1.1a
	unburned	10.2 + 2.3b	8.2 + 1.56
Artemisia ludoviciana	burned	0.1 + *a	0.1 + *a
	unburned	12.6 + 2.9b	a.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 psilostachya 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 32 years without fire (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).

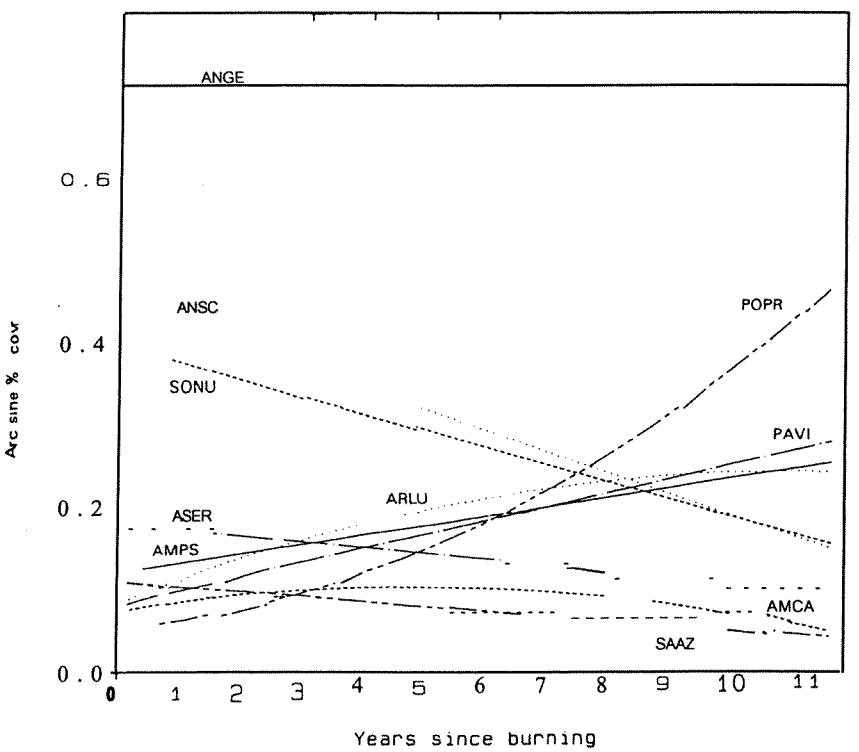

Fig. 1. Fitted 1st and 2nd degree polynomial regression lines of species distribution along a fire interval gradient identified by ordination analysis (Detrended Correspondence Analysis) (After Gibson and Hulbert 1987). ANGE = Andropogon gerardii; ANSC = A. scoparius; SONU = Sorghastrum nutans; PAVI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

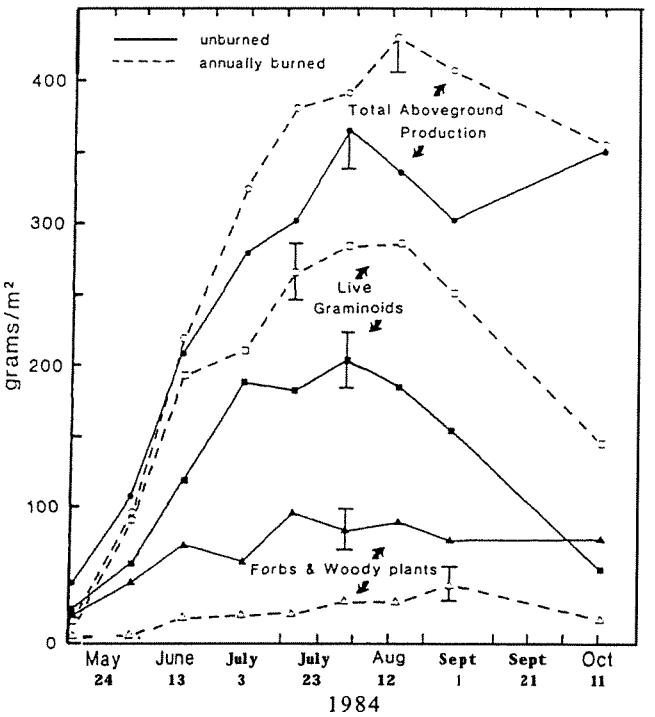

Fig. 2. The seasonal pattern of several components of aboveground biomass on a burned and unburned lowland soil during 1984 on Konza Prairie . Total aboveground production includes live graminoids, forbs, and woody plants, and current year's dead biomass. Vertical bar represents + standard error of the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

Invasion of Tree Species into Open Prairie

Woody species will rapidly invade open prairie in the absence of fire 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

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. Watersheds N4D and NIB contain large areas of gallery forest along the stream channels.

Site and Burn Treatment	Tree Density (number per hectare)	Number of Spec i es	Diversity (H')	Dominant Species (Density per hectare)
Annually Burned				
1A	2.5	6	1.23	Gleditsia triacanthos (1.5)
ID	2.9	4	0.94	Poputus deltoides (0.5)
Unburned (IO years)				
UB	12.0	a	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)
N1B	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. Cleditsia 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 fire has been excluded is a function of species dispersal vectors. Species such as Junioerus 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 - Quercus 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. Q. muehlenbergii and Q. macrocarna 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 xeric (group 4) (Abrams 1986).

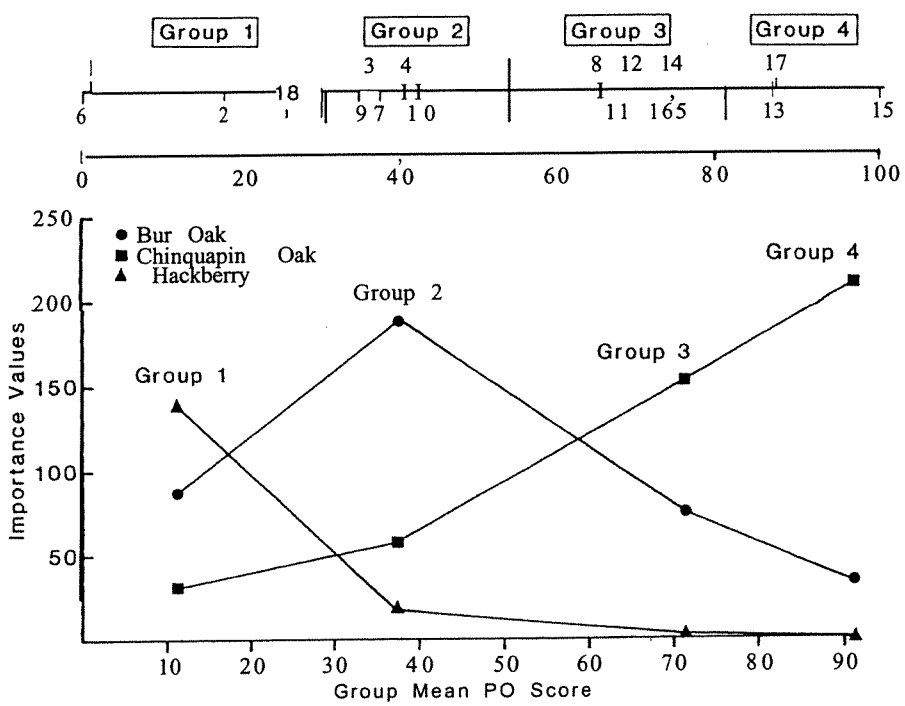

Fig. 3. Polar ordination analysis and the mean importance values for the dominant species in 18 gallery forest stands on Konza Prairie. The four stand types are identified.

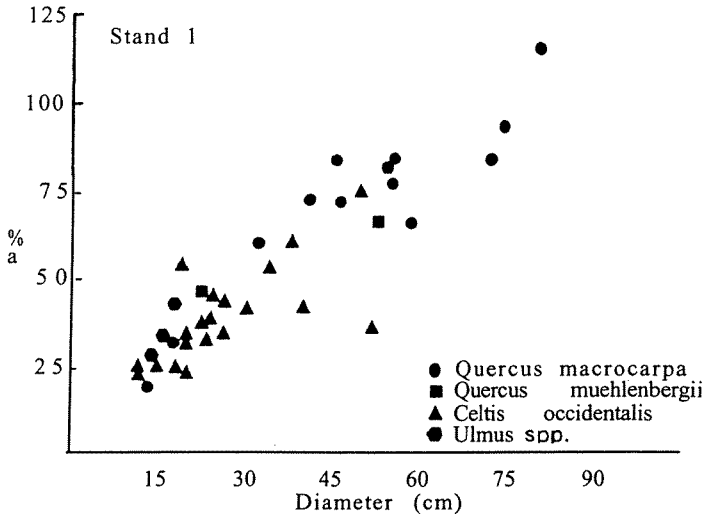

Fig. 4.
Age-diameter data
for gallery forest stand 1
on Konza Prairie.
(After Abrams 1986).

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. macrocarua oak stand in which Q. macrocarna stems were the largest and oldest present; most Q. macrocarna 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 tire 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

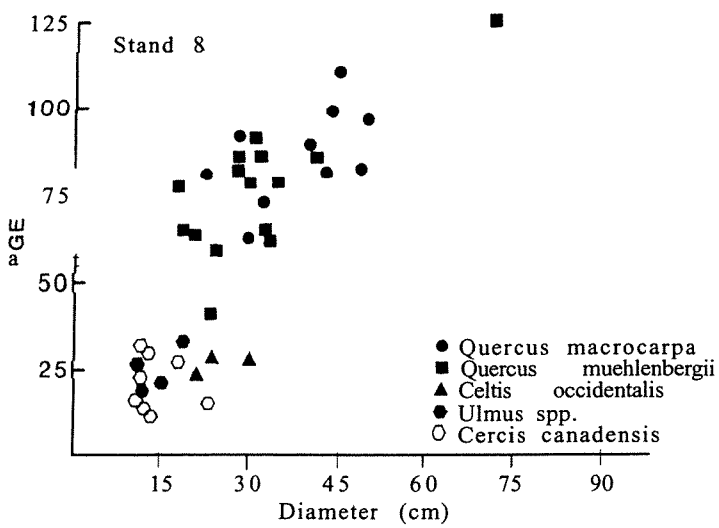

Fig. 5.
Age-diameter data
for gallery forest stand 8
on Konza Prairie.
(After Abrams 1986).

increased rapidly, which suggest that fire, rather than low precipitation, limited growth of woody vegetation in northcast 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. muehlcnbergii, 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. muehlcnbergii. The small stature of Cercis does not rule it out as a potential replacement species here because the size of Q. muehlcnbergii 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 fire 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 warn-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 1 l-year intervals. With increasing intervals between fire, total cover of fort) 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, Celtis, Ulmus and Celtis. e s t a b l i s h e d woodlands along stream channels and ravines had overstories dominated by Quercus and Celtis with Celtis Cercis and Ulmus in the understories. Distribution o f t h e s e gallery forests since 1850 and successional changes resulting in oak replacement by more shade tolerant species are attributed to reduced fire 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.

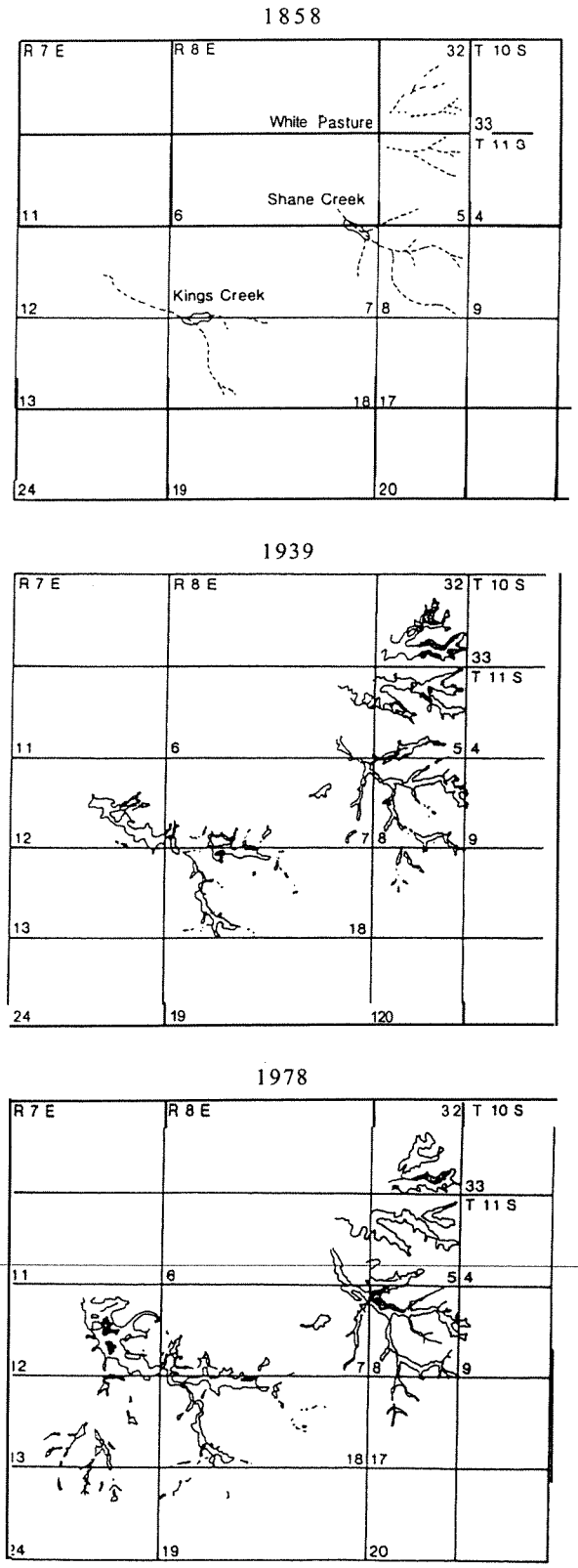

Fig. 6. Areal extent of gallery forests and shrublands (shaded) in 1858, 1939 and 1978 on Konza Prairie.

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FIRE MANAGEMENT FOR MAXIMUM BIODIVERSITY OF CALIFORNIA CHAPARRAL

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Abstract-Two reproductive modes present in chaparral shrubs are affected very differently by fire. Some species, called "tire-recruiters," are dependent upon fire 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 fire, rather they require long fire-free periods in order to establish seedlings. These species are vigorous resprouters, not only after fire, but throughout their lifespan. Older stands of chaparral are continually rejuvenated by recruitment of new resprouts and seedlings of these fire-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 "fire-type" vegetation based on the fact that all species are resilient to the modem fire regime of fires every few decades (Keeley 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 fire-dependent vegetation. This is based on both population and community level phenomenon. Certain species, Adenostoma fasciculatum (Rosaceae), Arctostaphvlos spp. (Ericaccae) 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 modern fire regime "a strategy," since most acreage in southern California burns 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 fire-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 recut-rent fire, may actually decline after repeated tires. Included here are species such as Ouercus dumosa (Fagaceae), Heteromeles arbutifolia Rosaceae), Prunus ilicifolia (Rosaceae), Cercocarpus betuloides (Rosaceae) and Rhamnus spp. (Rhamnaceae). These shrubs are resilient to tire 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 Wanes (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.

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My focus has been on the demographic structure of stands free of tire 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, Cercocamus and Heteromeles (Keelcy unpublished data). It is apparent that long fire-free conditions are required for seedling establishment by these tire-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 fire, and these are called fire-recruiters. Other shrubs, however, are not fire-dependent. They persist after fire but these fire-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 tire 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 tire-persisters.

RESILIENCE TO LONG FIRE-FREE INTERVALS

Community stability is dependent on both fire-recruiters and tire-persisters being resilient to both short and long fire return intervals. The current fire 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.

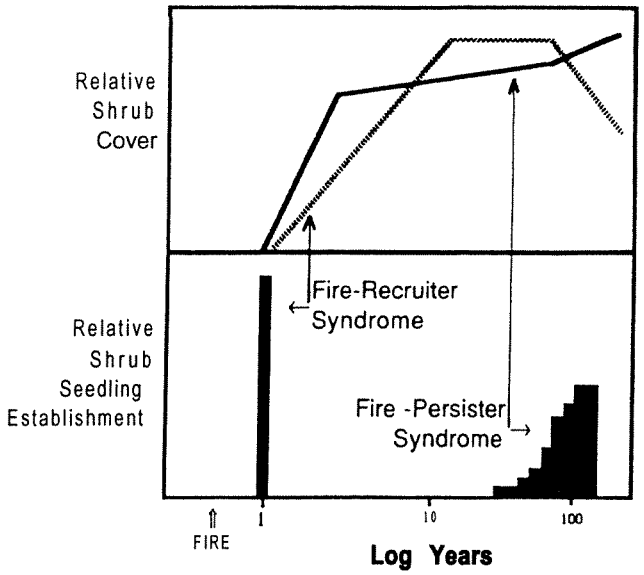


Figure 1.- Schematic illustration of the timing of seedling recruitment for chaparral shrubs described as fire-recruiters and as fire-persisters and longterm changes in relative shrub cover for tire-recruiters (dashed line) and tire persisters (solid line).

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.

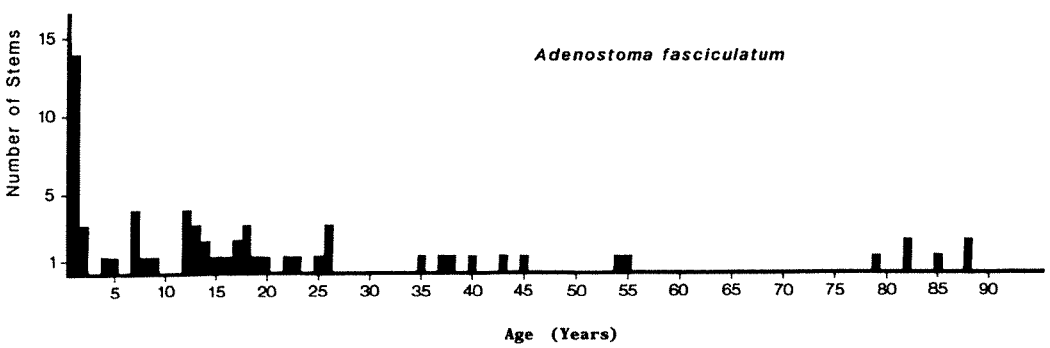


Figure 2.- Number of stems of different ages on a single resprouting shrub of Adenostoma fasciculatum in a stand of chaparral last burned 89 years ago (Keeley unpublished data).

How then did old stands of chaparral come to bc 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 tire. 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 tire-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. Modem 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 tire-free intervals, and different tire-return intervals, favor different components of the vegetation. Longterm stability and biodiversity of chaparral communities may require a mosaic of fire regimes.

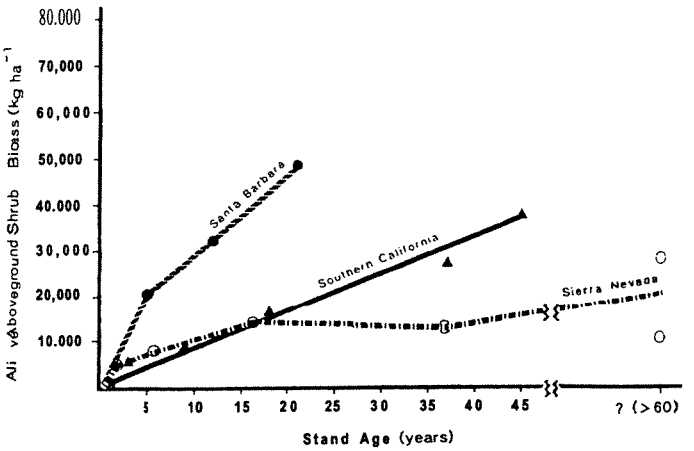
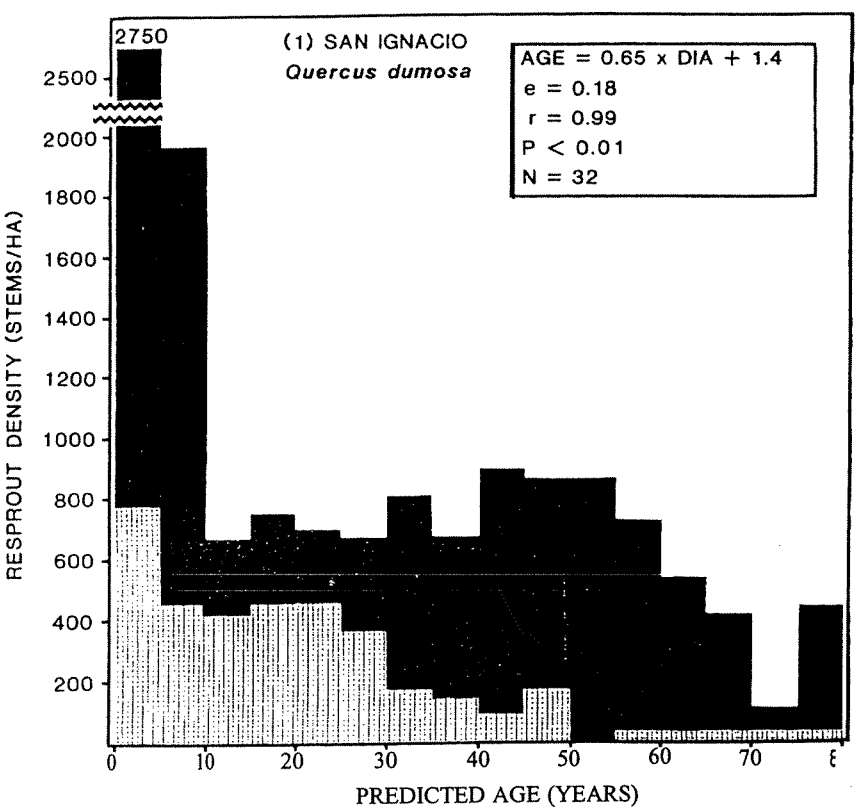


Figure 4.- Standing living biomass in chaparral stands as a function of age since last fire (from Keeley and Keeley 1988, with permission of Cambridge University Press, data from studies by Specht 1969, Conrad and DeBano 1974, Schlesinger & Gill 1980, Rundel and Parsons 1979, Stohlgren and others 1984, as cited in Keeley and Kcelcy 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 arc dead stems). Stem diameters wcrc 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 coeflicicnt, the estimate of relative error was calculated as the standard error divided by the mean value of y.



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FIRE AND OAK REGENERATION IN THE SOUTHERN APPALACHIANS

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Abstract-Oak forests throughout the southern Appalachians have been historically maintained in a regime of frequent tire. Frequent fire 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 tire 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 fire 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 arc 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 fire 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 arc tentative guidelines and must be tested prior to implementation as management recommendations.

THE ECOLOGY OF OAK REGENERATION

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 (Dartey-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 tire. 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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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 tires 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 (Carvell and Tryon 1961; Waldrop and others 1987).

At the turn of the century, summer tires 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 tire 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 fire. 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 tires 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

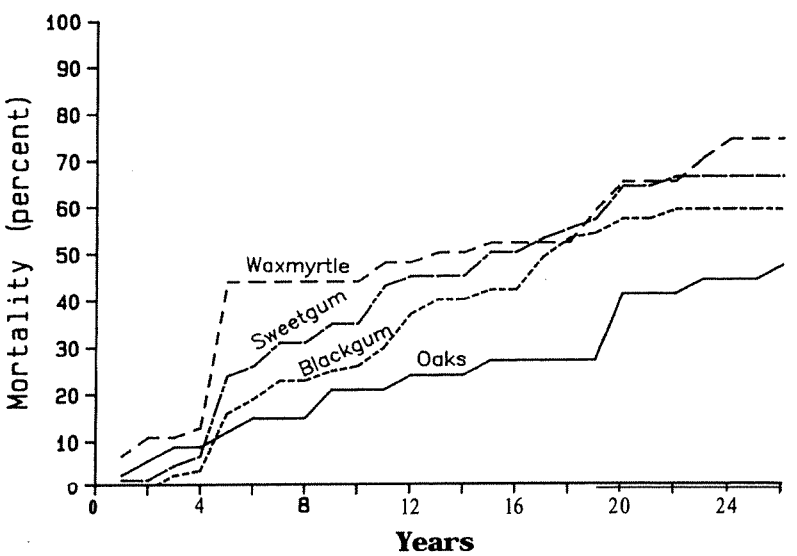

Figure 1. Cumulative mortality of hardwood roots over 26 years of biennial prescribed burning (From Langdon 1981).

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 understory 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 (Carvell 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 xcrify 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 fires 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 fire 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 arc 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 mockernut and pignut hickories, scarlet oak, red maple, and blackgum arc 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 areal extent (Van Lear and Waldrop 1989; Martin 1989). Impenetrable thickets of ericaceous species such as mountain laurel and rhododendron now often dominate midstorics 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 silvicultural 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 guidelines for using fire in oak management. Further research will be necessary to test and line 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 burns 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, while 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 fire, all advance regeneration species would respond to the favorable light conditions in an open stand.

Preharvest 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

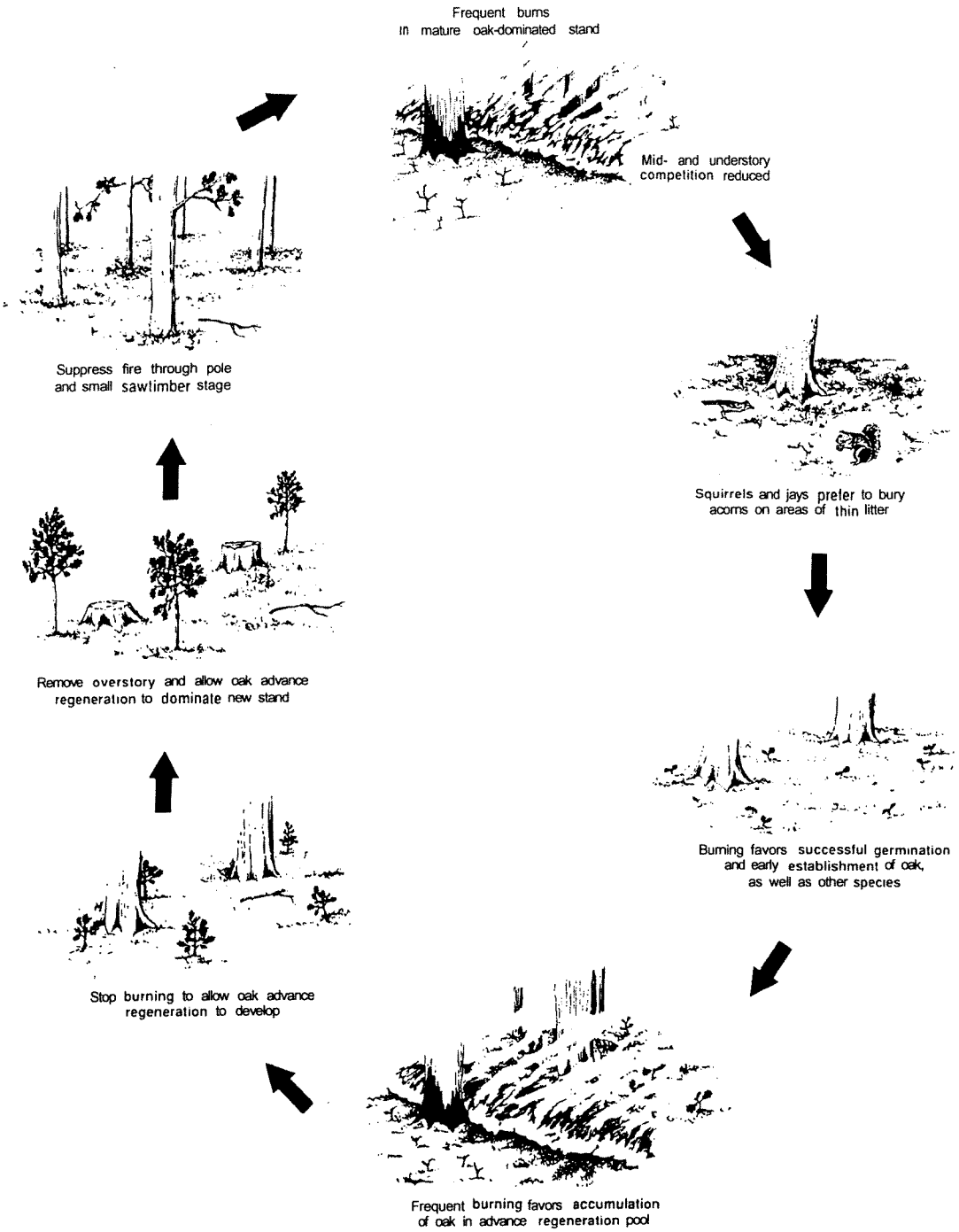

Figure 2. Tentative scenario of using prescribed fire to encourage advance regeneration of oak.

that currently documents what this mix of bums 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 (Teuke 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-bum 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 bums, 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.

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RESPONSE TYPES TO PRESCRIBED FIRE IN OAK FOREST UNDERSTORY

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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 live years) burns and no burn. Each was replicated three times.

Species number declined dramatically under the no-burn regime. Tree seedling establishment was inhibited and sprout size decreased in the annual and periodic burns--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-burn 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 fire years when cover was generally highest; legume cover peaked in four of the five fire years; other forb cover generally increased in tha 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), Daubenmire (1968a), Wright and Bailey (1982), Vogl (1974), and Collins and Wallace (1990). Summaries of the effects of fire 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 1965-1970 the understory of the burn 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 burn 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 burns. 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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Early surveyors report a few places with no forest, and such modern sites as the May Prairie have a physiognomic and floristic resemblance to midwestern 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 burns began in 1963; periodic burns 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 Fcmald (1950).

Data reported here are cover (sum of hits per species x 2) along each 50-foot line. Cover values are averages of the three replications. No frequency or relativized data are reported. Years have been segregated into early 1965-1972, 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 are 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 spccics: 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 styracillua (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 burn 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 sylvatica, Qucrcus coccinea, Q. falcata, Q. velutina and Vaccinium arborcum were recorded most to all years (Nyssa and Q. coccinea were decrcasers). Qucrcus stellata, Q. marilandica and Carya tomentosa occurred in early or middle years. Liquidambar and Cornus 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 burn plot strips, six taxa occurred widely (Carya, Nyssa, Q. coccinea, Q. stellata, Q. velutina and Sassafras albidum). coccinea and Q. velutina were decreasers, Q. stellata and Sassafras were increasers. Cornus florida, Q. falcata and Vaccinium arboreum occurred in early and/or middle years. Qucrcus 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 fires--they were burned back by the fires. Taxa with decreased cover on two to five fires were Carya, Nyssa, Q. coccinea, Q. falcata, Q. marilandica, Q. stellata, Q. velutina, and Vaccinium [illegible] (present six years) and Q. lyrata (present two years) barely survived these fires. Acer rubrum was seen only recently (1982-1988). [illegible] 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 fire (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. Ascyrum stragalum, Pyrus melanocarpa, Rhus glabra and Salix humilis persisted only one to three years (1965-1967). Ascyrum 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. [illegible] these, Ceanothus decreased in cover while Rubus erect, Salix tristis and Vaccinium vacillans increased in cover. Ascyrum hypericoides 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 control plots, Vitis occurred 1965-1968 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 burn 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 tire year, remained constant one tire 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 burn plot strips increased irregularly to 1973, fell, peaked again in 1978, fell irregularly until 1988 and peaked again in 1989. Biomass of Schizachyrium 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 Schizachyrium 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 burn 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	54.6	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	34.6	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	44.9	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 burn plots. Taxa present almost every year arc Andropogon gerardii and Sorphastrum 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. a b o v e 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 spiculata after 1968. 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 burns 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 gerardii 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 burn plot strips numbered 19 species A few taxa occurred 11 or more years, Andropoyon gerardii, Panicum commutatum, P. dichotomum, P. laxiflorum, P. microcarpon and Sorghastrum nutans. A. gerardii was a bulge species, Sorghastrum was an increaser.

Two taxa were seen in the early or early and middle part of the series, Agrostis hycmalis through 1976 and Muhlenbergia tcnuifolia 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 tire, 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 1957, Oosting 1942). Annual burn 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 I).

Composites (Compositae, Asteraceae)

Sixteen composite taxa, including unknown categories, occurred in the control burn 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, Coreopsis tripteris and Solidago odora. All but A. hcmisphericus 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 Scnecio anonymus. Several taxa appeared only in late or middle and late years; these were Ambrosia artimisiifolia seen first in 1987, Erectites 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, a d e n s i s w e r e weedy taxa locally.

Helianthus hirsutus and Coreopsis major were dccreasers--in the late years these taxa were present live 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 burns 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 tire).

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 gronovii, Senecio 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. Chrvsopsis 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 silphioidcs 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-fire 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 burn plot strips. Taxa which occurred only in the early years were Amphicarpa bractcata, Dcsmodium virginianum and Psoralea psoralioides. Species which occurred in middle or early and middle years were Dcsmodium 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, Stvlosanthes 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 rcportcd by Wahlenberg and others (1939). L. procumbens has a low-middle, and Schrankia microphylla 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 Tcphrosia virginiana, Lespedeza repens a decreaser, and L. intermcdia 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, Calactia volubilis 1981, Lespedeza hirta 1967, Psoralea psoralioides 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 occurred in the periodic burn years. The two highest peaks (1979 and 1988) arc amplified by high cover of Cassia nictitans. An increase in frequency of C. nictitans with burning has been rcportcd (Cushwa and others 1970). Four other taxa had high cover in three to four fire years compared to non-tire years: Clitoria mariana, Lespedeza repens, L. procumbens and Schrankia microphylla. The cover of these taxa decreased in the years after each fire. Lespedeza intermedia peaked in two fire years only. Cover of Lespedeza virginica and Tcphrosia increased on three of five 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 tire years. it was another species influenced negatively by fire.

Other Forhs

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, Ipomea pandurata, Leehea 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 Pvcnanthemum 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 dcnsiflorum, disappeared--it was last seen in 1978. A few taxa occurred only in the middle of the year series: Acalvpha virginica, Convolvulus sepium, Diodia virginica, Gerardia pectinata, Houstonia caerulea, Lechea minor and Lobelia nuberula. e 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 tire years was 3.0; mean cover in non-tire years was 4.0; the difference suggested a depressing effect of fire on forbs. The year following the tire the mean cover was 5.8--the rise suggests a positive fertilization or release-from-competition effect. These effects can be seen in Potcntilla simplex in which percent cover in fire years was low; in non-tire years it was intcrmediatc; 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 (Daubcnmire 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-burn 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 burn 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 fire 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 fires. Of low tolerance were taxa which were early and early and middle retrcaters, decreaser-retrcaters, 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 fire 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 bum 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 after 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 burns (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 arc 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 allclopathic 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 burns, five of 12 invaders appeared for the first time the year of one of the five periodic fires. That one species invading per (periodic) fire compares to the annual burns 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 fire. 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, burn plot trees had 11 responses. Rhizome spreading shrubs had seven responses, other shrub six. Among herbs, annuals had nine responses and occurred only in burn plots. Chamaephytes (two species) had two responses in burn plots. Geophytes (five species) had three responses in burns and did not occur in check plots. Stolmferons herbs (three species) had live responses in fire plots. Climbing herbs (live species) had six responses in burn 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 fire. 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
WD	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
WAO	P	2	T
WAN	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
WC	A		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
O	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. conallina, which was present throughout, peaked in fire 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 burn (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 after 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 tire years, and high cover between fires; 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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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 heliantboides) 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 (Stipa spartea) 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 fire 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 reline the understanding of fire's role in grassland ecosystems with an increased focus on fire frequency (the number of years between bums) and fire season (the season during which fire is applied). Grassland fires 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 fire 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 fire 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 fire 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-lie 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 grams [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 tilifolia 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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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 fire 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 fire 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, fires 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 (Steutcr 1987).

The C_3 grasses of the northern mix&prairie appear to be a fire-adapted guild (Steuter 1987). The tendency for cool-season grass species to increase or to bc 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 (Elvmus canadensis L.), and Scribner dichanthelium [Dichanthelium oligosanthes (Schult.) Gould var. scribnerianum (Nash) Gould] (Hensel 1923; Ehrenreich 1959; Hadley and Kieckhefer 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 Owcnsby 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 psilostachya DC.) and white aster (Aster ericoides L.), which were most positively affected by fail burns, blue lettuce (Lactuca oblongifolia Nutt.) most effected by summer burns, and stiff sunflower [Helianthus rigidus (Cass.) Desf.] and wavy-leaf thistle [Cirsium undulatum (Nutt.) Spreng.] most effected by spring burns. Only pasque flower (Anemone patcns 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) burns adversely affected species such as prairie violet (Viola pedatifida G. Don), white-eyed grass (Sisyrinchium campestre Bickn.) and downy gentian (Gentiana puberulenta Pringle); gay-feather (Liatris aspera Michx.) and smooth blue aster (Aster laevis L.), however, ad significantly more leaves with late than with early spring bums (Lovell 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 Udorthent 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 11 E) 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, 7-1 1% 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 strati&d, 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 burn treatment plots were not sampled in 1983 since treatment had not yet been applied: evaluations for 1981 were used to represent pre-burn 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 burn 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 (Gwmvs 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 fire, reflects only a change in the amount of a species and not necessarily changes in population size.

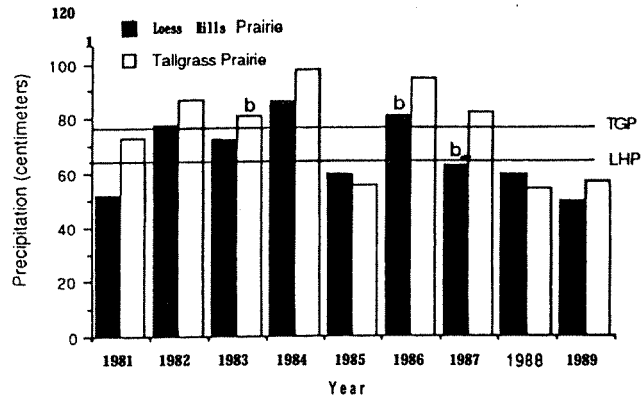

Fig. 1.-Precipitation for Sioux City, Iowa [Loess Hills (= LWP) Prairie site] and North Omaha, Nebraska [Tallgrass (TGP) Prairie site] weather stations for the years 1981 through 1989. Horizontal lines represent normal precipitation (National Oceanic and Atmospheric Administration 1989a, 1989b). "b" = burn 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 rhsn 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). H-H = no data; tr = <0.5 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	24±4.1
	1986	33±4.3	43±6.3	33±5.1	28±4.4
Bare Soil	1981		2±1.0	2±1.9	
	1963	6912.5	67±6.8		2[illegible].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
	1964	1±0.8	7±3.6	1±0.8	tr
	198.5	1±0.8	3±1.4	tr	tr
Canestens (leadplant)	1981	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	8±2.7	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	81±2.7	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)	1961	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	221.9	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	4±1.5	10±3.8	3±1.4	5±2.2
Ceanothuss (New Jersey tea)	1981	11±4.7	5±3.6	1±0.8	1±0.8
	1983	1G5.3	3±3.1	-	6±4.6
	1984	13±5.9	6±3.6	0	4±3.1
	1986	es.3	4±3.1	0	6±3.6
Conyzansis (horse-wed)	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	10±3.1	2±1.0	4±1.3	1±0.2
	1986	1±0.8	1±0.8	1±0.2	tr
Elymusnsis (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
	19%	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
		0	1±0.8	2±1.0	0
Euphorbia corollata (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	1023.4	9±3.8	8±3.8	1323.2
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	1fp.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	12±2.0	8±1.6	5±1.6
	1983	11±3.4	2±0.8		9±2.7
	1984	10±3.2	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 (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	3±1.4	6±2.3		5±1.5
	1984	10±3.8	8±2.7	16±3.7	16±4.8
	1986	22±5.4	8±3.1	2ois.o	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 5.6
	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 pratense (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	35±5.5	tr
	1986	tr	4x3.1	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 = 10.5 percent.

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	32k.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	40II.7	30+2.5	10+2.1
	1989	8±2.6	23±2.5	2123.0	1323.4
Andropogon gerardii (big bluestem)	1986	32±7.9	9±3.2	16+4.0	20+8.1
	1907	36+8.3	7±2.7	15+3.8	23+8.6
	1988	34±7.9	6±2.2	1423.1	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 (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	Go.3
	1989	1±0.8	2±1.0	2±0.7	110.3
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	22±2.4	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	3322.7	33±3.1
	1989	16±3.3	2622.6	24±3.1	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	2f0.7	4±1.3	120.2	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	431.5	tr
	1989	2±1.0	1214.0	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)	198.5	1+0.2	tr	tr	tr
	1987	tr	tr	1±0.8	tr
	1988	tr	0	tr	0
	1989	tr	tr	tr	tr

Table 2. (continued).

Species	Evaluation Year	Season of Prescribed Burn			
		Spring	Summer	Fall	Unburned
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 flex)	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	5f1.4	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	611.6	4±1.5	tr
	1989	10±3.4	5±2.2	4±1.5	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	3_2.0
Sisyrinchium campestre (white-eyed grass)	1986	5±2.1	6±1.8	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	1±0.4	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-burn 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 burn, 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 pm-burn 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-burn numbers. Thus, for both the loess hills and tke tallgrass prairie ecosystems, spring treatments, which represent the most widely applied time of fire management, showed the greatest long-term (f-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), g r a s:s [Sorghastrum nutans (L.) Nash], sideoats grama [Bouteloua curtipendula (Michx.) Torr.) , and sedge (Carex spp.) were sufficiently abundant to make comparisons between the tallgrass and loess kills sites. Tke 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 preburn amounts both without burning and with all burn treatments except spring burning (fig. 2). The most likely explanation for this difference in

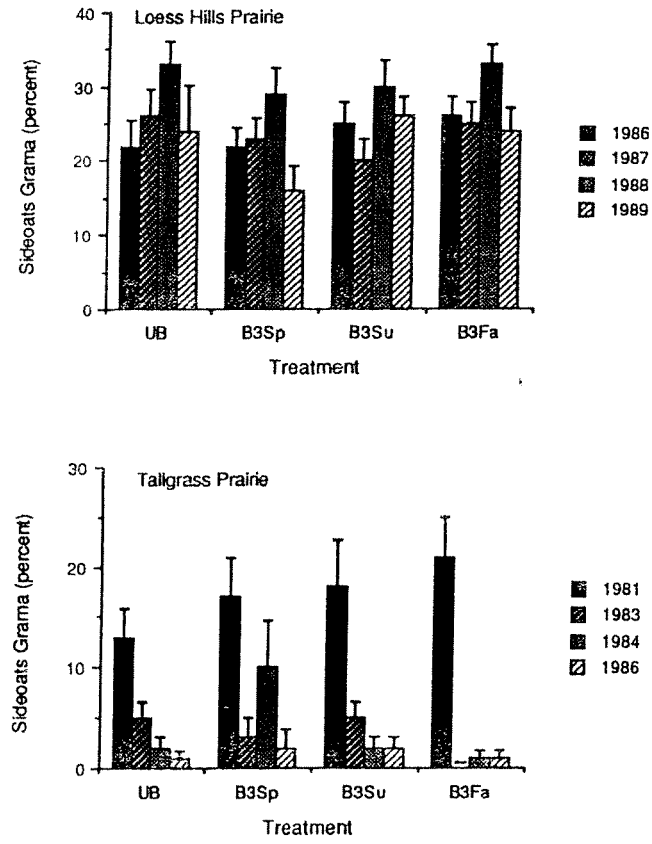

Fig. 2.-Sideoats grama cover for loess kills and tallgrass prairie sites contrasting the site-specific response of this species to burning. Vertical lines represent one Standard Error. B3 = three-year burn schedule, Sp = Spring, Su = Summer, Fa = Fall, UB = Unburned. Tallgrass site burn year = 1983; 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 fire'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, fire'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 fire-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 fire was found in the tallgrass prairie with summer burning of false sunflower [Heliopsis helianthoides (L.) Sweet var. scabra (Dun.) Fern.] (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 burns 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.

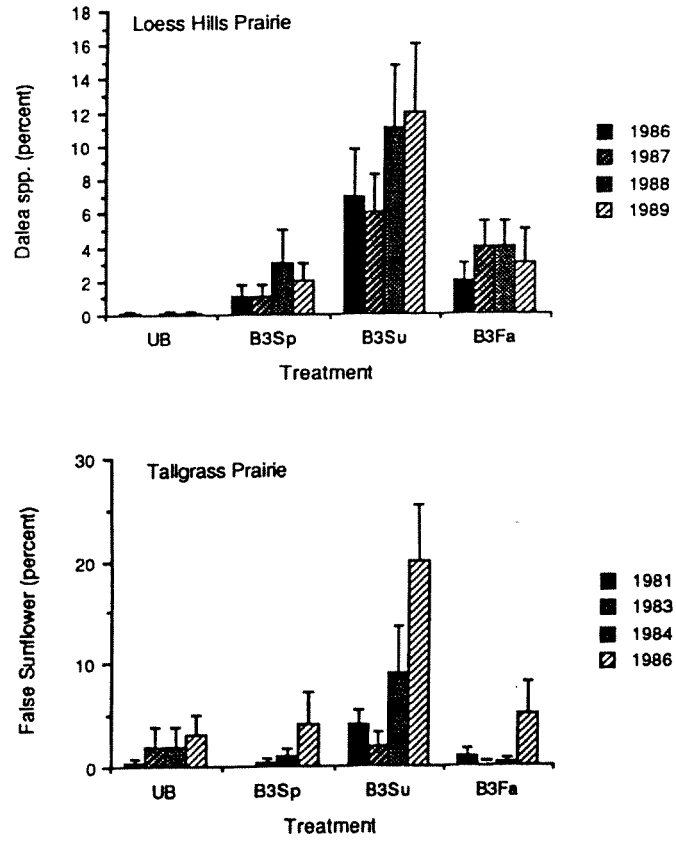

Fig. 3.-Canopy cover of Dalea spp. (prairie clover; loess hills prairie) and false sunflower (tallgrass prairie) showing the type of increase in cover hypothesized to reflect an increase in number of individuals in response to summer burning. Vertical lines represent one Standard Error. B3 = three-year burn 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. compactum (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. Little 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 dichanthelium 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 fire 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 area. 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 be given to some application of fire 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 burns.

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 burns, however, should not be so extensive as to adversely affect the resident invertebrate population of the area. Such small scale summer burns 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 fire.

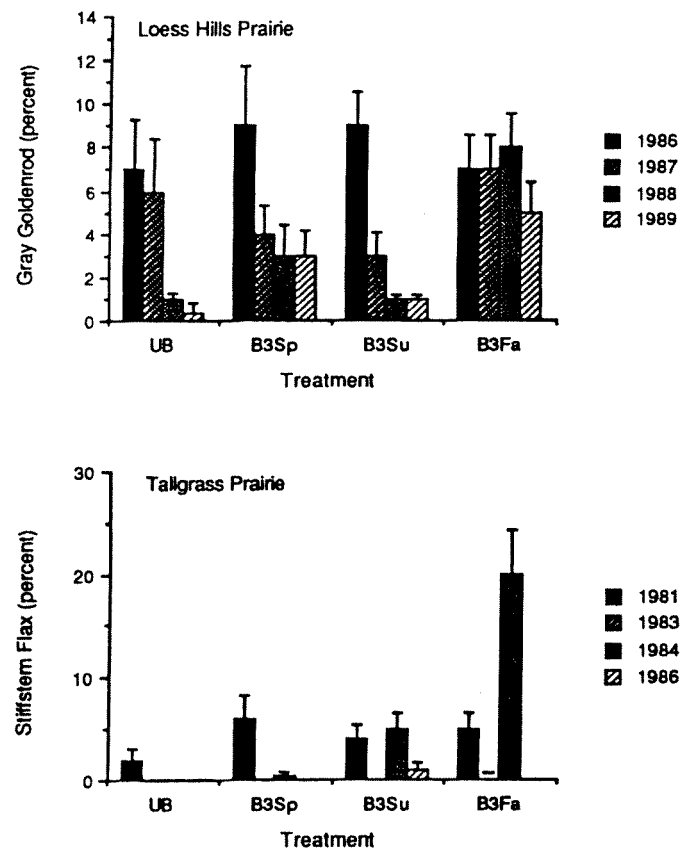

Fig. 4.-Canopy cover of grey goldenrod (loess hills prairie) and stiffstem flax (tallgrass prairie) indicating that their persistence may be dependent on summer or fall burns. Vertical lines represent one Standard Error. B3 = three-year burn schedule, Sp = Spring, Su = Summer, Fa = Fall, UB = Unburned; "-" 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.

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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 (Pinus taeda L.) stands over a 40-year period. Pine growth was unaffected by treatment. Above-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 (Bartram 1791; Harper 1962; Van Lear and Waldrop 1989). Frequent burning continued through the early 1900's, when fire 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 fire causes in plant communities can be slow and depend on fire 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 (Cornus 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 five 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 burns 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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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).

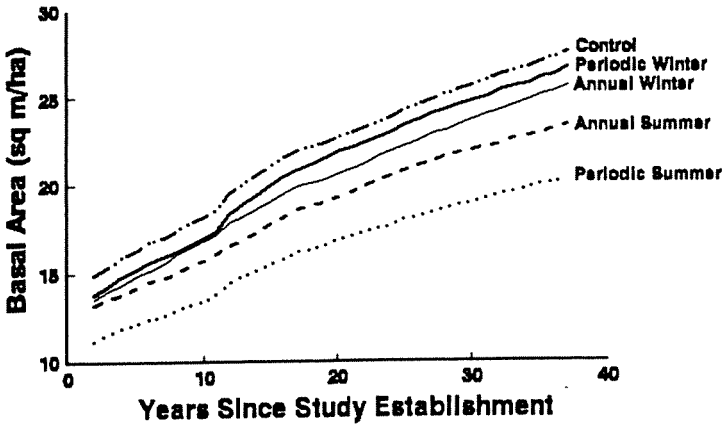

Figure 1.–Cumulative basal area of trees surviving from 1946 through 1984 by burning treatment.

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).

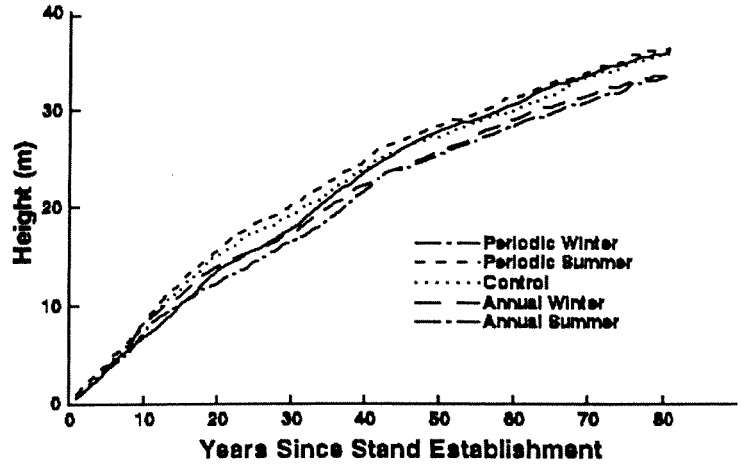

Figure 2.–Mean height of sampled trees by burning treatment from 1905 through 1984.

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 7.5-cm 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 7.5-cm 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

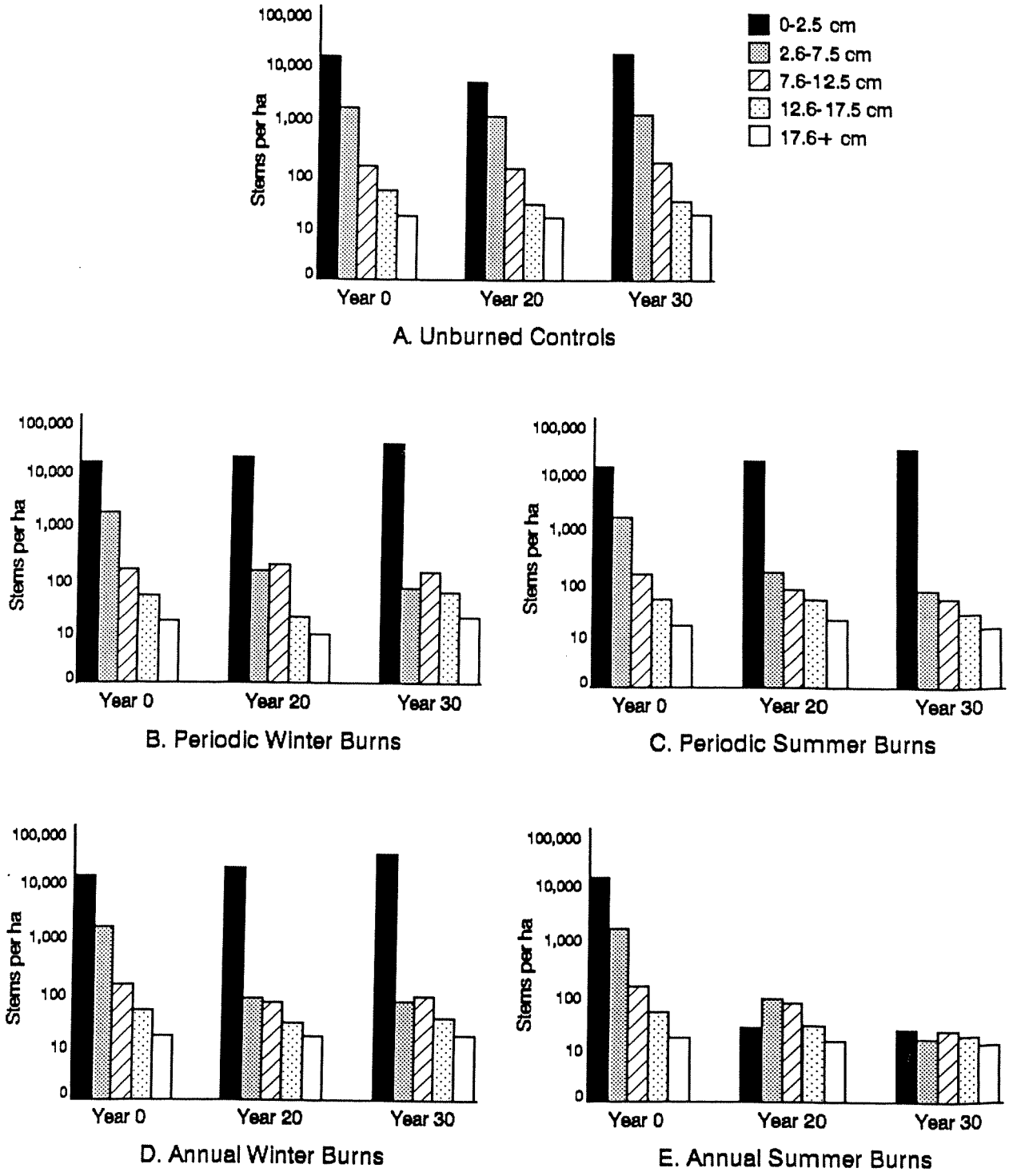

Figure 3.--Diameter distribution of all hardwoods at selected years for (a) unburned control plots, (b) period winter burn plots, (c) periodic summer burn plots, (d) annual winter burn plots, and (e) annual summer burn plots.

determine the number of burns required to kill their root systems. With annual summer burning (fig. 4A), mortality was rapid for sweetgum (Liquidambar styraciflua L.) and waxmyrtle (Myrica cerifera L.), nearing 100 percent within 8 years. Oaks and blackgum (Nyssa sylvatica 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 burns), 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.

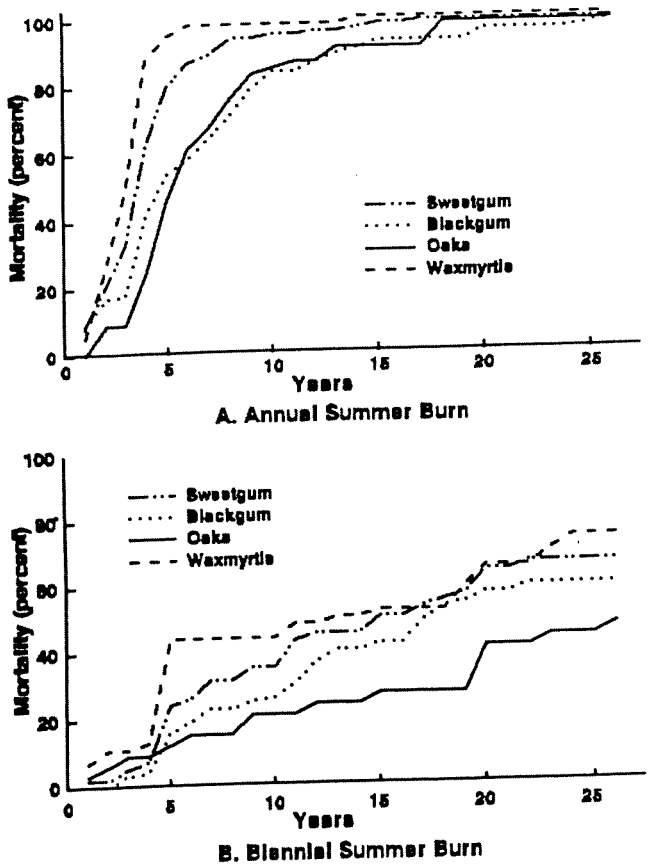

Figure 4.--Cumulative mortality of hardwood roots over 26 years of (a) annual summer burning and (b) biennial summer burning (Langdon 1981).

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 fire 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 burns due to increased sprouting of hardwoods and shrubs. Total coverage after annual winter burns 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.

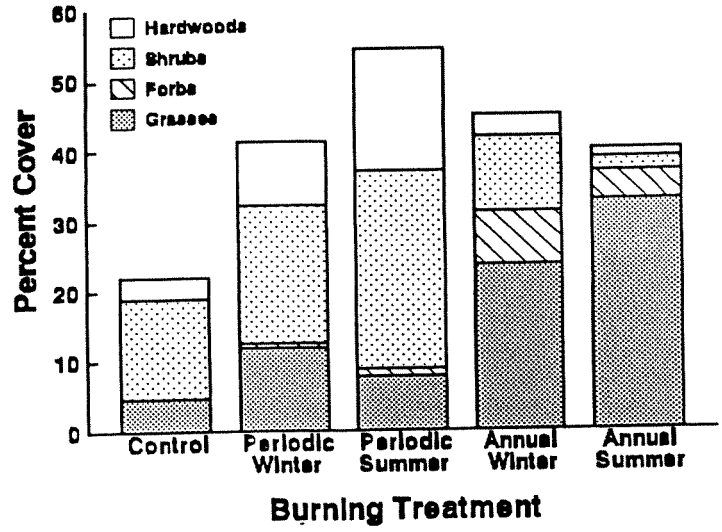

Figure 5.--Percent crown coverage of all understory plants after 44 years of prescribed burning (White and others 1991).

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 burns 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 burns 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 burns 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 fire or other disturbance would eliminate large hardwoods.

Although the Santee Fire Plot Study provides information on the frequency and number of fires 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 fires 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 fire, 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.

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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 burns. Understory cover has not changed in the past 20 years except in the annual winter burn plots where cover of trees $\leq$ 1.5 m in height declined and grass cover increased. Detrended correspondence analysis indentified four distinct understory plant communitites corresponding to season and frequency of burn. Distribution of understory species across a fire 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 burns 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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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 0.5- 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

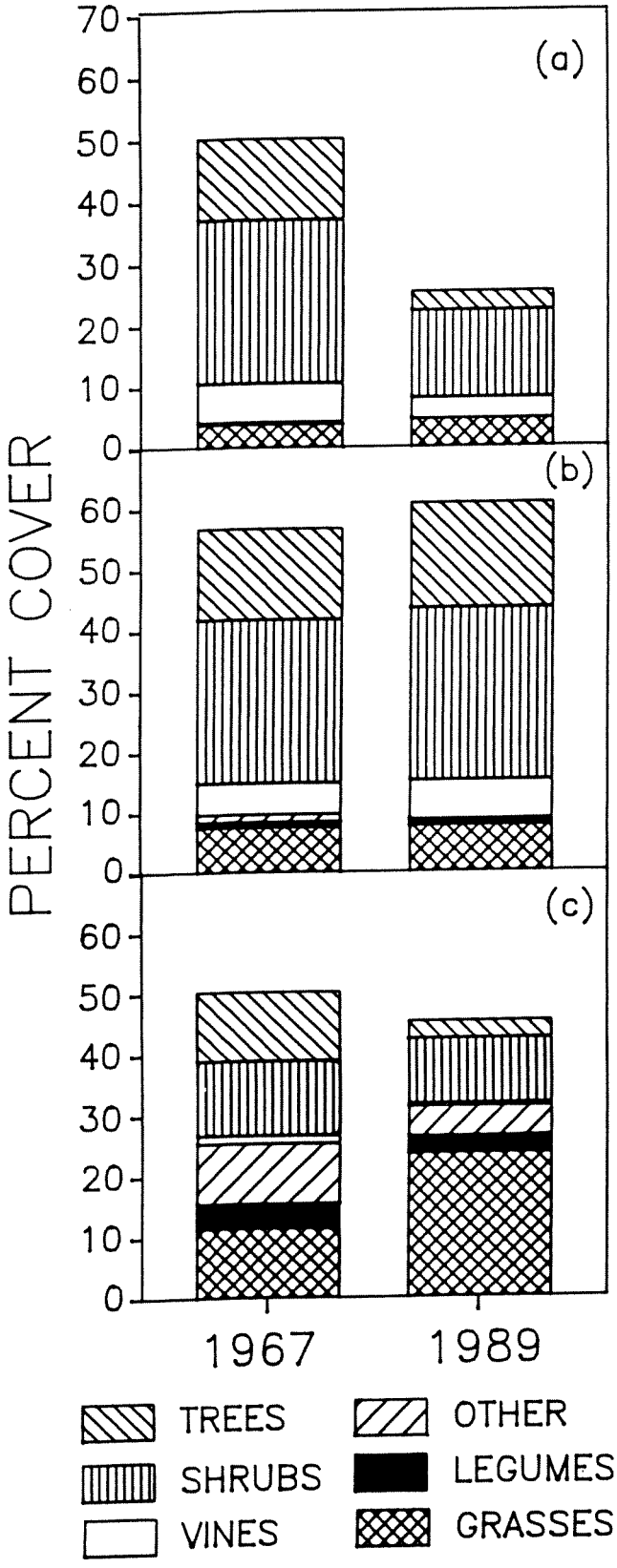

Figure 1–Understory cover by treatment, 1967 and 1989. Treatments: (a) no-burn control, (b) periodic summer burn, (c) annual winter burn. 1967 data are from Lewis and Harshbarger (1976).

the number reported by Langdon (1981) at year 30 (47,000 stems ha^{-1}). 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 burn 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 burns, annual winter burns, periodic burns, 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 burn 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 burn treatment is shown in table 1.

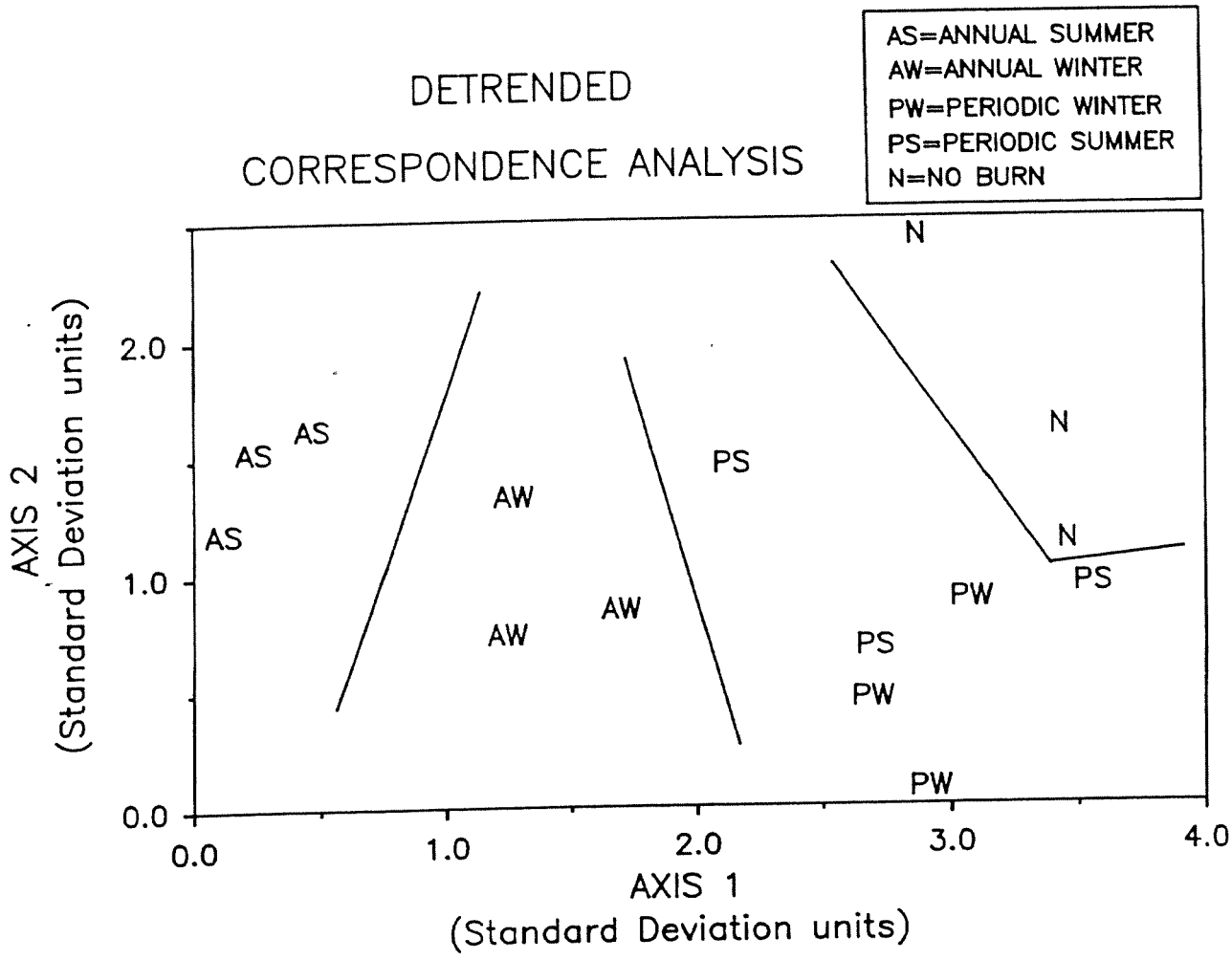

Figure 2–Results of detrended correspondence analysis of all understory plants in all treatment plots. Treatments indicated by the following codes: AS=annual summer burn, AW=annual winter burn, PS=periodic summer burn, PW=periodic winter burn, N=no-burn control. Lines are drawn to show separation between 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 1--Species synthesis table showing relative abundance[a] of each species across treatments (three plots per treatment)

Species[b]	Group	Treatment: Unburned control			Periodic summer			Annual winter			Annual summer		
Paspalum species	1										9	R	
Polygala lutea											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 biflora								4	1	8	4	9	
Galactia 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 nuttallii	3				+				9	R	+	6	4
Aster species					1			1	9	2	1	+	+
Solidago species					+		R	9	+	4	2	1	
Eupatorium species					+	+	R	8	9	7	2	3	+
Elaphantopus species					+		+	9	+		1	1	+
Panicum species					3	+	1	6	9	3	6	2	3
Andropogon virginicus					+		+		6	9	5	9	3
Hypericum species					+		8		8		+	2	1
Rubus species				1	4	5	5	+	1	5	+	R	
Rhus coppalina			+		+		R	2	R	1	1	R	R
Pinus taeda	4		+	1	8	+	+	R	+	+	7	9	6
Gaylussacia species		+	+	+	+	3	1	+	1	4	R		+
Vaccinium species			1	+	1	1	6	+	3	9	+		+
Uniola laxa		+	+	+	3	+	+	9	3	5			+
Myrica cerifera		1	+	+	9	2	1	1	R		+		
Liquidambar styraciflua		+	+	+	5	1	+	4	1	9			
Smilax species		9	1	1	2	+	R	1	+				
Vitis species		+	1	+	1	1	+	+		+	R		
Quercus species		+	+	+	6	4	3	+		9			+
Gelsemium sempervirens		+	+	+	7	9	1				+		+
Cornus florida	5		3	2	7	8	9				R		
Mitchella repens			4	+	3	9	2						
Persea borbonia		9	+	+			R						
Lyonia lucida			+	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. Cornus florida (dogwood) and Mitchella repens (partridge berry) were absent from annual burn plots, while Persea borbonia (redbay) and Lyonia 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 fire. 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 burn 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, Gaylusaccia spp. (Huckleberry) and Vaccinium spp. (blueberry), which sprout prolifically after fire. The greater abundance of all three woody plant groups in periodic winter burn plots was due to the fact that these plots had been burned the winter prior to sampling, which illustrates the immediate response to fire 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 burn 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 burn plots was in the range found in the studies cited above, most of which were conducted after single or periodic burns.

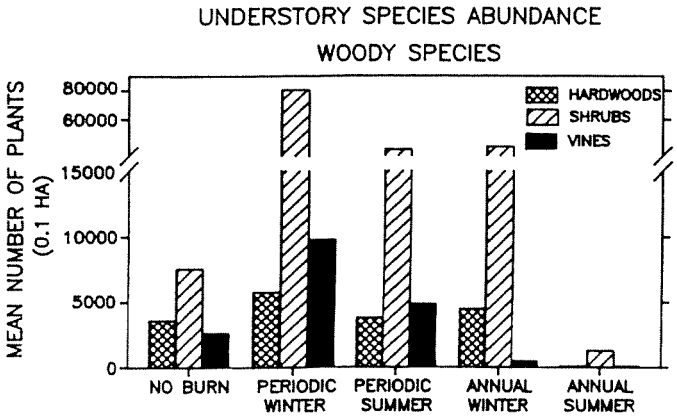

Figure 3--Mean number of stems 0.1 ha^{-1} for understory woody plant groups across all treatments. Note axis scale change.

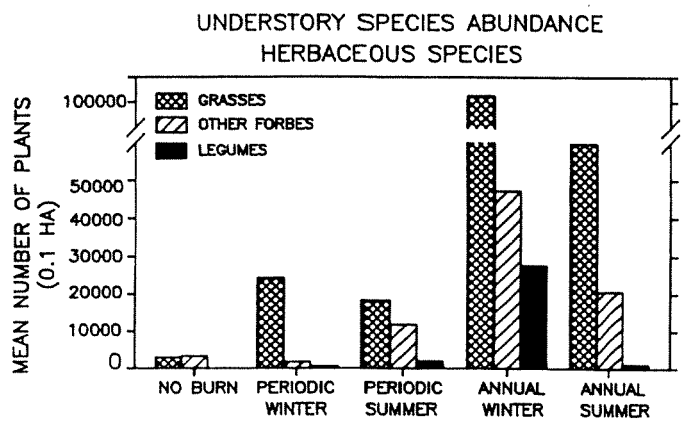

Figure 4--Mean number of stems per 0.1 ha^{-1} for understory herbaceous plant groups across all treatments. Note axis scale change.

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.

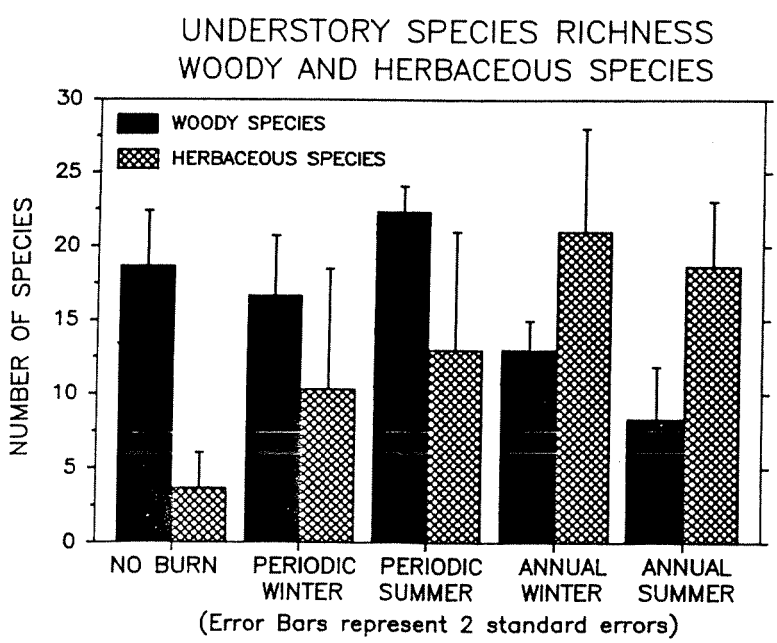

Figure 5--Understory species richness. Error bars represent two standard errors.

Table 2--Shannon diversity indices for understory 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 are 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 fire 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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FOREST DEVELOPMENT FOLLOWING DISTURBANCES BY FIRE AND BY TIMBER CUTTING FOR CHARCOAL PRODUCTION

Wayne K. Clatterbuck[1]

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 fire 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 (Quercus 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.

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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 (Thornthwaite 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

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 (Cornus florida L.), sourwood (Oxydendrum 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 Muenchh.), and blackgum (Nyssa sylvatica 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, 1-inch diameter class, and crown class (dominant, codominant, intermediate, or suppressed). Trees with diameters from 1.6 to 5.4 inches were tallied by 1-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 10-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[a]	10	6-21	75	40-135	11	6-24
			UNCUT AREAS			
Black oak	20	8-27	130	110-136	18	8-32
White oak	19	6-31	127	115-132	26	17-50
Hickories	13	6-22	91	63-125	8	3-16
Other species[a]	10	6-24	115	55-130	11	6-17

[a]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.

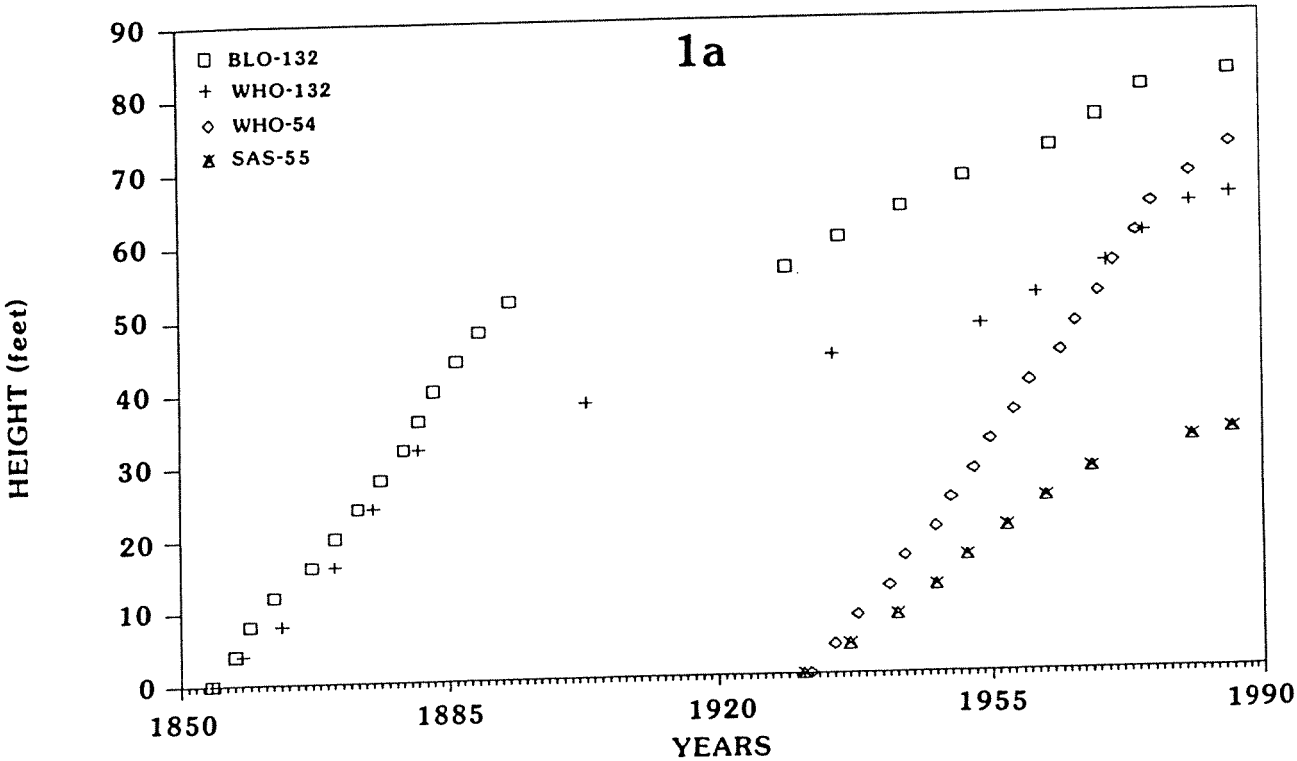
The charcoal hearths, with their circular shape, black soil, and absence of overstory vegetation, were conspicuous on the landscape. The soils in these hearths had lost their structure and were nearly sterile as a result of the intense heat associated with charcoal production. The only tree species to 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. 1a). 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. 1a) 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 50-year period (1885 to 1935) when fire and grazing was common, total height only increased 18 to 20 percent for both trees.



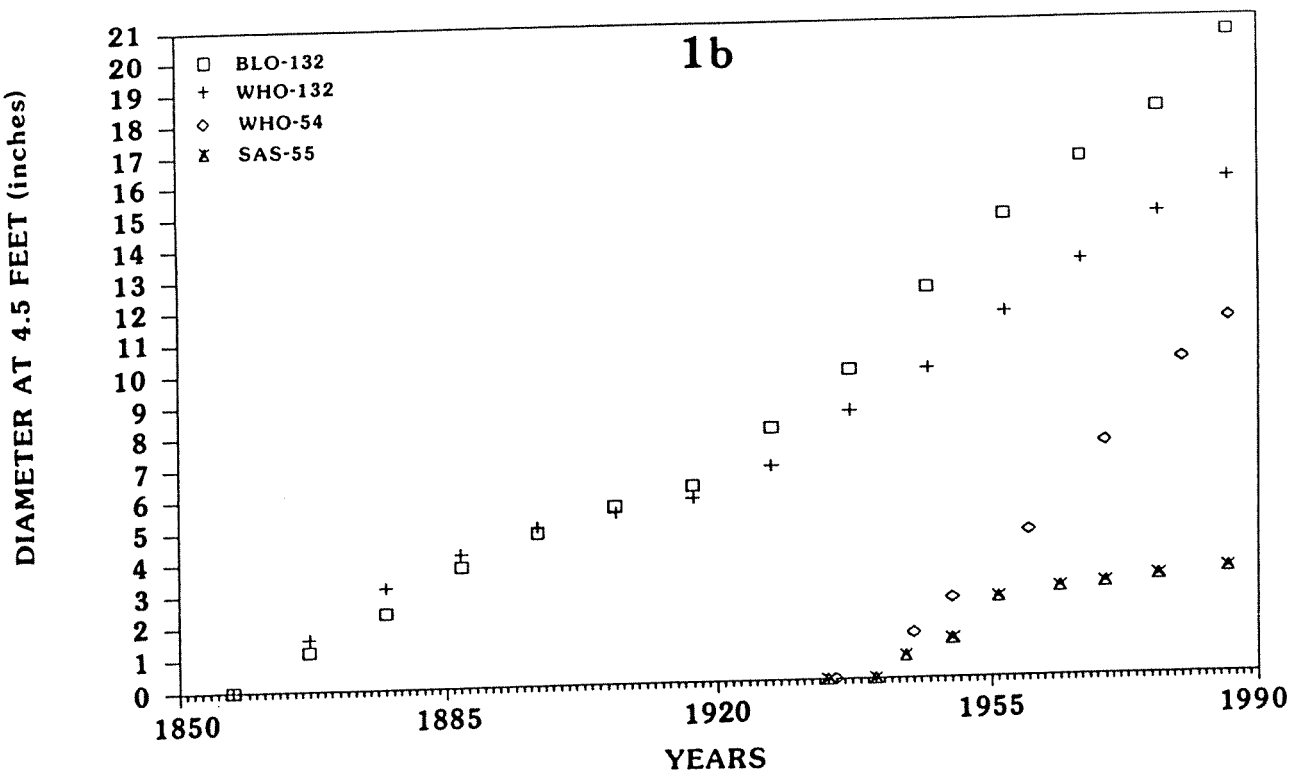


Figure 1.-Cumulative height (1a) and diameter (1b) growth patterns of a 132-year-old white oak (WHO-132), a 132-year-old black oak, a 54-year-old white oak (WHO-54), and a 55-year-old sassafras (SAS-55) from an area that was cut for charcoal.

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. 1b). 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 fires 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 burns 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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NATURAL REVEGETATION OF BURNED AND UNBURNED CLEARCUTS IN WESTERN LARCH FORESTS OF NORTHWEST MONTANA

Raymond C. Shearer and Peter F. Stickney[1]

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 fire 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 fire caused a marked change in composition of all vegetation. Herb cover, mostly fireweed, 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. Preburn 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) 31, 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: Xerophyllum tenax (XETE) on the drier south- and west-facing slopes, Menziesia ferruginea (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.

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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 fire treatments on south- and east-facing slopes.

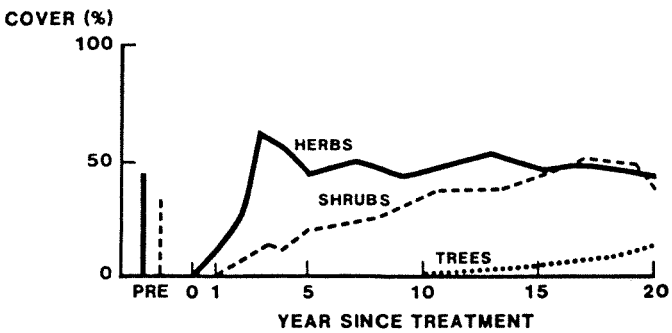
Reforestation of South-Facing Slopes

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 (Xerophyllum tenax), and prince's pine (Chimaphilia 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 fire 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 fireweed (Epilobium angustifolium) and bullthistle (Cirsium vulgare). Herbaceous cover developed rapidly. Fireweed quickly established; beargrass regrew less rapidly but more persistently than did fireweed, 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.

Herbaceous 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-fir, 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.



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.

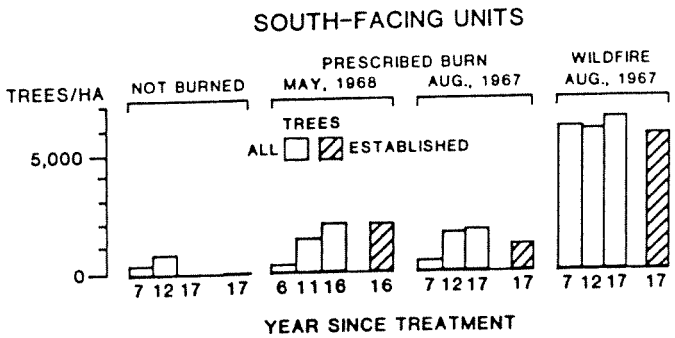


Figure 2. - Average number of all conifer seedlings and saplings per hectare (open bars) by years since treatment and number of established conifers (larch and pine at least 30.5 cm tall, others at least 15 cm) at the most recent measurement (crosshatched bar) on four south-facing units, Miller Creek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

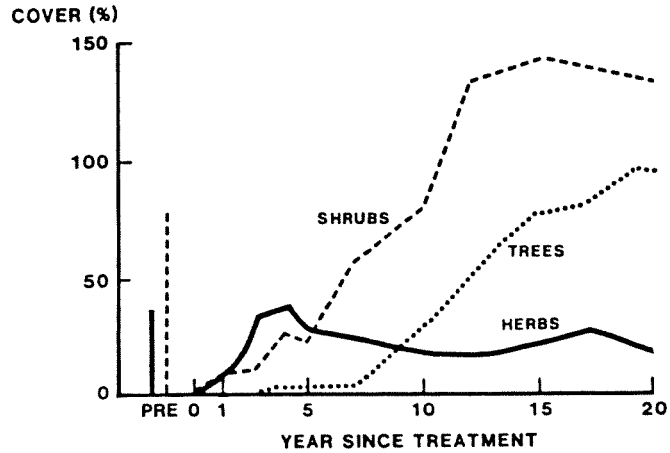
[b]CC = clearcut, UC = uncut;
PB = prescribed burned, WF = wildfire, NB = not burned

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 ashed 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 area (fig. 3, table 3). Trees occurred in 97 percent of the plots--the result of seedfall from fire-killed onsite trees.



Survivor:						
XETE (H)	23	2	5	10	10	8
SPBE (S)	9	2	11	18	23	26
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

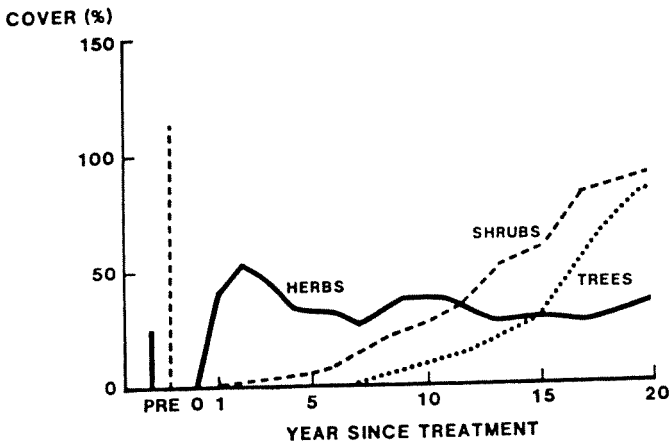
Figure 3. - Early succession development (cover) of major life form groups and prominent species from 1967 through 1987 of a south-facing uncut forest burned by wildfire on August 23, 1967, Miller Creek Demonstration Forest; CEVE = ceanothus, EPAN = fireweed, PICO = lodgepole pine, SPBE = spirea, VAGL = 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). As on 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: fireweed, 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	<1	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.

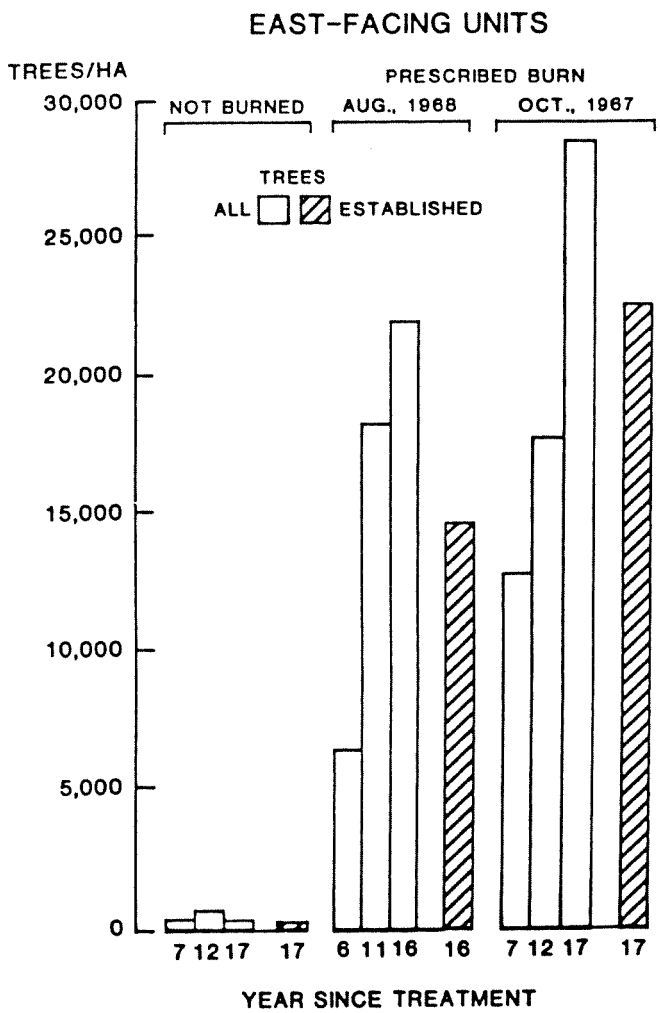
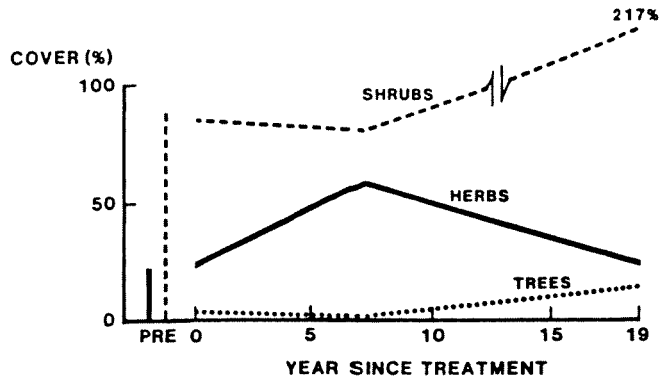


Figure 5. - Average number of all conifer seedlings and saplings per hectare by years (open bars) since treatment and number of established conifers (larch and pine at least 30.5 cm tall, others at least 15 cm) at the most recent measurement (crosshatched bar) on three east-facing units, Miller Creek 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 fire 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; fireweed, 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 fire, 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 suablpine 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 east-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, fireweed, 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, fireweed 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 fire to alter succession depends mainly on the composition of the forest community, the onsite seed source, and the severity of the fire. 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 fires 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).

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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.

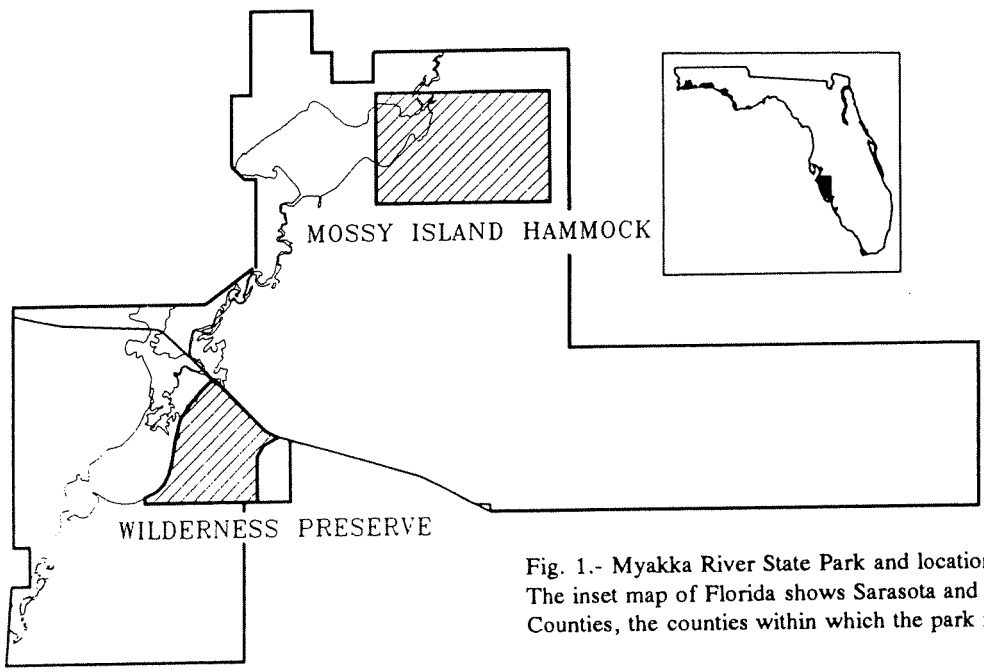

Fig. 1.- Myakka River State Park and location of study sites. The inset map of Florida shows Sarasota and Manatee Counties, the counties within which the park is located.

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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 fires 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 burns 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 fighting of fires at Myakka a high priority. Hundreds of miles of firebreaks were cut throughout the park and fires were extinguished whenever possible. Although many lightning fires were ignited, they were suppressed as quickly as possible. The result was not total fire exclusion but a much reduced fire 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 burns 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, Schizachyrium 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 Lyonia fruticosa), and saw palmetto (Serenoa repens). Florida dry prairie is a fire-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 hemitomon, 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 burns. Reductions in the cover of woody vegetation after one dry growing-season burn in the Wilderness Preserve study area, and after two, or in some sections three, dry-growing-season burns 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.

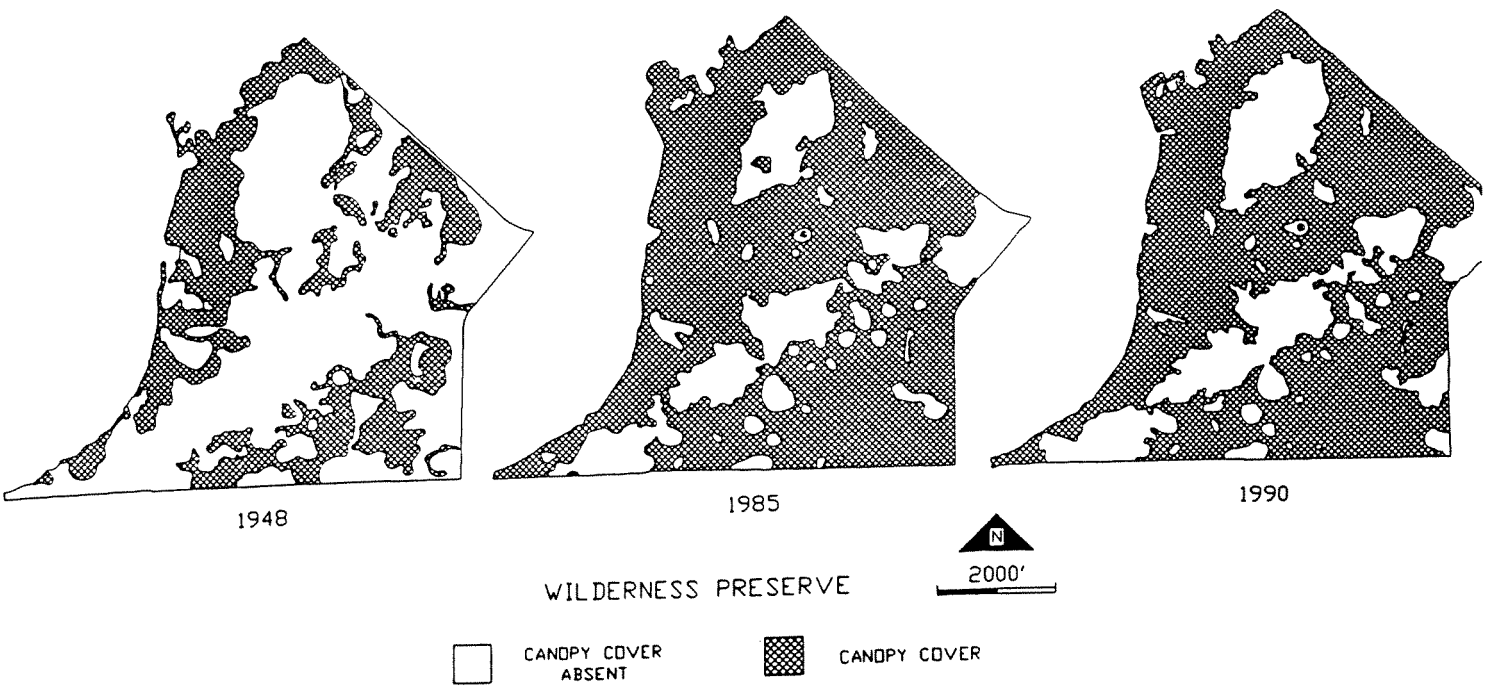
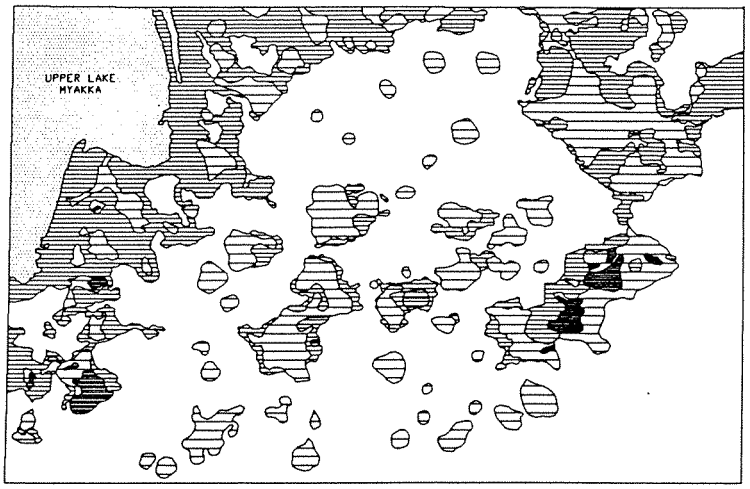
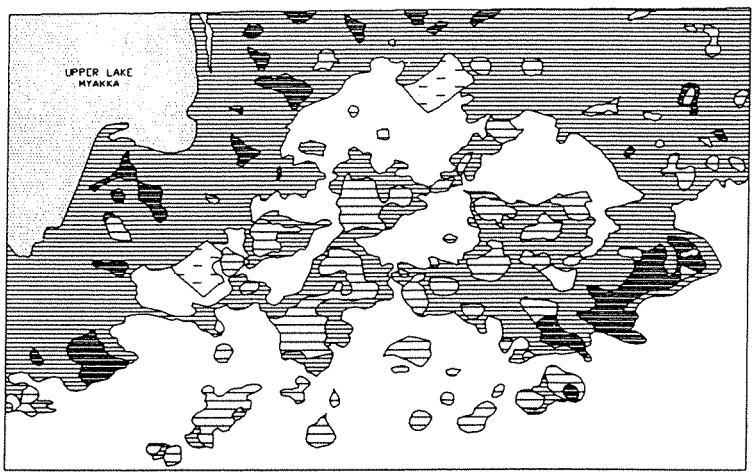


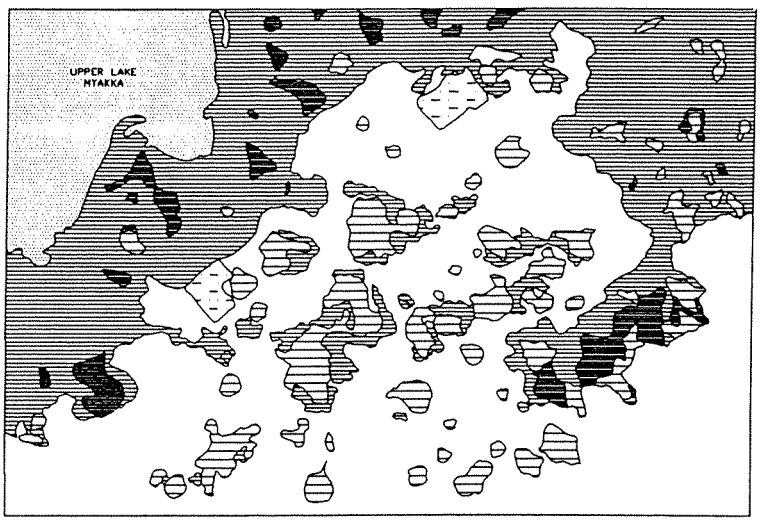
Fig. 2.- Wilderness Preserve canopy cover in 1948 before fire exclusion; in 1985, after fire exclusion; and in 1990, after one dry-growing season burn. Shaded areas indicate canopy cover. The north, east and southern edges are bounded by roads. The west side is bordered by the marshes of the Lower Lake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



1940

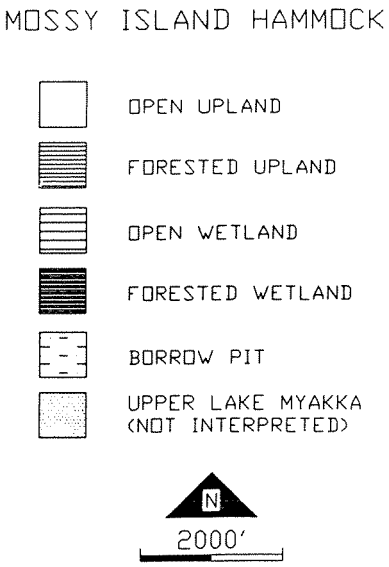


1986



1990

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 burns.



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

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 burn 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 Myrica 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 wetlands	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 burns were initiated in the park in 1983, but it was not until 1986 that a burn moved into oak-palmetto and woody wetland areas.

Mossy Island Hammock. Three burns 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 fire which occurred on August 21, 1985. This fire occurred late in the afternoon and was accompanied by high humidities and rain. Typical of earlier burns 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 burn were quite different from those of previous burns. 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 fire 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 burns 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 burn. 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 burn. The remainder of the area burned on May 24 and 31, 1990 with a milder burn. The 1990 map of the Mossy Island Hammock series (fig. 3) shows the extent of woody species cover reduction following the 3 burns 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 fire 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 burn 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 fire 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 fires, 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 fires 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 fire 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 burns are very useful for obtaining hardwood control. The growing season is recognized as the "natural" fire season in Florida. Growing season burns 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 fires 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 fire 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 burns in very dry conditions.

A dry growing-season burn should not be implemented in areas with large fuel accumulations. A fuel reduction burn 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 burns under very dry conditions.

CONCLUSIONS

In the absence of frequent fire, 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 fire after an extended period of fire 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 fire does occur in these areas usually very low or no mortality of well-established hardwoods occurs.

Observations of dry growing-season burns at Myakka indicate that such burns, 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 burns under conditions when fuel moisture and water levels are high may be causing significant shifts to occur in vegetation, especially in wetlands. Growing season burns under dry conditions at the end of the dry season, were almost certainly part of the presettlement fire regime. At least a periodic burns of this type may be necessary for the long-term maintenance of wetland plant communities.

Dry growing-season burns 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 fire-exclusion effects is a management goal.

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LIVESTOCK GRAZING ALTERS SUCCESSION AFTER FIRE IN A COLORADO SUBALPINE FOREST

William L. Baker[1]

Abstract—Plant succession after fires 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 (Connell 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 Lorenz 1986). There is some evidence of failure to restore pre-fire tree composition (Veblen and Lorenz 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.

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STUDY SITE

The study site consists of two hillsides in a subalpine forest about 7 km south-southeast of the summit of Pikes 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.

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.

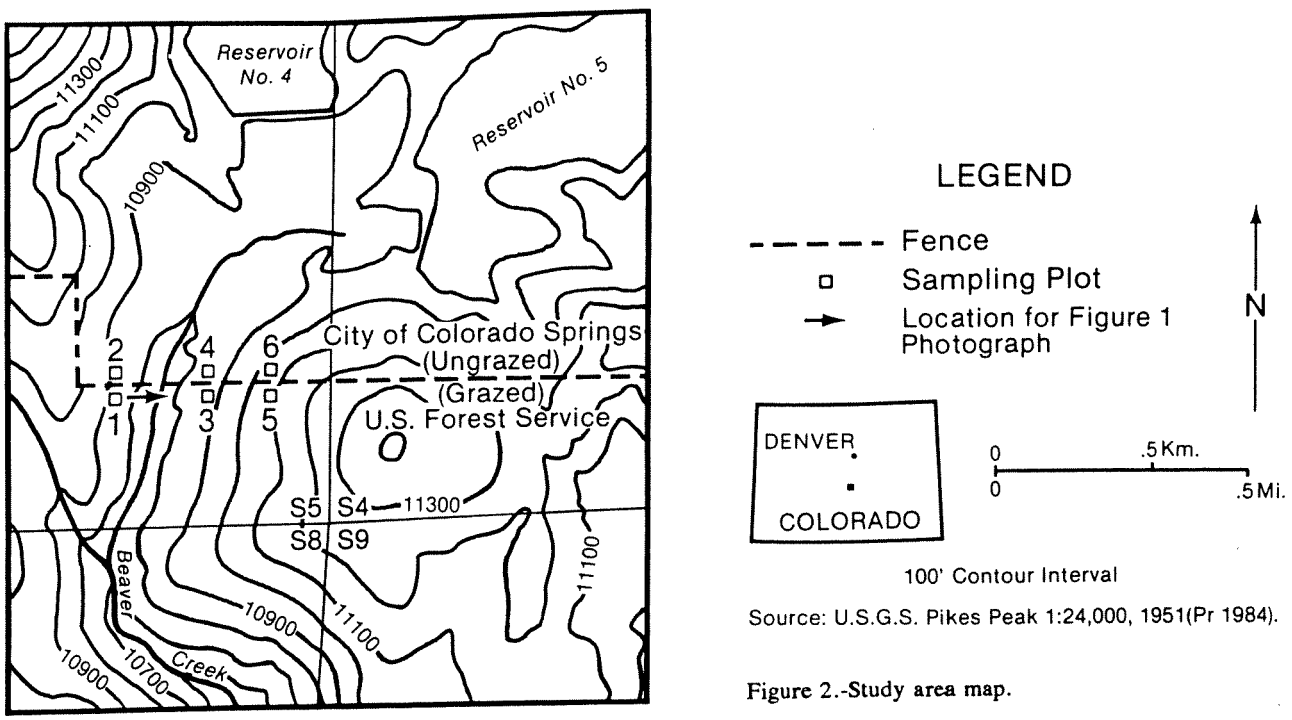

Figure 2.-Study area map.

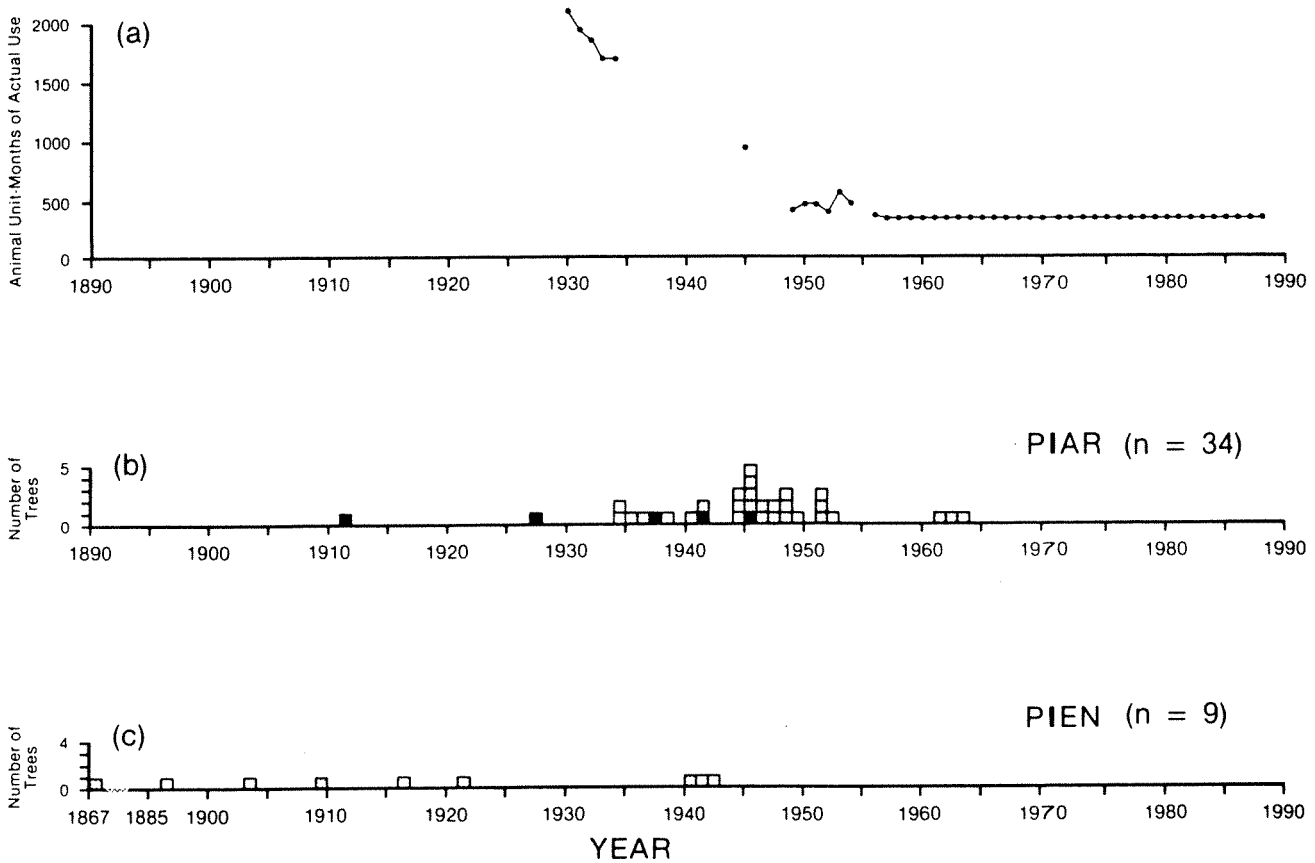

Figure 3.-(a) History of cattle use on the Deer Park Unit of the Beaver C&H Allotment. Data are from U.S. Forest Service-Pikes Peak Ranger District records. (b) Dates of establishment of largest Pinus aristata. Solid bars are dates from cores that contained the actual center of the tree. Shaded bars 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. Until 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.

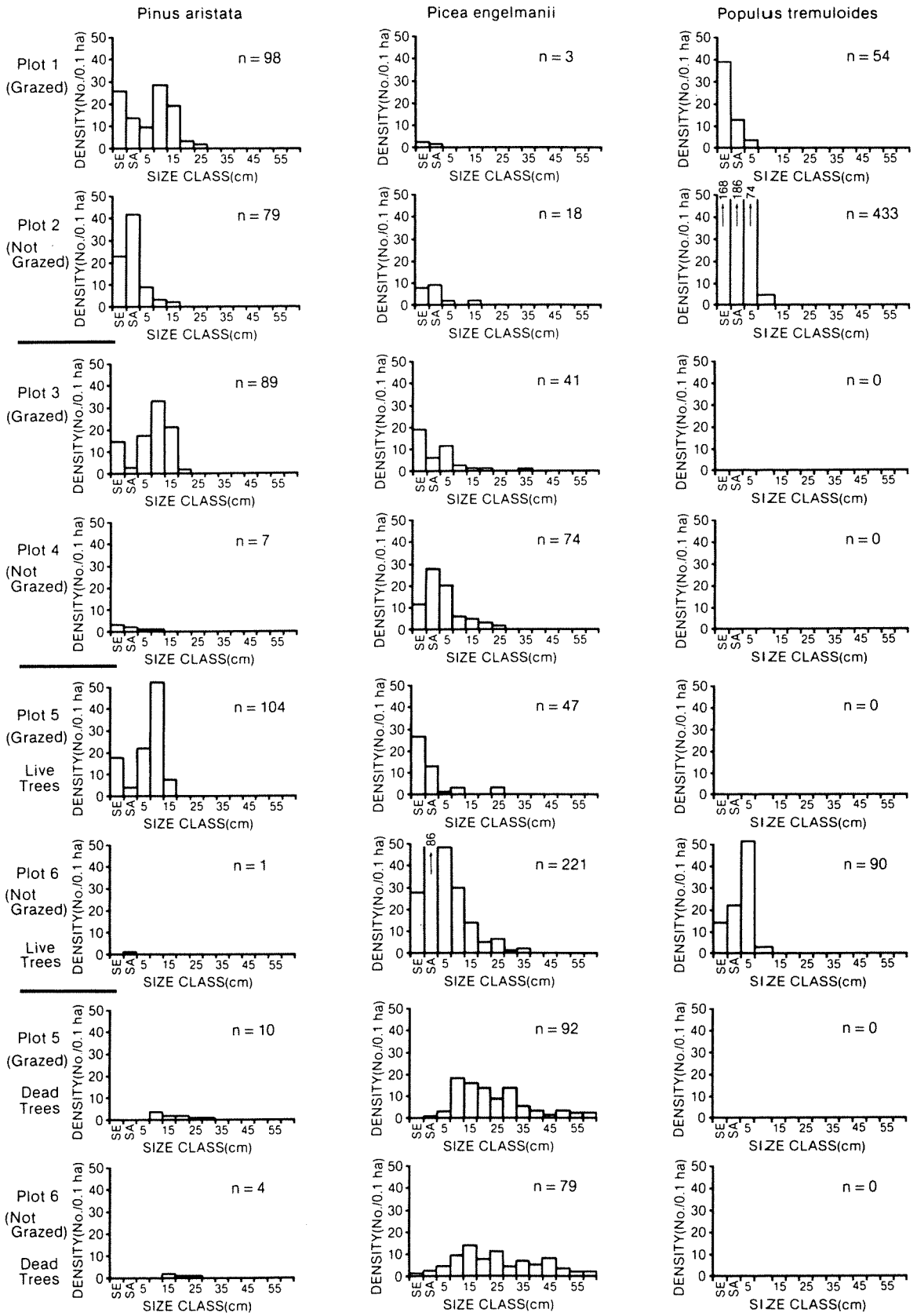

Figure 4.-Size class distributions for all live trees present in the six fenceline plots and for dead and downed trees in plots 5 and 6. Size classes are: SE=Seedlings (<1 m tall and <5 cm diameter), SA=Saplings (>1 m tall and <5 cm diameter). Other size classes are 5.0 cm wide, with the label indicating 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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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 furl loads and altered weather patterns will result in altered fire regimes. Altered tire 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 bc 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. We 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 garrigue (Malanson and Trabaud 1987). Wc 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. Wc modeled the dynamics of Californian coastal sage scrub over periods of 200 years under a variety of fire regimes, and wc 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 bc 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 fire weather from the recent past. These concepts may not lit the patterns of the future (cf. Van Wagcncr 1987).

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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 fire 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.

These fire 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 IO-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

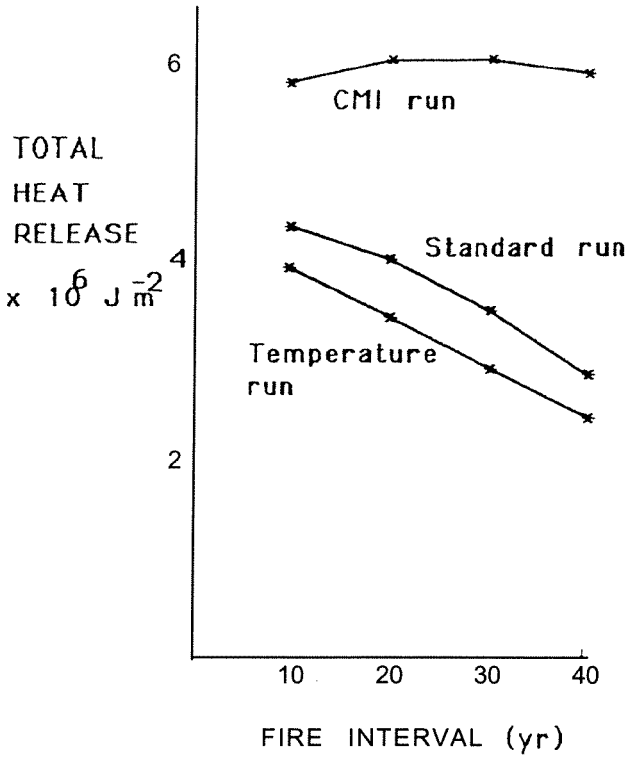

Figure 1. Fire intensities projected for coastal sage scrub under assumptions of altered climate (doubled carbon dioxide levels, GISS model). The Standard run is produced for current observed fuel loads; the Temperature run indicates the results of a decrease in fuel load assumed for an increase in temperature; the CMI (Composite Moisture Index) run indicates the results of an increase in fuel load assumed for an increase in precipitation.

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 fire 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 fire behavior and intensity, and thus in potential effects on vegetation. For the present, however, wc will discuss one change in the fuel load: the ratio of live to dead biomass.

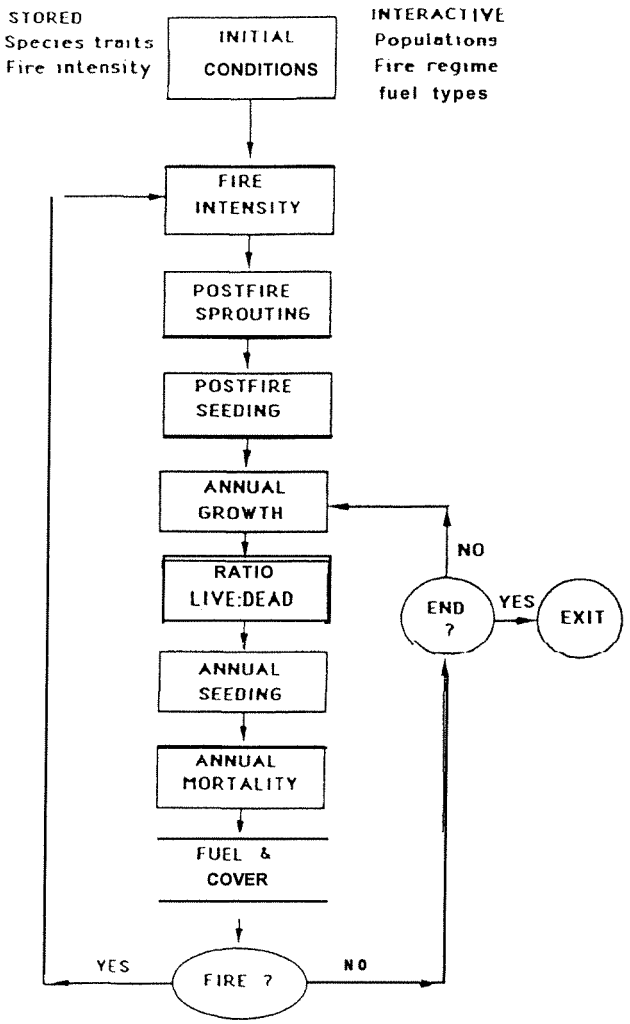

Figure 2. Vegetative response to fire and climate with a feedback to fire intensity through fuel load.

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

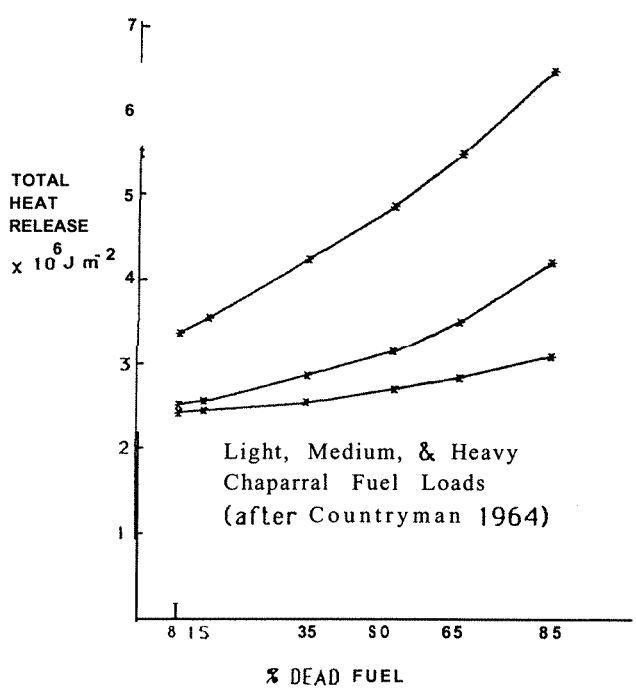

Figure 3. Fire intensities projected for three fuel loads apportioned into six classes of live-to-dead fuel ratio.

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.

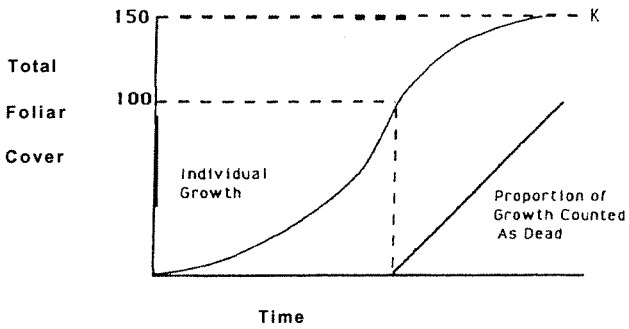

Figure 4. Apportionment of growth into live and dead fuel as overall growth is limited by crowding.

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 fire 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 will change with climatic change (cf. Clark 1988). Investments in the planning and implementation of wildland and fire management programs can be more efficient if models of the system in altered climatic conditions are incorporated in the planning process.

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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 tire 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 fire 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, fire 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 1983; Hemstrom and Franklin 1983; 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 (Bonnickscn 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 Gruell 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 (Botin 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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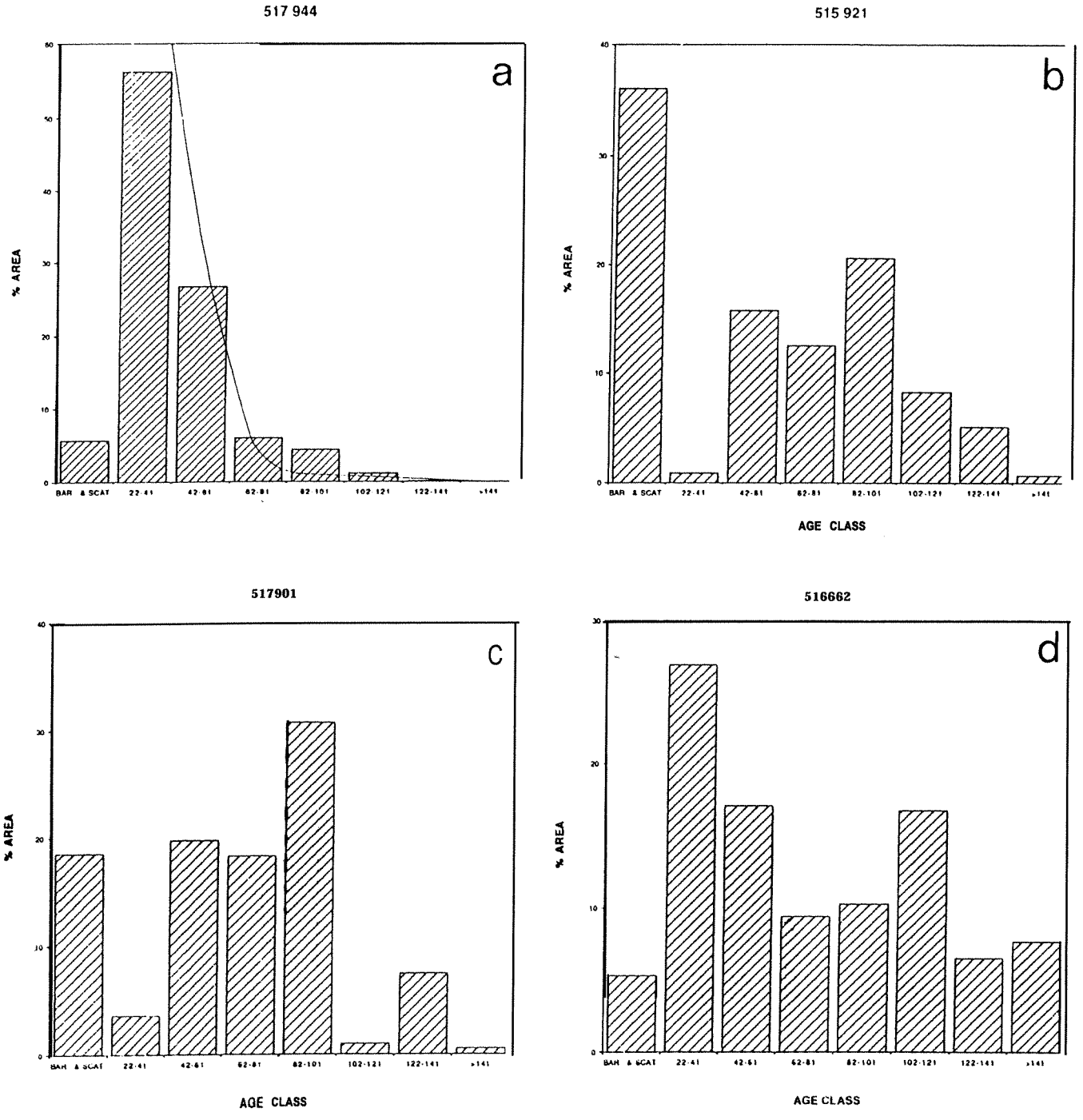

Figure 1 --Stand age-class distributions for Northwest Ontario for four areas ranging from most fire prone (la) to least fire-prone (Id). The data for the 4 graphs are stand ages of main stands since disturbance recorded on 1: 15840 Ontario Forestry Resource Inventory maps at the 8 locations shown on 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

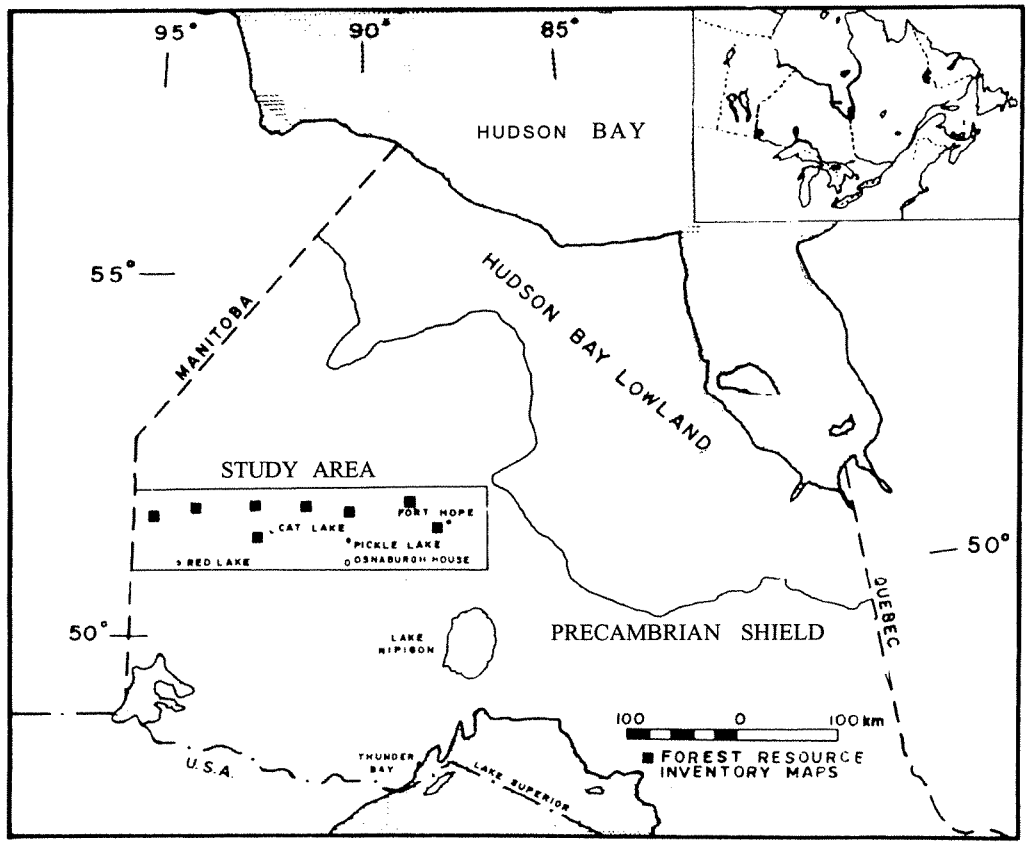

Figure 2--The location of the study area in Northwest Ontario

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 fires are stand-replacing crown fires, 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 tremuloides* 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 fire 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 fire 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 climinnted 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).

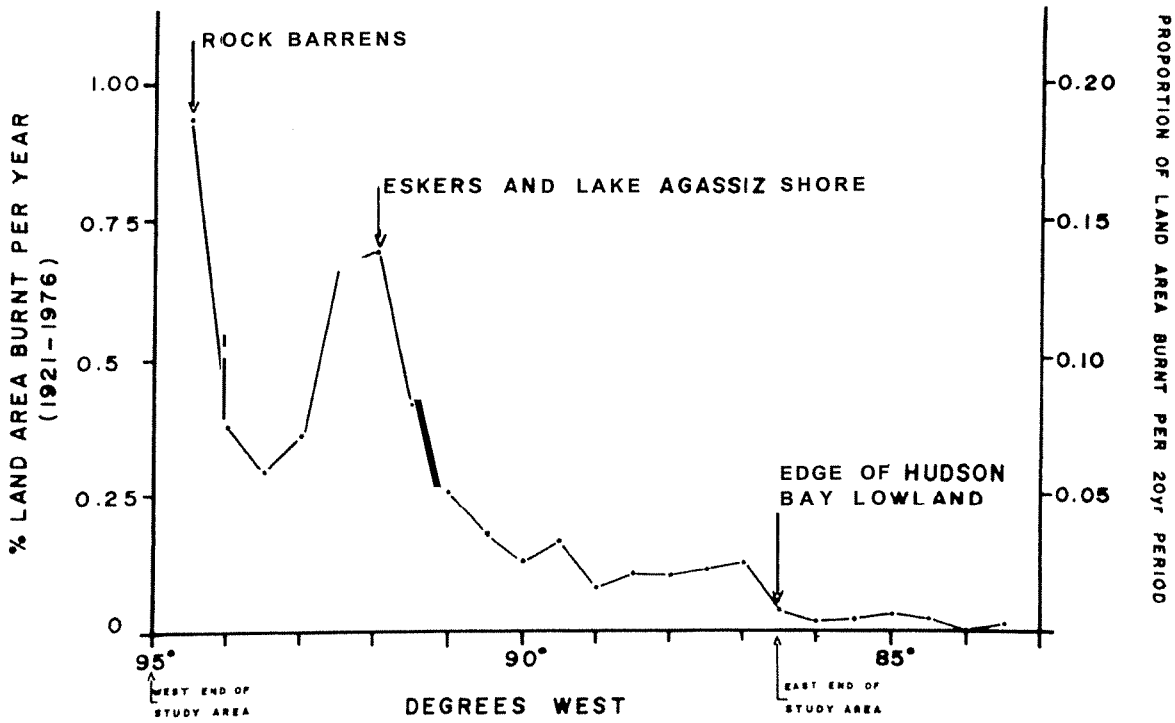

Figure 3--The gradient in fire occurrence across the study area in Northwest Ontario. (After Suffling and others 1988)

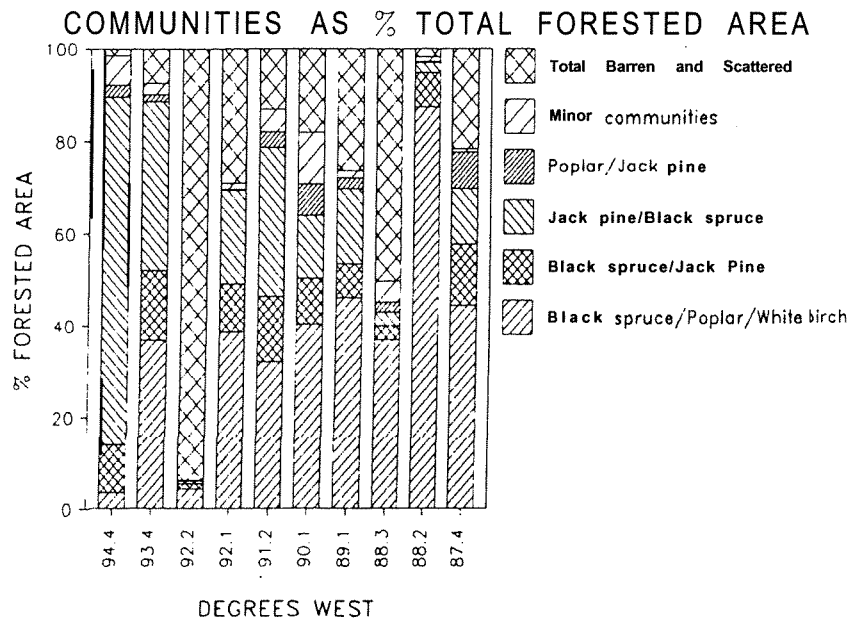

Figure 4--The change in community composition of forested upland sites across the study area in Northwest Ontario.(After Suffling 1988).

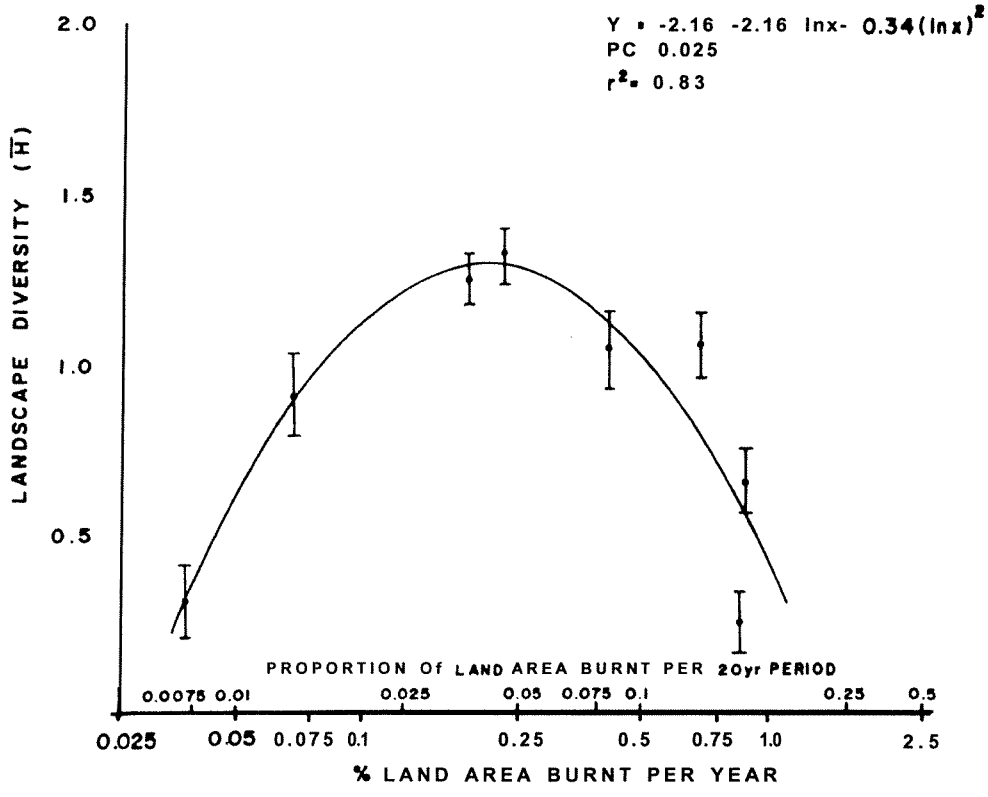

Fig. 5--The relationship of landscape diversity (Shannon's H statistic) in the Northwest Ontario study area, to disturbance by forest fires (After Suffling and others 1988).

FIRE MANAGEMENT IN AN ERA OF CLIMATE CHANGE

The policy of allowing natural fires to burn while suppressing human-caused tires (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 we 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 burn" 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 fire ecotone, and in the spatial relationships and patch sizes of different habitats (Suffling and others 1988; Turner 1989; Turner and others 1989).

The wildland fire manager's first reaction might be to attempt to control fires 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 fires 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 fires 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 fire 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.

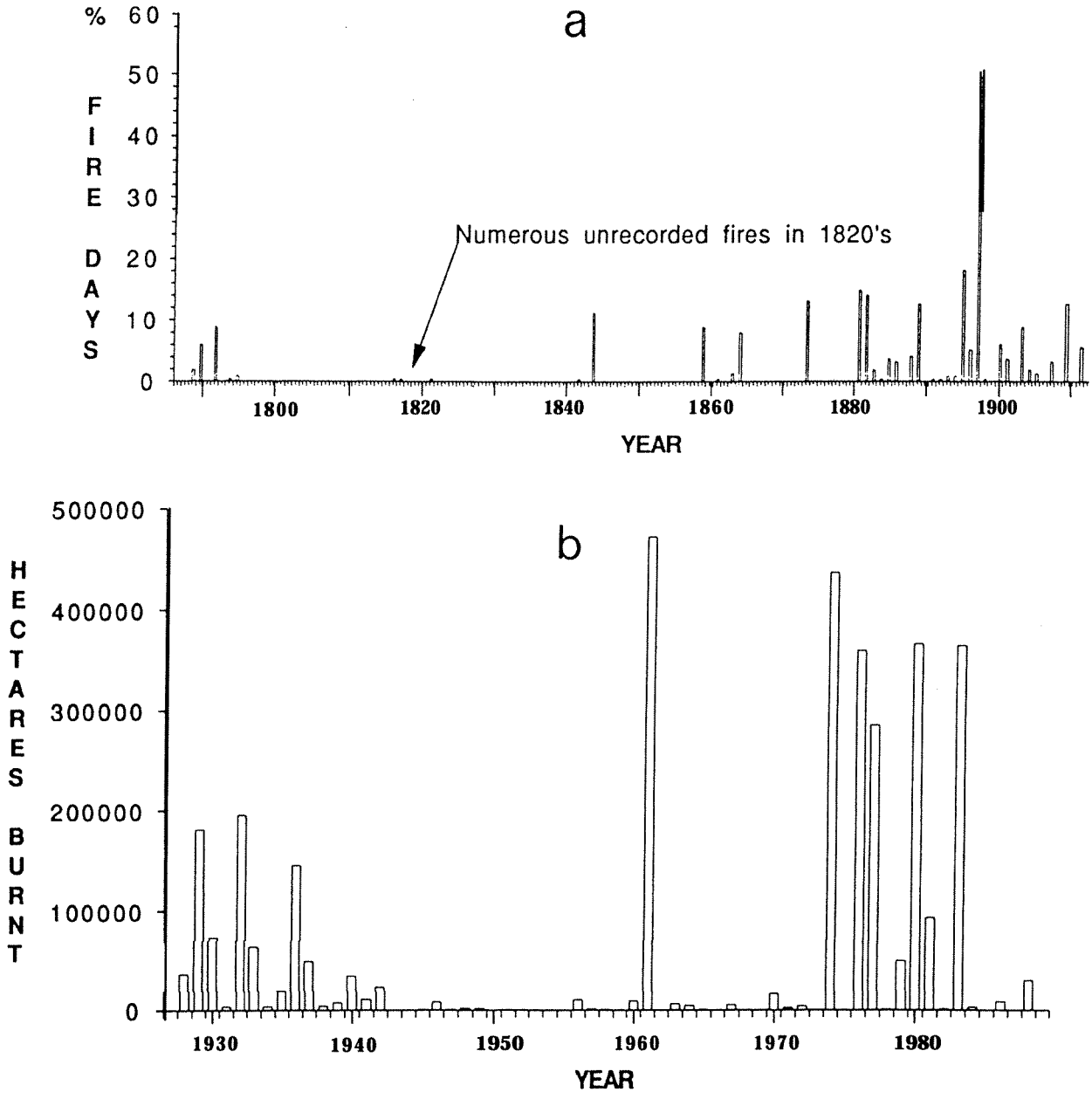

Fig. 6- Historical variation in fire occurrence in Northwest Ontario. a: Fire occurrence as represented by "fire days" (Suffling 1988) at Osnaburgh House. b: Ontario government statistics for area burnt in the Kenora District, 1927-1989 (Ontario Ministry of Natural Resources 1928-1990).

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 fires were frequent at that time. Data from other regions support the possibility that cyclical fire 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 300 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-Mikhaclian 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, tire 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 arc 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 bc 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.

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HAZEL PISTOL EROSION PLOT STUDY ON THE SISKIYOU NATIONAL FOREST IN SOUTHWEST OREGON

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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 SO 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 SO 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 revegetate 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 burns 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 burns 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 burns 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 burns, in the summer or early fall. Soil litter and the organic layer were often consumed.

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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, Willamctte 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 clear-cutting 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 7.5 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 wildfires. 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 s&stone, 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 are 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 11 1 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 (months)	Rainfall (in)	Average Plot Runoff (in) by Treatment 30B	SOB	70B	7ou
11/77-2/78	3 . 4	111	30.7	41.8	44.1	28.3
11177-1 1178	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 (months)	Rainfall (in)	Total Erosion (tons/ac) by Treatment 30B	SOB	70B	7ou
11/77-2/78	3.4	111	2.5(2.7)	4.6(5.8)	11.4(20.0)	2.2(3.8)
11/77-1 1178	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.

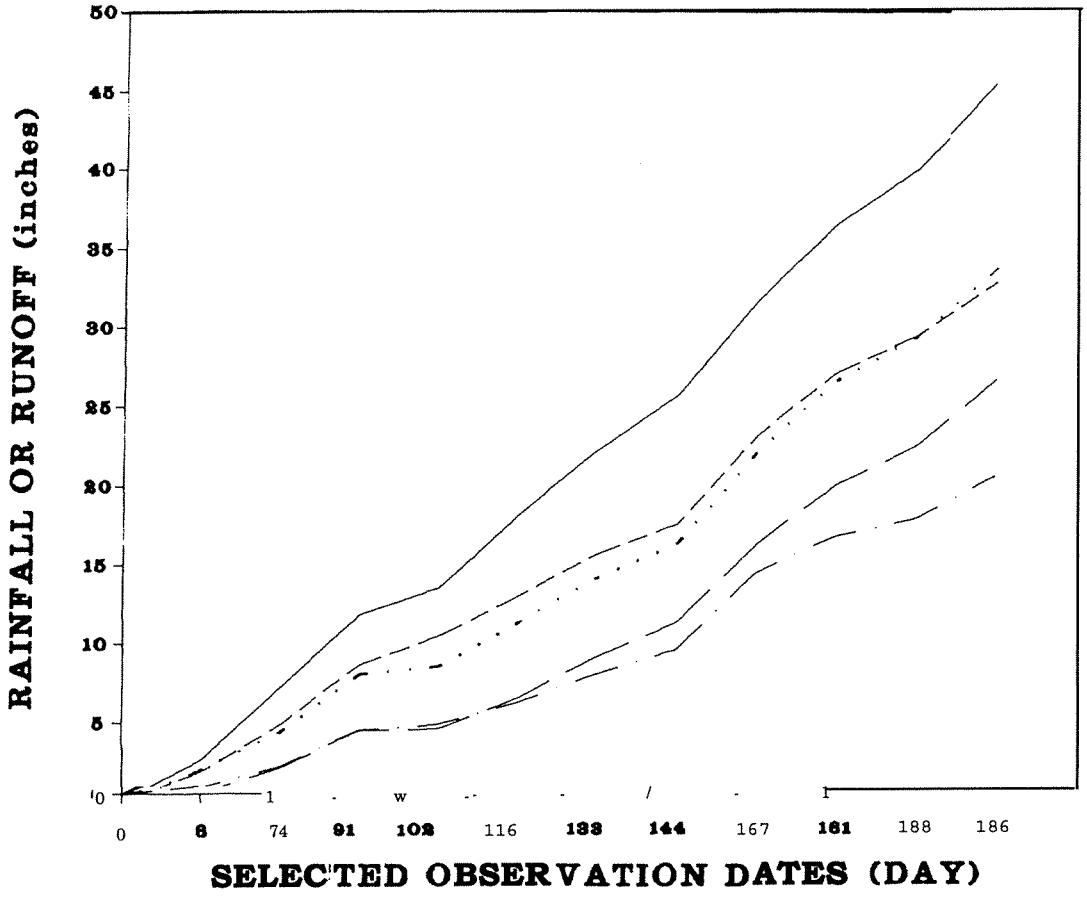
Several types of erosion processes were observed on the area, including raindrop, sheet, and rill erosion. These were detected or inferred by close observations during intense rainfall periods or inspection during the study period on the erosion plots.

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 bum 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

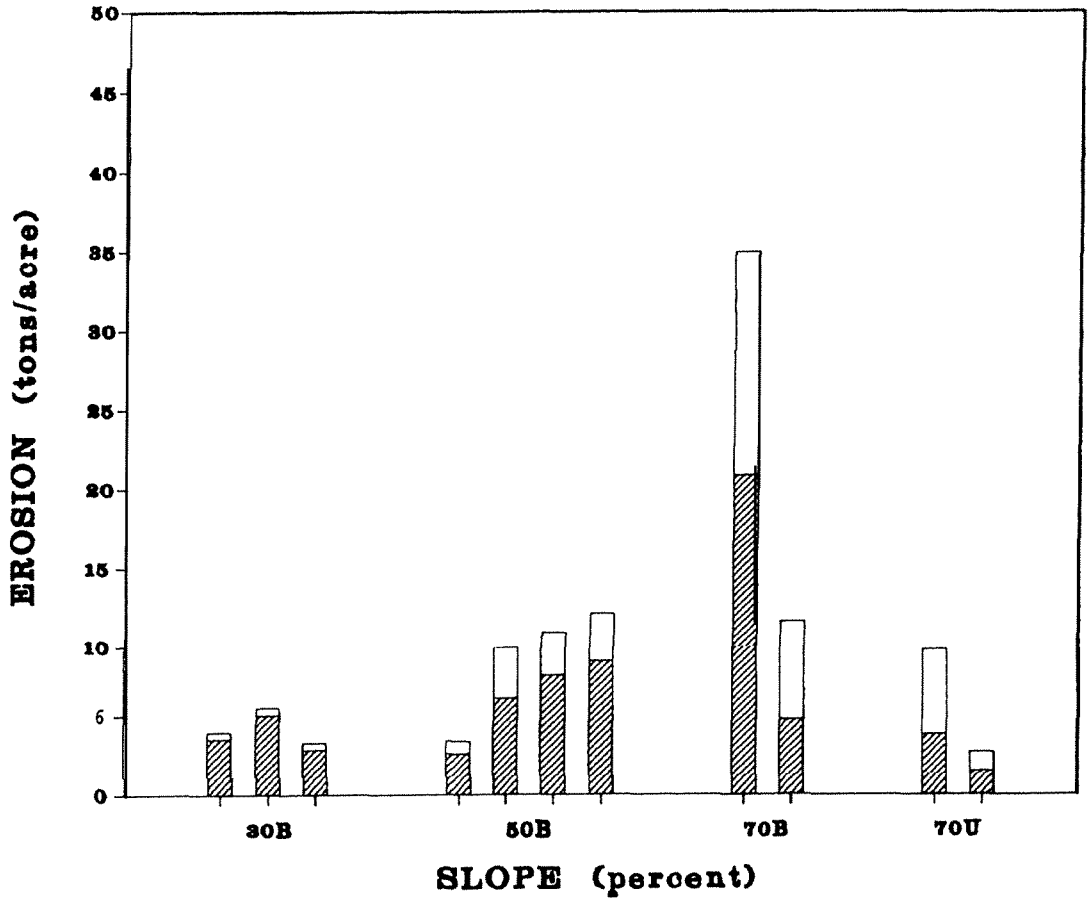
Figure 1
CUMULATIVE RAINFALL AND RUNOFF BY TREATMENT FOR SELECTED DATES



LEGEND

———	RAINFALL	B = BURNED
	RUNOFF 30B	U = UNBURNED
- -	RUNOFF 50B	30, 50, 70 = PERCENT SLOPE
- - - - -	RUNOFF 70B	
—— · ——	RUNOFF 70U	

Figure 2
SOIL EROSION BY SLOPE AND TREATMENT 11/77 TO 11/78



LEGEND

COARSE >2mm — B = BURNED

SOIL <2mm — U = UNBURNED

30, 50, 70 = PERCENT SLOPE

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 tire 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 1/2 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 tire impacts to soil resources. Strategies such as helicopter lighting also reduced fire 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 arc 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 crodiblc 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

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THE SIGNIFICANCE OF FIRE IN AN OLIGOTROPHIC FOREST ECOSYSTEM

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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 fire in several components of an oligotrophic lower Coastal Plain pine flatwoods ecosystem. Except for some loss of nitrogen (N) from the forest floor, experimental burns 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 lo 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 (1943) 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.

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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 (P. palustris Miller--17 percent). Other canopy species were sweetgum (Liquidambar styraciflua L.--4 percent), black gum (Nyssa sylvatica Marshall--3 percent), and shortleaf pine (P. echinata Miller--Z 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.

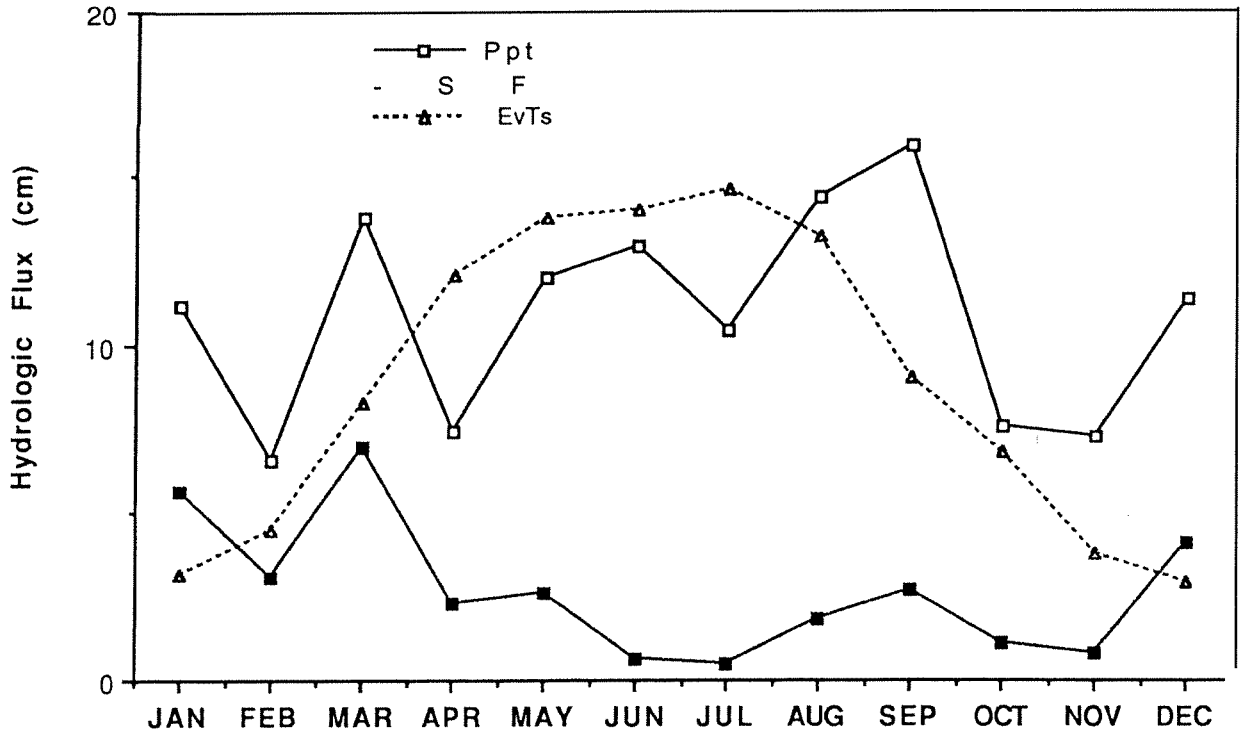

Figure 1 .-Mean monthly fluxes of precipitation (Ppt), stream flow (SF), and evapotranspiration (EvTs) for WS77

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 fires administered during this study. See Gilliam and Christensen (1986) for a complete description of compartments and fire treatments. Briefly, nine compartments receiving either winter-only fires, 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 IO-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 compositcd 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 hcrbaceous layer, defined as all vascular plants $\leq$1 meter in height, was sampled in five 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 five 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 0.5meter transects. These transects were subdivided into 75 0.5meter 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 live 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 spectrophotomctry (Isaac and Kerber 1971). Ammonium ($NH4^+$) was determined by isocyanurate colorimctry (Reardon and others 1966), NO_3^- by Cd reduction and azo-dye colorimetry (APHA 1976), PO_4^{3-} by molybdenum blue colorimetry (Mehlich 1953), and $SO_4^{=}$ by turbidimetry (Schlesinger and others 1982).

Mineral Soil

Samples of mineral soil were air-dried and ground in a hammer mill to pass a 2-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 Mchlich (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-burn soils. T-tests were also used to test the effects of fire 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 arc 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 1976-1982.**

Input-Output	H^+	Na^+	K^+	Ca^{++}	Mg^{++}	NH_4	NO_3	$SO_4^=$	Cl	$PO_4^{\equiv}$
	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_3^-. 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 were balanced for K and P (table 1), suggesting strongly that K and P (in addition to N) may be grow&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 NH_4^+. For winter burns, however, there were significant increases in pH and extractable K^+, Ca^{++}, and NH_4^+. 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 fire. 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 fire 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.

Summer burn

Depth/Treatment	pH	K^+	Ca^{++}	Mg^{++}	NH_4
			μeq/g		
0-5 cm/Pre-burn	4.38	0.7	12.2	5.5	1.1
0-5 cm/Post-burn	4.35	0.7	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*
10-20 cm/Pre-burn	4.58	0.2	6.1	4.7	0.4
10-20 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

Winter burn

Depth/Treatment	pH	K^+	Ca^{++}	Mg	NH_4
			μeq/g		
0-5 cm/Pre-burn	4.16	0.9	4.8	2.5	0.7
0-5 cm/Post-burn	4.26*	1.1*	7.3*	3.0	0.9*
5-10 cm/Pre-burn	4.35	0.5	3.4	2.2	0.3
5-10 cm/Post-burn	4.45*	0.5	3.2	1.9	0.4*
10-20 cm/Pre-burn	4.48	0.4	3.6	2.8	0.3
10-20 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

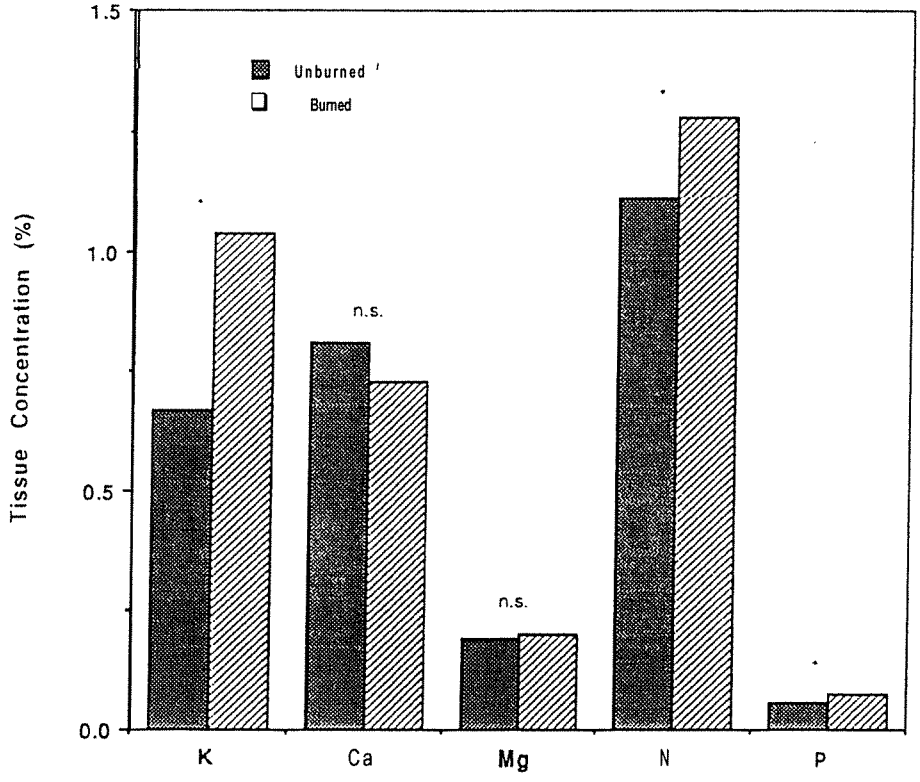

Figure 2.-Nutrient concentrations of burned and unburned plot herb layer vegetation. *Indicates significant difference between burned and unburned treatments at $p < 0.05$.

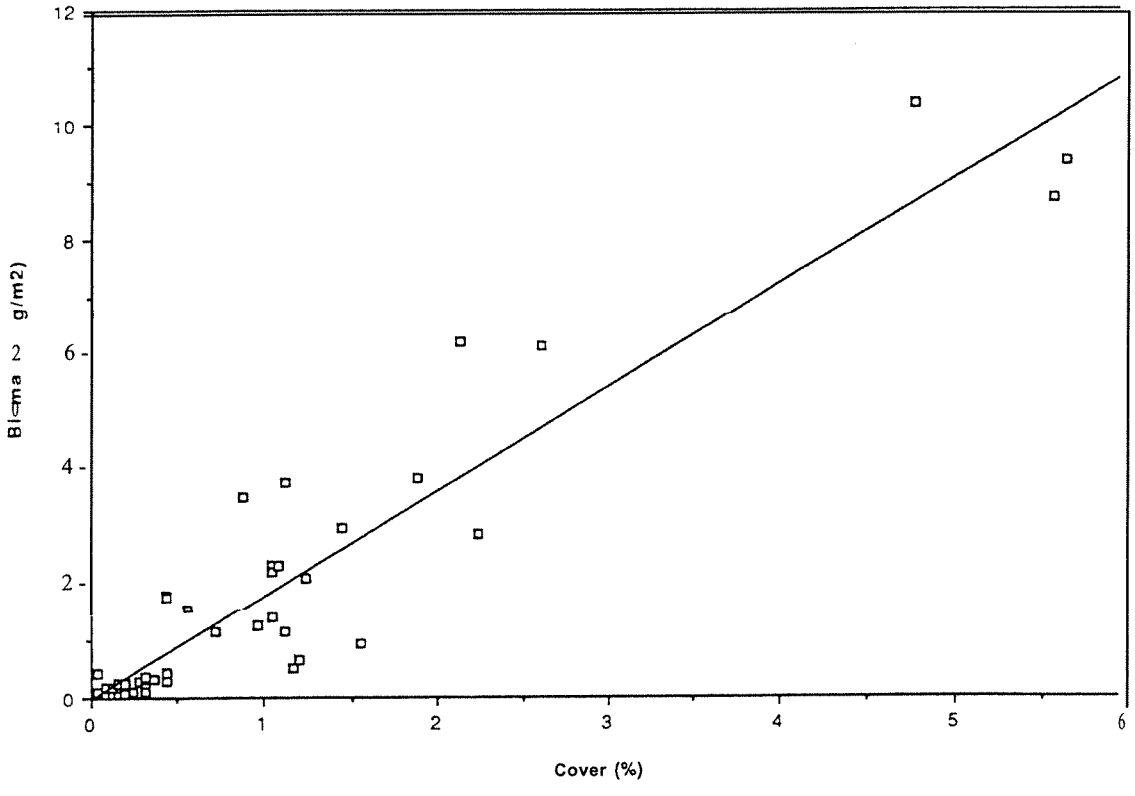

Figure 3.-Relationship of herb cover and harvested herb biomass for WS77. Each point represents average biomass and cover values for individual species. See text for equation.

Table 4. Herbaceous Layer cover, biomass, species richness, Shannon-Weiner diversity, and nutrient content for burned and unburned plots of WS77. Error vatues 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 bum" 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 lirc 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 bum and control compartments as the Shannon-Weiner Diversity Index (H), using the equation

$$H = -\sum_{i=1}^{n} [p_i \cdot \ln(p_i)] \qquad (2)$$

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 WS77. Nomenclature follows Radford, and others (1968).

Control Species	Relative Cover (%)	Winter burn Species	Relative Cover (%)
Lonicera japonica	16.3	Andropogon virginicus	21.4
Andropogon virginicus	15.2	Liquidambar styraciflua	8.5
Ilex gtabra	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 betulifotius	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 fire frequencies, but actually are dependent on fire 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 fire 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 tire-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 fire frequencies cause sharp declines in longleaf pine populations.

Conclusions

This Coastal Plain pine flatwoods ecosystem is distinctly oligotrophic and fire, 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 fire.

The importance of fire on the plant community level was evident in its effects on the herbaceous layer. Although these effects were variable (especially varying with season of burn), fire 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 fire 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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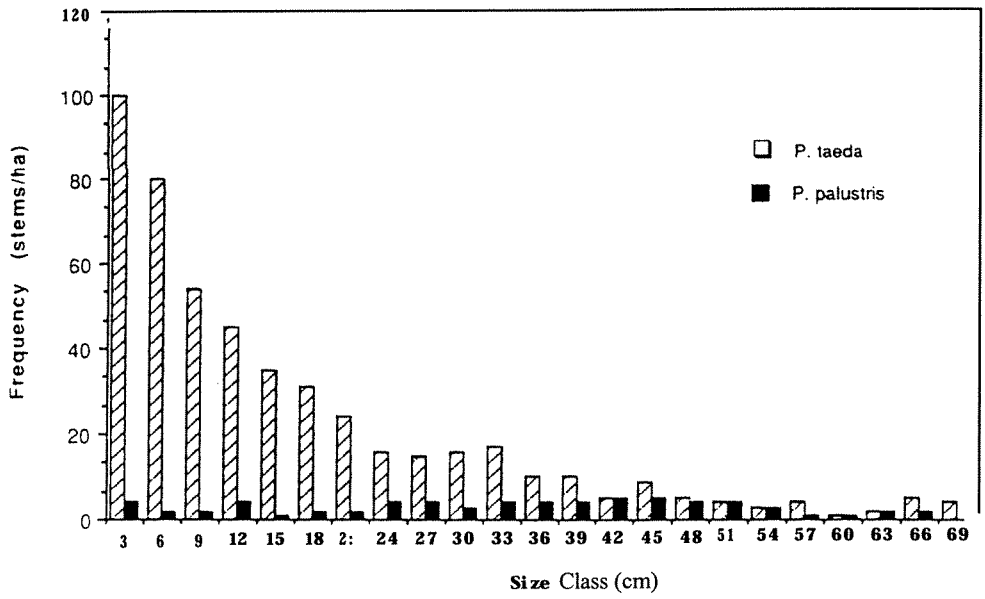

Figure 4.-Size-class distributions for loblolly pine (P. taeda) and longleaf pine (P. palustris) for WS77.

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THE EFFECT OF A HIGH INTENSITY FIRE ON THE PATCH DYNAMICS OF VA MYCORRHIZAE IN PINYON-JUNIPER WOODLANDS

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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 burn, 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 cover 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-burn spore numbers were significantly reduced under tree canopies (up to X8 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 suhcanopy 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 mycorrhizae many plants show a decreased growth rate or fail to develop beyond germination (Harley and Smith 1983; Masse 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; Klopatck 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).

Klopatck 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) (Klopatck 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. Klopatck 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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(1988) found significant reductions of three VA mycorrhizal species following a tire 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 arc 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 1985). 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 Engclm.) 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 hystrix (Nutt.) J.G. Smith), Stipa sp.] and shrub species [snakeweed (Guttierrezia sarothrae (Pursh) Britt and Rusby), rabbitbrush (Chrvthothamnus sp.), cliffrose (Cowania mcxicana 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 burn. 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 burn (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 $\pm$ standard errors of the mean. Significant differences ($p < 0.05$) in spore numbers were isolated using Tukcy'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 ectomycorrhizai, 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 roofs (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 I.--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.

Gtomus macrocarpum Tut & Tut
G. occultum (Walker)
G. mosseae (Nicot & Gerd) Gerd. & Trappe
Scutettospora calospora (Nicol. & Gerd.) Walker & Sanders
G. deserticuta Trappe, Bloss & Menge
G. aggregatum Schenck & Smith
G. fascicutatum (Taxter sensu Gerd.) Gerd. & Trappe
Acaulospora 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-burn 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 I). 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.

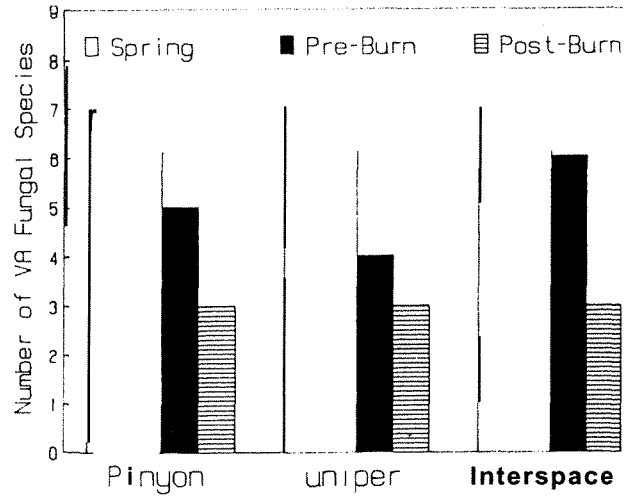

Figure 1 .--Change in the number of VA mycorrhizal species in soils taken from beneath pinyon and juniper and interspaces due to change in season and effect of fire

Spore Densities

Spore density varied under pinyon, juniper, and interspaces during the spring and pre-burn samplings (fig. 2). Overall spore counts under pinyon were not significantly higher in the spring than in pre-burn 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-burn 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-burn 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 burn, 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

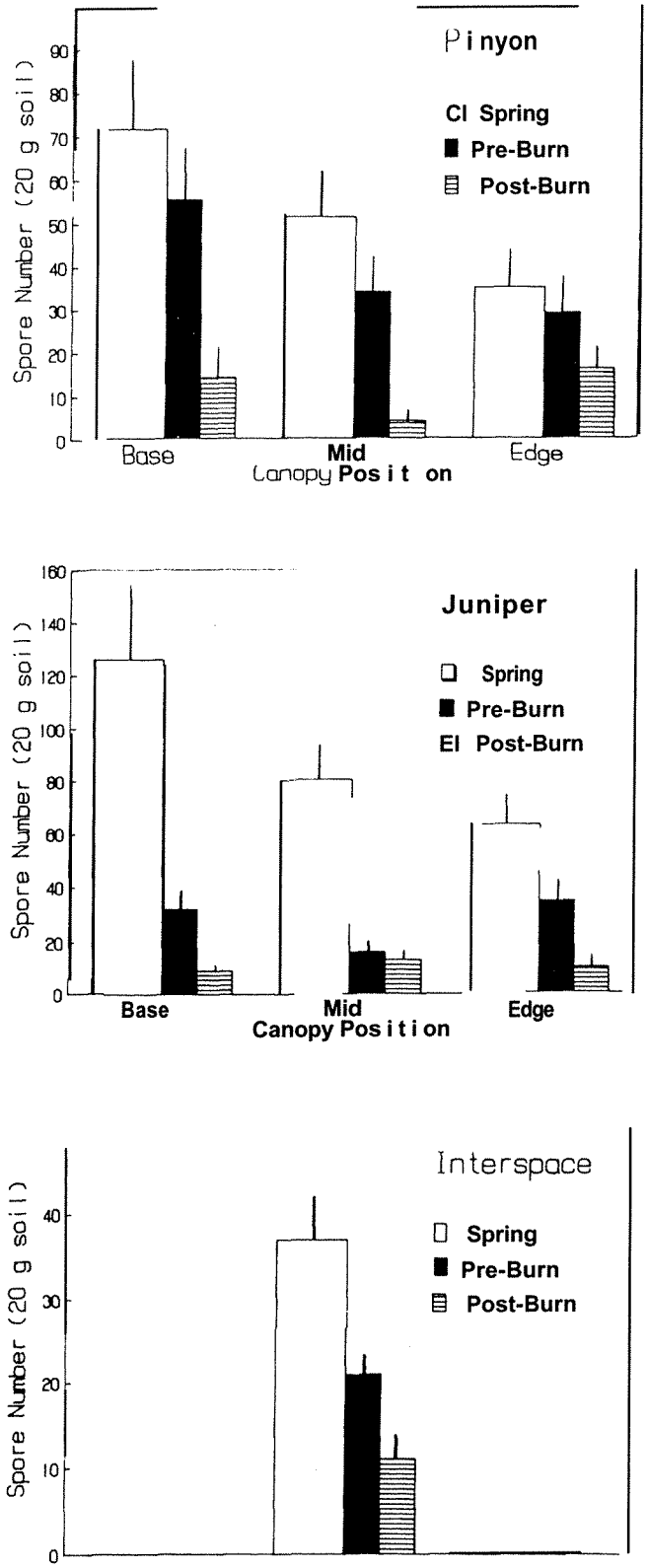

Figure 2.--Number of VA mycorrhizal spores per 20-gram soil sample taken from beneath pinyon and juniper canopies and interspaces. Samples were taken at three locations under tree canopies--base, mid and canopy edge and from grass covered interspaces

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 fire 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 tire 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 fire.

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FOREST SOIL CHARACTERISTICS FOLLOWING WILDFIRE IN THE SHENANDOAH NATIONAL PARK, VIRGINIA

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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 arc as, therehy 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 Dovel Mountain in the Shenandoah National Park and adjacent private lands. Dovel Mountain is located approximately 6.5 km northeast of the town of Shenandoah in Page county, Virginia. The mid-July wildfire burned approximately 350 ha before being brought under control and declared extinguished on August 8, 1988.

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The study area is located in the Blue Ridge Physiographic region and is underlain by the Erwin (Antictam) 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 predominatly 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 fire occurrence. High intensity burn levels represent greater than 75 percent overstory mortality of basal area and crown cover, whereas low intensity burn levels represent less than 25 percent overstory mortality. A combination of crown and surface fires resulted in high intensity burn sites whereas surface fires represented low intensity burn 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 burn 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 burn 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 fire 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 burn areas the first year after the fire (fig. 1).

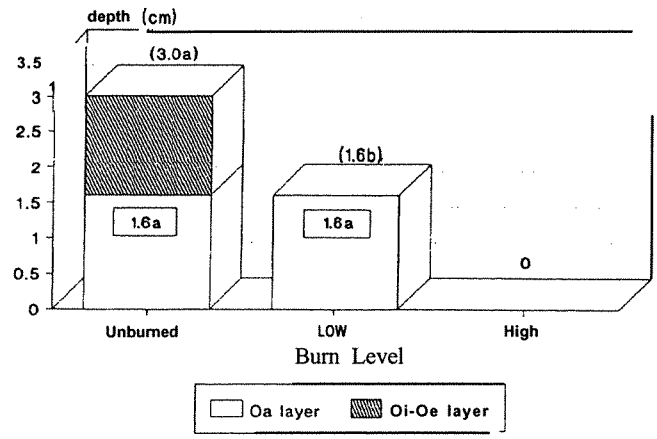

Figure 1 - Forest floor depth one year after fire occurrence. [Values in boxes represent comparisons among Oa layers while values in parentheses represent totals (Oi-Oe + Oa). Means followed by the same letter are not significantly different at the 0.05 level.]

Although the Oi-Oc 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.

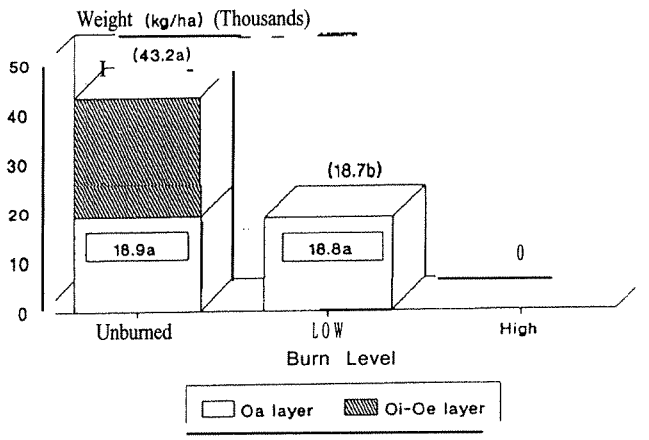

Figure 2 Forest floor weight (kg ha^{-1}) one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

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 bum 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 .O 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 bum sites. Overall, however, total C content for the entire forest floor was 50 percent lower on low bum areas, compared to unburned areas, due to the consumption of the overlying Oi-Oe layer.

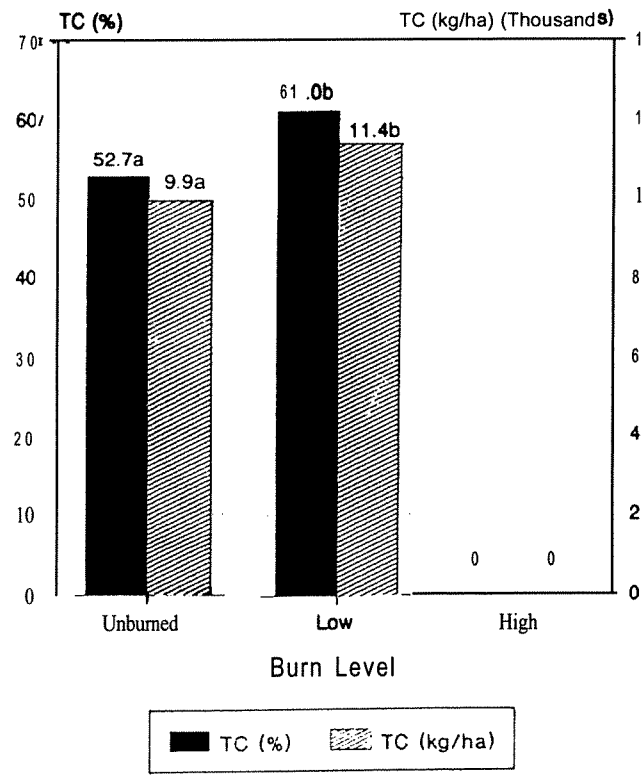

Figure 3 . Total carbon concentration (%) and content (kg ha^{-1}) of the Oa layer one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

The major elemental components of organic matter include N, O, H, and C. During normal decay processes of organic matter, some C is converted to CO_2, 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 burn 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 fire 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 are also produced chemically by soil heating and microbially after fire. Unlike NH_4-N, NO_3-N is not produced during soil heating, but is formed during subsequent mineralization and nitrification 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 nitrification processes following fire 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 fire. N2-fixation may contribute 10 to 100 kg ha^{-1} of N annually (Stevenson 1986).

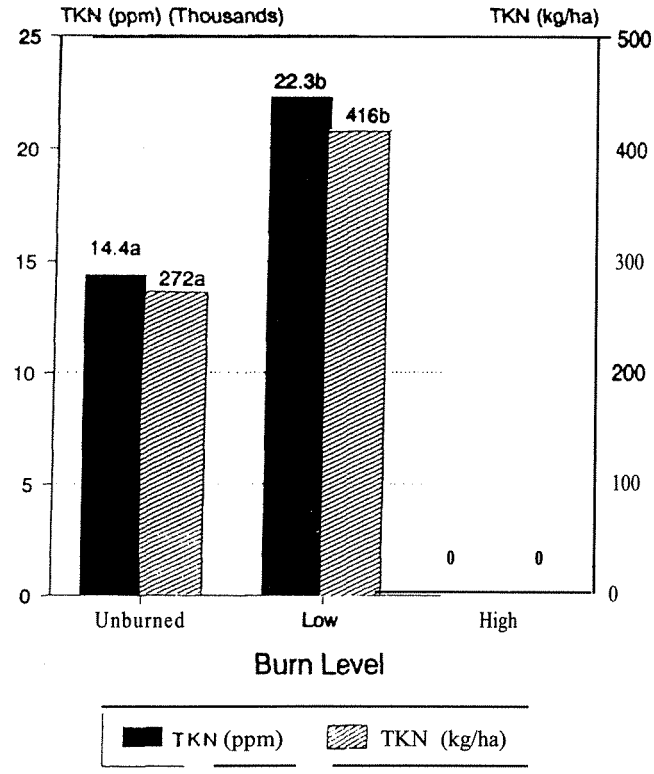

Figure 4 Total nitrogen concentration (%) and content (kg ha^{-1}) of the Oa layer one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

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 burn 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 fires 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.

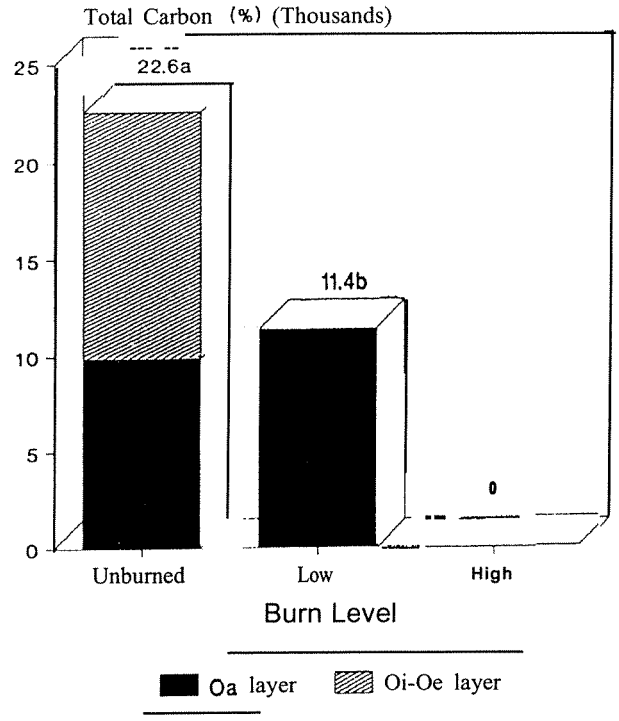

Figure 5 - Total carbon content (kg ha ^{1}) of the entire forest floor (Oi-Oe + Oa values) one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

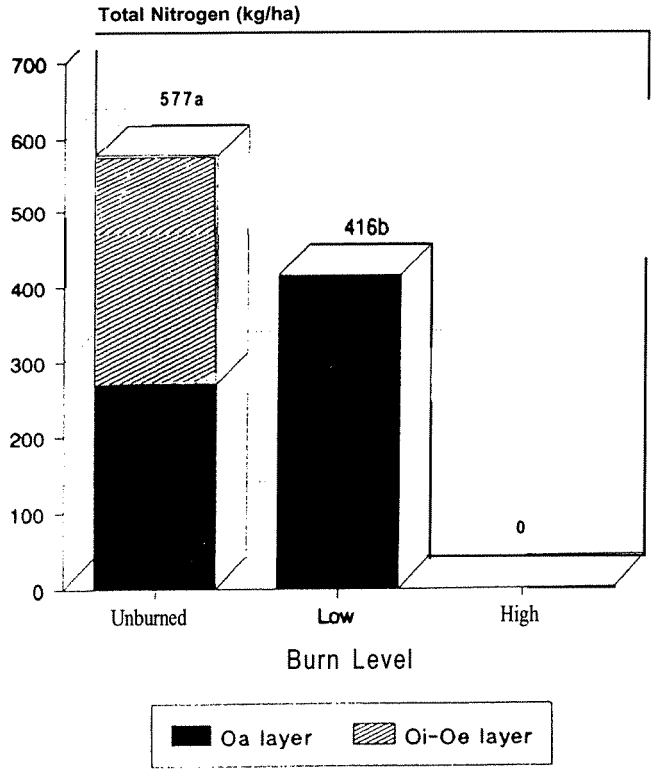

Figure 6 - Total nitrogen content (kg ha^{-1}) of the entire forest floor (Oi-Oe + Oa values) one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

Mineral Soil Parameters

Fire generally results in a decrease in soil acidity. Soil acidity in the surface 10 cm of mineral soil was 4.3 in unburned areas and significantly higher than low and high burn areas which measured 4.6. This rise in pH following fire is generally attributed to an influx of nutrient-rich ash and a resultant increase in exchangeable cations in the surface mineral soil. The magnitude of change in soil acidity is dependent upon such factors as nutrient concentration of the overlying litter, cation exchange capacity (CEC), buffering capacity and original pH of the soil, and rainfall frequency and amounts (Grier 1975; Metz and others 1961). McKee (1982) found that soil acidity decreased in the surface (O-8 cm) mineral soil following a combination of different prescribed burn treatments on four coastal plain pine sites. Changes in pH ranged from 0.1 to 0.4 units across the four study areas. Greater changes in pH may occur, however, most studies indicate changes of less than one pH unit following prescribed tires which return to preburn levels within a few years.

Total C and N levels in the surface 10 cm of mineral soil were higher on low burn sites compared to unburned areas (figs. 7, 8). Conversely, high bum areas had lower total C and N levels than unburned sites. An increase in total C following low intensity fires may be associated with the redistribution and movement of colloidal-sized charred material, high in elemental carbon, downward from the overlying residual ash into the mineral soil by gravity and water (Metz and others 1961), and/or by isoelectric precipitation of alkali humates produced during burning (Viro 1969). A large portion of the mineral soil organic matter (humus) is associated with the forest floor-mineral soil interface and within the top 2-3 centimeters of the mineral soil. Following the removal of the entire forest floor by high intensity fires, soil humus may also be destroyed where temperatures exceed 250°C. These temperatures are easily achieved during high intensity fires where temperatures have been shown to exceed 700°C at the mineral soil surface (Debano and Rice 1971). Another factor which may contribute to a loss of total C from the mineral soil is the physical removal of the surface mineral soil and associated C due to erosion. Once the protective forest floor mantle is removed from the site, such as by high intensity fires, erosion may lead to a direct loss of C and other nutrients from the site. In this study, erosion was not measured, but was observed by the accumulation of mineral soil at downslope positions below the high intensity bum areas. Low and unburned sites did not show any observable signs of surface erosion.

Total N followed similar trends to total C levels. Increases in total N following fire are likely due to an increase in organic and inorganic forms of N. Reasons for these increases in total N following tire have already been discussed earlier in relation to forest floor material.

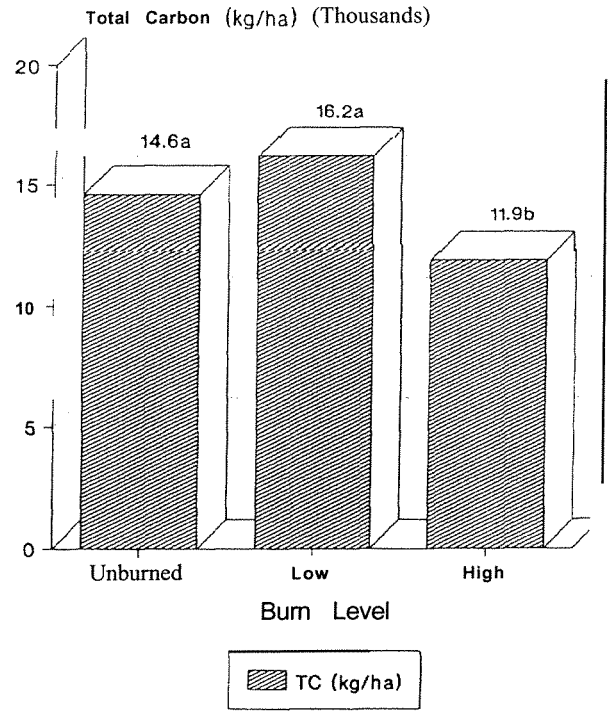

Figure 7 - Total carbon content (kg ha $^{-1}$) within the top 10 cm of the mineral soil one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

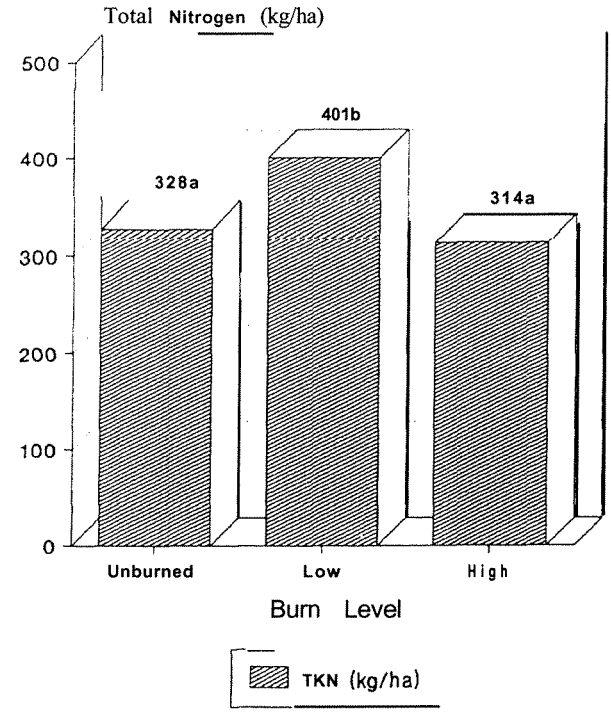

Figure 8 - Total nitrogen content (kg ha^{-1}) within the top 10 cm of the mineral soil one year after fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

Inorganic N levels were signiticantty higher on burned areas compared to unburned areas (fig. 9). Similar results by other authors (Burns 1952; Wells 1971; Alban 1977; White 1986a; Covington and Sackct 1986) have also shown increases in inorganic N following burning which is generally attributed to an increase in mineralization rates (Likens and others 1970; White 1986b; Lodhi and Killingbeck 1980) following a disturbance such as fire or clearcutting. Mineralization (ammonification + nitrification) is the process whereby organic N is converted to plant available inorganic forms through microbial-mediated biochemical transformations and is influenced by factors which affect microbial populations and activities such as pH, temperature, soil moisture, and the presence of compounds such as polyphenolics, tannins, and monotcrpenes. Following tire, increases in soil pH, temperature, and moisture, and the removal of inhibiting compounds favor increased rates of mineralization. An increase in inorganic N may also be associated with the downward translocation and rcprecipitation of N gases at cooler mineral soil depths. Klemmendson and others (1962) showed that burning accelerated N movement from the overlying forest floor into the mineral soil. Although mineralization rates vary over time with fluctuations of the factors which influence this process, the results of our point-in-time sampling of inorganic N reflects the conditions found by other investigators.

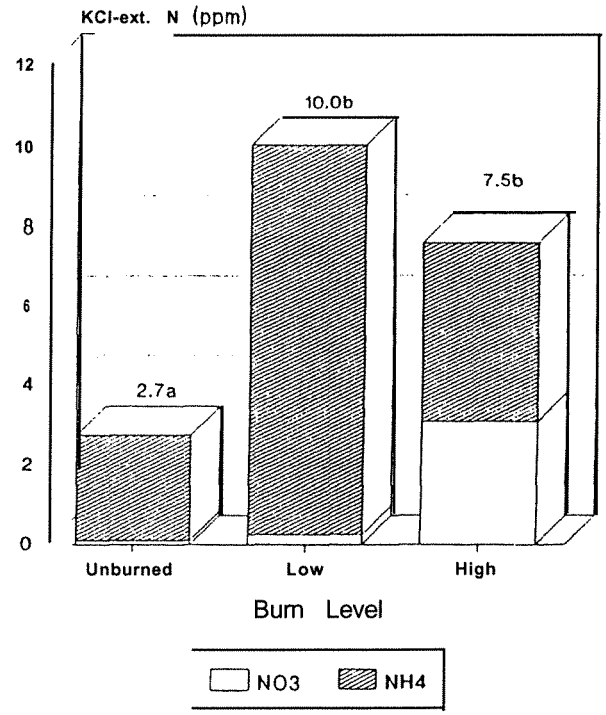

Figure 9 - KCl-extractable nitrogen concentration (ppm) within the top 10 cm of the mineral. soil one year alter fire occurrence. Means followed by the same letter are not significantly different at the 0.05 level.

Most of the increase in inorganic N following low intensity fires is due to NH_4-N, whereas most of the increase in inorganic N following high intensity fires is due to an increase in both NH,-N and NO,-N levels (fig. 9). A lack of NO,-N in low and unburned areas suggests that nitrification processes may be inhibited by some factor. Nitrification processes are severely limited at pH values below 4.5, insufficient soil moisture and cool temperatures, and in the presence of inhibitory compounds such as phenols, tannins, and monoterpenes (Stevenson 1986; White 1986b; Lodhi and Killingbeck 1986). Given the fact that low and high intensity areas had a pH of 4.6, the increase in NH,-N and the lack of NO,-N following low intensity fires suggests that the process of ammonification may be enhanced or less affected than nitrilication in the presence of factors such as monoterpenes, phenols, and tannins in the residual forest floor material. White (in press) suggested that monoterpenes may have a greater inhibitory effect on Nitrosomonas and Nitrobacter populations, responsible for nitrification, than on microorganisms responsible for ammonification. Lodhi and Killingbeck (1980) found that water extracts laden with soluble polyphenolics, tannins, and monoterpenes reduced numbers of Nitrosomonas by 93 percent. Other factors possibly contributing to an increase in the NO,-N to NH,-N ratio, following high intensity fires, is the fact that the overstory canopy was left mainly intact following low intensity fires, whereas complete overstory mortality resulted following high intensity fires. This overstory removal following high intensity fires results in more direct solar radiation and a resultant increase in soil temperature. Sub-surface soil moisture also increases due to removal of transpiring vegetation. Increased soil temperatures and moisture favor rapid nitrilication (Stevenson 1986).

Since N *is* the most limiting nutrient on most forest sites and C sources contributing to the "Greenhouse Effect" are important considerations, changes in these pools should be considered. Total C and N pools (forest floor + mineral soil) in low burn areas one year after fire occurrence were 25 and 10 percent lower, respectively, than unburned areas. Unlike low intensity burn areas, total C and N pools in high intensity burn areas were 68 and 65 percent lower, respectively, than unburned areas. Low intensity fires resulted in a partial redistribution of C and N from the forest floor into the mineral soil with a slight overall reduction in the combined nutrient capital. High intensity fires, however, resulted in no redistribution of nutrients and a greater loss of combined C and N capital from the site. Although reductions in these pools may be severe following high intensity fires, losses may not be altogether detrimental when considering the synecology of mixed pine forests on these poor sites. Periodic severe fires may be necessary to prevent stagnation and to promote successful regeneration and establishment of these species while inhibiting more nutrient- and moisture-demanding hardwood species.

The impacts of fire on soil are highly variable and depend on such factors as fire intensity and duration, weather conditions, and forest floor and mineral soil characteristics at the time of burning. Overall, low intensity fires in this ecosystem seem to have little deleterious effects on soil properties and may, in fact, facilitate increased mineralization rates, thereby releasing a pulse of nutrients to the site. Increases in pH, microbial activity and nitrogen fixation may also occur. Conversely, high intensity fires result in the removal of the protective forest floor and a much greater loss of nutrients from the site. However, a question must be raised in relation to the overall impact of high intensity fires in relation to site quality and the associated vegetation occupying a site. Is the loss of nutrients more significant on better sites where there is a greater buffer capacity and the total loss of nutrients in proportion to the whole is small? Or is the loss more significant on poorer sites where a small loss may represent a large portion of the nutrient capital for that site? Given adequate time without disturbance, forest floor and mineral soil properties tend to increase in both depth and fertility. On minimally developed soils as in this study, where soil depth is shallow and inherent fertility of parent material is low, much of the sites' fertility is derived from and dependent upon the turnover of forest floor material and external inputs. Considering the five major soil-forming factors, and in the absence of disturbance, depth and fertility of the mineral soil should increase, thereby allowing more nutrient-demanding species to invade and compete for site resources.

Tree species occupying better, more productive sites generally have higher nutrient requirements; therefore, even a small change in nutrient levels may result in a species shift. Conversely, tree species occupying poorer sites may have lower minimal nutrient requirements and may actually depend on periodic fire to disrupt the progress towards site quality improvement. In fact, one of the possible secondary functions for the high content and slow turnover rate of monoterpenes in fresh litter of fire-adapted Pinus species, may be to increase probability of fire occurrence. Terpenes and resins have a heat of combustion of 7720 calories per gram, which is twice that of cellulose (Rothermal 1976). These extractives are outgassed early in the pyrolysis process and may contribute three-fourths of the total flame height *and* intensity of the flame zone (Philpot 1969).

It is possible that low intensity fires would not provide the necessary conditions required by Tahle Mountain pine to successfully regenerate and compete, whereas high intensity fires generally result in (1) opening of serotinous cones; (2) removal of the forest floor providing favorable seed bed conditions; (3) removal of inhibitory compounds such as monoterpenes, tannins, and polyphenolics; and (4) ironically, limiting site quality improvement by preventing nutrient buildup to occur. Thus, a combination of these factors may result in retarding the invasion of more nutrient-demanding competitors and sustaining the endemic Table Mountain pine on nutrient- and moisture-limiting sites.

SUMMARY

Total forest floor thickness and weight were significantly reduced following low and high intensity tires. However, low intensity fires consumed only the Oi-Oe layer, leaving the Oa layer relatively intact, whereas high intensity fires resulted in the complete removal and destruction of the entire forest floor. Total C and N content of the Oa layer was higher on low burn areas compared to unburned Oa material. However, an overall reduction of forest floor total C and N resulted following both low and high intensity tires due to the partial or complete destruction of forest floor material.

Mineral soil pH was significantly higher in both low and high intensity bum areas compared to unburned areas. Additionally, total C and N content of the surface 10 cm of mineral soil was also higher on low bum areas compared to unburned areas. However, high burn areas had lower total C and N levels. Inorganic N levels were significantly higher in both low and high intensity bum areas, thereby providing a pulse of available N for plant uptake.

ACKNOWLEDGEMENTS

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THE INTERACTION OF PRESCRIBED FIRE, MONOTERPENES, AND SOIL N-CYCLING PROCESSES IN A STAND OF PONDEROSA PINE (Pinus ponderosa).

Carleton S. White'

Abstract—Monoterpenes, principal components of turpentine, have been shown to be inversely correlated with N mineralization and nitrification rates in ponderosa pine (Pinus pondcrosa Dougl. ex Laws.) soil. and are suspected to be allelopathic substances causing germination inhibition or growth regulation. Because monoterpenes are highly flammable, prescribed fire may represent an efficient method of lowering monoterpene concentrations in both organic and mineral soil horizons. Samples of the forest floor and the 0- to 10-cm soil horizon were collected from four separate plots within a pondcrosa pine stand immediately before and after fire treatment. The prescribed tire treatments resulted in a greater proportionate loss of monoterpenes than of forest-floor biomass: loss of 55 percent of the forest-floor mass corresponded to a 99 percent loss of monoterpenes. Forest-floor inorganic N content was doubled following treatment, with all the increase as NH,'-N; the mineral soil inorganic N content was unchanged. During incubation for potential N mineralization, only the burned forest-floor samples produced nitrate. Thus, the prescribed fire treatments resulted in potentially favorable changes in organic matter quantity and quality, levels of inorganic N, and potential rates of N-cycling processes.

INTRODUCTION

Management of southwestern pondcrosa pine (Pinus ponderosa Dougl. ex Laws.) often includes the USC of prescribed burning to reduce accumulated fuels. Studies have documented increases in the inorganic N content of forest-floor or mineral soil horizons immediately after burning (White 1986a; Kovacic and othcrs1986) or within the first growing season after burning (White 1986a; Ryan and Covington 1986; Covington and Sackett 1984; Covington and Sackett 1986). The increase in inorganic N is accompanied by a decrease in total N within the forest floor (White and others 1973 ; Klemmedson and others 1962; Kovacic and others 1986) and by an increase in biomass and nutrient content of understory vegetation (Harris and Covington 1983; Vlamis and others 19.55).

White (1986a) conducted research on the effects of prescribed burning on four plots within a ponderosa pine stand located in the Jemez Mountains of New Mexico. The bum treatments resulted in an immediate increase in the amount of NH,+-N in the forest floor. Potential N mineralization and nitrilication, as determined by laboratory incubations, were increased in samples of the forest floor collected within 12 hours of the burn. Nitrogen mineralization and nitrification potentials of the mineral soil were significantly increased in only 1 of 4 plots immediately after the burns; however, both processes were significantly increased in the mineral soil from all plots 6 months after the burn and remained elevated 10 months after the bum. White suggested that the immediate increase in nitrilication in the forest floor and the subsequent increase in nitrification in the mineral soil could be explained by the loss of volatile inhibitors from the forest floor.

The roles of volatile and water-soluble inhibitors of N mineralization and nitrification in the forest floor of the same pondcrosa pine ecosystem were studied by White (1986b). Water extracts of unburned forest floor inhibited nitrification by 17 percent when applied to actively nitrifying mineral soil from the same pondcrosa pine ecosystem after the bum treatment. Placing vials containing unburned forest floor or selected monoterpenes of ponderosa pine in sealed jars that contained actively nitrifying soil inhibited nitrification by 87.4 percent and 100 percent, respectively, and inhibited N mineralization by 73.3 percent and 67.7 percent, respectively. White (1986b) suggested that organic compounds that are water-soluble and volatile act as inhibitors of N mineralization and nitrilication in this ponderosa pine ecosystem. Inhibition of nitrification was also observed by Lodhi and Killingbeck (1980), who found that water extracts of pondcrosa pine needles applied to soil suspensions reduced numbers of *Nitrosomonas* by 93 percent. They suspected that polyphenolics and condensed tannins were the active compounds inhibiting nitrification. It appears that a number of secondary compounds produced by ponderosa pine could act synergistically to inhibit nitrilication and N-mineralization processes.

Laboratory bioassays (White, in press) showed that monotcrpenes could interact with N-cycling processes through four mechanisms: (a) by reducing net N mineralization; (b) by inhibiting nitrification; (c) by enhancing assimilatory uptake of NO_3^--N; and (d) by stimulating immobilization of inorganic N. The net effect of monoterpene addition on soil

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inorganic N content was to reduce the amount of NO_3^--N relative to NH_4^+-N, leading to net immobilization of inorganic N at high monoterpene additions (fig. 1). White (IN PRESS) also showed that monoterpene concentrations were highest in the L horizon and declined by an order of magnitude with each descending organic and mineral soil horizon (fig. 2). Prescribed burning has the potential to reduce the total monoterpene content of the soil profile drastically because the organic horizons rich in monoterpenes would be consumed preferentially.

The goal of this study was to identify the changes in monoterpene and inorganic N concentrations in the forest floor and mineral soil immediately following (within hours) prescribed burning of plots within a ponderosa pine stand, and to identify the change in potential N mineralization and nitrilication characteristics of these horizons.

METHODS

The present study was conducted on the same site where White (1986a, in press) had worked. The site is in north-central New Mexico, within the Jemez National Forest, near Bear Springs (elevation 2225 m). It is located on a small knoll of volcanic ash and pumice, with very uniform A horizon soils. Slope of each plot was less than 7". The overstory was composed entirely of pondcrosa pine. Scattered seedlings and saplings of pinyon pine (Pinus edulis) and various species of junipers (Juniperus spp.) were present. White originally chose the plots to avoid heavy fuel deposits and to favor areas with approximately equal accumulations of forest floor material and woody debris. Four of the 8 original plots were treated with prescribed burning on 7 November 1983. The 4 remaining plots were used in this study following a study of seasonal dynamics in monoterpene content and potential N mineralization and nitrification characteristics (White, in press).

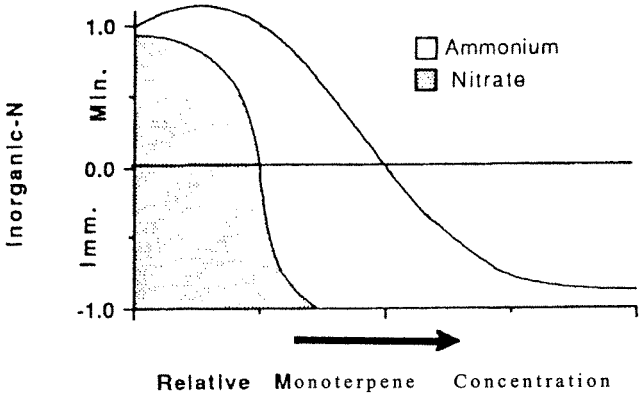

Fig. 1. Generalized response of soil inorganic-N levels to increasing monoterpene additions. Monoterpene additions are relative values, not actual concentrations (from White in press).

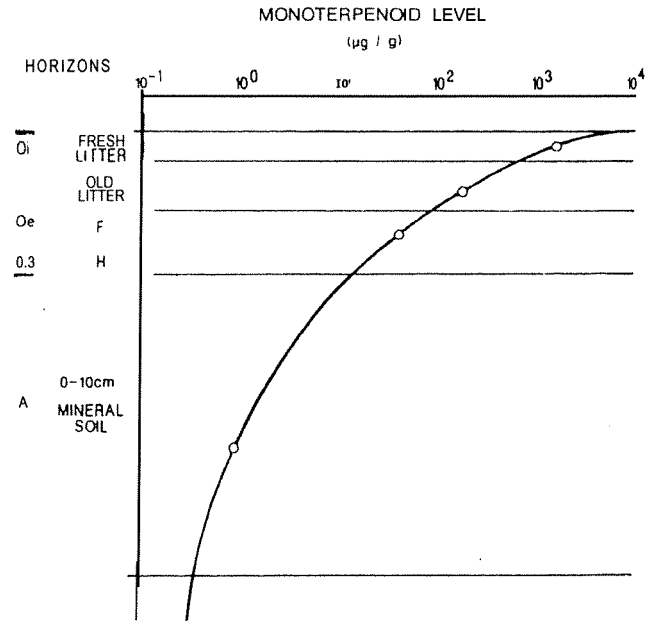

Fig. 2. Mean monoterpene concentration (n = 8) within the designated soil horizons of a ponderosa pine stand in New Mexico. The fresh litter was collected in October 1987; other horizons were collected in November 1987. Horizons are drawn in approximate proportion to actual depth in the field based upon the mineral soil horizon equal to 10 cm.

The plots were burned by U.S.D.A. Forest Service personnel on 27 October 1988. A fire break was scraped around the perimeter of each plot and the associated 5-m buffer zone. The plots were burned by igniting three strips about 5 m apart parallel to the length of the plot. Rates of fire spread ranged from 0.02 to 0.05 m s^{-1}. On 3 of the 4 plots, postburn samples were collected within one hour of burning. The fourth plot, which had a southern aspect, burned the longest; glowing combustion was observed about 2 hours after ignition. Samples from the fourth plot were taken approximately 3 hours after ignition. The amount of forest floor consumed by the burning was determined as the difference between ash-free mass of the preburn and postburn samples.

Collections were made from each plot on 27 October 1988 immediately before and after burning. Each plot measured 4m by 9m. A 5-m buffer zone around the perimeter of each plot was also burned. One sample per plot was collected before burning, and one sample along the same line transect was collected after burning. For each sample, all of the forest-floor material (0 horizon) beneath a 0.25 m^2 template was harvested. The template was placed on the forest floor, a

knife was used to make cuts around the template border, and the surrounding forest floor was scraped away. Mineral soil was collected to a 10-cm depth with a 10-cm-diameter corer. The soil collection was made at the center of the area from which the forest floor was harvested.

All samples were placed in resealable plastic bags and kept in the dark on ice during transport to the laboratory. In the laboratory, all samples were kept refrigerated at 4 "C. Roots with diameter greater than about 1 mm were removed by hand sorting. All material larger than 6.4 mm in diameter was removed from all samples by sieving. Needles and other materials too long to lit into the incubation cup were cut into appropriate lengths (usually into halves or thirds). All samples were corrected for ash content by determining weight remaining after ignition at 500°C.

Nitrogen mineralization and nitrification potentials were measured by aerobic incubation. After a portion of each sample had been adjusted to 50 percent of determined water-holding capacity (WHC) by methods described in White and McDonnell (1988), a total of 17 subsamples per horizon were apportioned into 125-ml plastic cups. Each cup received approximately 10 g dry-weight (DW) of mineral soil or 3 g DW of forest floor. One subsample of each horizon was immediately extracted with 100 ml 2 N KCl for NO_3^--N and NH,+-N analyses, and another subsample was frozen (-5 "C) prior to processing for monoterpene analysis. The remainder of the cups were covered with plastic wrap, sealed with a rubber band, and incubated in the dark at 20 "C. As reported by Jones and Richards (1977), the plastic wrap minimized water loss during incubation, yet exchange of CO, and 0, was sufficient to keep the subsamples aerobic during incubation. Moisture content was monitored by weight loss and replenished as needed

At weekly intervals to 10 weeks, a subsample of each horizon was removed for NO_3^--N and NH,+-N analyses. After extraction with 100 ml 2N KCl for 18-24 hours, the clarified supernatant was analyzed for NH,'-N and NO_3^--N + NO_2^--N (NO_2^--N was never detected) on a Technicon AutoAnalyzer. White (1986a) has described the procedures employed.

After incubation for 1, 2, 4, 7, and 10 weeks, a subsample of each horizon was frozen (-5 "C) prior to processing for monoterpcnc analyses. Subsamplcs of mineral soil were transferred to plastic scintillation vials and stored at -80 "C. A mortar and pestle were used to gring the forest floor subsamples separately under liquid nitrogen to break apart the larger material. These subsamplcs were then transferred with liquid nitrogen to a Tecator¿ centrifugal grinder fitted with a l.O-mm screen. After grinding, the forest-floor material was transferred to plastic scintillation vials, sealed, and stored at - 80 °C until monoterpene analyses could be performed. Subsamples (ranging in weight from 9 to 10 g for mineral soil and 2 to 3 g for forest floor) were extracted with 10 ml of ether, which contained a known amount of fenchyl acetate for use as an internal standard, in a 50-ml Erlcnmeyer flask that was covered with paraffin film and aluminum foil. After 1 hour extraction at room temperature, the ether was decanted and centrifuged (mineral soils did not require centrifugation).

The clarified supematant was pipetted into a ground-glass-stoppered culture tube, sealed with paraffin film, and refrigerated at 4 "C. A 4-μl portion of the refrigerated ether extract was injected into a Shimadzu GC-9 fitted with a split injector (split ratio was 50:1), a bonded methyl silicone capillary column (25 m in length, 0.25 mm in inside diameter, 0.25 micron in film thickness), and a flame-ionization detector. The injector temperature was 270 °C, flow rate was 4 cc min^{-1}, and initial oven temperature was 60 °C. Oven temperature was increased by 4 °C min^{-1} to 109 "C, then by 40 °C min^{-1} to 250 "C. Individual monotcrpene standards (verified with CC-MS) were added to sample extracts, and monoterpenes were identified by co-chromatography. Peak area was converted to mass of individual monoterpencs by means of calibration curves generated with standards. An average calibration factor was used to convert the peak area of each unknown to relative mass.

The effects of the prescribed fire treatment were determined for each analysis by comparing the 4 pretreatment samples to the 4 post-treatment samples by analysis of variance (control vs. treatment, n=4). Ash-free mass lost upon ignition was used as a measure of burn intensity since rates of spread and flame heights were approximately equal for each plot. All concentration data were converted to mass per unit area for seasonal comparisons. Net N mineralization was defined as the increase in the amount of inorganic N (NH,'-N + NO, - N) over the entire 10-week incubation. Net immobilization was defined as the decrease in the amount of inorganic N over the entire 10-week incubation. Relative nitrification was defined as the percent of the total inorganic-N pool comprised by NO_3^--N at the end of the incubation period. All statistical analyses were performed with SAS-PC ⌐ (Statistical Analysis System, SAS Institute Inc.) or with StatView⌐ (Brainpower, inc.). The a *priori* probability level accepted to be significant was <0. 10; however, the probability level for each statistical analysis will be given below.

RESULTS

The amount of forest floor remaining after the prescribed burning treatments was significantly less than before treatment ($P<0.003$), but varied from 38 to 80 percent (fig. 3). The lowest amount of mass lost was approximately equal to the mass of the L horizon alone as determined in previous collections (White in press), while the greatest amount of mass lost was approximately equal to the entire L horizon and about half of the combined F and H horizons.

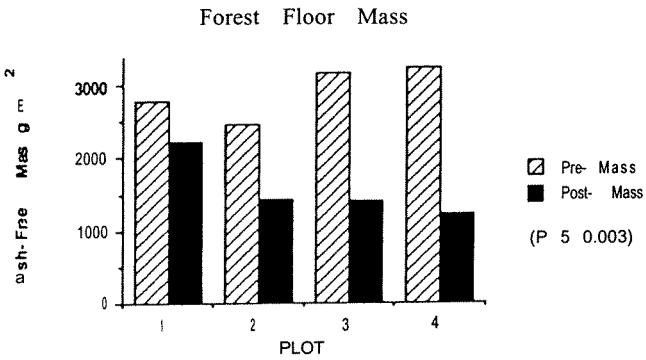

Fig. 3. Ash-free forest floor mass before (Pre-Mass) and after (Post-Mass) prescribed burning. Probability level for the comparison of preburn and postburn mass is shown (n=4).

Total monoterpene concentration in the postburn forest floor declined in 3 of the 4 plots and increased in the plot with the smallest loss of mass (fig. 4). When expressed on an area basis, the total amount of monoterpene declined in all plots ($P=0.067$, fig. 5). Monoterpene content of the postburn forest floor was a function of the fraction of original forest-floor mass ($r^2=0.993$, $P < 0.01$; fig. 6). The burn treatments reduced the content of some monoterpenes to a greater extent than others. Monoterpenes with a double-bonded carbon atom in a terminal position on the molecule (including camphene, b-pinene, sabinene, limonene, myrcene, and limonene oxide; fig. 7) and monocyclic monoterpenes (including p-cymene, a-phellandrene, limonene, and g-terpinene; fig. 8) were reduced to very low or undetectable levels, even in the plot that lost the least amount of forest floor (plot 1).

The burn treatments significantly increased the amount of inorganic N in the forest floor ($P=0.012$; fig. 9), with all the increase due to higher NH_4^+-N content and no change in NO_3^--N content. The amount of inorganic N in the mineral soil was unchanged by the burn treatment ($P=0.91$; fig. 10). Measurement of potential N mineralization and nitrification for the prebumed forest floor showed net immobilization of inorganic N and no net nitrification (net decline in inorganic

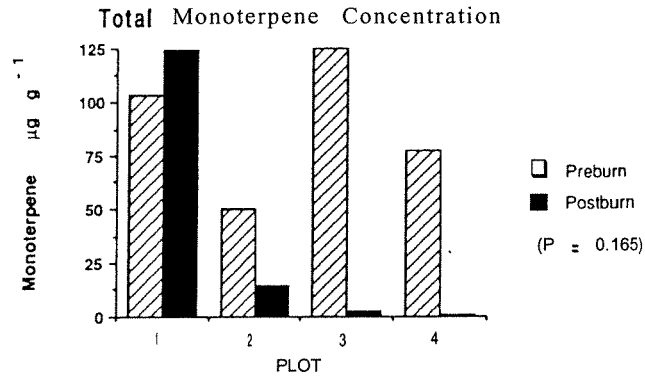

Fig. 4. Total monoterpenc concentration of the 0 horizon before (Preburn) and after (Postbum) prescribed burning. Probability level for the comparison of prebum and postburn concentrations is shown (n=4).

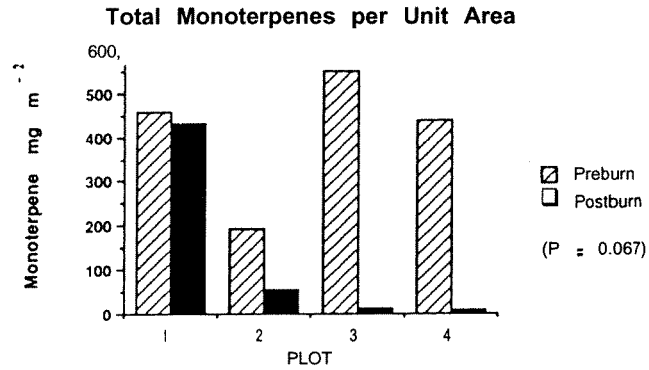

Fig. 5. Total monoterpene content of the combined organic and 0- to 10-cm mineral soil horizons before (Pre-bum) and after (Postbum) prescribed burning. Probability level for the comparison of prebum and postburn content is shown (n=4).

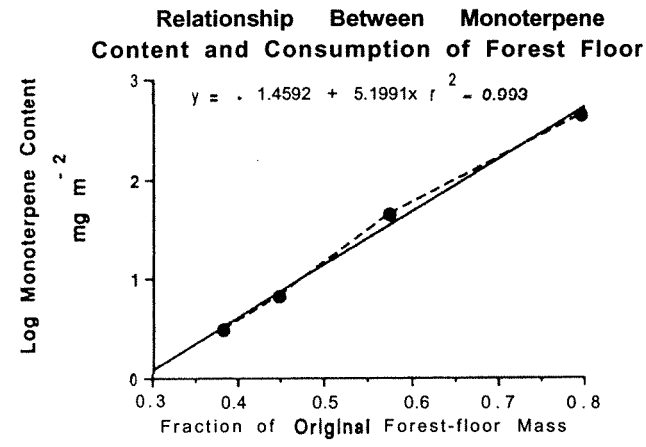

Fig. 6 Relationship between monoterpene content of the combined postburn organic and 0- to 10-cm mineral soil horizons and the amount of consumption (expressed as the remaining fraction of original forest-floor mass) by the prescribed burning.

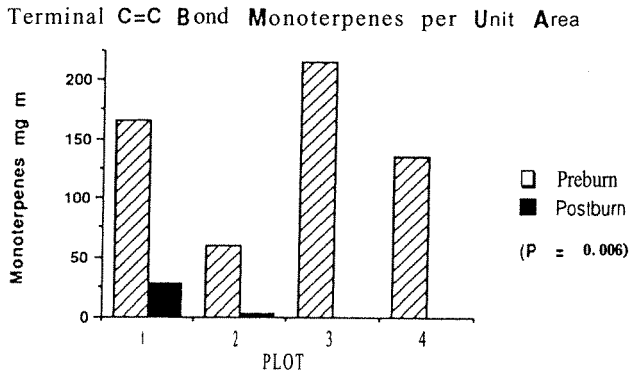

Fig. 7. Content of monoterpencs that contain terminal unsaturated carbon-carbon bonds for the combined organic and 0- to 10-cm mineral soil horizons before (Prebum) and after (Postbum) prescribed burning. Probability level for the comparison of prcbum and postburn content is shown (n=4).

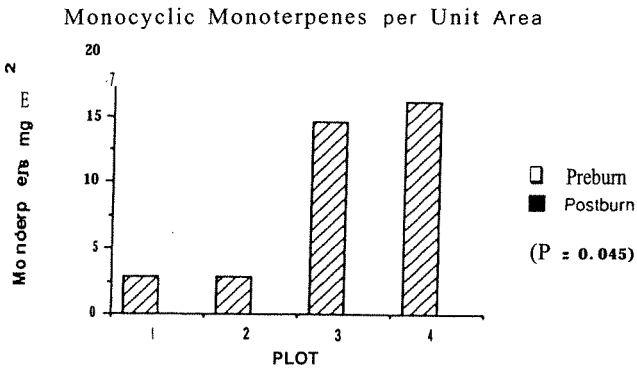

Fig. 8. Content of monocyclic monoterpcnes for the combined organic and 0- to 10-cm mineral soil horizons before (Prcburn) and after (Posthum) prescribed burning. Probability level for the comparison of preburn and postburn content is shown (n=4).

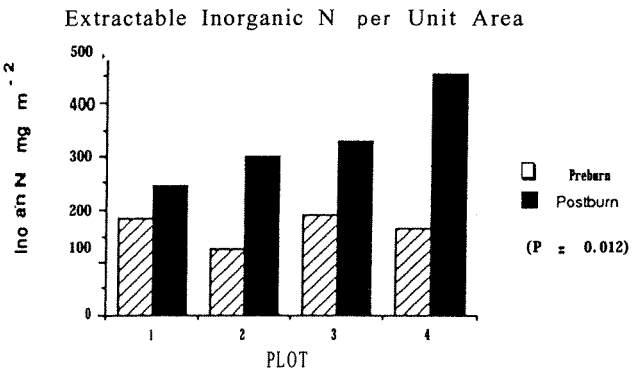

Fig. 9. Extractable inorganic N content of the 0 horizon before (Prebum) and alter (Postburn) prescribed burning. Probability level for the comparison of prebum and postburn content is shown (n=4).

N, shown by comparison of prebum values in figures 9 and 11). Although the burned forest floor showed the same basic pattern of net immobilization (difference in postburn values in figures 9 and 1 1), the potential N mineralization and nitrification pattern for the burned forest floor substantially deviated from the pattern shown by the pre-burned forest floor in two ways. First, net inorganic N levels in the burned forest floor began to increase rapidly over the final 3 weeks of incubation (fig. 12), whereas the pre-burned forest floor showed very little increase over the same period. Second, forest floor samples from all of the burned plots produced NO_3^--N during the 10-week incubation, whereas all of samples from the pre-burned plots showed no detectable amount of NO_3^--N after the 10-week incubation. When the amount of NO_3^--N present at the end of incubation in the four burned forest floor samples was compared with the amount in the preburned samples (none in all 4 prcbumed), the difference was not statistically significant (P=0.18). In part, the lack of significance was due to the large variation in the amount of NO_3^--N produced by the burned forest floors. The plot that had the greatest reduction in forest-floor mass (plot 4) produced the most NO_3^--N, but NO_3^--N production was not significantly correlated (P > 0.10) either with forest floor consumption or with the amount of NH,'-N present in the sample (representing substrate for nitrilication; fig. 13).

DISCUSSION

The plots burned in the present study were the control plots for a previous study (White 1986a) on the effects of prescribed burning in ponderosa pine. In the previous study, there was a greater range in preburn biomass (from 1650 to 3590 g m^{-2} ash-free weight) and in the amount of forest floor consumed by the bum (from 150 to 2070 g m^{-2}). The prescribed burning treatments were conducted under similar conditions (same prescription in both studies) and had similar characteristics, and therefore had very similar effects on soil inorganic N levels. In both studies, the increase in forest-floor inorganic N was proportional to the amount of forest floor consumed, with all the increase as NH,'-N. This relationship was highly significant in the first burn (r^2=0.97, P<0.01; White 1986a), where the range in forest floor consumption was greater, but was not as strong in the current study (r^2=0.78). Burning did not significantly change mineral soil inorganic N levels in either study, except in the plot where consumption of forest floor was greatest (White 1986a). Potential N mineralization and nitrilication in the mineral soil was unchanged in both studies.

Prescribed burning reduced weight of monoterpenes proportionally more than it reduced forest-floor mass. Removal of the upper organic horizon with the highest monoterpene concentration could explain a large portion of the decline, but monoterpene concentrations after burning were even lower than those measured in pm-burned F-H

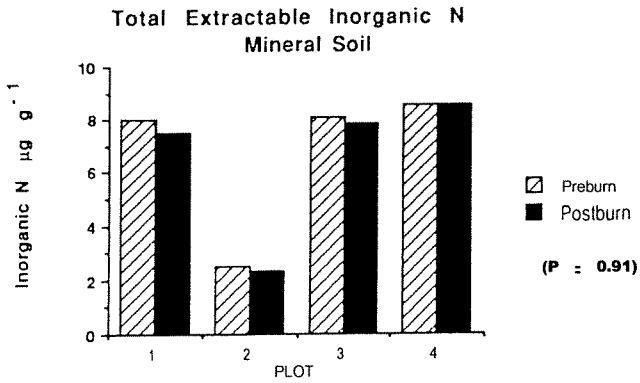

Fig. 10. Extractable inorganic N content of the 0- to 10-cm mineral soil horizon before (Preburn) and after (Postburn) prescribed burning. Probability level for the comparison of preburn and postburn content is shown (n=4).

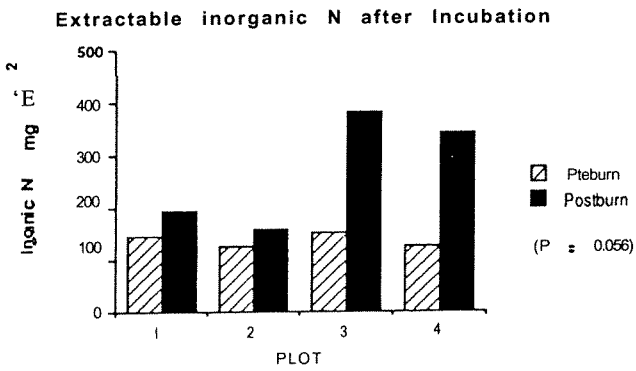

Fig. 11. Extractable inorganic N content of the 0 horizon before (Preburn) and after (Postburn) prescribed burning at the end of IO-week aerobic incubation for potential N mineralization. Probability level for the comparison of preburn and postburn content is shown (n=4).

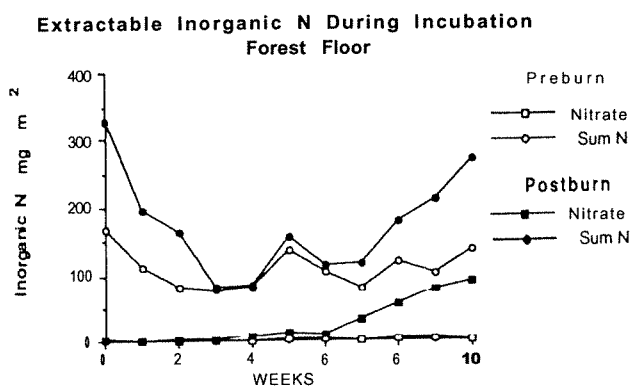

Fig. 12. Mean values (n-4) of extractable nitrate and ammonium + nitrate (Sum N) content of the 0 horizon before (Preburn) and after (Postburn) prescribed burning at weekly intervals during aerobic incubation at 20 °C.

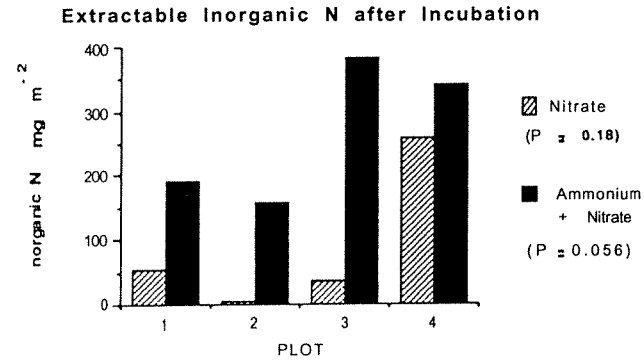

Fig. 13. Extractable nitrate and ammonium + nitrate content of the postburn 0 horizon at the end of IO-week aerobic incubation for potential N mineralization. Probability level for the comparison of preburn and postburn nitrate and ammonium + nitrate content is shown (n=4).

horizons in 4 other collections before the burn (White IN PRESS). The lower-than-expected concentrations suggest that monoterpenes were volatilized and probably combusted. The relationship between monoterpene concentration and residual forest-floor mass (fig. 6) suggests that reduction in forest-floor fuels by 50 percent can reduce monoterpenes by over 90 percent. Removal of monoterpenes would reduce the probability of fire and enhance the potential for higher rates of N mineralization and nitrification. White (1986a) observed increased rates of N mineralization in the forest floor and mineral soil in burned plots 10 months after treatment. If burning that reduces forest-floor mass by 50 percent results in increased soil moisture as in other studies in ponderosa pine (Haase 1986, Ryan 1978), field conditions will become more favorable for N mineralization. Thus, bums that consume half of the forest floor could increase site fertility significantly.

ACKNOWLEDGMENTS

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LOSS, RETENTION, AND REPLACEMENT OF NITROGEN ASSOCIATED WITH SITE PREPARATION BURNING IN SOUTHERN PINE-HARDWOOD FORESTS

Lindsay R. Boring, Joseph J. Hendricks, and M. Boyd Edwards'

Abstract—High-intensity site preparation burning is a common forest regeneration practice on harvested pine and mixed pine-hardwood sites in the southeastern USA. This practice could result in excessive losses of forest floor organic matter and nitrogen, and could subsequently decrease long-term productivity. In general, intensive burning may result in large losses of forest floor nitrogen, primarily by combustion and convection of N gases. However, past studies may have overestimated combustion losses due to inadequate knowledge of potential gaseous N retention mechanisms. Long-term inputs of N from biological fixation and atmospheric deposition may replace large amounts of N lost from fire, but more information on N_2-fixation processes is needed over time and space. Also, additional studies are needed to determine practical N_2-fixation management applications, such as retention of coarse woody debris and enhancement of N_2-fixing plant populations.

INTRODUCTION

High-intensity site preparation burning is a common and cost-effective regeneration tool on harvested pine and mixed pine-hardwood forest sites in the southeastern United States (Abercrombie and Sims 1986). Few studies have comprehensively examined the immediate and potential long-term impacts of this practice upon site productivity (Van Lear and Johnson 1983; Van Lear and Waldrop 1986). Site preparation effects are a central concern of many forest managers since the technique may alter forest floor organic matter and nutrient reserves that provide long-term site productivity for future stand rotations (Van Lear and others 1983).

Although low-intensity prescribed burning has been shown to have no deleterious effects upon the productivity of loblolly pine forests in the southeastern Coastal Plain (McKee 1982), high intensity site-preparation burning could result in excessive losses of forest floor organic matter and nitrogen. Several studies have provided gross mass-balance estimates of organic nitrogen loss in logging residues up to several hundred kg ha^{-1} from site-preparation burning (Van Lear and Kapeluck 1989). However, few detailed, process-level studies have been conducted to examine forest floor nitrogen losses and the mechanisms of nitrogen loss and retention during and following burning (fig. 1; Jorgensen and Wells 1986; Little and Ohmann 1988; Van Lear and others 1983). In addition, long-term replacement of nitrogen through biological fixation and other inputs has not been adequately examined to assess the potential contributions to the nitrogen balance of intensively-burned sites (Boring and others 1988, Hendricks 1989).

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In this paper, we summarize the state of knowledge concerning key processes regulating N losses, retention, and replacement associated with intense fire in southeastern pine and mixed pine-hardwood forests, as well as in other related ecosystems. We synthesize the research results and perspectives from our work, as well as those from other investigators, and identify key areas for further research.

NITROGEN LOSSES AND RETENTION

There are several mechanisms by which N may be lost during and following intensive burning, including combustion and convection of N gases and particulates, leaching of NO_3^- in the soil solution, denitrification of residual inorganic N, and erosion of organic matter by water and wind (fig. 1). Although each of these mechanisms may play a role in the loss of N reserves, past studies suggest that the combustion losses may exceed the others in importance (Christensen 1987; Raison and others 1985; Van Lear and Waldrop 1989).

Intensive burning results in large losses of N by volatilization and the removal of gases and particulates in wind currents (Jorgensen and Wells 1986). The amount of N lost varies and depends primarily on the fire severity, which in turn is determined by the amount and flammability of organic matter, moisture conditions, and the residence time of the peak thermal pulse. Mass balance estimates based upon loss of woody debris and other forest floor fuels have indicated losses may range as high as 300 kg ha" for severe site-preparation fires in the southeastern Piedmont region (Van Lear and Kapeluck 1989; Wells and others 1979), and up to 1000 kg ha^{-1} for intense fires in western Douglas-fir forests (Binkley 1986; Little and Ohmann 1988).

Although a considerable amount of the lost N may have originated from the smaller-sized fuels of residual logging slash and young colonizing vegetation, the potential losses from the original forest floor and soil organic matter may have the greatest impact upon N balance and long-term site

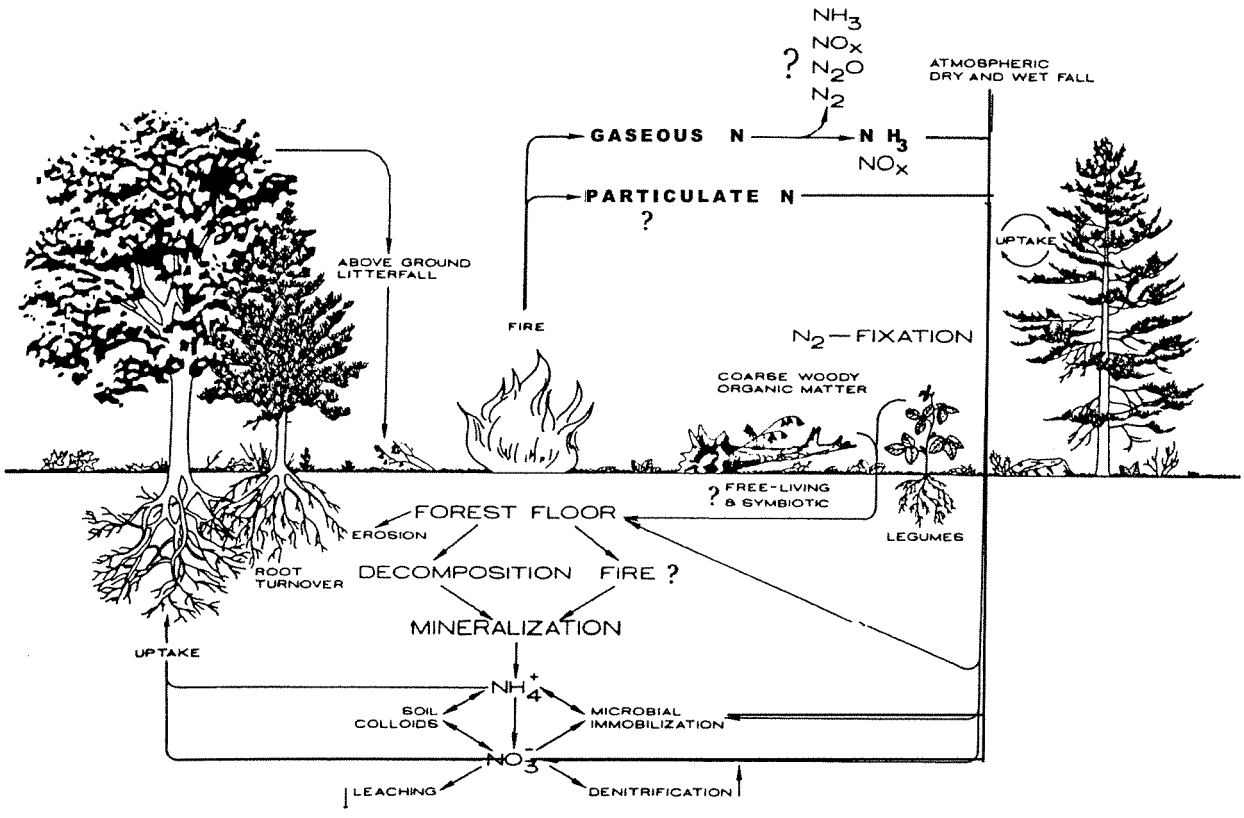

Figure 1. Nitrogen cycling processes and their relationships to losses, retention, and replacement

productivity (Van Lear and Kapeluck 1989). Losses of N from forest floor mass have been estimated to range from 130 to 170 kg ha^{-1} (Van Lear and Kapeluck 1989), depending primarily upon the severity of the burn, with hotter and slower tires causing greater losses (Knight 1966).

Most N loss from fires is associated with gaseous loss rather than particulates (Raison and others 1985). Using controlled ignitions in a muffle furnace, volatile loss of N was shown to begin at approximately 300°C and increase to 60 percent at 700°C. Such controlled experiments formerly assumed that most of the N was lost as N_2, and that it was convected offsite following oxidation (DeBell and Ralston 1970; Knight 1966). However, other workers have shown that ammonia gases may be liberated at temperatures as low as 100°C, and subsequent information has revealed more complex processes regulating these losses (Raison 1979).

Combustion studies with southern pine litter-soil systems have shown a complex scenario of N loss, which includes significant volatilization of NH, and NO, at relatively low temperatures (Lewis 1975). Although we now appreciate the complexity of N volatilization, we still have few detailed case studies that accurately document N losses from southern pine and pine-hardwood forests. We also suggest that there may be retention mechanisms in southern pine forests which have not been examined by early studies (Lewis 1975; Raison 1979).

Some researchers have reported surprisingly variable and low losses of N from burned forest floors of different types, and some of the increases in inorganic N availability have been attributed to rapid increases in nonsymbiotic N fixation or to the occurrence of legumes on the sites (Jorgensen and Hodges 1970, Mroz and others 1980). Although replacement of N from these sources is known to occur, some of these rapid increases in inorganic N availability are not explainable by decomposition and nitrogen fixation since the increases appear immediately (hours to a day) following burning (Raison 1979).

Instead, it is likely that thermal mineralization of organic matter occurs, where inorganic N is released and retained in significant amounts in subsurface layers of the mineral soil. Studies in some soil-plant systems have documented elevated inorganic N immediately following burning as NH_4-N, NO,-N, and possibly as labile organic compounds. This may happen by ammonia hydrolysis and vertical translocation as gases are volatilized by the initial thermal pulse of the tire and are subsequently condensed by cooler temperatures in lower soil mineral horizons (DeBano and others 1976, 1979; Kitur and Frye 1983). Although this process has been examined in North American chaparral and in Australian eucalyptus forests, the mechanism has not been documented in southern pine or pine-hardwood forests.

Biological transformations related to decomposition and nitrification become more important with time after burning, and play dominant roles in the well-documented but short-term (weeks to months after burning) increases of inorganic N availability in southern pine forests (Christensen 1987; Raison 1979; Schoch and Binkley 1986). The magnitude and duration of such effects may be highly specific to individual forest floor types and burn characteristics, especially as related to initial litter quality and N contents. Mroz and others (1980) found widely variable ammonification, nitrification and immobilization responses among different forest floor types, and concluded that it was difficult to make universal generalizations about microbial processes following burning. Although stimulation of nitrification may be a key burning response in southern forest ecosystems, elevation or reduction of microbial immobilization and gaseous N_2O flux also play significant roles in regulating the availability of NO_3-N (Christensen 1987). Nitrification and gaseous nitrogen transformations require further research and it is not clear to what degree N retention after burning may be quantitatively affected by either NO_3-N leaching or gaseous losses. Further, these processes likely interact with the recovery rates of microbial and plant nitrogen uptake which may minimize N losses through biomass immobilization.

NITROGEN REPLACEMENT

Although site-preparation burning may cause large losses of forest floor nitrogen reserves, natural sources of replacement may help maintain or improve the productivity and quality of these forest ecosystems. Two major pathways of nitrogen replacement are atmospheric deposition and biological nitrogen fixation (Boring and others 1988) (fig. 1). Atmospheric deposition includes the input of a variety of nitrogen-containing compounds by both dry and wet modes. Atmospheric N_2 may be biologically fixed (and converted to organic N) by symbiotic and nonsymbiotic organisms. A thorough understanding of the magnitudes of these nitrogen inputs and their impacts on nutrient cycling is incomplete for any single ecosystem. Furthermore, knowledge of these fundamental processes is essential to accurately assess the impact of site-preparation burning on the nitrogen balance and long-term productivity of forest ecosystems.

Atmospheric Deposition

A variety of nitrogen forms may be deposited in terrestrial ecosystems from the atmosphere (Boring and others 1988). Some of these, such as dissolved NH_4^+ and NO_3^-, can be rapidly incorporated into terrestrial nitrogen cycles following wet or dry deposition. Other constituents, such as those in aerosol and gaseous forms, may be transferred directly to vegetation surfaces (Okano and Machida 1989). Many factors that may affect the spatial and temporal patterns of these deposition inputs. One is the proximity to nitrogen sources such as industrial emissions. Also, factors that regulate the transport and transformation of atmospheric nitrogen forms, such as precipitation patterns and meteorological conditions, are important considerations.

Measurements of all of the potential forms of nitrogen deposition are unavailable for any terrestrial ecosystem. However, although conservatively estimated, nitrogen inputs measured in bulk precipitation provide some measure of the relative importance of atmospheric deposition to forests. Estimates of wet deposition inputs to southeastern forest ecosystems may range from 5.1 to 12.4 kg ha^{-1} yr^{-1} (Kelly and Meagher 1986; Richter and others 1983; Riekerk 1983; Swank and Waide 1987; Van Lear and others 1983; Wells and Jorgensen 1975). The upper value of this range was recorded at Walker Branch in eastern Tennessee which is in close proximity to coal-fired power plants (Kelly and Meagher 1986).

Dry deposition may also contribute significant amounts of nitrogen to forest ecosystems. The dryfall contribution to the total NH_4^+ and NO_3^- deposited in open collectors exceeds 20 percent at Coweeta (Swank and Waide 1987) and exceeds 50 percent at the Walker Branch site (Kelly and Meagher 1986). These figures primarily represent large particulate inputs and are not representative of all nitrogen in aerosols and gases which may originate from combustion processes. Combining both wet and dry N inputs, general estimates for southeastern forest ecosystems may range from 6 to 14 kg ha^{-1} yr^{-1} excluding aerosol and gas fractions which may also be high (fig. 2).

Nitrogen Fixation

In southeastern forest ecosystems, detectable nitrogen-fixation activity may occur in the forest floor and surface mineral soil horizons, coarse woody debris (CWD) on the forest floor, and the nodules of symbiotic nitrogen-fixing plants. In general, the fixation rates of symbiotic organisms are greatest during the early successional stages of forest development (Boring and Swank 1984; Boring and others 1988). The harvesting of merchantable timber, followed by the felling of residual stems and intense site-preparation burning creates an early successional environment and may therefore promote detectable, if not significant, nitrogen-fixation activity among a variety of organisms.

Forest Floor and Soil

Clearcutting may increase nonsymbiotic nitrogen-fixation in the forest floor (excluding CWD) and soil through the transfer of large carbon pools in the form of dead roots and small fractions of logging debris (Boring and others 1988). At the Coweeta Hydrologic Laboratory, maximum fixation rates of 4-6 kg ha^{-1} yr^{-1} were measured three to five years following clearcutting (Waide and others 1987). These high rates are likely to be short-lived, however, due to the sensitivity of nitrogen-fixing bacterial populations to substrate quality, moisture, temperature, and pH (Jorgensen and Wells 1986;

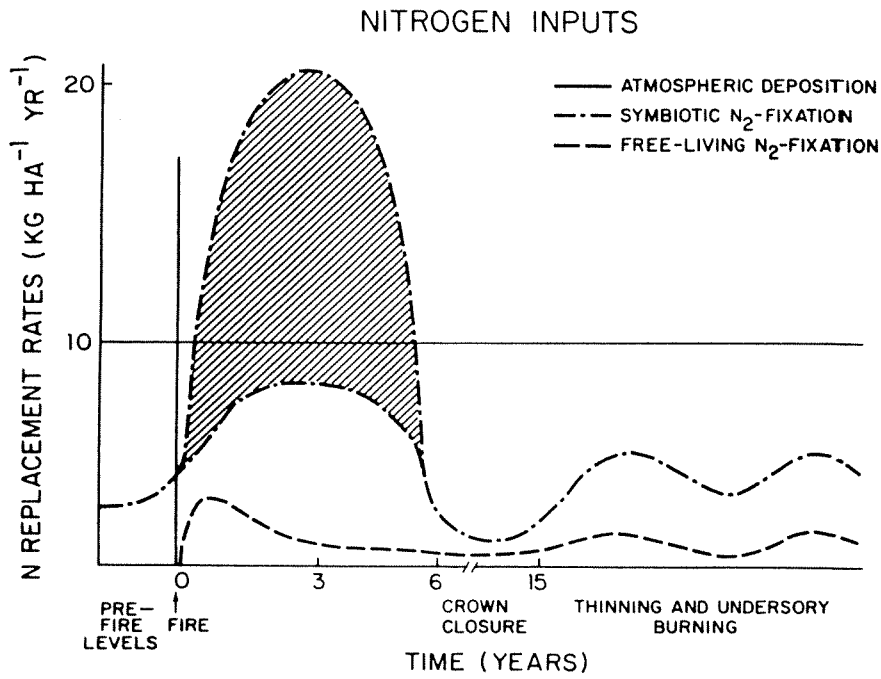

Figure 2. Range of temporal dynamics of nitrogen replacement in relation to forest succession; based upon studies of sites with at least moderate N-fixing plant populations.

Vance and others 1983). Most estimates of nonsymbiotic fixation in southeastern temperate coniferous and deciduous forest are much smaller and range from 0.1 to 3.7 kg ha^{-1} yr^{-1} (Di Stefano and Gholz 1989; Gholz and others 1985; Grant and Binkley 1987; Jorgensen and Wells 1986; Van Lear and others 1983).

There appears to be a paucity of information concerning the effect of intense site-preparation burning on nonsymbiotic forest floor and soil nitrogen fixation. However, research on the effects of less intense understory burning on this form of fixation have been contradictory. Maggs and Hewett (1986) reported a three-fold increase in nitrogen-fixation activity following understory burning, whereas Vance and others (1983) and DiStefano and Gholz (1989) reported little or no response to burning. Even given these conflicting results, it is generally assumed that such low nonsymbiotic fixation activity in the forest floor and soil will not make a significant contribution to the replacement of nitrogen following intense site-preparation burning.

Coarse Woody Debris

Silvicultural clearcutting of southeastern forests may deposit from 15 to 50 tons ha^{-1} of non-harvestable coarse woody debris (CWD) to a site (Sanders and Van Lear 1988). The majority of this CWD remains on the site following burning since even the most intense fires generally consume stems only up to 10 centimeters in diameter. This CWD may play a significant nitrogen replacement role by serving as a carbon substrate for a highly diverse group of nonsymbiotic nitrogen-fixing organisms, as well as for wood-eating insects that form symbiotic relationships with nitrogen-fixing gut bacteria (Dawson 1983; Roskoski 1980; Silvester and others 1982).

Research conducted in old-growth Douglas-fir stands of the Pacific Northwest has revealed that nonsymbiotic fixation rates in large masses of well-decomposed wood by such organisms as bacteria, fungi, blue-green algae, and lichens may reach 1.4 kg ha^{-1} yr^{-1} (Silvester and others 1982). In a northern hardwood forest at the Hubbard Brook Experimental Forest, comparable annual nitrogen fixation rates in decaying wood ranged from 0 to 2 kg ha^{-1} yr^{-1}, with the rates being directly correlated to the standing crop of decaying wood (Roskoski 1980, 1981). Although the nitrogen replacement role of CWD in southeastern forest ecosystems is less well understood, Todd and others (1975, 1978) reported values of 1.22 to 1.66 kg ha^{-1} yr^{-1} for an oak hickory forest at Coweeta and DiStefano and Gholz (1989) measured high specific rates in low masses of decomposing wood of slash pine plantations in North Florida.

It is important to note that these area estimates of non-symbiotic nitrogen fixation are a function of CWD biomass as well as actual rates of fixation activity. Also, Silvester and others (1982) suggested that fixation rates generally increase as the CWD, which may remain on the site for several years, becomes more highly decomposed. Therefore, nonsymbiotic fixers (even with low specific activity) in the abundant CWD of southeastern clearcut sites may potentially contribute significant amounts of nitrogen during the decomposition process of the debris.

As stated earlier, CWD serves as a substrate for wood-eating fauna such as termites, bark beetles, and cockroaches, which may contain nitrogen-fixing bacteria in their gut (Dawson 1983; French and others 1976; Potrikus and Breznak 1977). Among these organisms, the process of nitrogen fixation has been best established for temperate and tropical termites

(Bentley 1984; Prestwich and others 1980). Due to numerous difficulties preventing accurate measurements, nitrogen fixation values for termites have not been related to nitrogen-balance estimates, although their contribution could be significant on some forest sites.

Higher Plants

Symbiotic nitrogen-fixing plants commonly occur on sites where nitrogen is limiting, early successional areas, or sites subject to substantial N loss, such as from intense and/or frequent fires (Boring and others 1988). In southeastern forest ecosystems, fire-adapted native herbaceous legumes generally thrive during the first few years following clearcutting and intense site-preparation burning (Cushwa and others 1969; Czuhai and Cushwa 1968).

Legume populations are typically largest during early stages of stand development for a number of reasons. The seed of several legumes have their highest germination rates following scarification with moist heat at temperatures approaching 80° C (Cushwa and others 1968, 1970). Also, it is believed that these seeds remain viable in the litter layer and soil for prolonged periods of time. Finally, these fire-adapted, early successional species thrive under the high light environment of pine stands prior to crown closure (Brunswig and Johnson 1972; Cushwa and others 1971).

Nitrogen fixation rates of these herbaceous legumes are predicted to be highest during this early stage of stand development (fig. 2). The absence of a developed overstory and the reduced competition from non-fire adapted species should result in larger quantities of photosynthate available for the energetically expensive nitrogen fixation process. Hendricks (1989) assessed the nitrogen fixation activity of three dominant legume species (Desmodium viridiflorum, Lespedeza hirta, and L. procumbens) in a cleared and burned area of a Georgia Piedmont pine forest. In the early to middle part of the growing season, D. viridiflorum and L. procumbens exhibited specific acetylene reduction activity per nodule biomass comparable to those of black locust, Robinia pseudoacacia (Boring and Swank 1984), and greater than those of many actinorhizal nitrogen-fixing species, although total nodule biomass was considerably lower (Binkley 1981; McNabb and Geist 1979; Tripp and others 1979). This nodule activity, however, declined substantially during the remainder of the hot and dry growing season, and the third species L. hirta was rarely observed to nodulate.

The total amount of nitrogen fixed by herbaceous legumes on these Georgia Piedmont sites was roughly estimated to range from <0.5 kg N ha^{-1} yr^{-1} for areas with small legume populations (500 - 700 individuals ha^{-1}) to 7 - 9 kg N ha^{-1} yr^{-1} for areas with relatively large populations (20,000 - 30,000 individuals ha^{-1}; Hendricks 1989). These values represent broad ranges of estimates and illustrate the potential importance that factors controlling the spatial and temporal variation of legume populations may have on forest floor and soil nitrogen reserves. Sites with larger legume populations than ours may have substantially more nitrogen fixation.

The spatial variation of herbaceous legumes depends upon many factors including the fire-history of the site. Table 1 gives the results of a legume population survey for two similar Georgia Piedmont sites that were cleared and burned following southern pine beetle infestation. These sites, which were sampled two years following the intensive burn, differed primarily in their fire history as one had no previous burning and the other had received periodic winter understory burns since 1962. The site that had been managed under a burning regime had a substantially higher diversity and density of

Table 1. Density (#/ha) of native and naturalized herbaceous legume species on cleared and burned sites in the Georgia Piedmont. Site 1 had no previous burning history, whereas site 2 has been managed under a 4 year burning regime since 1962

SPECIES	DENSITY (#/ha) SITE 1	SITE 2
Cassia nictitans	12	3,429
Centrosema virginianum	12	381
Crotalaria sagittalis	-	143
Desmodium		
ciliare	-	238
laevigatum	32	1,048
marilandicum	74	2,333
nuttallii	-	1,238
rotundifolium	-	381
tenuifolium	-	333
viridiflorum	28	3,952
Other spp.	3	334
Lespedeza		
bicolor*	-	619
cuneata*	42	667
hirta	-	3,333
nuttallii	-	1,048
procumbens	380	6,905
virginica	6	2,333
Other spp.	-	476
Tephrosia spicata	-	667
TOTAL	731	29,858

legumes due primarily to increases in species of Desmodium and Lespedeza (table 1). Although these data only represent two sites, other reports also underscore the importance of regular burning to generate a cycle of high seed germination and plant establishment rates (Cushwa and others 1966, 1969, 1970; Czuhai and Cushwa 1968; Devet and Hopkins 1967; Speake 1966).

Brunswig and Johnson (1972) studied the temporal variation of legume populations in southeastern pine plantations during the first seven years following intense site-preparation. The results indicated that annuals, primarily C. nictitans, were the predominant legumes in one-year old plantations. By the third year, perennial legumes (primarily species of Desmodium and Lespedeza) were more abundant than annuals. In older stands, the annuals were essentially eliminated and the perennials decreased substantially due to crown closure. However, in latter stages of stand development when light gaps appear and understory burning is commonly initiated, legumes may still influence nitrogen availability via the temporal dispersal of a viable seed bank.

Approximately 300 native legumes occur in the southeastern United States (Wilbur 1963). A majority of these are herbaceous legumes that are tolerant of acidic soils, shading, and litter accumulation on the forest floor, and commonly occur in pine and mixed pine-hardwood forest ecosystems. Although the value of these legumes to wildlife has long been recognized, their nitrogen accretion role as well as their contribution to functional biodiversity are just beginning to be recognized in southeastern forest ecosystems.

SUMMARY AND RESEARCH NEEDS

Our present knowledge of the impacts of intensive fire upon ecosystem nitrogen cycling processes and long-term productivity in southern forests is incomplete, and many key questions require additional research. We generally know that large amounts of forest floor nitrogen are lost with severe burns, and that long-term replacement sources may be potentially significant but variable. However, in the past we may have overestimated N volatilization on some sites by not examining potential retention processes in humus and mineral soil horizons below the litter. Simultaneously we have not examined the potential for additional and smaller short-term gaseous losses via N_2O flux from residual inorganic N following burning, or examined the interactions of immobilization by microbial or plant biomass with nitrification and gaseous N flux (Matson and Vitousek 1987).

Our interpretation of intensive fire effects upon long-term N balance is uncertain until we better understand how adequately nitrogen fixation processes replace N losses over time and space. We need to better understand how to more effectively manage nitrogen fixation inputs. More effective management may require retention of coarse woody debris, increased populations of nitrogen-fixing plants, and modification of environmental factors that control their fixation rates (e.g. P fertilization). A more complete understanding of these processes and their potential management need to be integrated into a whole-ecosystem perspective, possibly with the use of simulation models, to better interpret their impacts upon long-term N balance and forest productivity over several stand rotations.

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FIRE EFFECTS ON NUTRIENT POOLS OF WOODLAND FLOOR MATERIALS AND SOILS IN A PINYON-JUNIPER ECOSYSTEM

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Abstract—The total pools of carbon and nitrogen in the litter, duff, and soil compartments were quantified in a mature pinyon-juniper woodland. One hectare of the woodland was burned in a fire similar to a severe wildfire, where almost all aboveground vegetation was killed. Soil temperatures reached as high as 325° C at 5 cm below the soil surface. The total nutrient pools were again quantified after fire indicating significant losses of both C and N from forest floor material. The litter loss of C was as high as 92 percent and N loss was as high as 88 percent. Loss of C from the duff layer was estimated from 78-80 percent, while nitrogen loss was 75 percent. Soil N displayed a slight, significant increase under canopy, but not in the interspaces. The greatest initial effect was the reduction of the C/N ratios favoring mineralization. The total amount of C and N lost from the woodland was 12.6 Mg ha^{-1} C and 167 kg ha^{-1} N.

INTRODUCTION

Pinyon-juniper woodlands occupy a significant expanse of the semiarid United States (Klopatek and others 1979). They are characterized by extreme variability in climate, soil, and topography that produces units of canopy-covered and non-canopy covered (interspace) patches. Therefore, a seemingly uniform disturbance, such as fire, to this patchy mosaic ecosystem type may result in complex, non-uniform responses. Despite the expansiveness of the pinyon-juniper woodlands and their susceptibility to fire, studies of fire effects in pinyon-juniper woodlands have only been recent and limited (DeBano and others 1987; DeBano and Klopatek 1988; Gifford 1981; Klopatek and others 1988).

Studies on the effects of fire upon soil nutrients, and specifically soil N, have produced conflicting results. Some investigators have reported no significant changes in total soil N contents (Covington and Sackett 1986; Jurgensen and others 1981; Kovacic and others 1986; White 1986). Waldrop and others (1987) found no changes in either soil organic matter or total N after 30 years of various prescribed burning treatments in loblolly pine.

Stock and Lewis (1986) reported significant increases in N that were due to leaching of ash material in fynbos (chaparral) ecosystems, whereas DeBano and others (1979) reported a significant loss of total N from laboratory burnings of chaparral soils. Fuller and others (1955) described that loss of soil N was proportional to the fire intensity in ponderosa pine forests with a concomitant decrease in C/N ratios. Grier (1975) noted significant nutrient losses from an intense fire on the eastern slope of the Cascade Mountains of Washington and estimated a loss of 855 kg ha^{-1} of N. Covington and Sackett (1986) found a 37% reduction in forest floor material following a low-intensity prescribed fire in ponderosa pine forest with an additional 20% reduction 7 months after burning, but no significant soil N loss.

In a comprehensive study of the effects of prescribed burning, Wells (1971) noted that while periodic burns had caused significant losses of forest floor material immediately after the burn, there seemed to be a tendency for the system to regain its organic matter (both C and N) over time and approach the control condition. Additionally, he found a small increase in available P, but the increase may be short lived in calcareous soils (DeBano and Klopatek 1988).

Christensen (1973) found greater NH_4 availability and nitrification rates following burning in chaparral, and Jurgensen and others (1981) found that broadcast burning caused a minor net loss of N (approximately 100 kg ha^{-1}), but resulted in greatly enhanced soil N, nitrification, and base cation availability from a clearcut site in Montana. They concluded that no significant long-term losses of N occurred. Schoch and Binkley (1986) found that prescribed burning increased decomposition rates and N availability (as indexed by incubation) in loblolly pine stands in North Carolina. Similar results of increased levels of NH_4 and NO_3 have been reported in ponderosa pine (Covington and Sackett 1986; Kovacic and others 1986; White 1986) and Douglas-fir ecosystems (Jurgensen and others 1981). Increases in NH_4 are presumably the result of physicochemical reactions caused by the elevated temperature (Kovacic and others 1986). Subsequent, post-fire increases in NO_3 are attributed to increased nitrification rates, that are possibly enhanced by the reduction of allelochemical compounds (White 1986).

In summary, the results of fire on C and N losses from shrubland and coniferous forest ecosystems are mixed, but appear related to fire intensity. With this as a background, we attempted to document changes in the total pools of C and N in a pinyon-juniper woodland resulting from fire. The objective of the study was to determine if the patchy nature of

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this ecosystem was reflected in the fire effects on its nutrient pools. Initially, we conducted our experiment using microcosms and determined that there might be a substantial loss of nutrients from the ecosystem (Klopatek and others 1990). Here, we report on the effects of the subsequent field study. While a complete inventory of the pools of both C and N was undertaken in this ecosystem, only the effects of fire on the forest floor and soil components are reported on in this paper.

METHODS

In September, 1989 a burn was conducted of a 1-ha section of mature pinyon-juniper woodland in the Kaibab National Forest in northcentral Arizona. The meteorological conditions at the beginning of the burn were: a wind speed of 6.0 m sec^{-1}, temperature of 27° C, and a relative humidity of 18 percent. Moisture content of the large downed fuel and litter was 9 and 6 percent, respectively. Fire temperatures were monitored at the litter surface and the 0, 2, 5, and 10 cm depth of soil by a series of chromel-alumel thermocouples connected to a data logger. Burning was conducted by U.S. Forest Service personnel from the Tusayan Ranger District and Grand Canyon National Park staff. The burn and a nearby control site were fenced with barbed wire to prevent disturbance from local livestock. Prior to the burn, an inventory was conducted of the biomass of all trees, shrubs and herbaceous species on the site using previously developed allometric relationships. The site contained 340 pinyons and 167 juniper ha^{-1} (all of which were marked with permanent brass id tags) with a tree cover of 4286 m^2 ha^{-1}. Aboveground tree biomass totaled 135.2 mt ha^{-1}. Tree-ring analysis revealed that many of the trees were > 350 years old without any fire scars and, combined with replacement patterns, indicated a substantial time since intense burning. Soils were primarily sandy loams with Ph values ranging from 7.3 to 8.1. The site was part of the Dillman mature site described elsewhere in this volume (C.C. Klopatek and others 1990).

The site was divided into four relatively equal-sized quadrants. Samples were taken of litter and duff accumulations from under the mid-canopy of four randomly selected trees of each species in each quadrant using 25 cm x 25 cm quadrats. Five quadrats were sampled for litter in the interspaces of each quadrant. There was no duff in the interspaces. These measurements were combined with identical measurements taken from the nearby control site to yield a statistical population (n = 32) used to calculate regression coefficients of total C and N relative to the cross-sectional area of the bole and canopy cover.

Subsamples of litter and duff were taken back to the laboratory for analysis of organic C and total N. Additionally, soil samples were taken from the 0-10 and 10-20 cm depth along with the litter and duff samples, yielding 16 soil samples from each depth and in each cover type. Sampling was repeated from 24 to 48 hrs post-burn when the canopy sites had cooled down. Although a qualitative separation of litter and duff ash were possible for estimation of loss by ignition, samples were combined for nutrient analysis.

Litter, duff, and ash samples were analyzed for C content by ashing in a muffle furnace at 550° C for 8 hrs with the oxidized portion multiplied by 0.58 to yield organic C; soil organic C was analyzed by the Walkley-Black Method (Page and others 1982). All material was analyzed for N by digesting the material following methods of Raveh and Avnimelech (1979) and measuring the digest with a Wescan ammonia analyzer. Statistical analyses were conducted using simple linear regressions for calculating duff and litter biomass per tree and AOV procedures for measurements of before and after burning differences (SAS 1985).

RESULTS

To understand the effects of fire on the nutrient pools in the landscape it was necessary to quantify the partitioning of nutrients relative to the patch mosaic of the woodland. We multiplied the total amount of pre-burn C and N in the litter, duff and soil (0 - 20 cm depth) per unit area by the area occupied by each cover type to obtain the total woodland floor and soil nutrient pools. Figures 1a,b show that, despite the fact that the interspace and its associated vegetation covered 57.1 percent of the area compared to 42.9 percent by the trees (28.4 pinyon, 14.5 juniper), the trees partitioned the majority of the resources under their canopies, accumulating nearly 68 percent of the total C and 70 percent of the total N.

There existed significant differences between the pre-burn organic C concentrations of litter, duff, and soil material of all three cover types (table 1). Total N concentrations of pinyon, juniper, and interspace litter were not different. The C:N ratios of pinyon and juniper litter (83 and 77, respectively) were similar but differed with that of the interspace litter (120). Higher C:N ratios for the interspace litter compared to under the canopies is typical of mature pinyon-juniper ecosystems in Arizona and may represent greater competition for available N in the interspaces (Klopatek 1987). Total N of litter and duff were not statistically different under pinyon but were under juniper; both differed from their respective underlying soil.

Peak fire temperatures experienced under the canopy were as high as 374, 305 and 260° C at the 2, 5, and 10 cm soil depths and 68° C at the 2 cm depth of the interspaces. The effect of fire was most noticeable on the litter and duff pools of the tree patches. Figures 2 and 3 represent the amount of C and N per unit area by cover type. Organic C was reduced an average of 92 and 80 percent in pinyon litter and duff, and 91 and 78 percent of the juniper litter and duff, respectively (fig. 2a,b). The resulting post-fire concentrations of organic C did not differ between types (table 1).

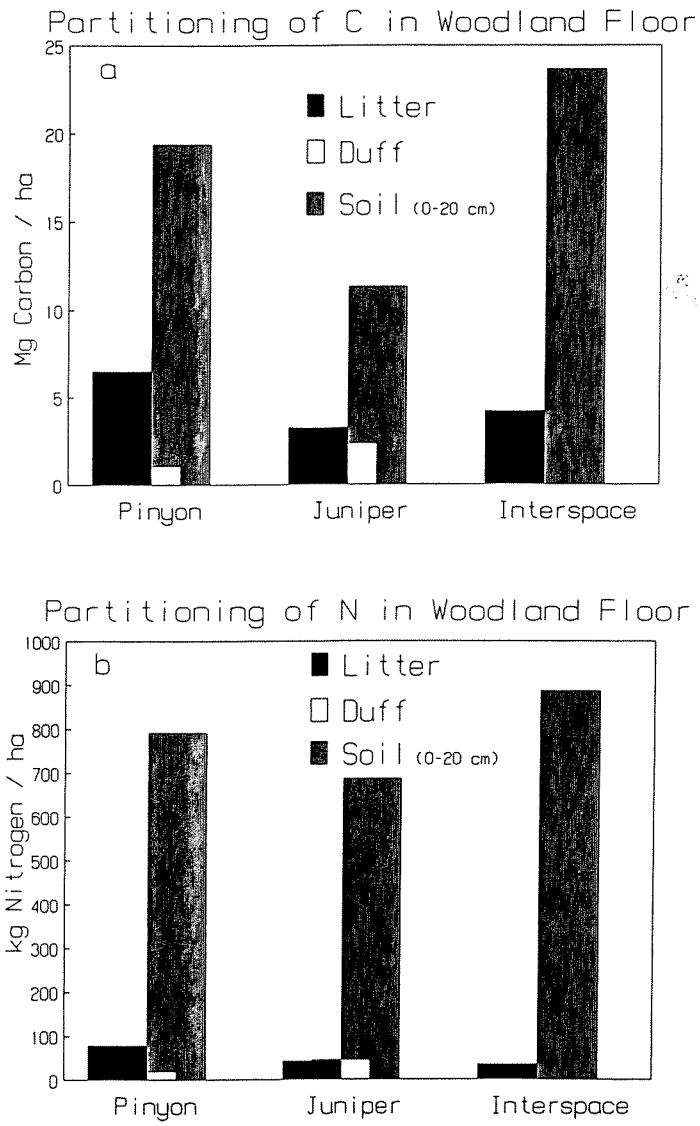

Figure 1.--Total organic carbon (a) and nitrogen (b) in a pinyon-juniper woodland floor located in northern Arizona.

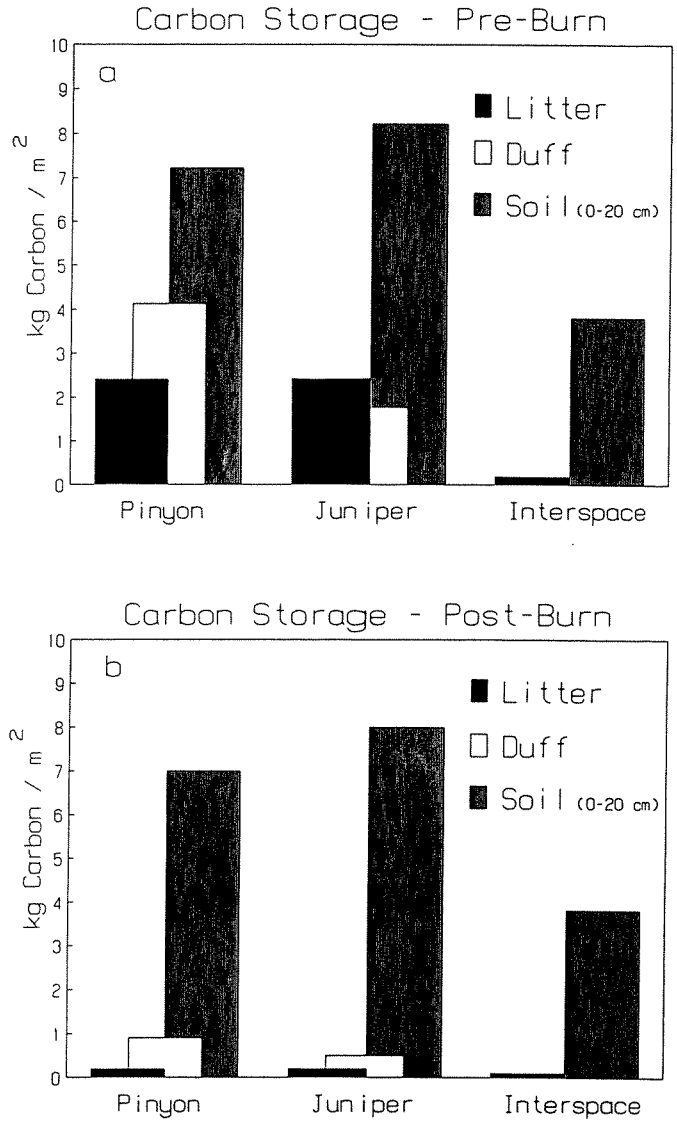

Figure 2.--Carbon storage pre- (a) and post- (b) burn in the woodland floor of a pinyon-juniper ecosystem in northern Arizona.

Nitrogen exhibited similar results (fig. 3a,b), but the relative concentration of total N did not decrease as much as C (table 1). If corrections are made for weight loss due to combustion, loss of N from the pinyon litter and duff compartments was 87 and 75 percent, and 88 and 75 percent of the juniper litter and duff, respectively. The loss of C and N closely parallel the results reported by Raison and others (1985). An important result of the fire is the change in the C:N ratios of the ash as compared to the litter and duff (table 1), being significantly reduced for both pinyon and juniper.

The effect of burning on total N and organic C were less pronounced in the underlying soil compared to the overlaying duff and litter. Both pinyon and juniper soils at the 0-10 cm depth displayed significant increases in concentrations of total N (table 1) although no significant differences in organic C. Decreases in the soils at the 10-20 cm depth were not significant. The interspace soils followed a similar pattern, but differences were not significant. Increases in both C and N in underlying soils are consistent with reports that organic materials are translocated downward in the soil during burning and are wicked up from lower depths (DeBano and others 1976). Soil C:N ratios exhibited no significance before and after differences.

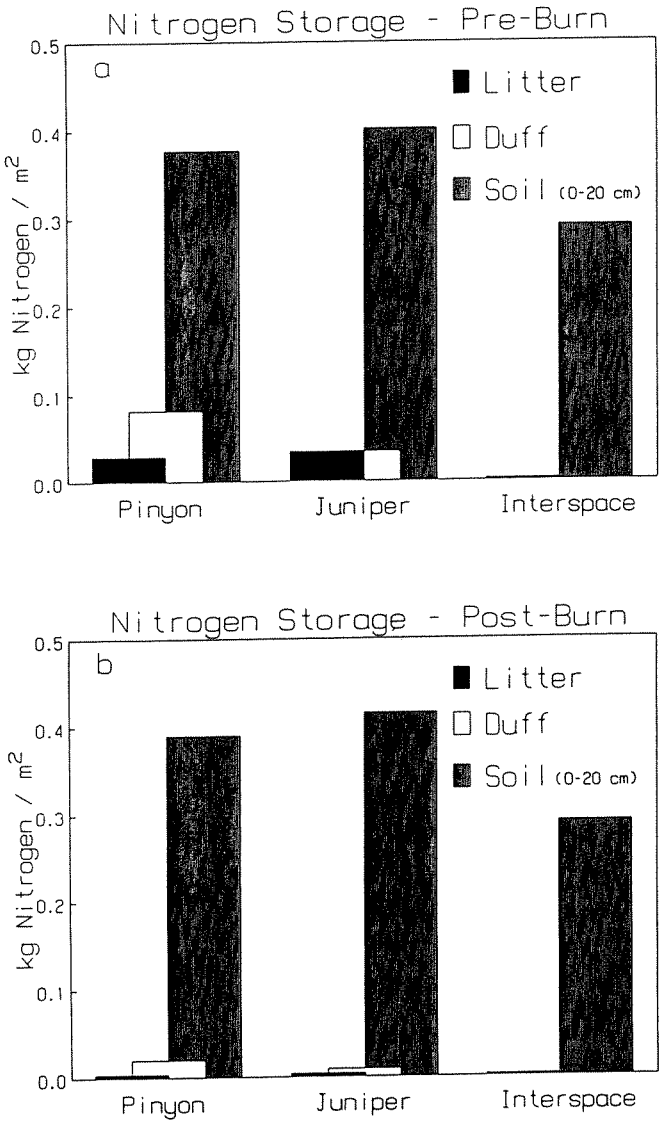

Figure 3.--Nitrogen storage pre- (a) and post- (b) burn in the woodland floor of a pinyon-juniper ecosystem in northern Arizona.

DISCUSSION

The effect of burning a pinyon-juniper woodland had surprisingly similar results to our microcosm experiment in which simulated burns conducted over both pinyon and juniper soils led to a large loss of C and N [as well as 50 percent of the P] (DeBano and Klopatek 1988; Klopatek and others 1990). Loss of N agreed with that reported by Raison and others (1985) in that nitrogenous compounds are usually lost proportionally to the amount of C oxidized.

The effect of burning on soil N has presented an interesting paradox that has been vigorously debated in the literature for years (e.g., Knight 1966; McKee 1982). As stated previously, some authors have reported insignificant total N increases, while others reported significant increases in soil N that were caused by the leaching of the above ash material. We found significant losses of N from the woodland floor. When the loss of C and N are applied to the spatial distribution of pinyon-juniper-interspace mosaic, the losses total nearly 12.6 Mg ha^{-1} of C and 167 kg ha^{-1} N. Although large amounts of C and N were lost from the litter and duff in this study, the changes in total N of the combined soil depths were minimal. However, the soils at the surrounding field sites that had been previously (10-90 years) burned all had significantly less soil N than the unburned (Klopatek 1987). Our findings do not indicate why the loss of N occurs, although we hypothesize it may be due to the loss of C. This is a result of a combination of reduced C/N ratios of the ash (compared to the litter and duff) and the increase in decomposable substrates in dead root material. It should be mentioned that our reported organic C concentrations include the reduced charcoal that probably is not available for microbial utilization. The newly available root material will lead to a initial immobilization of soil N, but a release after decomposition has occurred. Our preliminary findings indicate an increase in CO_2 release from the forest floor of the burn site when compared to the nearby control site, indicating increased decomposition similar to that reported by Shoch and Binkley (1986).

Pinyon-juniper woodlands in Arizona are often situated between fire adapted ecosystems: chaparral and grasslands on the xeric end and ponderosa pine on the more mesic end. Clearly, pinyon-juniper is not a fire adapted system as many of its trees have low-lying branches that act as ladder fuels resulting in the trees "torching" or crown fires. This torching adds considerable heat to the system, effectively consumes all litter and duff, and may sterilize the upper soil layers. The result is an initial greater loss of nutrients and provides a positive feedback mechanism to accelerate subsequent losses.

Table 1.--Organic carbon, total nitrogen and carbon:nitrogen ratios of pinyon, juniper, and interspace litter and duff material before and after burning

	Carbon g kg^{-1}		Nitrogen g kg^{-1}		C/N	
	Pre-burn	Post-burn	Pre-burn	Post-burn	Pre-burn	Post-burn
Pinyon						
Litter (ash)	432a,w	41b,x*	5.2a,x	2.1b,x*	83.1a,x	19.5b,x
Duff (ash)	231a,x	41b,x	4.6a,x	2.1b,x	50.2a,y	19.5b,x
Soil 0-10 cm	40a,y	43a,x	1.9b,y	2.1a,x	21.1a,z	20.5a,x
10-20 cm	27a,z	28a,y	1.6a,y	1.5a,y	16.9a,z	18,7a,x
Juniper						
Litter (ash)	352a,x	47b,x	4.6a,x	1.8b,x	76.5a,y	26.lb,y
Duff (ash)	169a,y	47b,x	3.2a,x	1.8b,x	52.8a,y	26.lb,y
Soil 0-10 cm	39a,z	40a,x	1.8b,y	2.3a,x	21.7a,z	17.4a,y
10-20 cm	33a,z	31a,y	1.7a,y	1.5a,x	19.4a,z	20.7a,y
Interspace						
Litter (ash)	445a,x	34b,x	3.7a,x	0.9b,x	120.2a,x	37.2b,x
Soil 0-10 cm	13a,y	14a,y	1.0a,y	1.0a,x	13,4a,y	14.1a,y
10-20 cm	16a,y	16a,y	1.3a,y	1.3a,x	12.3a,y	13.3a,y

*Post-burn litter and duff ash values represent composites due to the difficulty in separating ash material for chemical analysis.

Common letters (a,b) following values indicate no significant differences ($p < 0.05$) between pre- and post-burn for the same element, while common letters (x,y,z) indicate no significant differences within columns for the same cover type.

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EFFECTS OF FELL-AND-BURN SITE PREPARATION ON WILDLIFE HABITAT AND SMALL MAMMALS IN THE UPPER SOUTHEASTERN PIEDMONT

Timothy L. Evans, David C. Guynn, Jr.[1], and Thomas A. Waldrop[2]

Abstract—The fell-and-burn site preparation technique is an effective means of regenerating low-quality hardwood stands in the Southern Appalachian Mountains to more productive pine-hardwood mixtures. This technique offers a number of advantages over conversion to pine monoculture. These include: lower cost, increased vegetation diversity within the stand, improved aesthetics, and continued mast production. However, the technique has not been fully tested in the Piedmont and other regions. This study reports the early successional effects of several variations of the fell-and-burn technique on small mammal communities and wildlife habitat in the Upper Southeastern Piedmont. Burning was increased forage production and species richness of vegetation. Winter felling of residual stems was more effective than spring felling in stimulating forage production and increasing species richness of vegetation.

INTRODUCTION

The fell-and-burn site preparation technique has proven successful as an inexpensive means to regenerate low-quality stands to more productive pine-hardwood mixtures in the Southern Appalachian Mountains (Phillips and Abercrombie 1987). Complete descriptions of the technique are given by Abercrombie and Sims (1986), Phillips and Abercrombie (1987), and Van Lear and Waldrop (1988). Briefly, the technique involves a commercial clearcut followed by a spring felling of residual stems (> 2 m in height) and a summer broadcast burn, after which pines are planted on a 3 m by 3 m (10 by 10 feet) or wider spacing. It is anticipated that the technique will produce results in the Upper Southeastern Piedmont similar to those observed in the mountains. However, differences in climate, soils, topography, and rainfall may make refinements to the technique necessary (Waldrop and others 1989). This method could become an attractive alternative to pine monoculture management for nonindustrial private forest landowners, who control approximately 80 percent of the commercial forested land in the Piedmont.

Benefits to wildlife have not been documented. However, it has been supposed that use of fell-and-burn methods would benefit certain game species, but their has been little consideration of effects on small mammals, insects, and herpetofauna in treated stands. For these reasons it is important to determine the effects of the technique on all components of the natural community before promoting its use in the Piedmont.

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METHODS

Study Area

Study areas were located in the Upper Piedmont Plateau region of western South Carolina, on the Clemson University Experimental Forest in Pickens and Oconee Counties. Soils were sandy loams of the Cecil and Pacolet series. Annual temperature and precipitation average 15.5° C and 148 cm, respectively. During 1989, mean annual temperature was 0.8° C below normal, and mean annual precipitation was 23 cm above normal (NOAA 1989).

Prior to harvest, stand ages ranged from 45 to 55 years. Site indexes for shortleaf pine (Pinus echinata Mill.) at base age 50 years averaged 18 m (range 15 to 20 m). Stands consisted primarily of low-quality hardwoods dominated by upland oaks (Quercus spp.) and small numbers of shortleaf pine, loblolly pine (P. taeda L.), and Virginia pine (P. virginia Mill.). Basal area averaged 8.6 m^2/ha. Aspects ranged from 180 to 230 degrees, and slope averaged 13.5 percent (range 10.0 to 20.0 percent).

Treatments

Each of three replications was divided into five 0.8 ha treatment areas. Each treatment area contained 5 to 7 sample plots, 0.1 ha in size. Treatments included clearcutting followed by winter-felling with and without summer burning; spring-felling with and without summer burning; and an unharvested control.

Habitat Analysis

Procedures for habitat analysis were modified from United States Fish and Wildlife Service Habitat Suitability Index (HSI) models (Mengak 1987, Mengak and others 1989, and Sanders 1985). Prior to the harvest, 10 to 20 0.04 ha vegetation plots were established along a transect within each treatment area. Plots were spaced at varying distances along the transect to best utilize the available area, avoid overlap, and maintain a southerly aspect. Permanent small-mammal

trapping stations were also established at each plot center. Sampling was conducted during three sampling periods in 1989. Periods were chosen to evaluate the habitat at the lowest level of vegetation production (Jan. 1 to Mar. 31), the peak of production (May 1 to July 31), and the end of the growing season (Sept. 1 to Nov. 31). Ground cover estimates (by species) were obtained using a 35 mm ocular tube (James and Shugart 1970). Estimates were made at 1-m intervals along two 10-m transects within each sample plot. Transects were centered on the trap station.

Aboveground forage biomass was determined by clipping the current year's growth of all plants in a 1 m by 1 m plot randomly located within each 0.04-ha plot to a height of 1.5 m; forage was weighed in the field. Clipped material was separated into three categories: woody, forbs, and grasses. Moisture content of forage biomass was determined in the laboratory after drying in a forced-air oven at 60 degrees C° for 72 hours.

Trapping

Trapping took place during the three periods when vegetation was sampled. Traplines were prebaited with peanut butter for 5 nights with the traps closed and then sampling was conducted for 5 consecutive nights during each trapping period. Four trap types were used in each treatment area: Victor rat traps, Victor mouse traps, Museum special traps, and pitfalls with drift fences. All traps were rebaited each day during the prebaiting and trapping periods. Trapping design was identical for all periods.

One snap trap of each type was placed within 2 m of each randomly located trap station. Trapping stations were marked with 1-m sections of rebar in order to establish permanent trap locations. Pitfalls were randomly located on each site by overlaying a grid on the site map and using a random number table to determine their coordinates. A modification of the trap design described by Williams and Braun (1983) was used. Each drift fence consisted of three 5 m by 51 cm legs of aluminum flashing that met at a common point centered on the pitfall, with 120 degrees between each pair of legs. Flashing was set in a ditch 8 to 10 cm deep. These ditches were then packed with soil and the fences supported with wooden stakes. At the center of the fences, a 19-1 plastic bucket was buried flush with the ground. Buckets were kept one-third to one-half full of water to drown captured animals, and were covered with a lid when not in use. All traps were checked daily during trapping periods.

Vegetation and trapping data were used to calculate Shannon diversity (H′), evenness (J), and species richness (S) for each trapping period. Shannon diversity was calculated as $H' = -\Sigma P_i (\ln P_i)$ where (P_i) is the proportion of the ith species in the population (Shannon and Weaver 1949). This function measures the uncertainty in predicting the identity of any randomly selected individual based on the total number of species in the sample (S) and the number of individuals (N), or the proportion of that species to the whole sample (P_i) for each species represented in the sample. (J) is a measure of the evenness of the distribution of individuals within the species present, and is calculated as $J = H'/(\ln S)$ (Pielou, 1977).

Insects were collected in ten randomly located 600-ml pitfalls on each site. Traps were used for biomass collection, since terrestrial insects are more susceptible to capture in pitfalls, their numbers would be overestimated if individuals were singled out for identification (Southwood 1978). Traps were kept one-third to one-half full of equal parts of water and ethylene glycol, to keep the insects flexible. Traps were emptied daily during the 5-day period when small mammal trapping took place. All insects were identified to family and weighed for biomass.

All habitat and trapping data were summarized for each site and treatment type. Analysis of variance was used to test for differences between treatments, blocks, and collection periods. Differences were tested for significance at the 0.05 level.

RESULTS AND DISCUSSION

Vegetation

Biomass. Total forage biomass was greatest on winter-felled sites and on burned sites (Fig. 1). All treatments that included felling produced more forage biomass than the unharvested control plots. Total woody biomass, which was highly variable, did not differ significantly among treatments. Woody biomass production varied within the treatments depending on the species of woody vegetation present on the site. This variation within treatments masked any between-treatment differences that might have been developing. Forb production was greatest on burned sites, particularly with winter felling. This forb response resulted from removal of the litter layer which improved seed germination conditions. Grass production was significantly higher on the winter-felled no-burn sites than all other treatments as a result of sprouting from pre-existing rootstocks beneath the little layer. The controls had significantly lower grass production than all other treatments as a result of the heavy litter layer and almost complete shading of the forest floor. Increases in grass and forb coverage at the expense of woody vegetation are common after burning and have been documented by (Langdon 1981, Waldrop and others 1987, Van Lear and Waldrop 1989).

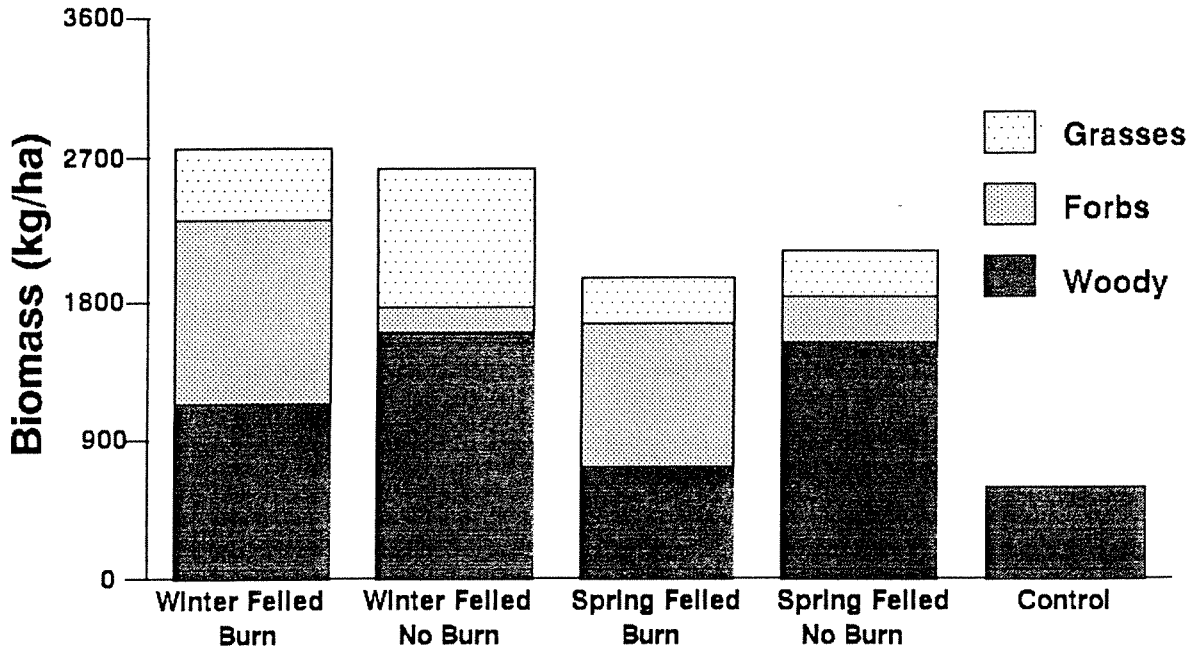

Figure 1. Forage biomass production by species group and treatment on fell-and-burn site-prepared areas in the Upper Southeastern Piedmont.

During the first sampling period after the burn, considerable browsing occurred on blackgum (Nyssa sylvatica Marsh.), American holly (Ilex opaca Ait.), sassafras (Sassafras albidum (Nutt.) Ness.), and smilax (Smilax spp.) seedlings and sprouts. During the second sampling period, utilization of the same species continued. Pokeweed (Phytolacca americana L.) however emerged as the most heavily browsed species. Pokeweed was often browsed to the point of being stunted. During the final sampling period, utilization of woody browse seemed to decline, probably due to the lignification of the woody tissue. While utilization of pokeweed and smilax remained steady. Because summer rainfall was higher than normal forbs on these sites remained succulent into October and November, when they would normally have hardened and been abandoned as preferred browse species.

Diversity, Richness, and Evenness. Diversity of vegetation (H′) increased slightly as a result of winter felling, but there were no significant differences in H′ between treatments. Species differences did occur among treatments as a result of burning, but these differences did not significantly affect H′. Burning favored grasses and forbs while unburned areas were dominated by sprouts of trees and shrubs.

Species richness of vegetation (S) was significantly higher on burned areas than in unburned areas and unharvested controls (fig. 2). Among the burning treatments, winter felling produced significantly greater species richness values[3]. Due to the absence of leaves on the slash, winter-felled sites typically did not burn as evenly or completely as spring-felled sites (Geisinger and others 1989). Therefore a mosaic of burned and unburned microsites was created, with each one capable of supporting a different complement of species.

Vegetative evenness (J) did not differ significantly among treatments. However, J was slightly higher on winter-felled no-burn sites due to increased grass production on those sites.

Small Mammals

Diversity, Richness, and Evenness. Diversity of small mammals (H′) showed no significant differences among treatments until the third sampling period (Sept. 1 to Nov. 31) (table 1). At that time, small mammal abundance on all site-prepared areas declined with the winter decline of vegetative browse and ground cover. This pattern agrees with the finding of Briese and Smith (1974) that small mammals shift the centers of their ranges throughout the year to take advantage of the distributional change in food and cover. H′ was greater on the unharvested controls than on the treated sites during the third period as a result of the fall mast crop and the greater cover afforded by the undisturbed little layer.

Species richness (S) values were low in the first sampling period and there were no significant differences in S among treatments (table 2). In the second sampling period, winter-felled, burned sites had significantly higher S values than other sites. However, in the third sampling period, species richness was significantly lower on winter-felled burned sites as a result of the early senescence of the forb species that dominated those sites. Both food and cover declined much earlier on winter-felled burned sites than on those where grasses or woody vegetation were more dominant. Evenness (J) values did not differ significantly among treatments in any period.

[3]See Evans (1990, unpublished thesis) for a full species listing.

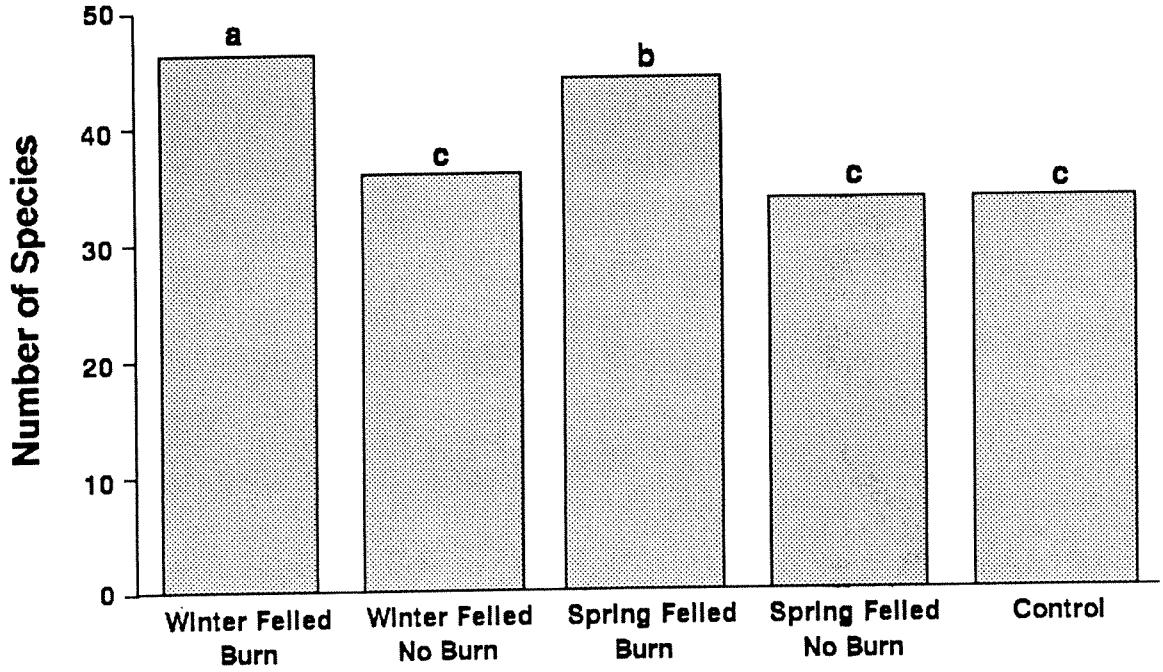

Figure 2. Plant species richness on fell-and-burn site-prepared areas in the Upper Southeastern Piedmont (columns with the same letter were not significantly different at the 0.05 level using Duncan's Multiple Range Test).

Table 1. Small-mammal diversity (H′) on felled-and-burned study sites in the Upper Southeastern Piedmont, 1989.

Treatment	Period		
	Jan. 1-Mar. 31	May 1-July 31	Sept. 1-Nov. 31
Winter-Fell, Burn	0.0a	0.261a	0.092a
Winter-Fell, No-burn	0.1a	0.173a	0.360ab
Spring-Fell, Burn	0.0a	0.235a	0.409ab
Spring-Fell, No burn	0.0a	0.191a	0.192a
Control	0.0a	0.000a	0.519b

-Values followed by the same letter within a column were not significantly different at the 0.05 level using Duncan's Multiple Range Test.

Table 2. Species richness (S) of small mammals on felled-and-burned study sites in the Upper Southeastern Piedmont 1989.

Treatment	Period		
	Jan. 1-Mar. 31	May 1-July 31	Sept. 1-Nov. 31
Winter-Fell, Burn	0.333a	2.667a	1.333a
Winter-Fell, No-burn	1.333a	1.667ab	2.667ab
Spring-Fell, Burn	0.667a	2.000ab	3.333b
Spring-Fell, No burn	1.000a	2.000ab	2.000ab
Control	0.667a	0.333b	3.333b

-Values followed by the same letter within a column were not significantly different at the 0.05 level using Duncan's Multiple Range Test.

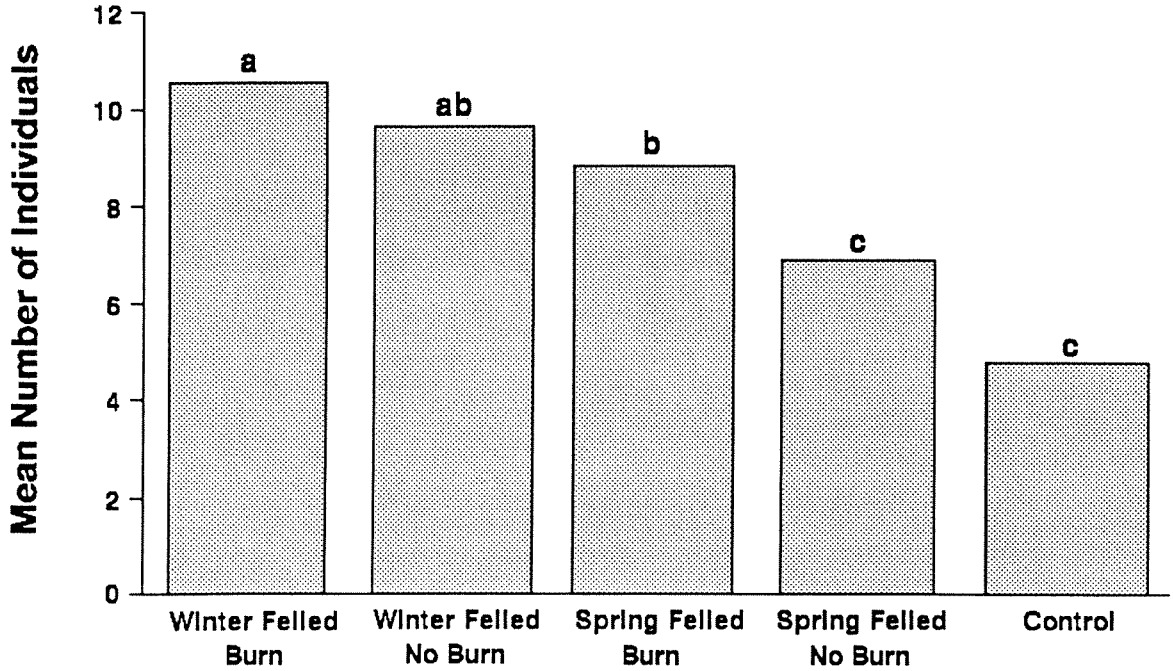

Figure 3. Number of individual small mammals on fell-and-burn site-prepared areas in the Upper Southeastern Piedmont (columns with the same letter were not significantly different at the 0.05 level).

Number of individuals. Both winter-felling and burning resulted in higher numbers of small mammals (N) utilizing an area (fig. 3). This increase is probably a response to the increase in available forage (vegetation biomass) that resulted from this treatment combination. Not all small mammal species increased in numbers in response to disturbance. Species that were trapped most often, such as white-footed mice (Peromyscus leucopus), were those that are best adapted to an early successional environment (table 3). This finding agrees with a number of other studies that show an increase in Peromyscus spp. following fire (Ahlgren 1966; Krefting and Ahlgren 1974; Hingtgen and Clark 1984). The increase in Peromyscus spp. was most pronounced during the first two sampling periods and was no longer evident by the third sampling period. By that time the habitat was sufficiently developed to support a larger number of species with more varied food habits and cover requirements.

Table 3. Relative abundance and total number of individual animals (N) captured, by species, on all fell-and-burn study sites in the Upper Southeastern Piedmont 1989.

SPECIES		N	ABUNDANCE (PCT)
MAMMAL			
white-footed mouse	(Peromyscus leucopus)	97	63.8
golden mouse	(Ochrotomys nuttallii)	13	8.5
house mouse	(Mus musculus)	10	6.6
eastern cottontail rabbit	(Sylvilagus floridanus)	7	4.6
cotton rat	(Sigmodon hispidus)	6	3.9
cotton mouse	(P. gossypinus)	2	1.2
eastern chipmunk	(Tamias striatus)	1	0.7
least shrew	(Cryptotis parva)	1	0.7
southeastern shrew	(Sorex longirostris)	1	0.7
black rat	(Rattus rattus)	1	0.7
	TOTAL=	139	91.4
BIRDS			
mourning dove,	(Zenaida macroura)	1	0.7
	TOTAL=	1	0.7
HERPETOFAUNA			
American toad	(Bufo americanus)	3	2.0
Woodhouse's toad	(B. woodhousei)	2	1.2
eastern box turtle,	(Terapene carolina)	2	1.2
southern leopard frog	(Rana sphencocephala)	1	0.7
eastern narrow-mouthed toad	(Gastrophyrne carolinensis)	1	0.7
ring-necked snake	(Diadophus punctatus)	1	0.7
	TOTAL=	10	6.5
OTHER			
brown grand-daddy longlegs,	(Phalangium opilio)	1	0.7
Carolina locust,	(Dissostiera carolina)	1	0.7
	TOTAL=	2	1.4
	GRAND TOTAL=	152	100.0

1-indicates an incidental capture in a snap trap

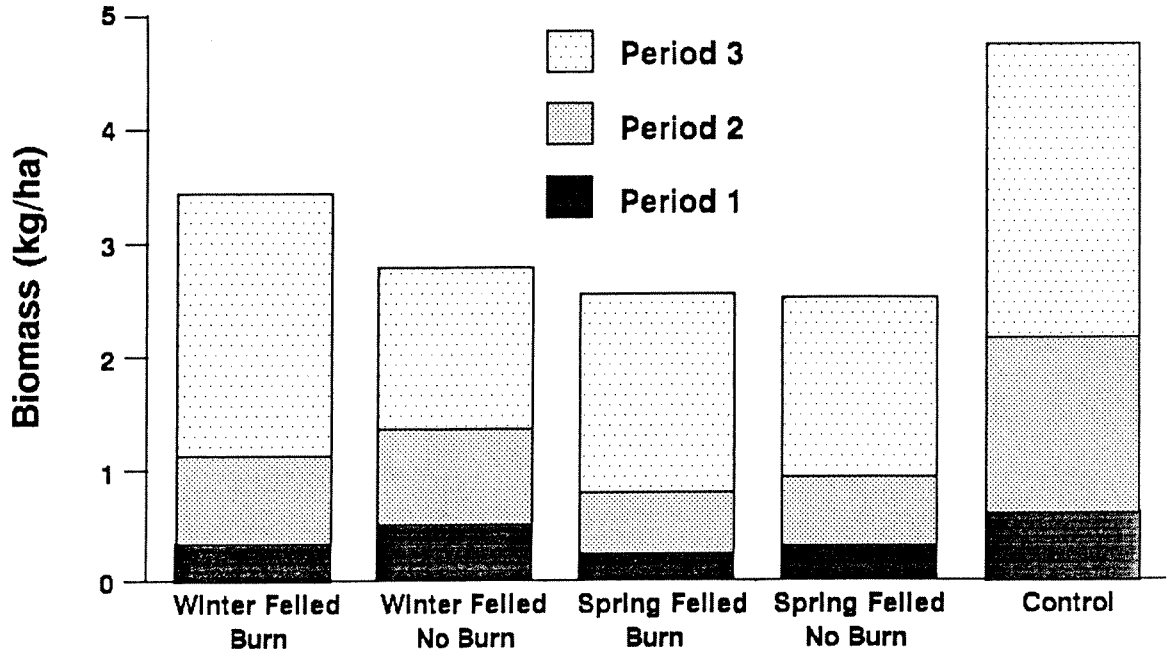

Figure 4. Insect biomass production on fell-and-burn site-prepared areas in the Upper Southeastern Piedmont, 1989.

Insects

Biomass. Total insect biomass was decreased temporarily by all site preparation treatments (fig. 4). Control sites averaged 4.7 kg/ha, while treated sites averaged 2.8 kg/ha. Insect biomass did not decrease as dramatically on winter-felled sites as on other sites, probably because fire intensities were lower on the winter-felled sites. Insect biomass was significantly higher on control sites than on other sites during the first sampling period. Both winter-felled and control sites were significantly higher than other sites during the second sampling period. Recovery of insect biomass production was rapid and there were no longer significant differences by the third sampling period.

SUMMARY AND CONCLUSIONS

Vegetation biomass production was greater for all site preparation treatments than for the control. Burned plots supported richer, more productive plant communities and higher numbers of small mammals than did unburned plots. Winter-felling and burning yielded richer, more productive plant communities and higher numbers of small mammals than spring felling and burning. As vegetation biomass production declined in the fall, small-mammal numbers became highly variable within treatments. Insect biomass production was reduced by all site preparation treatments due to disturbance of the litter layer. However, this decrease in production lasted less than 1 year.

This study indicates that the fell-and-burn site preparation technique, as it is practiced in the Southern Appalachian Mountains, can be used in the Upper Piedmont without adversely affecting forage production for wildlife habitat. If felling of residual stems is conducted in the spring, as is recommended in the Southern Appalachian Mountains, site preparation burns can significantly reduce fuel loads and provide uniform planting conditions (Sanders and Van Lear 1987; Geisinger and others 1989). Burns conducted after winter felling are less uniform (Geisinger and others 1989) and leave more of the slash and logs that provide cover and foraging sites for small mammals. More complete burns also result in a more homogenous habitat than the mosaic of burned and unburned microsites found on winter-felled areas.

The fell-and-burn technique is a relatively inexpensive method to regenerate pine-hardwood mixtures but its application in the Piedmont requires additional study. Effects on wildlife, water quality, and soil as well as on stand regeneration and development are currently being studied. As Van Lear and Kapeluck (1989) have shown, burning prescriptions on Piedmont sites must be modified if erosion is to be controlled. Species composition and soil characteristics of Piedmont sites are different from those of mountain sites, and it may be necessary to modify fell-and-burn techniques because of those differences. Finally, this study addressed only the early successional habitat changes that resulted from this technique. The impact of this type of site preparation on wildlife as the stands continue to develop is yet to be determined.

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EFFECTS OF FIRE AND TIMBER HARVEST ON VEGETATION AND CERVID USE ON OAK-PINE SITES IN OKLAHOMA OUACHITA MOUNTAINS

Ronald E. Masters[1]

Abstract—This study compared vegetation response and cervid browse use within the Ouachita Mountains following an array of timber harvest and fire regimes. Nine treatments were replicated 1-3 times in a completely randomized design on 23 (1.2-1.6 ha) units. The treatments were a no treatment control, a winter rough reduction burn treatment, a clearcut, mechanical site preparation and summer burn treatment, a harvest pine (Pinus echinata) only and annual burn treatment, and 5 harvest pine and thin hardwood treatments with no burn, 4, 3, 2, and 1 year winter-burn intervals. Pine timber was harvested in June and July of 1984 and hardwoods selectively thinned to a basal area of 9 m^2/ha in appropriate treatments. Clearcut treatments were sheared, raked, and windrowed in spring 1985 followed by a summer site preparation burn, and then contour ripped prior to planting in early April 1986. Winter burns were strip headfires applied in mid- to late winter in 1985 through 1988. Little bluestem (Schizachyrium scoparium) and big bluestem (Andropogon gerardi) dominated harvested and winter burned (retrogressed) treatments. Plant frequency and percent ground cover of these 2 species increased on sites burned more frequently. The clearcut and summer burned sites were initially dominated by forbs and panicums (Dicanthelium spp. and Panicum spp.). Then as forbs declined, little bluestem increased in frequency and percent ground cover. Plant species richness was significantly ($P < 0.05$) increased by timber harvest and fire. Among harvested sites, frequency of burning had no significant effect on plant species diversity or plant species evenness. Longer burn intervals or no burning on retrogressed sites allowed woody browse species used by white-tailed deer (Odocoileus virginianus) and possibly elk (Cervus elaphus) to increase. Frequency of browse use by cervids in 1988 was greatest on the harvest, thin, 3-year burn interval; harvest, thin, no-burn; harvest, thin, 2-year burn interval; and clearcut treatments. The harvest, thin, no-burn and clearcut treatments also provided screening and bedding cover for cervids, in contrast to other treatments. Winter prescribed fire at 1- or 2-year intervals favored legumes and created habitat conditions favorable for bobwhite quail (Colinus virginianus). Timber management strategies that create a mosaic of retrogressed burned and unburned sites, and regeneration clearcuts with adequate provisions for hard mast production should provide management flexibility to meet habitat needs of most game species.

INTRODUCTION

The oak (Quercus spp.)-shortleaf pine forest is the most extensive forest type in the eastern United States (Lotan and others 1978), and is widely considered to be a fire subclimax association (Oosting 1956). In spite of the type's prevalence and importance, there has been insufficient research on forest management and fire ecology in the oak-shortleaf pine type and specifically in the Ouachita Highlands (Lotan and others 1978).

Segelquist and Pennington (1968) documented the lack of an adequate understory forage base for deer in the Ouachita Mountains of Oklahoma. Winter mortality of deer has been related to mast failure and may be compounded by the lack of an evergreen winter browse (Segelquist and Pennington 1968; Segelquist and others 1969, 1972). Forage production in late summer and early fall may be of critical importance in the advent of mast shortfall (Fenwood and others 1984).

In 1977, the Oklahoma Department of Wildlife Conservation began using timber harvest and prescribed fire to improve habitat conditions for deer and elk on the Pushmataha Wildlife Management Area. Harvested settings were maintained in early stages of secondary succession with prescribed fire (site retrogression). Although the effects of forest management and fire on wildlife have often been studied, little research has dealt with manipulation of forested ecosystems for the purpose of benefiting wildlife (Ripley 1980).

My objective was to compare site retrogression through timber harvest and periodic prescribed fire, with regeneration clearcutting and understory rough reduction burns. Changes in plant species richness, diversity, evenness, composition, percent ground cover and browse utilization by cervids were used as measures of treatment effects.

STUDY AREA

The 29.1-ha study area was located within the Forest Habitat Research Area (FHRA) on the 7,395 ha Pushmataha Wildlife Management Area near Clayton, Oklahoma. The Pushmataha Wildlife Management Area lies along the western edge of the Ouachita Highland Province. Study area soils belong to the Carnasaw-Pirum-Clebit association with areas of rock

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outcrop. The soils developed from cherty shales and resistant sandstones and were thin and drought prone. The climate was semihumid to humid with hot summers and mild winters (Bain and Watterson 1979).

Prior to acquisition from 1946 to 1954, Pushmataha Wildlife Management Area was grazed, selectively harvested, and frequently burned (Oklahoma Department of Wildlife Conservation 1972). The FHRA was protected from further logging, grazing and fire from acquisition until 1984 (R. Robinson, Area Biologist, Oklahoma Department of Wildlife Conservation, personal communication). From 1983 to 1988 the Pushmataha Wildlife Management Area supported an average deer population of 540 $\pm$ 40 (SE) and 9 $\pm$ 1 (SE) elk (Masters 1991).

Post oak (Q. stellata), shortleaf pine, and to a lesser extent, blackjack oak (Q. marilandica), and mockernut hickory (Carya tomentosa) dominated the overstory. Common woody understory species included tree sparkleberry (Vaccinium arboreum), Virginia creeper (Parthenocissus quinquefolia), greenbriar (Smilax spp.), and grape (Vitis spp.). Common herbaceous plants included little bluestem, panicums, and sedges (Carex spp.) (Masters 1991).

METHODS

Cultural Treatments

Beginning in summer 1984, 9 treatments were applied to 23, 1.2-1.6 ha contiguous, rectangular units on the FHRA in a completely randomized experimental design (Chambers and Brown 1983). Treatments, burning sequence, treatment code, and number of replications (n) were:

(1) no treatment (control) (n=3);
(2) rough-reduction winter prescribed burn at 4-year interval, 1985 (RRB) (n=3);
(3) clearcut and summer site prep burn, 1985 (CCSP) (n=3);
(4) harvest pine timber only, winter prescribed burn, 1-year interval, 1985 to 1988 (H-NT-1) (n=3);
(5) harvest pine timber, thin hardwoods, no burn (H-T) (n=1);
(6) harvest pine timber, thin hardwoods, winter prescribed burn at 4-year interval, 1985 (H-T-4) (n=3);
(7) harvest pine timber, thin hardwoods, winter prescribed burn at 3-year interval, 1985, 1988 (H-T-3) (n=2);
(8) harvest pine timber, thin hardwoods, winter prescribed burn at 2-year interval, 1985, 1987 (H-T-2) (n=3); and
(9) harvest pine timber, thin hardwoods, winter prescribed burn at 1-year interval, 1985 to 1988 (H-T-1) (n=2).

In appropriate treatments merchantable pine timber was harvested and hardwoods selectively thinned by single stem injection using 2-4 D, to a basal area of 9 m^2/ha (includes stems > 5 cm diameter at 1.4 m height), in summer 1984. Prescribed burns using strip headfires were conducted in winter 1985 and in succeeding years at appropriate intervals. Several replications were dropped because they were either burned out of sequence by spotovers or not burned because of rain. The clearcut site-prep treatment included shearing, raking and windrowing of logging debris with a site-prep burn conducted during summer 1985. After contour ripping, genetically improved loblolly pine (P. taeda) was planted on a 2.1 m by 2.4 m spacing, in early April, 1986.

Vegetation Sampling

Understory, midstory and overstory vegetation was sampled using nested quadrats (1 m by 1 m and 4 m by 4 m) (Oosting 1956:47-50, 62). On each treatment unit, 10 permanent plots were established at 19.8 m intervals on two randomly located lines perpendicular to the contour. In order to avoid bias caused by influences from adjacent treatment units, I did not sample within 19.8 m of any edge (Oosting 1956; Mueller-Dombois and Ellenberg 1974). Data collected included plant species density, frequency, percent ground cover, and utilization.

Utilization was categorized based on proportion of current annual growth (CAG) browsed. The categories were none, trace--less than 25 percent, moderate--25 to 50 percent, and heavy--greater than 50 percent utilization.

Overstory and midstory vegetation were categorized by vertical strata and crown position relative to stand canopy structure. Strata designations were 0 to 1 m, 1 to 3 m, and greater than 3 m. Strata greater than 3 m were categorized by position relative to stand canopy structure and were suppressed, intermediate, codominant, and dominant canopy position (Smith 1962). On harvested treatments strata designation of residual trees was based on prior stand structure. No tree or shrub regrowth was greater than 3 m. Overstory vegetation was further quantified using the variable radius plot method (Avery 1964). Basal areas were taken using a 10 basal area factor prism with plot center at the center of each 4 m by 4 m plot. Vegetation sampling and browse use determinations were conducted in September and October of each year because this was a critical period of the year for deer (Fenwood and others 1984). A baseline survey was conducted in 1983.

Data Analysis

Species diversity, evenness, richness, density, and frequency were calculated from vegetation samples (Ludwig and Reynolds 1988). A modification of Krueger's (1972) preference index (RP1) combined across years and treatments was used to rank plant species used by deer and elk. Analysis

Table 1.--Average percent cover for major species groups 1983-88. Timber harvest was applied in summer 1984 and prescribed burns were conducted in 1985 and following.[1]

VEGETATIVE GROUP	TREATMENT[2]								
	CONT	RRB	H-NT-1	H-T	H-T-4	H-T-3	H-T-2	H-T-1	CCSP
YEAR=83									
GRASSES	3	6	.	7	12	8	4	.	7
FORBS	2	2	.	1	1	tr	2	.	3
LEGUMES	1	1	.	1	1	1	2	.	1
VINES	1	<1	.	<1	<1	1	<1	.	<1
SHRUB 0-1M	6	13	.	6	10	11	7	.	6
SHRUB 1-3M	1	3	.	0	1	1	<1	.	2
TREE MID[3]	14a	10a	.	4b	2b	1b	4b	.	4b
YEAR=84									
GRASSES	9	10	.	14	14	8	5	.	7
FORBS	5	6	.	7	1	1	2	.	2
LEGUMES	2	2	.	<1	1	1	2	.	2
VINES	1	1	.	<1	<1	1	1	.	<1
SHRUB 0-1M	10	24	.	16	11	8	9	.	7
SHRUB 1-3M	3	5	.	1	2	<1	4	.	1
TREE MID	23a	24a	.	9ab	1b	7b	3b	.	9ab
YEAR=85									
GRASSES	7b	6b	.	23a	22a	20a	14ab	.	5b
FORBS	2	2	.	25a	17b	11b	14b	.	3
LEGUMES	1	1	.	2	4	3	6	.	1
VINES	1	<1	.	0	<1	1	1	.	<1
SHRUB 0-1M	7	9	.	20	13	17	19	.	4
SHRUB 1-3M	5a	3ab	.	1b	<1b	0b	0b	.	<1b
TREE MID	24a	17a	.	1b	2b	0b	2b	.	<1b
YEAR=86									
GRASSES	7b	8b	30a	20ab	29a	27a	20ab	28a	17ab
FORBS	3c	5bc	13bc	16bc	18b	17b	19b	18b	37a
LEGUMES	2	2	4	4	5	6	7	9	3
VINES	2	<1	<1	<1	1	1	1	1	<1
SHRUB 0-1M	9	19	10	27	20	14	19	14	9
SHRUB 1-3M	6a	1bc	1bc	3bc	2bc	2bc	4ab	<1bc	0c
TREE MID	22a	10b	3bc	4bc	2c	0c	1c	0c	0c
YEAR=87									
GRASSES	4c	7c	34a	19b	25ab	21b	21b	35a	25ab
FORBS	1	2	11abc	10bc	9bc	7c	17ab	13abc	20a
LEGUMES	1b	1b	6ab	8a	4ab	3ab	9a	5ab	4ab
VINES	1	<1	<1	<1	1	3a	1	1	<1
SHRUB 0-1M	6c	14abc	10bc	29a	21abc	24ab	22abc	8bc	13abc
SHRUB 1-3M	4	2	2	12	6	5	3	2	3
TREE MID	22a	10b	4c	2c	<1c	2c	1c	0c	0c
YEAR=88									
GRASSES	3d	6d	31ab	11cd	25ab	32ab	20cb	37a	28ab
FORBS	1b	2b	7ab	4b	5b	7ab	8ab	6ab	13a
LEGUMES	1c	1c	5abc	2bc	3abc	5abc	9a	8ab	5abc
VINES	1	<1	<1	<1	1	1	<1	1	<1
SHRUB 0-1M	7c	15abc	10bc	29a	26ab	28a	23ab	10bc	17abc
SHRUB 1-3M	4b	2b	2b	24a	11b	2b	9b	1b	12b
TREE MID	16a	9bc	2c	12ab	1c	0c	<1c	0c	0c

[1] Row means with the same letter are not significantly different ($P < 0.05$).

[2] CONT = control, no treatment; RRB = rough reduction burn in winter, at 4 year intervals; H-NT-1 = harvest pine timber, no thinning of hardwoods, winter prescribed burn at 1 year intervals; H-T = harvest pine timber, thin hardwoods; H-T-4 = harvest pine timber, thin hardwoods, winter prescribed burn at 4 year intervals; H-T-3 = harvest pine timber, thin hardwoods, winter prescribed burn at 3 year intervals; H-T-2 = harvest pine timber, thin hardwoods, winter prescribed burn at 2 year intervals; H-T-1 = harvest pine timber, thin hardwoods, winter prescribed burn at 1 year intervals; CCSP = clearcut, windrow logging slash, summer site prep burn, rip.

[3] TREE MID = Suppressed trees > 3 m height in the midstory, but not extending into the upper canopy layer.

was performed using PC-SAS (SAS Institute 1985, 1987) and SPDIVERS.BAS (Ludwig and Reynolds 1988). Statistical analysis of treatments was by one-way analysis of variance (ANOVA) for unequal sample size. To determine treatment preference by cervids, browse utilization frequency for all sample plots was summed by unit (replication), ranked and analyzed by ANOVA, the equivalent of the Kruskal-Wallis nonparametric procedure (SAS Institute 1985). Mean ranks were separated by Duncan's Multiple Range Test (Steele and Torrie 1980).

RESULTS

Vegetation Response

Pretreatment vegetation sampling in 1983 indicated higher ($P < 0.05$) percent cover of midstory trees in control and RRB replicates than on other treatment units (table 1). Values for utilization and other descriptors of vegetation did not differ among units prior to application of treatments. The only significant differences found between control and RRB treatments in succeeding years were in percent cover of suppressed trees. Rough reduction burning reduced ($P < 0.05$) percent cover in that stratum by 1986-88 (table 1).

Understory response varied after initial timber harvest and thinning of residual hardwoods. In 1984, species diversity increased, and evenness declined ($P < 0.05$) on all harvested and thinned treatments compared to the control and RRB treatments. Species evenness provided an adequate measure of shrub response only in 1984. Species richness of herbs and shrubs immediately after timber harvest was unchanged (figs. 1 and 2).

In 1985 and 1986 after all burning and timber harvest treatments had been applied species richness of herbaceous and shrub vegetation on treated areas were significantly ($P < 0.05$) higher (figs. 1 and 2). Grass cover on treated areas was dominated by little bluestem, big bluestem and panicums. The predominant forbs were horseweed (Conyza canadensis), white snakeroot (Eupatorium rugosum), and fireweed (Erechtities hieracifolia). Shrub response on harvested and burned treatments was composed of primarily winged sumac (Rhus copallina), dewberry (Rubus spp.), and post oak sprouts. Only legume and vine categories showed no difference in cover among treatments (table 1).

In 1986, values of most vegetational characteristics of CCSP areas did not differ significantly from corrresponding values for areas that were harvested and burned (table 1). However species composition and shrub species richness differed by treatment ($P < 0.05$) (fig. 2). Panicums and little bluestem were respective grass dominants on CCSP and all the harvested, thinned and burned treatments. Crabgrass

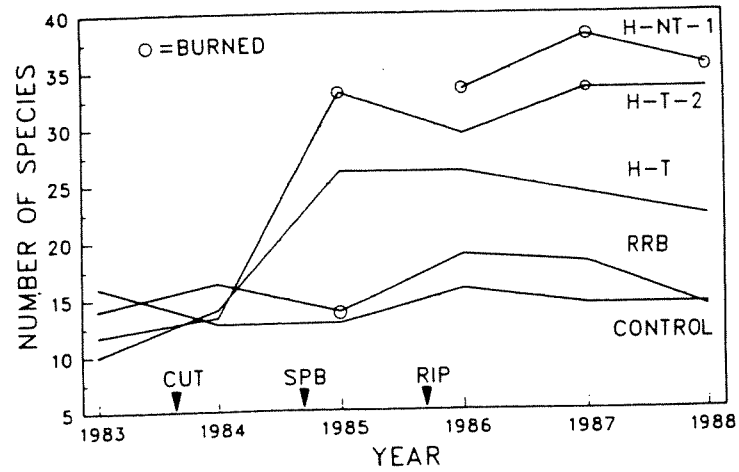

Figure 1.--Mean species richness of herbaceous plants 1983-88. For clarity of presentation some burned treatments were not depicted. Those not depicted were intermediate in response.

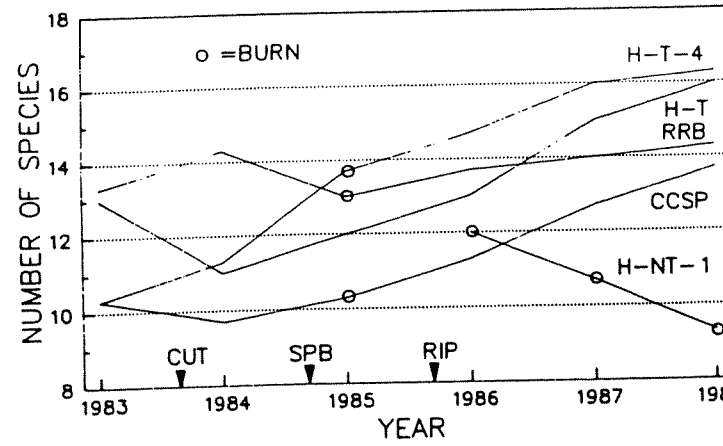

Figure 2.--Mean species richness of shrubs 1983-88. For clarity of presentation some burned treatments were not depicted. Those not depicted were intermediate in response.

(Digitaria violescens) was a significant component of the grass response of the CCSP treatment and occurred infrequently on other treatments. Broomsedge bluestem (Andropogon virginianus) also occurred more frequently on CCSP treatments than on other treatments. Forb response was greatest during 1986 on the CCSP treated areas and was significantly higher for this treatment than for others ($P < 0.05$) (table 1).

By 1988, percent cover of all plant groups, except vines, differed among treatments (table 1). For herbaceous plants, species richness and evenness differed significantly among treatments. Species richness and diversity differed significantly among treatments for shrubs (fig. 2). Timber harvest and prescribed fire decreased herbaceous species evenness but increased shrub and herb richness and shrub diversity (figs. 1 and 2). Bluestems and panicums were dominant grasses on harvested and burned treatments. In the CCSP treatment areas, the grasses were mainly comprised of panicums and to a lesser extent little bluestem. Broomsedge bluestem occurred more frequently on this treatment than others.

Dominant shrub species on harvested and burned sites included winged sumac, dewberry, post oak sprouts, tree sparkleberry, and winged elm (Ulmus alata). On the H-T treatment, sumac was not prevalent, but the above species and shortleaf pine seedlings and saplings were prominent. Dewberry, post oak, coralberry (Symphoricarpos orbiculatus) and loblolly pine were primary shrub constituents on CCSP treatments.

Abundance of preferred forbs increased ($P < 0.05$) (fig. 3) after timber harvest and prescribed fire then declined as grass cover increased (table 1). Preferred browse increased ($P < 0.05$) in all except RRB, control and annual burned treatments (fig. 4). Percent cover of preferred browse in the annual burned treatments were not different from percent cover of preferred browse on the control or RRB sites. By 1988 legumes, preferred forbs and preferred browse responded differentially by treatment (figs. 3-5). More frequent burning intervals favored legumes and preferred forbs while less frequent intervals favored shrubs (figs. 4 and 5).

Utilization

Cervids utilized 74 species of plants and 17 plant groups identified to genera. Forbs of 31 species, and additional plants identified only as members of 7 genera were used. Thirteen species of legumes and additional legumes identified to 1 genus (Desmodium spp.) were used. Utilization occurred on 29 species and an additional 7 genera of woody browse. Grass-likes utilized included panicums, sedges, and little bluestem. Rankings of relative preference revealed that woody browse was used more than forbs (table 2).

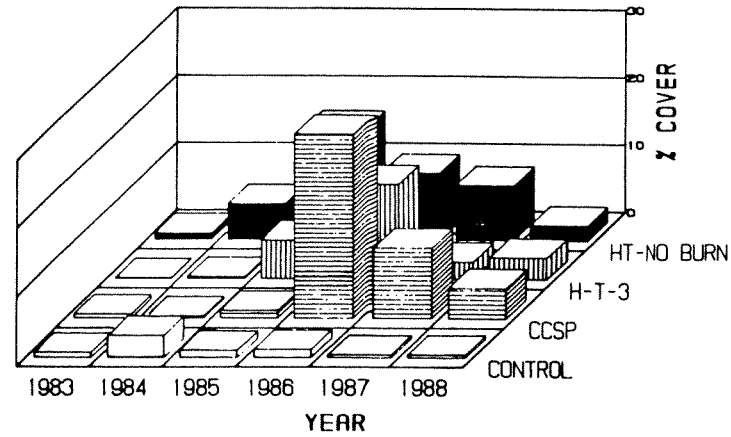

Figure 3.--Percent cover of preferred forbs 1983-88. For clarity of presentation some burned treatments were not depicted. Those not depicted were intermediate in response.

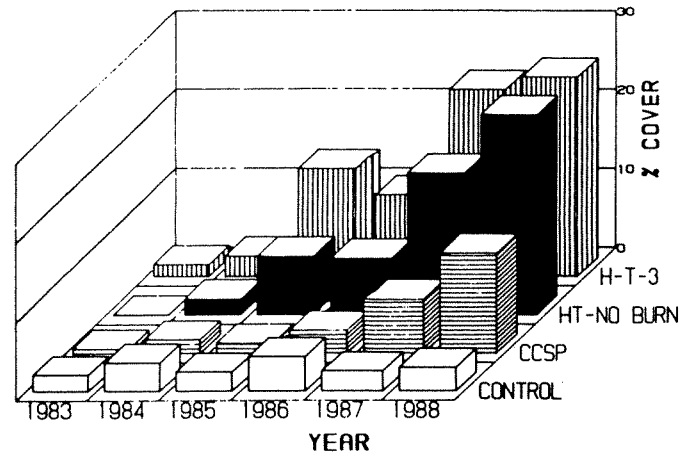

Figure 4.--Percent cover of preferred browse 1983-88. For clarity of presentation some burned treatments were not depicted. Those not depicted were intermediate in response.

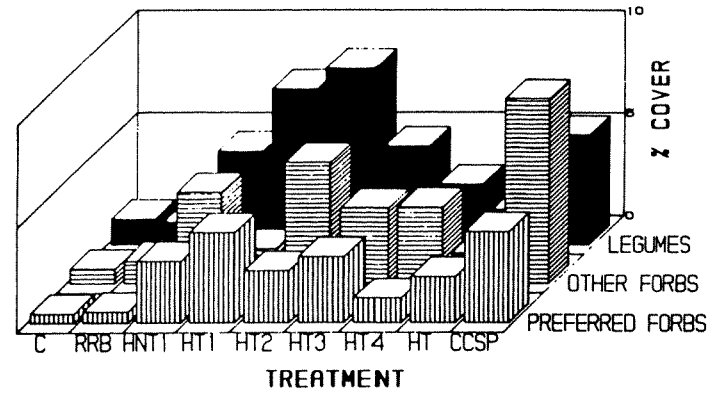

Figure 5.--Percent cover of preferred forbs, other forbs, and legumes after all burn intervals had been completed in 1988.

Table 2.--Rankings of preferred cervid food plants based on a summed preference index for all years and treatments.

Browse	Index	Forbs	Index
Smilax spp.	808	*Lespedeza* spp.	322
Ulmus alata	745	*Aster patens*	311
Amelanchier arborea	448	*Solidago ulmifolia*	201
Vitis spp.	422	*Monarda fistulosa*	135
Vaccinium spp.	201	*Phytolacca americana*	128
Hypericum spp.	195	*Conyza canadensis*	120
Rhus glabra	167	*Solanum carolinense*	116
Rhus copallina	159	*Aster* spp.	106
Nyssa sylvatica	103		
Rubus spp.	103		

Cervid Use

Mean ranks of cervid frequency of utilization on replicates was significantly different ($P < 0.001$) among treatments (table 3). Annual burn and RRB treatments had significantly lower frequency of utilization than other treatments.

DISCUSSION

Vegetation response varied by species. Some plant species increased on retrogressed sites and others decreased from pretreatment levels. Species evenness was highest on the control and pretreatment, which indicated that herbaceous species were equally abundant. Site perturbation, caused some plant species, particularly tallgrasses, to become more abundant relative to other species.

Community progression on harvested and burned sites was similar to that reported by Hebb (1971) for clearcutting. Successional stages after harvest were; (1) disturbed site with pretreatment understory ground cover; (2) profusion of grasses and annual forbs; (3) increase in perennial forbs and grasses, decrease in annuals and increase in shrubs; and (4) in the absence of periodic prescribed fire, increases in shrubs and grasses and declines in forbs.

Chronosequences of vegetation on retrogressed sites subjected to fire at varying frequencies was similar to response of burned mesic tallgrass prairie (Anderson and Brown 1986). Longer fire intervals allowed woody species to increase (Bragg and Hulbert 1976; Petranka and McPherson 1979). Summer site-prep burns and ripping associated with the CCSP treatment caused a lag in plant community progression. Species composition was different under this treatment regime with forbs dominating the year following the summer site prep burn. As grasses increased, panicums were the primary dominant followed by little bluestem. The broomsedge bluestem component was higher on the CCSP treatment than others. The summer site prep burn apparently set back bluestems and allowed cool season grasses (panicums) and sedges to increase. Shrub species richness and percent cover were slower to increase on CCSP than retrogressed and winter burned sites (table 1 and fig. 2).

Rough-reduction burns caused smaller increases in herbaceous cover and species richness than they have in other cases (Oosting 1944, Lewis and Harshbarger 1976). However, oak-pine forest in the Ouachita Mountains do not have well

Table 3.--Mean ranks of 1988 cervid utilization frequency by treatment on the Pushmataha Forest Habitat Research Area.[1]

TREATMENT[2]								
H-T-3	H-T	H-T-2	CCSP	CONT	H-T-4	H-T-1	H-NT-1	RRB
19.8	18.5	17.2	17.2	13.2	9.8	8.5	7.3	2.3

[1] Means underscored with the same line are not significantly different ($P < 0.05$).

[2] H-T-3 = harvest pine timber, thin hardwoods, winter prescribed burn at 3 year intervals; H-T = harvest pine timber, thin hardwoods; H-T-2 = harvest pine timber, thin hardwoods, winter prescribed burn at 2 year intervals; CCSP = clearcut, windrow logging slash, summer site prep burn, rip; CONT = control, no treatment; H-T-4 = harvest pine timber, thin hardwoods, winter prescribed burn at 4 year intervals; H-T-1 = harvest pine timber, thin hardwoods, winter prescribed burn at 1 year intervals; H-NT-1 = harvest pine timber only, winter prescribed burn at 1 year intervals; RRB = rough reduction burn in winter, at 4 year intervals.

developed midstories. Herbaceous species will increase as repeated fire eliminates smaller diameter overstory hardwoods and as pines assume dominance (Lewis and Harshbarger 1976).

Browse use on a treated area was probably related to percent cover of preferred browse and shrub species richness (table 3 and figs. 2 and 4). Woody browse is the major component of deer diets in all months except May (Jenks and others 1990). However when hard mast is available in fall and winter it comprises the major portion of deer diets (Fenwood and others 1985). Presence of preferred forbs, panicums, and sedges on a treatment probably affected use because of the selective foraging nature of deer (Vangilder and others 1982).

Screening, bedding, or escape cover may be important because deer were flushed frequently out of beds only in the H-T and CCSP treatments. The shrub component on H-T and CCSP treatments in the 0-1 m and 1-3 m categories was primarily pine saplings. Pines probably provided a more dense horizontal cover but this parameter was not measured in this study. The presence of cover on HT and CCSP treatments may have increased use on these areas. Deer use increases on recent clearcuts but is limited to 100 m from cover on large clearcuts (Tomm and others 1981). As pine stands develop in height on regeneration areas, deer use of the central portion of the stand will increase. All portions of large (128-276 ha) 4-5 year old pine stands were used in a southeast Oklahoma study (Melchoirs and others 1985).

CONCLUSIONS

The primary values associated with controlled burning and overstory removal were increased species richness and availability of preferred food items for deer, elk and possibly bobwhite quail. By varying frequency of fire, managers can shift plant communities to benefit target game species. Winter prescribed fire at 1- or 2-year intervals favored legumes and created habitat conditions favorable for bobwhite quail. Less frequent burning or no burning allowed woody browse species prefered by deer to increase on retrogressed sites (Landers 1987). A prescribed burning rotation at 2- or 3 year intervals on retrogressed sites will allow growth of important deer and quail foods. Clearcutting and site preparation provide benefits in terms of food and cover for deer. However benefits from regenerated clearcuts last only until canopy closure. Site retrogression without burning provides an important cover component to deer.

Timber management strategies that create a mosaic of retrogressed burned and unburned sites, and regeneration clearcuts with adequate provisions for hard mast production should provide management flexibility to meet habitat needs of most game species. The effects of growing season burns on maintaining retrogressed sites for forage production should be evaluated in a similar manner. The long-term effects of prescribed fire on vegetation response and site quality in mountainous terrain should also be evaluated.

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