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Scope and Method of Study: This report is essentially a survey of the literature dealing with fire as an ecological factor in grassland areas. However, investigations which deal with anatomy, physiology, and non-grassland habitats have also been reviewed when relevant. The associations discussed in detail are the tall, short, and mixed grass prairie, the desert plains, and chaparral. Practical suggestions for burning are also included. Major botanical journals and miscellaneous publications are the main source for the paper.

Findings and Conclusions: The effect of fire on any given habitat is determined by a complex interplay of factors. For this reason it is difficult to generalize from one habitat to another or to form value judgements concerning the usefulness of fire as a tool. It is concluded, however, that the presence or absence of fire will affect climax conditions in many areas. From a practical point of view fire in tall grass prairie is useful in promoting increases in livestock weight if burning is done properly. In short and mixed grass prairie the slow rate of mulch accumulation and small annual rainfall make burning a hazardous procedure. In desert plains, fire may be necessary for protection from noxious shrubs while in chaparral it is the important factor in maintaining climax conditions.

ADVISER'S APPROVAL ______________________

FIRE

AN ECOLOGICAL FACTOR IN GRASSLAND

By

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PREFACE

The scientific study of ecology is a relatively recent endeavor so there are many areas where knowledge is incomplete or scattered. It was my purpose in this paper to review the available literature dealing with fire ecology both to provide a source for anyone wishing to do research in this area and to stimulate such research. There are many apparent contradictions in the literature and many aspects of fire ecology which have been practically neglected so the field is a fertile one for further investigation.

I wish to thank Dr. Jerry Crockett for his suggestions and careful reading of this paper, as well as for his patience in introducing a Michigander to the ecology of the plains. A debt of gratitude is due to my wife who typed, read, and criticized (constructively) this manuscript.

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INTRODUCTION

The relationship of fire to natural vegetation is both a complex and important topic. It is the purpose of this paper to review the literature dealing with the ecological effects of fire. Special attention is given to grassland formations.

The utility of such a study can be illustrated by the following unsolved problems of applied ecology in managing grassland areas: (1) what place will be left for palatable grasses and herbs under full fire protection; (2) what is the change in fire hazard as full protection is attempted; and (3) what are the risks and returns with controlled burning.

Besides the practical questions of applied ecology, there are many fire-related problems of theoretical interest, such as the question of whether the grassland formation is a pyric climax, or does fire play no role whatever in maintaining climax grasslands.

The author will try to organize research data on the role of fire on ecology into one source. No rigid boundaries have been drawn; thus material of general interest as well as that which might illuminate the problem of grassland fires will be included.

CHAPTER I

THE REACTION AND ADAPTATION OF PLANTS TO FIRE

The ecological limits of any plant are determined by the reactions to environmental stimuli. For this reason, knowledge of the anatomical and physiological reactions of plants to fire is both useful and interesting. However, a paucity of anatomical and physiological literature exists in this area.

Resistance of Plant Tissue to Heat

The resistance of living plant tissue to heat and (or) desiccation is thought to be indicative of its chances of survival under extreme conditions such as hot weather or fire. Levitt (31) points out that cold, drought, and heat resistance are all basically related and a resistance to one of these factors carries with it a resistance to the others. He also points out that conditions which lead to adaptation to low temperatures (drying out with increase in osmotic pressures) at the same time raises heat resistance.

Heat resistance appears to vary from plant to plant, season to season, and from day to day. Variation in resistance is well illustrated by the studies of Jameson (29) on Pinyon-Juniper vegetation. He found that lethal temperatures were highest in winter and lowest in late spring for the plants he tested. The tissues of most species also showed a secondary high lethal temperature in midsummer and secondary low in September. With respect to species differences he found the culm bases of *Hilaria jamesii*, *Bouteloua gracilis*, *B. eriopoda*, and *B. curtipendula* were the most sensitive of the tissues studied, while *Juniperus deppeana* and *Pinus edulus* twigs were the least sensitive. In general, the tree twigs were found to have higher lethal temperatures than the grass culm bases. This might explain why, under certain conditions, fire can kill invading weed trees without killing grasses (keeping in mind that temperatures during a fire are usually higher a few inches above the ground than at ground level). Jameson further found that variation in heat resistance is inversely correlated with depression of the wet bulb thermometer, so that during hot, dry weather, air temperature at the soil surface was near the lethal level for most culm bases. Therefore, it is probable that fires at these times would be more damaging to grass plants than during cooler weather when lethal temperatures for culm bases are found to be higher.

Viability determination studies such as those performed by Jameson can be done by gradually increasing tissue temperatures and testing with 2, 3, 5 - triphenyltetrozolium chloride (TTC). Parker (35) reports that, after 24 hours, the cambium of twigs and grass tissue exposed to TTC was colored a deep red if viable, while non-viable tissue remained uncolored. TTC turns deep red when reduced in the presence of active dehydrogenase. He further reports that the oxidation reaction which reverses the color change reaction in methylene blue does not occur or occurs only slowly.

Responses of Plant Tissues to High Temperature

Little is known about the changes occurring in normal plant tissue as the environmental temperature is raised. Parker (33) studied anatomical changes in the leaves of Pinus strobus and P. nigra in response to desiccation and dehydration. It was assumed that the changes induced by desiccation are similar to those produced by high temperature. Parker observed that when excised leaves of white and Austrian pine lose moisture and are unable to replace it, cells of the chlorenchyma, endodermis, and transfusion tissue decrease in size. One result of this shrinkage is that the epidermis and hypodermis bend inward. In Austrian pine the adaxial surface bends inward, and in white pine all three surfaces bend inward. Eventually the upper corners of the leaf bend in toward each other and longitudinally the needles become warped into a slight curve.

The change in shape of the cells inside the hypodermis depends to some extent on their position. Parker further observed that some chlorenchyma cells collapse lengthwise, pulling the epidermis and hypodermis inward. Others stretch when they are attached to the hypodermis at the corners of the needle. The speed of drying appeared to cause variation in the relative rates of shrinkage of both transfusion and chlorenchyma tissue. The endodermal cells flatten out while the transfusion tracheids and transfusion parenchyma collapse or become distorted. The xylem and phloem remain approximately the same size during desiccation. A change in color of the leaves from grass green to light green during drying was observed. Parker believes this color change is caused by the contracted condition of the chlorenchyma cells or by physical changes within the chloroplasts, but not by a change in the chlorophyll structure itself.

Reproduction and Fire

In general, it appears that the occurrence of vegetatively reproduced species on burned-over lands depends primarily on the resistance of their reproductive parts to fire. Examples of such resistant species as listed by Ahlgren (1) include: Cornus canadensis, Maianthemum canadense, Vaccinium angustifolium, Clintonia borealis, and Calamagrostis canadensis.

Resistance of reproductive parts to fire may be due to the presence of specialized reproductive structures or to modifications within the seed itself.

One example of a modified reproductive organ is the lignotuber (Fig. 1), a peculiar feature of many Australian plants. This structure is most common in the Myrtaceae and Proteaceae, and is entirely lacking in the Leguminoseae, Rutaceae, Casuarinaceae and most Epacridaceae. Lignotubers are frequently large organs and usually are buried sufficiently deep to avoid high temperatures. Beadle (5) showed by examination that plants with lignotubers are rarely killed during a natural fire, and that the lignotuber's depth below the ground surface is of great importance in its survival.

Another distinct modification of a reproductive structure selected in response to temperature extremes is the serotinous cone (one not opening spontaneously upon maturation) found in the Conifers. Ten North American pines have cones exhibiting some degree of serotiny. Beaufait (6) has described both the structure and opening mechanism of the Jack Pine (Pinus banksiana) cone. The female cone consists of a central axis with bracts spirally arranged around it. In the axils of

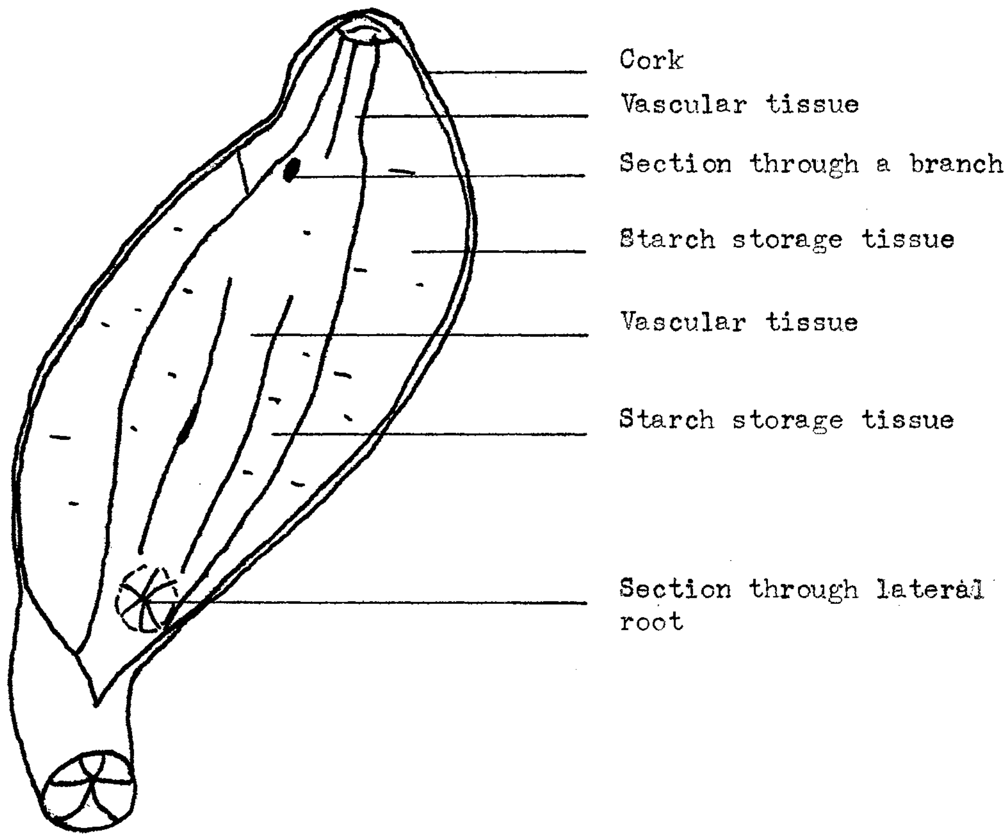

Fig. 1. Lignotuber (side view, $\frac{1}{2}$ actual size). Redrawn from original sketch. Beadle, N. C. W. 1940. Soil temperature during forest fires and their effect on the survival of vegetation. Journal of Ecology 28: 187.

the bracts are potentially simple cones reduced to one sporophyll with two ovules. The cone scales (ovuliferous scales) are physical barriers to seed dispersion from a mature cone. The lower one-third of the Jack Pine cone does not produce seeds but the scales often restrict full opening of those above. Cones which remain closed do so because of a resinous bonding material which seals the scales together and forms a vapor-resistant protective coating over the entire cone. Temperatures exceeding those usually found in tree crowns are required for melting this resin and freeing the scales. If the resin seal is melted, longitudinally oriented structures in the cone scales curve away from the cone axis to liberate the seeds. The strongest curvature occurs nearest the point of attachment to the cone axis, decreasing with proximity to the scale tip.

Beaufait conducted tests which show the dependence of cone opening on ambient atmospheric humidity (mature cone tissue does not receive moisture from the living portion of the plant). Cone moisture content was found to vary from 350 percent of oven dry weight when green to 7 percent when mature; the mature cones remain in equilibrium with the atmospheric moisture. That desiccation alone will fail to open the mature cones was shown by subjecting cones to desiccation at low temperatures. The stresses incurred failed to break the resinous seals on the cones scales.

Further tests conducted by Beaufait showed that elevated temperature is necessary for cone opening. Serotinous cones from all parts of northern lower Michigan were exposed to temperatures within the range expected in wild crownfires or prescribed burns. The cones responded consistently by opening over a range of 80 seconds at 200 F. to 2 seconds at 1300 F. The cones which ignited retained no viable seed, while unignited cones suffered little reduction in the germination capacity of their seeds.

As stated earlier, the seed itself may contain some modification rendering it resistant to the effect of high temperature. Wright (51) states, however, that:

> no one factor is likely to be responsible for the variation of seeds in enduring high temperatures. There are many factors to consider; among the most important is the chemical composition, the effect upon colloidal material in the cells, and on enzymatic activity, the effect of light on germination, and the color of the seed coat.

The experiments of Wright show that seed of certain shrubby plants such as _Rhus laurina_ and _R. ovata_ endure higher temperature than coniferous or grass seed. This may account for the aggressive invasion of shrubby plants on burns in some areas. However, the ability of seed to endure high temperature cannot be satisfactorily explained on the basis of varying degrees of desiccation. Wright suggests that resistance to high temperature may possibly be related to seed coat thickness. However, since the temperature rose in all seeds at the same rate regardless of seed coat thickness, it might be assumed that heat increases seed coat permeability and thus aids in breaking dormancy.

Beadle (5) found that seeds whose testae are permeable to water at any temperature have a low resistance to high temperature in the wet condition. On the other hand, those seeds whose coats are impermeable to water at room temperature may be subjected to high temperatures in the wet condition for relatively long periods without injury. Such treatment increases the percentage of seeds capable of immediate germination.

The effect of field-burning on germination of Rhus ovata was duplicated in the laboratory by Stone and Juhren (46). They found temperature to be responsible for germination, and came to the following conclusions about untreated seeds: 1) The embryos are not dormant. 2) The seed coat as a whole is impermeable to water. 3) Impermeability of the seed coat is caused by a second seed coat layer. 4) No chemical inhibitor exists in the seed coat, the remains of the nucellus, or the endosperm. 5) Germination of seeds exposed to elevated temperatures is induced by a rupturing of the second seed coat layer along the edge of the seed immediately above the micropyle. This allows for initial water entry through the underlying third seed coat layer.

The extreme resistance to heat of certain seeds is shown by Beaufait (6). Normal extracted Jack Pine seeds were exposed to high temperature and demonstrated an ability to remain viable until the wings ashed and the seed coats cracked from the heat. At 700 F, this took between 10 and 15 seconds; and at 1000 F, between 1 and 5 seconds.

CHAPTER II

DESCRIPTION OF GRASSLAND AREAS

The grassland or prairie formation is the nost extensive and the most varied of all the climaxes of North America. It ranges from northern Saskatchewan, Alberta, and central British Columbia to the highlands of central Mèxico and from western Minnesota and Iowa to the coast of California and Lower California. In the form of a closely related subclimax it extends eastward to Indiana and portions can be found still further east in Ohio and Michigan. The eastern half is broken only by the fringing forests of river valleys but the western half is interrupted by many mountain ranges.

The general grassland formation can be divided into three major associations on an empirical basis. The first of these associations, the tall grass prairie, borders on the deciduous forest, receives the most rainfall, has the greatest north-south diversity, and has the greatest number of major dominants. Bunch grasses are the conspicuous species, but sod forming species are also dominants. The mixed grass prairie occupies an area between that of the tall grasses and the short grasses and the dominants are derived from both these communities. The western limit of the association may be taken as the line where tall grasses disappear due to lack of precipitation and beyond which only short grasses are dominant. The last association, the short grass prairie, extends westward from the mixed grass prairie to the woodland zone of the Rockies with the relic short grasses as dominants.

Sometimes included in the grassland associations are the desert plains which extend from southwestern Texas through southern New Mexico and Arizona and northern Mexico. In composition, the desert plains resemble the short grass prairie of the Great Plains, and, when overgrazed, can hardly be distinguished from them in general appearance.

Intermediate between grassland and forest is the chaparral community which extends over a wide area and a diversity of habitats, and has a proportionately diverse composition. It includes at least forty species of evergreen shrubs with varying degrees of dominance. These may occur in many combinations, but invariably form low, dense thickets. The long, dry summers and the nature of the vegetation make frequent fires the rule.(33).

Types of Fire

Fires, whether occurring in grassland, chaparral, or forests, are divided by Daubenmire (12) into three types. Fires of the type that are flameless and subterranean are called ground fires. These occur wherever the soil is overlain with thick accumulations of organic matter which may catch fire and smolder for long periods. Almost all plants rooted in the burning material are killed.

Fires which sweep rapidly over the ground surface consuming little herb grasses and shrubs, and scorching the bases of trees are called surface fires. Subterranean organs and seeds may escape serious injury if not contained in the horizon of litter.

Crown fires are those which travel from the canopy of one plant to another in dense woody vegetation. Usually everything from the ground upward is consumed or killed, but sometimes the ground is moist enough so that many subterranean organs and burried seeds escape destruction. Depending on the burning conditions any one of the above fire types can be converted into any other type.

The Problem of Origin and Succession

Two important theoretical questions in ecology are why are grasslands found where they are and does fire play a role in maintaining them. Sauer (42) points out that grassland is found chiefly (a) where there are dry seasons or occasional short periods of dry weather during which the ground cover dries out; and (b) where the land is smooth and rolling. These conditions are universal in grassland areas and foster one known factor that operates effectively across such surfaces--fire. He believes there is no basis for a climatic grassland climax and that fire, as a chiefly cultural phenomenon, is the cause of vegetational drift toward grassland. This belief is based upon Sauer's observation that suppression of fire results in a gradual recolonization by woody species in every grassland known to him.

Anderson (4) believes fire is an important ecological factor. Climate favors grassland and this in turn favors fire. He differs from Sauer in believing that fire was set by natural causes before man appeared and that man merely utilized this phenomenon for his own ends.

A similar view is held by Transeau (47) who says that fire favors the persistence of prairie species in contrast to tree species. It seems, therefore, that fire retards development in forest climates and may promote shrubby growth, but does not retard development of grasslands. In a prairie climate, fire helps maintain and perhaps slightly enlarges the prairie.

There are many actual cases which show that fire has an effect on the extension of prairie. Gleason (20) observed that the location of forests throughout central and northern Illinois and adjacent states is closely connected with prairie fires. These fires drive the forests back toward the east, produce isolated groves of trees, and restrict forests on the west side of a stream to a narrower belt than on the east side of the same stream. He describes the process whereby thousands of acres of forest have been converted into prairie as follows:

> The prairie fire was a slowly moving fire, with its flames reaching heights of three to ten feet, or rarely more. When such a fire reached the margin of the forest, with even less fuel, its intensity and destructive power were further decreased, so that it is doubtful if mature trees were ever killed by fire. But the seedlings must certainly have been destroyed in large numbers, and the repeated charring of the bark of the larger trees led after a few years to their death.

Another interesting case of conversion from arboreal to herbaceous vegetation is reported by Buechner and Dawkins (8). In Murchinson Falls National Park near the equator in Uganda, East Africa, all types of woody vegetation are in the process of conversion to grassland under the combined influence of elephants (Loxodonta africana) and fire. Large trees are killed by fire damage to tissues exposed by the action of the animals in gouging, peeling, and ripping while foraging in the boles of the trees. Over most of the area south of the Victoria Nile conversion to treeless grassland has been completed. Without protection from fire, the continued existence of woodland is impossible. As more flammable grass material becomes available, the destructive force of fire with respect to trees increases in intensity and spreads over a wider area. Under present conditions 30 to 40 fire resistant species of trees are unable to attain maturity. Thus, grassland becomes readily established.

The effect of fire on climax vegetation in various areas is reported by Garren (19), who believes it is probable that the long leaf pine (Pinus palustris) forest of the southwest originated as a result of fire. He also thinks the southeastern grass-sedge bogs are definite fire sub-climaxes since they change to forest areas when protected from fire.

No conclusions can yet be drawn concerning the true role of fire in forming a grassland climax. The conflicting opinions probably stem from hasty generalizations based on local conditions. Edaphic, climatic, and biotic factors probably interact differently in different locales. These complex interactions and a lack of information prevent us from finding universal patterns of grassland development at the present time.

CHAPTER III

THE EFFECTS OF FIRE ON TALL GRASS PRAIRIE

Weaver and Fitzpatrick (49) describe the tall grass prairie as an area of moderately long, cold winters followed by hot summers with average day time temperatures between 70°F and 85°F. The growing season is characterized by sunshine, considerable wind, and average daily evaporation of 20 to 30 cc., and an average relative humidity of 40 to 80 percent. Mean annual precipitation varies from 25 inches in the northwest to 36 inches in the southwest. About 78 percent falls in fairly well distributed showers during the growing season.

Only recently have quantitative studies been undertaken to determine the exact effects of fire on the vegetation of this area. Older studies of this nature are characterized by qualitative approaches and sweeping generalizations covering all grassland areas. The more recent experimenters are more cautious in this regard and seem to be waiting for all the pièces of the picture to fall into place before making any generalizations. In 1941, Elwell, Daniel, and Fenton (18) reported that from their observations in Oklahoma, all burning should be be stopped because it reduces the quantity and quality of forage, causes a loss of nitrogen due to dissipation in smoke, destroys organic matter, and increases soil and water loss. Graber (22) in 1926 studied Wisconsin prairie and argues that burning appears to be injurious especially in bluegrass pasture. More optomistic and more cautious is Clements (9) who reported in 1928 that:

> Fire is of especial value in destroying the old stems of bluestem and bunch grasses, and making the new growth available for grazing. There is still a wide difference of opinion as to the ordinary effect of fire upon grassland and this is one of the many grazing problems which need exact investigation. Theoretically the burning of prairie every few years should constitute a desirable practice, if the year and season are chosen in such a way as to avoid injury to the underground parts. In the short grass and desert plains, fire could probably do more harm than good due to the dry soil. Annual fires in grassland are probably always harmful.

The time of year during which burning occurs in important when making a value judgement on the effects of fire. Aldous (3), working in a Kansas bluestem pasture (Andropogon scoparius, A. gerardi, etc.) where the rainfall is 31.14 inches per year, burned four times during the year: early spring (March 20), medium spring (April 10), late spring (May 5), and late fall (December 1). He found that the plots burned in late spring yielded more mature vegetation than those burned at the other times. Also, burning had little effect in controlling weeds and brush unless it was done in the late spring. The bluestem grasses on the burned plots were more leafy during the early part of the growing season than on the unburned plots, with the nutritive content depending on the amount of growth. In early June, the protein content was highest for the vegetation on the plots burned in the late spring followed by forage on the unburned plot, medium spring-burned plots were third, with fall and early spring-burned plots having the lowest protein content. The moisture content of the soil on the unburned plot was higher than on any of the burned plots. The plant population was greatest on the plots burned in the late fall and least on those burned in the late spring. Burning did not cause any decrease in organic matter or total nitrogen during a five year period. A three year study was conducted by Kucera and Ehrenreich (30) to observe the effects of annual spring burns on dry matter production and mineral composition in native prairie vegetation in central Missouri. The principal species were Andropogon gerardi and A. scoparius. The primary effects of spring burning were a marked increase in growth on burned plots and more numerous flower stalks of A. scoparius, A. gerardi, and Sorghastrum nutans. Ehrenreich (17) obtained the same results while working in the Haydn Prairie in northeastern Iowa. These findings are probably caused by the higher soil temperature in early spring due to removal of matted residues and to the greater absorptive capacity of a dark surface (4 to 17.5°F higher on burned plots). Under conditions of heavy litter and poorly drained profiles, the soil remains wet and cold for extended periods. Warm season grasses such as the bluestems are slow to resume growth but respond readily to higher soil temperatures. This fact is reflected in the early resumption of growth on the burned plots (7 to 10 days earlier). A growth stimulus due to the release of plant nutrients may also occur. Ehrenreich suggests that the removal of large quantities of carbonaceous materials and the probable effect on availability of soil nitrogen may be significant and require further study. No significant differences were noted between seasonally burned and unburned plots in total ash and nutrient composition.

Penfound and Kelting (37) not only noted the effects of burning at a certain time of year but included the factor of snow cover. They burned tall grass pasture near Norman, Oklahoma, when there was an uneven snow cover. Burning resulted in earlier growth in the spring, a reduction of aerial cover, a greater degree of utilization by grazing animals, increased light intensity, higher midday subsurface temperatures, decreased relative humidity, increased wind velocity at the surface, decreased soil acidity, and increased percentages of replaceable calcium and nitrogen. Burned over soils, therefore, exhibit slightly more favorable chemical characteristics but considerably less favorable physical characteristics than do soils in unburned areas. They suggested that controlled burning in the winter, with at least two inches of snow on the ground, might increase forage utilization in little bluestem (Andropogon scoparius) pastures.

To determine the effects of fire on soil moisture, Bieber and Anderson (7) burned an upland bluestem range site covered by "true" prairie vegetation in excellant range condition. Burning treatments included burning in winter (December 1), early spring (March 20), mid spring (April 10) and late spring (May 1). Forage yields were found to be largest on unburned plots with those burned in late spring ranking second. Early spring burning appeared to reduce moisture content in the soil, while no significant difference was observed between unburned plots and those burned extremely late in the spring. The greatest decline and fluctuations of moisture occurred in the upper two feet of soil.

Several studies have been done on the way forage is effected by burning mulch. One of the best of these studies was done by Dix and Butler (14) who compared burned and unburned portions of a thin-soil prairie in southwestern Wisconsin. They found that a mulch cover of 2.3 inches was completely removed by fire. At the end of the first growing season, the burned prairie had produced 0.68 inches of mulch while 0.2 inches were added to the unburned area. At this rate the mulch cover would accumulate to its original depth in about five years. Flower stalk production was greatly stimulated during the first year following the fire (prairie dropseed--25 fold, big bluestem--25 fold, and little bluestem--3 fold). The only species to show a sharp decrease was Sorghastrum nutans (4 fold). All except prairie dropseed and goldenrod showed a decrease in cover the first year after burning. Stimulation to flower production caused by burning or mulch removal will necessarily reduce the number of leaves produced, and consequently cover will show a decline.

The stimulation of flower production on burned areas was investigated by Curtis and Partch (11). They give the following reasons for profuse blooming of Andropogon gerardi after spring or autumn burning:

1. The fire's heat may have some direct effect on the buds although this is probably not important.
2. Liberation of mineral fertilizers from the ashes is responsible for a small increase in flower production.
3. The most important cause is the removal of the insulating blanket of old stems, thus permitting the plants to begin growth early and to build up a carbohydrate reserve before the normal period of flower initiation (responsible for a six times increase in flower production).

While a community may appear to react as a whole to some influence the reaction is nothing more than the composite reaction of individual species composing the community. For this reason, two similar communities may react differently to the same influence. The response of individual species is pointed out by Curtis and Partch (11) who made annual and biennial burns in March, May and October in a field of bluegrass where prairie plants had been artificially introduced. The response of the prairie plants to the fire varied with the species. For example, fire had no effect on Baptisia leucantha while the spread of Andropogon gerardi, Solidago rigida and Liatris aspera was favored.

The effect of fire on the chemical composition of an individual species was investigated by Smith and Young (44). They found that little bluestem samples collected from a burned pasture in Kansas were higher in crude protein and ash, and ranked somewhat higher in calcium than similar samples from non-burned pasture. Samples from the burned pasture were also lower in ether extract. No difference was found with respect to crude fiber, nitrogen-free extract, and phosphorus.

The best conclusions about burning in tall grass prairie areas is that it is probably not harmful, and is perhaps helpful, if frequency and time of year are considered. Aside from theoretical interest the problem of burning to increase meat production is a vital one, and can best be answered by studying the local conditions before applying a pasture burning program. Anderson (4) offers the best general summary of the effects of fire in tall grass prairie:

1. Burning removes protective mulch, allows surface soil to puddle during rain, increases runoff, and reduces the rate of moisture intake. The earlier the burning, the drier the

soil.

2. Fire does not kill weeds unless burning has been delayed until the last week in April. Weeds increase in plots burned during winter or early spring.

3. Burning does increase gains per head--at least for a number of seasons--but the reduced yields of forage make it necessary for the rancher or farmer to allow increased acreage if overgrazing is to be avoided.

4. Late spring burning (May 1) results in average annual gains of 266 pounds per head compared with 242 pounds under early spring burning (March 20) and only 235 pounds on unburned ranges.

5. Ranges burned in early spring have deteriorated severely in terms of bluestem grass cover and vigor of growth, while ranges burned during late spring have been maintained fairly well.

CHAPTER IV

THE EFFECTS OF FIRE ON MIXED GRASS PRAIRIE

Since the mixed grass region contains species characteristic of both the tall grass prairie and the short grass plains, the question arises as to whether this is simply an ecotome or a distinct association. The answer to this question is more one of definition than of absolute distinction. The primary factor to be considered is the decreased amount of rainfall. In the tall grass prairie, mulch accumulates rapidly and the high humidity and rainfall are effective in reducing damage due to burning. In the mixed grass prairie, there is less mulch and it accumulates less rapidly, allowing damage to plants and soil due to increased evaporation and runoff.

Hopkins, Abertson, and Riegel (25) studied 750 acres of mixed grass prairie in West Central Kansas composed of three general habitats: short grass--*Buchloe dactyloides* and *Bouteloua gracilis*; little bluestem habitat on hillsides--*Bouteloua curtipendula*, *Andropogon gerardi*, and *A. scoparius*; and lowland habitat--*Agropyron smithii*, *Andropogon gerardi*, *Elymus canadensis* and *Panicum vergatum*. All areas were spring (March 27) and fall (November 22) burned.

Observations showed that on all three areas there were losses in forage production and percent of basal cover. There were also losses in soil and organic matter due to increased erosion. The potential yield of this area in pounds of air dried forage per acre is 2,198,322 pounds while the actual yield was 959,473 pounds per acre. This means that burning caused a loss of 29,733 pounds of beef (assuming 60 percent utilization of 25 pounds of forage to produce one pound of beef). Spring burning proved to be more harmful than fall burning, and was especially destructive in areas where grazing had been light and accumulation of litter was heavy. Increased growth of ragweed, stimulated by spring burning, caused injury to the short grasses. Most damage was done to the individual species which maintained life in above-ground stems or crowns.

The authors of this investigation feel that the detrimental effects of pasture burning--accidental or planned--cannot be overemphasized. Their conclusion is consistent with their results, but this reviewer would like to see more research done before any hard and fast rules are made.

CHAPTER V

THE EFFECTS OF FIRE ON SHORT GRASS PRAIRIE AND DESERT PLAINS

The short grass prairie and desert plains are discussed together because of their similarity in climate and vegetational forms, and because a relatively small amount of work has been done in both regions.

Dix (13) found that in western North Dakota, where the annual rainfall is 16 inches, herbage production was positively correlated with mulch accumulation on unburned and completely protected relic grassland. The effect of mulch in this area contrasts with the retardation of plant heights and forage production due to mulch accumulation on the tall grass prairie. The importance of mulch in low rainfall areas is pointed out by Glendening (21) who found mulch aids in germination and emergence of native grass seedlings on depleted semidesert grassland. Therefore, fire appears harmful in short grass prairie where mulch destruction means deterioration of climax flora.

There are two schools of thought as to the value of fire in desert grassland (southeast Arizona, southwest New Mexico, and southwest Texas, 3,000 to 3500 feet elevation, 12 to 18 inches of annual precipitation in the west to 20 to 30 inches in the east, and a very high evaporation rate). One school would attribute all grassland area to the effects of fire, while the other school views these effects as negligible or lacking. Humphrey (27) feels the combined evidence is conclusive that fires in the desert grassland have been instrumental in preventing the establishment of woody species. One reason cited by Humphrey is the difference in the length of time required for grasses, as contrasted with most desert grassland woody plants, to mature sufficiently to produce seed. Since the dominant invading shrubs do not normally produce seed for several years, fires occurring at intervals shorter than this and killing the plants or burning them to the ground will continue to keep seed production suppressed. Recurrent fires may also maintain woody species in a juvenile non-fruiting stage which is as effective as completely killing them. Humphrey also feels that the slow invasion of fire protected grassland by shrubs is due primarily to the problem of seed distribution.

Grasses have a competitive advantage over shrubs because grasses are morphologically better adapted than shrubs to withstand the effects of fire. The growing points in dormant grasses are close to ground level where they escape the severest heat, while shrubs have their growing tissue exposed on the ends of branches and in the cambial layers just beneath the bark.

One problem facing the grassland ecologist is why most desert grassland ranges now produce much less forage than they once did. Today there is almost complete dominance of noxious shrubs such as Aplopappus tennicectis, Prosopis juliflora, Opuntia fulgida, Opuntia spinosa, and Larrea tridentata over many millions of acres of range land that were formerly grassland.

Humphrey and Mehrhoff (28) believe the invasion of the southern Arizona semidesert grassland is due to reduction of range fires. Such fires maintained the desert grassland prior to the introduction of livestock. Two other factors contributing to the shrub invasion are grazing by domestic livestock which has affected the composition of the vegetation in part because of seed dissemination, in part because of selective grazing, and in part because of the removal of grass by grazing that formerly served as fuel for range fires; and the fact that rodents bury mesquite seeds and transport chollo cactus joints, thus serving to propagate those plants. For example, Merriam kangaroo rats (*Dipodomys merriami merriami*) have been found by Reynolds (9) to become reduced in number where increasing perennial grass density forces out weedy annuals. Humphrey and Mehrhoff rule out climate as a factor in shrub invasion since no climatic change has been observed.

Reynolds and Bahning (40) have shown the destructive nature of fire in southern Arizona (7 to 27 inches annual rainfall). They burned a plot in June. One year after burning, herbage production of perennial grasses on the burned area was about half that of the controll area. One year later the perennial grass production of the burned area was equal to that of the unburned. Three years after burning, both areas were still comparable.

It is apparent that direct benefits in terms of improved range conditions are not obtainable by burning in low rainfall areas. However, in desert grassland, fire may be the one necessary factor in maintaining the grassland free of noxious shrubs.

CHAPTER VI

THE EFFECTS OF FIRE ON CHAPARRAL

Chaparral communities are extensive in California and Mexico, along the shores of the Mediterranean Sea and along the southern coast of Australia. A large number of plant species may serve as dominants, depending on the region. Usually, however, the climax vegetation consists of trees or shrubs with hard, thick evergreen leaves. In chaparral, fire favors shrubby species. In contrast, fire in grassland areas prohibits invasion by woody species.

In chaparral, the density of the brush stand is increased by burning and, as Horton and Krasebel (26) show, a scanty chaparral cover can usually withstand repeated burning without a loss of vitality. These investigators further report that summer and fall fires repeated at intervals of twelve years or more change a chaparral cover only temporarily. In the first few years after burning a temporary cover develops rapidly. This cover helps to stabilize the soils but does not prevent the eventual formation of a normal brush cover. While the relative abundance of the several dominant shrubs may be changed by fire, the general type of shrub cover remains unchanged.

The abundant germination of chaparral species in the first season following a fire was studied by Wahlenberg, Green, and Reed (48). They found germination of some seeds is increased by the heat of fire but germination of others is decreased. However, germination of certain plants in the burned areas was not due to the effect of the fire on their germinability but was due to conditions created by the fire, such as lack of competition by actively growing plants and by removal of litter. Certain plants were found to inhibit the germination of some species while having no effect on others. For example, *Brassica nigra* inhibits germination of *Salvia mellifera* but not *Ceanothus crassifolius*. The authors of the study concluded that removal of competition is the major cause of post fire germination in chaparral.

Finally, studies by Sampson (41) of soil moisture relations show such slight quantitative differences in freshly burned, as opposed to unburned, chaparral soils as to be of little ecological or economic importance.

CHAPTER VII

THE EFFECTS OF FIRE ON MISCELLANEOUS AREAS

Pickford (38) observed the effects of promiscuous burning on areas in Utah (5 to 20 inches of annual precipitation) which had been protected from grazing. These areas were spring-fall ranges, which include the lower mountain slopes and adjacent foothills. They consist of the following chief forage plants: *Agropyron spicatum*, *A. inermi*, *A. Smithii*, *Poa sandbergii*, and *P. nevadensis*. Pickford's observations indicate that burning tends to deplete the stand of perennial grasses and to allow annual grasses such as *Bromus tectorum* to increase in density. Sagebrush cover was destroyed and a slight decrease of grazing capacity occurred. However, the combined effect of grazing and burning resulted in a 50 percent reduction in grazing capacity.

Several investigators have turned their attention to the longleaf pine forests of the southwest. Garren (19) reports that summer fires or annual fires result in destruction or suppression of longleaf reproduction, and that frequent winter fires in the proper ratio to fire free years are essential to perpetuation of the longleaf forest. This conclusion is substantiated by Wahlenberg, Green and Reed (48) who found that annual winter burning maintained more favorable forage than did exclusion of fire. The smothering due to pine litter and accumulated dead grass retarded the growth of native grasses and legumes, and reduced the number of plants per acre. Cattle on burned areas gained 37 percent more than those on unburned areas.

Succession after fire in the longleaf fire area is reported by Hodgkins (24) to follow a pattern of forbs to perennial grasses to perennial woody species. This succession depends on the seedling and sprouting habits of the various species, and the ability of the various plant forms to develop in size and to avoid smothering under organic litter. Invading shrubs and woody vines offer the most substantial competition to trees.

Succession is similar in northeastern Minnesota forests as reported by Ahlgren (1). He observed that burned areas rapidly became covered with a lush vegetation of herbs the first and second growing seasons after burning. The first cover was important in determining subsequent plant succession since the cover created a shady, moist, cool microenvironment conducive to the early growth of woody plants. The first cover also trapped and retained nutrients released to the soil by ash, reduced leaching, and began rebuilding damaged organic layers. Animal life, especially small mammals and birds, was also observed to find suitable food and cover in this herb region. The early plant invaders retained a position of dominance for several years, but after the third growing season woody species began to dominate and establish the future vegetational pattern.

CHAPTER VIII

BURNING AS A TOOL

Most authors agree that fire can be used as a tool; fires can be purposefully set or excluded from a given area. However, before using fire, a thorough ecological knowledge of the area should be gained to insure effective land management. Several applications of fire have been made and are cited to show possibilities, not to form generalizations.

Fire is an essential factor in the environment of the extensive grasslands of East Africa and, for maintainance of pasture, it is accepted as a necessity. Edwards (16) reports that in the tall grass savannah, Themeda triandra has remained dominant only where periodic burning was practiced. Where burning has been suppressed, Digitaria abyssinica has largely replaced it. He concludes that in order to maintain suitable pasturage, it is necessary to employ fire periodically in the dormant season of the year after the bulk of the grass seed has ripened. Burning need not be annual if grazing is sufficient, and would probably suffice if used every second or third year.

In a central Louisiana grassland, Duvall (15) has found that prevention of large accumulations of herbaceous litter is the key to high herbage yields. He suggests burning ranges that have been ungrazed for several years before stocking them with cattle. Further, he states that on lightly grazed ranges, burning on a three to four year cycle maintains high yield, but does not appear to benefit herbage production on heavily grazed fields.

Most authors agree that burning on bluestem ranges will benefit beef production. Smith, Anderson, Koch, Brown, and Walker (43) found steers increased in weight on bluestem pastures burned April 1 to May 1 but also found reduced forage production. These results are explained by the research of Smith, Young, Anderson, Ruliffson, and Rogers (45) who compared the digestibility of forage from unburned and burned bluestem pasture. Andropogon gerardi, A. scoparius, and Sorghastrum nutans made up 50 to 60 percent of the total vegetation of the study area. Four digestion trials were conducted with 32 steers on spring burned (April 1 to 15) pasture. Apparent digestibility of crude fiber and dry matter was increased by burning in each trial. Ether extract digestibility was increased in three of the four trials. Burning increased digestibility of nitrogen free extract, of dry matter, but not of protein. Apparently the pasture benefited from mid-spring burning; however, the benefit was due to increased digestibility of vegetation and not to increased forage production, since there was no significant increase in forage consumption.

If burning of bluestem ranges is to be attempted, certain precautions are necessary. Anderson (4) suggests the following rules for burning bluestem pastures:

1. Do not burn unless accumulation of old tops is extreme.
2. Wait until late April before burning, or until the bluestem have begun to show green tops.
3. Burn only where the soil and plant crowns are wet. This prevents close burning and reduces damage to plant crowns.
4. Burn range downwind during a gentle wind (8 to 12 mph).

Another application of fire has been in the reduction of medusahead (Elymus caput-medusae). Medusahead matures later in the spring than most associated species and has a seed head moisture content of 30 percent for approximately one month after leaves and stems begin to dry. High temperature is most injurious to seed viability when seed moisture content is high. Coincident with these facts, McKell, Wilson, and Kay (32) found controlled burns of medusahead-infested rangeland were most effective in late afternoon when burning slowly into a mild wind, and at the soft dough stage of medusahead development.

Pechanec and Stewart (36) explored the possibilities of burning the dense sagebrush-grass ranges in southeastern Idaho. Here, due to the dense sagebrush cover, the livestock cannot graze satisfactorily. Lamb losses are great due to straying and palatible plants are deprived of soil moisture. They found good results following planned burning. The grazing capacity was increased 69 percent; perennial grasses increased 60 percent; and a change in availibility from 64 to 93 percent occurred. Soil losses from planned burning were light and soil movement, accelerated immediately after burning, was arrested almost completely by the end of the first spring season. The authors suggest reseeding the first fall after burning in range lands where the understory of perennial grass and weeds is light. Also, they point out that proper management after burning prevents the return of sagebrush and greatly promotes increases in the stands of perennial grasses.

Pechanec and Stewart give rules for proper burning in southeastern Idaho. Although these rules are indigenous to a specific area, they do have elements of good sense that should be followed regardless of the locale in which burning is to be done. Burning should be done:

1. Where fire can be controlled.
2. Where the principal use of the area is for livestock grazing.
3. Where soils are fairly firm and slopes are less than 30 percent.
4. Where fire resistant perennial grasses and weeds form more than 20 percent of the plant cover.
5. In the late spring or early fall, but not when perennial grasses are just making active growth or beginning to flower.
6. Not in drought areas.
7. Not earlier than 10 days after perennial grass seed is ripe and scattered.
8. On a hot, dry day with a steady moderate wind; fairly fast crown fires are needed in sagebrush areas.
9. Late enough in the day so that if the fire does escape, little time will remain before temperatures drop, humidity rises, and the wind goes down.

The following are suggestions for proper management practices to be followed after burning:

1. Burned areas should be protected from trailing by livestock during the first fall to prevent erosion.
2. Burned areas should be protected from grazing for one full year.
3. Light grazing should be permitted the second year, and thereafter should be no heavier than the range can support permanently.
4. The same management practice should be followed on areas burned accidentally as on those burned under planned burning.

The preceeding suggestions cannot be applied to all areas; however, they should stimulate those planning a burning program to anticipate the total management requirements.

CHAPTER IX

SUMMARY AND CONCLUSIONS

Dix and Butler (14) have commented on the research into the ecological effects of fire on vegetation:

> Prairie vegetation constantly varies because its many component species respond, each in its own way, to the multitude of environmental changes (biotic, climatic, etc.) occurring concurrently in the plant community. When the additional factor of fire is superimposed upon this already delicate sub-balance of natural forces, the responses become even more complex. Thus, the conflicting results obtained by workers in various parts of the grassland formation are to be expected since the many studies have been carried out under a wide range of experimental conditions and their results are not directly comparable. It is suggested that the place of fire in grassland management will be resolved only after considerably more experimental evidence is available from local areas, and, at that time the mosaic of local studies will demonstrate the general nature of the phenomenon.

Despite the caution necessary in generalizing from relatively few local investigations, certain generalizations can be made concerning the effect of fire on vegetation. The following list is based, in part, on the conclusions drawn by Ahlgren and Ahlgren (2):

1. Fire has been frequent in forest, shrub and prairie land for many centuries, and has probably been a major factor in determining the direction and rate of plant succession.
2. In most cases, severe fires increase erosion by lowering the ability of the topsoil to absorb and retain water.
3. The ultimate effect of the changed moisture relationship on

the water table apparently varies with different conditions and has not been investigated completely.

4. The temperature of the top soil during fire varies greatly, but below two inches, the temperature rise is not great.
5. Burning results in greater post-fire soil temperature extremes for a relatively long time after the fire. These temperature extremes may affect plant growth.
6. Reports of the effect of fire on soil productivity range from decreased plant growth to greatly increased growth, and each case should be considered individually.
7. The acidity of the soil is usually lower after fire. Generally there is also increased soil calcium, phosphorus, and potassium, but reports regarding increase and decrease in nitrogen are contradictory. Biotic nitrogen fixing activities in the soil are usually stimulated by burning.
8. In forest areas, fire frequently results in an increase in moss, lichen, and liverwort cover, certain species being characteristic of burned areas.
9. Fire influences the spread or destruction of numerous insect pests and plant diseases, especially in forest areas. Here again, each case must be considered individually.
10. Definite patterns of post-fire plant succession exist, but these are different for different sites and conditions.
11. A regrowth of herbs, grasses and shrubs occurs frequently the first few years following fire.
12. The effect of fire on plant reproduction varies with the species, largely because of different methods of seed

dispersal, seed survival and sprouting capacity.

13. As studies of Hank and Anderson (23) indicate, the long term effects of burning are important and may be different than expected.

14. The use of fire as a tool can increase beef production in certain areas.

Fire is most important in forest and grassland regions of temperate and tropical zones with dry seasons. In many areas it would be difficult to find virgin sections untouched by fire in the last fifty years. Primitive man regularly burned woods and prairie for practical reasons, while in other sections, lightening was, and is, a regular natural cause. Thus fire was a limiting factor long before the white man appeared on the scene in America. In his attempt to improve the environment man has protected many areas from fire. Results in some areas were favorable, while in others the land's productivity declined.

Research during the last thirty years has drastically changed many ideas about fire as an ecological factor. It is now evident that fire is an important component in the "climate" of many areas. As with most ecological factors man has modified its effects, especially since fire has not always been found to be detrimental to his interests. Properly used, fire can be an ecological tool of great value. It has potential since man is able to control it to a far greater extent than he can any other limiting factor.

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