FIG. 1. Sweeping grasslands of the Nyika Plateau (Malawi, Africa); roan antelope and zebra in foreground, near a natural pond.

Effects of Fire on Herbs of the Southeastern United States and Central Africa

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FIRE, as a tool for man, or as a powerful factor in natural ecosystems, has been of interest even before recorded history. Yet it is imperfectly understood for lack of carefully conducted studies and a tendency to misapply knowledge from one area to another. Various review articles or annotated bibliographies collect the literature on ecological effects of fire (Garren, 1943; Shantz, 1947; Komarek, 1964; and Phillips, 1965). Findings reported differ widely according to climatic setting and whether or not fire has been present sufficiently long to produce evolutionary adaptations in the vegetation. If fire is infrequent and erratic, or exceptionally severe, a community may be forced back to an early successional stage. But, if burning is frequent and mild, its effect may be the maintenance of a fire-conditioned community which would seem to many ecologists to be "natural" in a literal sense.

The information presented here is taken from two geographic situations deemed to be adjusted to frequent, though not necessarily annual burning. One is the southeastern coastal plain of the United States and the other a high grassland area, the Nyika Plateau in

Malawi, Africa. In both cases, fairly high rainfall is sufficient to produce broad-leaf or dicot forest, if not conditioned otherwise by fire. The Tall Timbers Fire Ecology Conferences (1962-1966) along with the usual scientific journals and even the popular press (Cooper, 1961 and Komarek, 1966) provide increasing documentation and understanding of the fire relations of our southeastern states. However, a bit of detail on this selected area of Africa is pertinent. (See also Shantz & Turner, 1958).

A comprehensive ecological investigation of the broad Nyika Plateau (750 square miles) was undertaken during 1963-64. It is a gently rolling plateau grassland which as yet is vacant or thinly populated by man. Nyika (Bantu term for wilderness or "empty grassland") is at elevations of 6,000 to 8,000 feet, and is centered at approximately 10° S. Latitude and 33° E. Longitude (Fig. 1). Though the days are quite long and the sun high, the climate is surprisingly temperate. Fire, as nearly as can be surmised, has occurred more or less regularly in the dry season, either set by man (Killick, 1963) or by lightning. Presence of eighteen or more endemic plant and animal species suggest stability of this habitat over a very long period of time (Lemon, 1964a). Grazing is largely by eland, zebra, and roan antelope, as well as a number of smaller herbivores. This ecologic influence is also presumed to have been a regular event, far into the past.

Therefore, it seems safe to assume that the whole area has burned with a frequency of 1 to 3 years, probably averaging near a two-year interval. Present estimates of the stocking by the large grazers is something equivalent to 10 acres per animal ("cow-sized") per month. If the grazing pressure were well distributed, this would be considered very light. The animals had certain favorite areas, but even these had only transitory use, rarely reaching 80% forage utilization.

IMPROVED GROWING CONDITIONS

Moderate grazing and occasional burning often seem to encourage vigorous growth and increased variety in herbaceous vegetation

(Lemon, 1964b; Biswell and Lemon, 1943; Boughey, 1963). Quite a number of suggestions have been advanced to explain this response but one of the most concrete may be the distinctly increased soil temperature that sometimes results. This can be vividly brought out with data collected in the long-leaf-slash pine type in the lower Coastal Plain of Georgia (Fig. 2). Wahlenberg (1937), working in Mississippi, had similar experience in that at the three inch depth the soil was 5.5° F warmer on burned areas. In Kansas, Aldous (1934) showed that soil temperatures on burned areas were somewhat higher than on protected areas, and considered that the higher temperatures were responsible for more rapid growth of the grasses until early June, at which time temperature ceased to be the limiting factor.

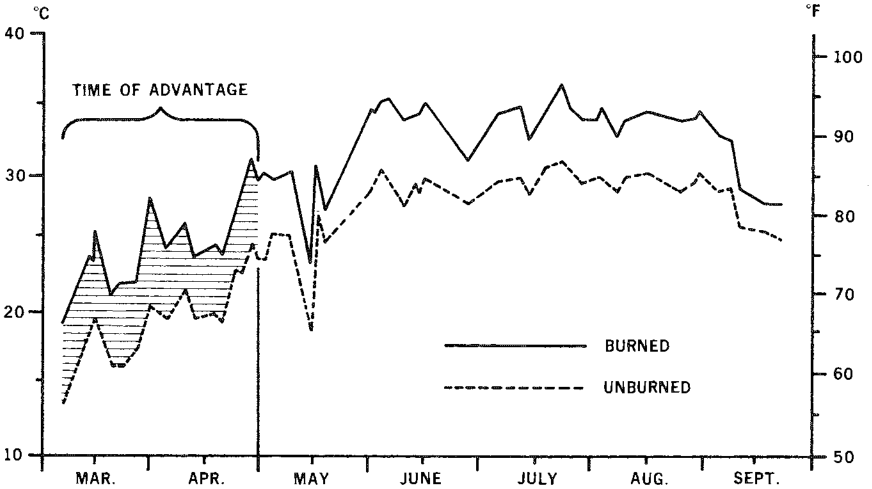

FIG. 2. Soil temperatures at three inches depth, 5 PM, comparing burned and unburned areas in the coastal plain of Georgia (U. S. A.).

In South Africa, Phillips (1920) found that a covering of unburned vegetation kept the soil at a more even temperature, inferring that this was an advantage over burning. Staples (1929), also working in South Africa, wrote of greater extremes of soil temperature after burning treatments.

Care must be used in interpretation of an alleged advantage due to higher soil temperatures. Perhaps two points give real benefits, particularly to herbaceous vegetation: (a) an earlier start in the spring growth and (b) certain increases in the activity of soil organisms. Notice that on Fig. 2 no advantage is claimed after about 1 May, when soil is sufficiently warm anywhere.

Haig (1938) reported an increased number of microorganisms, chiefly bacteria, as a result of burning. Ordinarily, any increases in the activity of soil organisms would be advantageous to plant life. On the other hand, Fletcher (1910) did not believe that the advantages of heating the soil could be attributed to increases in the bacterial flora nor to increases in soluble matter; he held rather that the heat destroyed some toxin that was normally present in the soil prior to treatment.

Most of the reports on mild burning show that the chemical characteristics of the soil are made slightly more favorable to plant growth by burning, or that at least the soil is not adversely modified. Alway (1927) found that the soil was somewhat more fertile after burning.

Heyward (1936), working in the southeastern coastal plain, reported increases in both soil nitrogen and organic content following burning treatment. Others attempt to explain the mechanism for replenishment of soil nutrients, as assisted by light fire. Leukel (1937) stated that most pasture plants produce entirely new shoot and root systems each growing season. Presumably he was referring to herbaceous plants, especially grasses and other plants that do not have a prominent tap root. If this is true, then the roots of the old plants are available for decay and return to the soil each year. Greene (1935) emphasized the fact that the replenishment of organic matter and nitrogen in the soil seems to come primarily from the decay of underground plant parts, rather than from material decaying on the soil surface. If these suggestions are true, they may help explain why loss of the surface litter by mild burning does not cause depletion of soil nutrients.

Some indirect evidence on soil nutrients is contributed by chemical analysis of plants from burned and unburned areas. American studies by Fraps and Fudge (1940), and Stoddart (1941) have shown that plants are materially affected by the soil on which they grow, producing forage with high mineral content when the soils are high in minerals. An exhaustive treatment by Beeson (1941), who reviewed 607 articles on the subject, indicated that soil minerals influence the mineral content of plants but that climate, age of plants, part of plant used, and other factors also influence the chemical composition. Tinley (1966) remarks about release of potassium brought about by burning plant litter.

RESPONSES OF HERBACEOUS LEGUMES

The sponsors of my African research* were interested in the carrying capacity of the Nyika grassland and, particularly, the nutritional welfare of the large antelopes and zebra. Thus, I stressed investigation of the relation of fire to forage quality and quantity. Various non-woody legume plants were observed and measured, primarily because they served to provide an index to the general nutritional picture of this community.

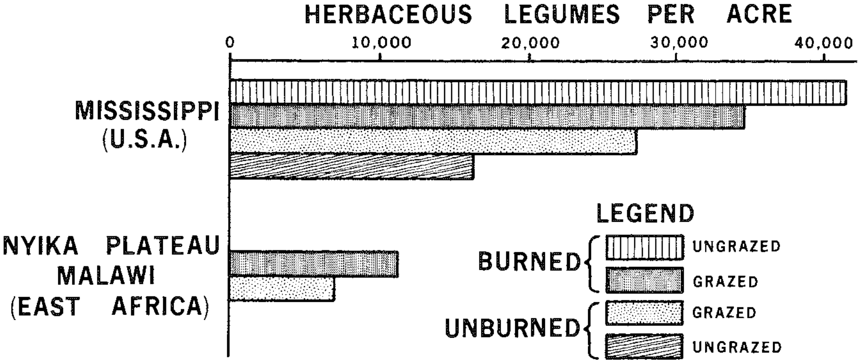

FIG. 3. Number of herbaceous legumes per acre, Mississippi (U. S. A.), and Malawi (Africa) compared.

In the first procedure, using a "modified quarter method" (Curtis and Cottam, 1962; or Lemon, 1962), field assistants were trained to throw a cross of two bamboo wands behind themselves. Falling at random, the cross formed four quadrants about a point. Measurements were made from the center to the closest herbaceous legume

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plant. Distances were recorded to the nearest centimeter, and each legume plant was identified. Compilation of the results was simple and allowed estimation of the number of plants per acre, as summarized in Fig. 3. This same graph allows comparison of findings reported in Mississippi by Wahlenberg *et al.* (1939).

A second method involved randomly distributed circular plots, each containing ¼ square meter area. This procedure was mainly carried out by two Grinnell College students* who tossed a hoop about so as to observe twenty or more plots on each ½ acre fire-history replicate. They recorded the number of legume plants occurring in each circular plot. This procedure yielded even more striking results. When annually burned areas were contrasted with unburned areas the number of legume plants was almost four times as great, where burned.

Finally another set of field assistants, uninformed about the first two methods, conducted a third survey. Elongate rectangular plots were studied, particularly to count the individual stems of *Aeschynomene oligophylla* (Fig. 4). To avoid a possible error in counting close neighbors that might seem as one plant, all stalks or stems were tallied, to give a grand total for each plot. In objectivity, it was thought that this method might be an improvement upon the first two procedures. Study plots were 2 x 20 meters in dimensions, one plot in each treatment replicate. The unburned area contained an estimated 22,750 stems per acre. In contrast, the annually burned area was estimated to have 66,000 stems of this nodulated legume per acre.

EFFECT OF FIRE ON REPRODUCTIVE PROCESSES

The impact of burning affects plants in a variety of ways. Applied plant physiologists have been interested for many years in environmental manipulations which induce fruiting, yet reports on use of fire to stimulate seed production are infrequent in the literature (Burton, 1944; Biswell and Lemon, 1943). Stoddard (1931) no-

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* John Edgren and Philip Northen.

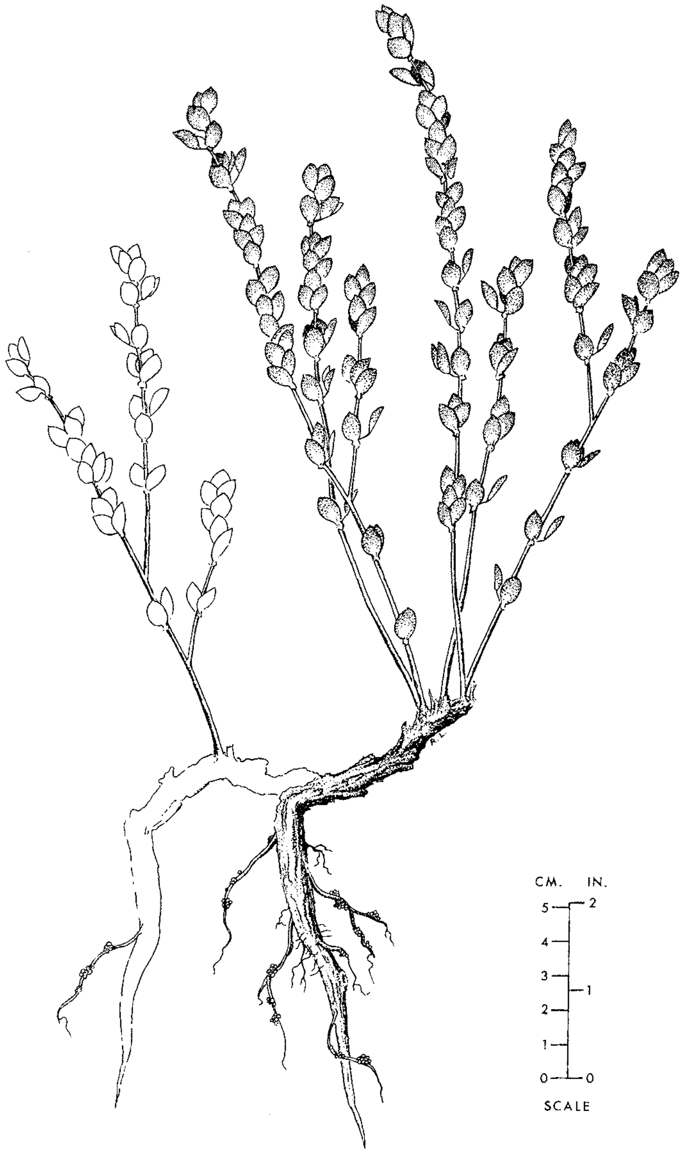

FIG. 4. *Aeschynomene oligophylla* Harms or "phunga" (Bantu dialect of East Africa), an herbaceous legume plant common on the Nyika Plateau of Malawi.

ticed stimulation of legume growth by fire, in Georgia, and suggested that it might be due to removal of dead portions of competing grasses, to "plant food" released in ash, to increased germination of hard seeds heated by fire, or a combination of all these factors. He also suggested that an occasional fire seemed to serve a useful function as a pruning agent which stimulated fruiting for several seasons.

My own field studies have yielded interesting data on the responses of certain fire-conditioned grasses to fire treatments. All of the grasses listed in Table 1 are dominant herbaceous species, either in the southeastern coastal plain or the Nyika grassland in Africa.

TABLE 1: SEED STALK PRODUCTION OF DOMINANT GRASSES, AS AFFECTED BY FIRE TREATMENTS

Species	Unburned	Burned
AMERICAN SPP.*:		
Andropogon tener (Nees) Kunth	35	112
Aristida stricta Michx.	0	88
Sporobolus curtissi (Vasey) Small	0	18
AFRICAN SPP.**:		
Annuals (*Eragrotis* and *Panicum* spp.)	24	128
Exotheca abyssinica Anderss.	12	62
Loudetia simplex (Nees) Hubb	10	18

* Figures given on a per clump basis, except that *A. tener* is an estimate for a square foot. (Coastal Plain of Georgia, U. S. A.)

** Figures given on the basis of 5 square meters. (Nyika Plateau, Malawi, Africa).

It is not necessary to assume that fire has a mysteriously beneficial effect upon the physiology of the plants. The more logical assumption is that these grasses (dominants) have made evolutionary adjustments for enduring fire, or possibly have taken advantage of the improved soil conditions that may follow burning. Not only did the grasses produce seed stalks, but it was found that the Georgia grass heads contained some 60 to 80% viable seeds. In addition to *A. stricta* and *S. curtissi*, many other coastal plain species produced more flower stalks on burned areas. At the time of the early leaf stage and the full leaf stage there was some tendency for the plants on the burned area to have higher nitrogen content. Yet at the time of anthesis only *Andropogon tener* had a higher percentage of nitrogen on the burned area. This species bloomed on both burned and unburned land, but other dominant species rarely flowered on unburned areas.

AMOUNTS OF HERBAGE PRODUCED

In addition to the features just discussed several studies have been made to determine the amount of herbaceous material produced, in the Georgia coastal plain. A comparison of the timing and amount of growth on burned and unburned areas showed that herbs started sooner and yielded more on the burned areas. Measurements of height growth and estimated ground cover of leading grass species indicated that growth was nearly a month earlier on the burned area as compared with the unburned area (Fig. 5). In fact, growth on the area burned in December was much ahead of the area burned in January. The final yield of herbage in the fall was determined by obtaining the dry weight of clippings. Although clippings for the first growing season provided a precise measurement, advantages were not confined to one season. The same trend was found also in estimates of the amount of ground covered. Considering all studies, there was a range of 6.4 to 41.3% more herbage produced on burned areas as contrasted with unburned.

Several factors influence interpretation of increased herbaceous growth on the burn. Higher soil temperature during spring and summer has already been mentioned and is doubtless an important influence contributing to earlier growth on burns. Chemical analyses gave some clue to possible increases in soil fertility after fire. In particular, greater nitrogen content in forage grown on burned areas may reflect increased vigor. In addition to my studies, Heady (1960) reports similar findings in East Africa.

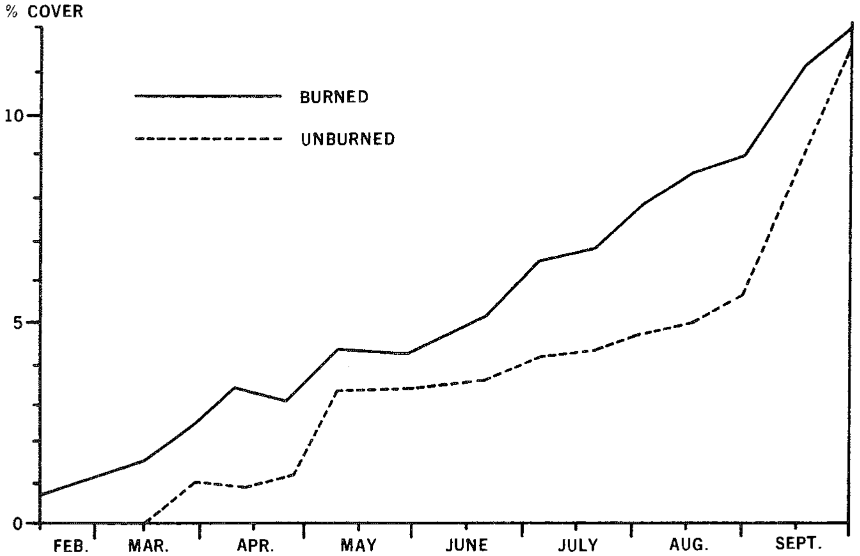

FIG. 5. Ground cover of Curtiss Dropseed, *Sporobolus curtissi*, on burned and unburned areas of the Georgia coastal plain (U. S. A.)

Besides favorable soil temperature and fertility there are two other factors of importance. The first is the removal of great accumulations of dead litter composed of grass leaves and other debris. This debris impedes growth because it obstructs light, intercepts rainfall, keeps seeds from reaching the ground, and is of great physical bulk, actually suppressing the upward growth of plants. Often tangled herb or grass leaves that are unable to push through it have been observed.

Another way in which burning assists in promoting growth of herbaceous vegetation is by removal of old shoots and foliage. This senescent tissue is less active and functions poorly, as compared with fresh young parts. It is farther from the roots and is furnished with water and nutrients with more difficulty. Leaves of *Aristida stricta* sometimes attain a length of more than 40 inches, but they often show loss of vitality and drying at the tip of the leaf. In compact bunchgrasses like *Sporobolus curtissi*, the removal of old leaves obviously makes room for new ones to grow.

NATURE OF ADAPTATIONS

Once the responses of plants to fire are well understood, it is of great interest to look into structural and physiological adjustments typical of successful fire-conditioned species. Frequent burning, extending far back into prehistoric times, has resulted in selection of species in such a way that present vegetation of the pine subclimax is predominantly made up of species which are well equipped to withstand fire (Hodgkins, 1958). The evolutionary adaptations which appear to be of survival value comprise features preventing destruction of vital vegetative tissues as well as large production and efficient dissemination of reproductive bodies.

The "principal herbs," *Sporobolus curtissi* and *Aristida stricta*, are bulky bunchgrasses that together constitute over half the herbaceous cover. When protected from fire, these two species retain their leaves for parts of two growing seasons, remaining green during the intervening winter. Their meristems are 1½ inches or more below the soil surface, safe from being killed by all but the most severe fires. The mature and dead leaves of these grasses, which are rich in lignin, gradually accumulate and eventually choke out many associated species. *Sporobolus curtissi*, *Aristida stricta*, four other important grasses, and some dicot herbs do not usually produce flower stalks when left unburned. The next season after being burned they fruit in profusion, more so on summer burns than on winter or early spring burns. This brings about the reseeding of an area at times favorable for germination and establishment of new plants.

The "secondary herbs" are a group of five species that are commonly associated with the principal herbs in lesser quantities. They have much the same characteristics as the two leading grasses.

"Fire-followers" constitute the third ecological group of herbs. They are highly mobile and seem to be able to colonize rapidly an area made available by fire. Many species of this group produce a large number of relatively small disseminules. The grass fruits often have awns or hairs that facilitate dispersal, and others have panicles that break off and roll about. Considering ground area covered, composites are the most important group of dicot herbs. Most of them have several heads per plant, and produce wind-carried achenes.

Many of the fire-followers have efficient vegetative methods of increase in addition to that of sexual reproduction. Several grasses and herbaceous dicots have rhizomes or crown buds, and some of the grasses are efficient in tillering.

DISCUSSION

Questions of the effect of fire on vegetation and the land have been troublesome in the past due to the complexity of the problem as well as difficulty in clearly expressing various reasons for intentional use of fire. Fire ecology continues to be an extremely complex subject, but perhaps we are overcoming some of the difficulty of language as well as accumulating a store of accurate data. Much of the improved understanding is attributable to better information about the physiology of fire effects along with general progress in the field of ecology.

The pattern of food reserves and vigor of plants can now be described in much simpler terms than previously. It has been long observed, by both primitive peoples and scholars, that fire gives a burst of new growth for almost all plant species. Whether or not it is a good thing depends upon the events just following this period of new growth. If the photosynthetic tissues increase quickly and are not grazed off severely, the plant will manage very well. Even if grazed, as long as ample food reserves are available a plant can continue its annual cycle normally. In situations where there is a strong economic interest it is highly advisable to make biochemical studies of the food regimen throughout the seasons. Collections should be made at biweekly intervals. It is important to study both foliage and root systems for assessing the quantity of stored foods.

Even without exhaustive biochemical studies it is possible to follow the vigor of each important species in a community. A skilled ecologist will make either cover or biomass estimates to determine whether a plant is participating in the normal community life of the vegetation type as expected. The present study attempts a comparison of fire effects on two very widely separated areas where climate and soil are also dissimilar in many respects. Yet, there is one significant way in which the two situations are comparable: the performance of legumes is used as an index to general health of the herbaceous cover or forage. This idea resembles numerous studies in the literature which report crude protein or other expression of nutritional value of burned plants vs. unburned plants (Edwards and Bogden, 1951; Heady, 1960; and others). The criterion employed in the present study is just as direct and perhaps a bit more concrete, within its obvious limitation. While the author is not attempting to estimate the total amount of forage produced, at least this specific attention to a nitrogen-fixing herbaceous legume should be strongly suggestive of nitrogen cycles in the community and should imply certain fertility relations. The information obtained in Mississippi by Wahlenberg, *et al.* (1939) and new data offered in Fig. 3 of this paper show that desirable legumes are encouraged by judicious use of fire. The mechanism bringing about this desirable condition is probably removal of litter and senescent foliage of the grasses, dicot herbs, and low shrubs, which often accumulates over a period of several years. If grazing or decay processes are too slow, fire is an effective way to induce new growth and permit the sunlight to strike the leaves without excessive shading. Secondary advantages such as higher soil temperature, release of ash nutrients, and other points have been mentioned from time to time.

On the other hand, deterioration of a community type results when two or more strains are placed upon plants in short succession with but a brief interval between. When fire removes foliage, it is necessary for replacement to occur and this requires a drain on reserve foods. If some combination of frost, fire, or grazing is so timed that two of these happen in short succession, there may be too great a demand for the plant's reserves. If this occurs at a point of natural ebb in stored foods, there may be a severe loss in physiological vigor. It is essential that there be sufficient photosynthetic activity to allow regrowth, supported by current production plus the available food reserves. Unless this can be assured, with at least a small margin of safety, plants fall behind in their ability to grow and compete normally. These compounded blows are sometimes responsible for the weakening or death of desirable plants.

SUMMARY

1. A brief survey of literature gives the background and present state of knowledge as it pertains to the method adopted in this paper. Although we now have substantial information on the broad aspects of fire effects, there is great need for precise quantitative data such as the annual cycle of plant food reserves, plant-animal interactions and similar questions.

2. A comparison is made between the southeastern United States and a selected area in East Africa (Malawi) with reference to effects of fire on grasses and herbaceous legumes. In both areas there appears to be a richer flora under light burning and moderate grazing.

3. Improved nitrogen cycling, and therefore greater community productivity, results from wise use of occasional burning, coupled with a reasonable intensity of grazing. Trained skill and judgment are required to determine the correct timing of burning and to care for the soil properly.

4. To conserve our natural resources, it is necessary to make repeated studies of vegetation and wildlife in order to currently revise plans for the best practices with respect to grazing and the use of fire. The two influences nearly always work together and thereby constitute a very potent ecological force. Beneficial guidance by man is a serious scientific undertaking.

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