Burning and Tropical American Savannas

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The question of the effect of fire on vegetation development has always been a controversial one. Especially for the scientifically little-known tropical American savannas, the scanty available information from local sources is often expanded and made to cover more than was originally intended by the authors. These generalizations are then repeated over and over again, without a thorough check to see if the extrapolation is valid, and soon they are accepted as facts by others who have to depend on the literature for their information.

As the term “savanna” is controversial by itself, some explanations are due here first. The origin of savanna is found in the language of the Caribbean Indians and adopted by the Spaniards as “sabana”; Habana in Cuba is another derivation of this term. The general indigenous meaning of open clearings in forest was later adopted by plant geographers to indicate a specific vegetation type. Thus we find it in Grisebach's treatise on the Vegetation of the Earth in 1872, where he relates savannas with lack of moisture (Page 340):

"Daechte man sich die Baume entfernt, so wuerde der Wasserdampf sich nicht so haufig verdichten, es wuerden Savanen entstehen . . ."

(Where the trees are wider apart, the humidity will frequently not be so great, savannas will be formed . . .)
One feature of the earlier descriptions of savannas, was the inclusion of trees in the savanna definition. Drude in 1897 expressed it in the following manner (Page 275):

"Le manque d'arbres est considéré comme une marque distinctive des steppes proprement dites . . . L'adjonction de plantes ligneuses, tropicales, de plantes grimpantes et d'epiphytes caractérise les savanas"

(The lack of trees is considered as a distinctive feature of the steppes proper . . . The addition of tropical woody plants, climbers and epiphytes characterizes the savannas)

The distinction between savanna and steppe on the basis of presence and absence of trees, was maintained by Schimper (1903) and Warming (1909). Schimper also maintained the climatic origins of the savanna, although he mentioned soil influences as an additional factor (Page 364):

"When the trees become closer, the savannah passes into savannah forest, and when the trees disappear it passes into steppe. Such transitions are frequent, and are sometimes occasioned by climatic causes, but more frequently by changes in the nature of the soil."

This characteristic presence of trees in savannas, was not included in the original indigenous meaning of the term, as mentioned by Oviedo (Page 1535):

"Este nombre de sabana se dice a la tierra que está sin árboles, pero con mucha y alta hierva, o baxa"

(This name savanna is given to areas without trees, but with much high grass, or short)

In the more modern work on savannas of tropical America, the definition of Beard (1953) is usually accepted:

". . . a virtually continuous, ecologically dominant stratum of more or less xeromorphic herbaceous plants . . . and with scattered shrubs, trees or palms sometimes present." (Italics mine)

Beard added a limitation to tropical America to this definition, a limitation which will be maintained here, because if African or temperate American savannas are added, the discussion can become endless.
As we have already seen, early investigators ascribed a climatic or edaphic origin to the savanna vegetation in tropical America. Apparently they were little impressed by fire as an environmental factor, except as a secondary influence once the savanna was formed. Controlled burning experiments, such as those of Trapnell (1959) in Africa, have not been undertaken in tropical America. At the most, the effect of 3 years of fire protection on savanna development was measured and data were accumulated over 2 years of burning in different seasons (Blydenstein, 1963). During this study, dry matter on the unburnt savanna just accumulated, new growth being added to the previous years' production, until 10,000 kg/ha of dry matter of standing herbaceous vegetation was measured in the third year. For 2 consecutive years, the highest dry matter production was measured in the rainy season on those plots that had been burnt early in the previous dry season. The regrowth on plots cut with a mower at the same time was significantly lower, and similar to the regrowth on plots burnt towards the end of the dry season (see Fig. 1).

Eden (1967), remeasured some of the plots in 1965, after 6 years of fire protection. Compared to 1962, total plant density had increased from 96 to 111 plants/square meter, although the percentage of grasses in the vegetation had remained stable at around 78 percent. Part of the experimental area had been burnt the previous year, in a particularly destructive fire running through the accumulated organic debris. On the burnt area, herbaceous density was significantly less, and several sedge species had increased at the expense of perennial grasses; many dead grass tufts could be observed.

The accumulation of dry matter, when unburnt, and the relatively high annual production of the herbaceous vegetation, leads to one generalization about fire in tropical vegetation which might safely be made. In order to burn, enough dry matter must be produced to provide sufficient fuel to carry a fire. In the tropics, where temperatures are fairly uniform throughout the year, the growing season coincides and is dominated by the rainy season. If the rain that falls during this period is sufficient, an abundant vegetation development will take place. If the climate is too dry, a desert-type vegetation is all that develops, and fires are not very prevalent. On the other hand,
FIG. 1. Large amounts of accumulated vegetative matter will burn easily during the dry season—Experimental burn in the Venezuelan llanos.

if there is no significant dry season, the desiccation of the vegetation and the production of a suitable fuel is not completed, and again fires are rare in standing vegetation.

Thus the tropical wet and dry climate, with its alternating rainy and dry seasons, is a prerequisite for good burning conditions. With no temperature limitations, a 6-month growing season with a 50-inch rainfall, produces a development during these 6 months almost equivalent to a similar period in a region with 100 inches of rainfall.

The tropical wet and dry climate has been called a “savanna climate,” because the long dry season following a continuously rainy wet season was considered “hostile to woodland” (Schimper, 1903). In actual fact, however, the major part of the region with a tropical wet and dry climate is covered by deciduous forest in the American tropics, or at least its visible remnants. The leaf-shedding of these tropical deciduous forests is rainfall-controlled, and physiological activity does not cease completely, as no low temperatures are in-
BURNING AND TROPICAL SAVANNAS

One effect of this is the prevalence of a flowering season during the last part of the dry season, with flowers blooming on the dry, leafless tree branches, and fruit and seed formation completed by the time good growth conditions return with the rainy season.

The dry leaves which are shed form a fuel which will carry a fire in the dry season, but the woody tree trunks and stems of shrubs are not too combustible and will largely resist consumption by the flames. The resprouting of the leaves in the following rainy season obliterates most of the evidence of burning during the previous dry season.

It is often postulated, that savannas derive from deciduous forests destroyed by repeated burning. Although there is little argument about the dominant role of fire in the environment of savannas, once these are formed, the role of fire in the destruction of forest must be studied in the forests which are supposedly destroyed, and not in the savannas which are the end-product. No long-term studies of this kind are available for tropical America, but the African experience (Trapnell, 1959) has shown that there the woodland persists in a shrubby grassland, even under burning conditions most unfavorable to woody vegetation development.

The most that can be done at present in tropical America, is to refer to the many observations of tropical deciduous forest which has given way to more or less open grassland. All these observations are based on the fact, that trained observers have been able to recognize the signs of forest relicts within these grasslands and the general tendency to vegetation succession in the direction of forest development. Such degraded forest is very common in tropical America and is usually associated with cultivation and forest clearing practices, among which fire plays an important, but not exclusive role.

The extrapolation of such information to all grasslands in the American tropics is not valid, however. Where the obvious signs of previous forest vegetation are absent, it is dangerous to assume that savanna development had the same origins as in other areas, where forest relicts can still be found. The usual defense for such extrapolation is that the process has been active for a longer time, and thus the forest was destroyed more completely.

Again we can cite an interesting publication about Africa (Buechner and Dawkins, 1961), to show how trained observers can even
recognize minimal signs of previous vegetation. On the basis of a few forest remnants and scattered forest trees in the present grassland, these authors postulated a grassland development initiated through overgrazing and debarking by elephants, and then expanded by burning. The question is, what observations are available for tropical America?
The most extensive woody grasslands and open woodlands are found in Brazil, where they are called “cerrado.” Ferri (1963) has written an excellent summary of the literature available on this vegetation type, and reached the conclusion that in some cases this vegetation must be considered a climax. Although its species exhibit certain characteristics of xeromorphy, the cerrado vegetation is not, as a rule, limited by lack of water; stored water in the very deep soils is tapped by the extensive and deep root systems of most of the woody cerrado species.

In the same Symposium publication, Rizzini (1963) gives a detailed account of the cerrado flora. He dismisses the herbaceous and suffrutescent component of this flora as no more than an extension of the open grassland (campos limpios) flora. Of the shrubby and tree species in the cerrado flora, 58 percent originate in the surrounding, more humid rainforest formations of the Amazon basin, while 42 percent are characteristic of the xeromorphic forest known as “cerradão,” peculiar to the Central Plateau of Brazil. The cerradão vegetation exhibits little dynamic behavior in the form of nutrient cycling between vegetation and soil, a very important factor in tropical forest vegetation. As an example, data are cited from Rizzini and Heringer (1952), which show a higher organic matter and mineral content in soils under a mesophyl forest grove compared to cerradão vegetation only a few meters away on similar soil.

On a floristic basis, cerrado vegetation grades into cerradão, with a significant herbaceous component coming from more open grassland vegetation, but no successional connection is established.

A different case is presented by the open grasslands of the Llanos region of Venezuela and Colombia. The herbaceous vegetation is dominant here, and woody plants form a minor component. Both the herbaceous and woody vegetation shows much variation over the whole of the region; Blydenstein (1967) distinguished 10 major savanna types, based on herbaceous vegetation, in the Colombian Llanos. The woody vegetation is distributed quite independently from this herbaceous cover, however. A typical tree of the drier savanna types was Curatella americana L., of the Dillenaceae, a spe-

*It should be pointed out here that “cerrado” means “closed” in Portuguese, while the ending “dão” is a superlative, in this case “more closed”.

7
FIG. 3. Especially fierce fires may destroy even highly fire-resistant trees in the open savanna—Curatella americana in various stages of fire damage in the Colombian llanos.

cies excellently adapted to an environment where burning is frequent. There are even indications that the germination of its seeds is improved after passing them through a flame.

Another example is the presence of Caraipa llanorum Cuatr., variously classified with the Guttiferae or Theaceae. This species is found in a restricted habitat within the Mesosem savanna. The savanna is characterized by seasonal inundations, the tree is found in low depressions, where water collects to form the start of small streams. At the edges of these depressions, just above the level of inundations, and in many similar, extremely moist habitats, Byrsonima crassifolia HBK, of the Malpighiaceae, is found. Other species of Byrsonima are found on inundable sites with heavy clay soils.

These examples of individual trees growing in the savanna, are cited here, as they all belong to old plant families and testify to the antiquity of some adaptations to the environmental conditions found in the savannas. Wymstra and Van Der Hammen (1966), in pollen studies of savannas in British Guyana and Colombia, found that for the last 10,000 years at least, or since the last ice age, an unstable equilibrium has existed between Byrsonima-dominated forest and
grasslands. These authors think that human influence on this balance has only acted to an important degree since the last 1000 years, previous fluctuations being principally due to natural factors, such as lightning fires or drought.

Quite another type of tree growth on the savannas is found in the scattered groves encountered in some landscapes. The development of such groves was studied first by Blydenstein (1962) in Venezuela, and encountered again in Colombia (Blydenstein, 1967), although with different woody species in a different savanna type.

One or two tree species, which can become established by themselves in the savanna, form the nucleus for such grove development. The presence of these nucleus species alters the environment apparently enough, so that other woody species can become established under their protection; these other species are rarely found by themselves in the open grassland. Fairly soon an outer ring of xeromorphic shrubs protects the developing grove from most grass
fires, by providing little in the way of fuel to carry a fire into the interior of the grove. Thus protected, the trees within the grove develop and further modify the environment, especially temperature and soil humidity, within the grove. Expansion of such groves is very slow, however. Blydenstein (1962) could measure no differences in grove size on aerial photographs and on the ground, over an 11-year period. The species composition of the groves was also different from the species composition of nearby forests in every case, indicating that such grove development was not a direct step in vegetation succession from savanna to forest. In the same area, Eden (1967) found that a few of the typical grove species did become established in the open grassland, when protected from fire. After 6 years of fire protection, these grove species added up to 9 percent of the total trees found in the savanna, the other 91 percent being formed by the 3 tree species commonly found in the open grassland. All the new trees were destroyed in a single fire at the end of the protected period.

González (1967), who studied seed germination in the same area, tested germination percentages of a group of species common to the groves, after submitting them to burning in the field and controlled high temperatures in the laboratory. Only one species, _Bowdichia virgilioides_, a leguminous tree common to the open savanna, showed appreciable germination after controlled high temperatures, although its seeds did not survive experimental burning in the field.

Blydenstein (1967) noted mortality caused by fire even in such highly resistant species as _Curatella americana_, in savanna areas of Colombia. Aerial photographs showed markings which indicated that such mortality apparently is widespread and fairly recent, but at the same time showed that, if such a woody vegetation previously existed, it took the form of widely scattered individual trees.

In other cases tree groves are found which are forest relicts. These groves can often be distinguished by a characteristic elongated shape, formed by fires always coming from the same direction under the influence of the trade winds; or the groves are located in protected sites and show no special structure or species composition, ranging from one or a few trees to several acres in size. Often these forest relicts are associated with particular savanna types.
The lack of evidence of immediate succession towards forest upon the cessation of burning, is often interpreted as a secondary effect due to the changes wrought in the soils through centuries of repeated burning. Highly emotional references are made to the burning up of organic matter in the soil and the consequent loss in nutrient status. Some of these references can be traced to a direct comparison between the fertile black soils of temperate grasslands and the poor latosols of tropical grasslands, without proper appreciation of the differences in climate on the respective soil formation processes. Savostin (1962), in Venezuela, showed that nitrification was actually increased after burning, although the accompanying volatilization of ammonia caused some loss of nitrogen from the soil. The total amount of this loss was minimal, however, except where a nitrogenous fertilizer was added to the soil immediately after burning. Varischi (1962) studied soil temperatures during burning of savanna vegetation in Venezuela, and found increases of only 3°C.
at a depth of 3 cm., with no rise in temperature at all at deeper depths. Blydenstein (1962) showed that the desiccation of the upper soil layers at the start of the dry season proceeded undiminished equally on burnt and unburnt plots, or even on mowed and mulched plots.

A semi-detailed soil survey of the Colombian Llanos (UNSF, 1965), found several cases in which the same soil series continued from savanna to forest, with only minor differences. Under the forest, root penetration was slightly deeper, colors were slightly darker in the deeper horizons, the mineral content was somewhat higher and the soils were more acid. Most of these differences can be attributed to the modifying effect of the vegetation on the soil, and would not prevent forest development on the savanna soils. The effect of burning of the savanna soils, is not apparent in these differences, except for the difference in pH. The lower acidity of the savanna soils can be attributed to the accumulation of ashes, high in potassium content, after grassland fires. Base saturation of forest and savanna soils was a uniformly low 1-5 percent, on an exchange capacity of around 16 meq/100 g. This shows that some tropical savanna soils have a low nutrient status, but so do some tropical forest soils unaffected by repeated burning.

As all this evidence accumulates, the hypothesis of savanna origin exclusively through repeated burning of forest, becomes untenable as a generalization. In many individual cases, forest destruction and replacement by grassland vegetation can be shown, often under the direct influence of man. Fire plays an important role in this forest destruction, but often many of the trees are felled first and partly dried to help along the combustion of the solid trunks. At present, it might even be safe to state that the man made savannas and open woodlands are in a majority, compared to natural tropical savannas. In this sense it is interesting to note that Ferri (1963) mentions unpublished studies on the germination of seeds of cerrado species. Germination was uniformly high under laboratory conditions, but actual establishment under field conditions was favored in soil cultivated for the establishment of new farm plots in cleared forest areas. Establishment on the hard sun-dried cerrado soils was poor.

Fire is maybe the dominant factor in the established savanna environment. Herbaceous savanna vegetation is excellently adapted to...
repeated burning, and has several advantages over forest vegetation under such conditions. The accumulated vegetable material which is burnt off is dead already and expendable; new growth may actually be stimulated by letting more light enter at the level of the basal growing points of bunchgrasses. The development cycle of the grasses and many broadleaved forbs, from sprouting through flowering to seed-setting, is completed within the rainy season, when fires are absent.

Most savanna fires nowadays are set by man. Although the onset of the rainy season in the tropics is often accompanied by lightning storms, little unburnt savanna is left by that time, and fires from natural causes are relatively uncommon. Burnt areas can easily be traced on aerial photographs, and here it becomes immediately apparent that fires do not burn on endlessly. The majority of visible fire traces measured on a selection of aerial photographs from the Colombian Llanos, did not extend beyond 2 km., only a few burnt areas of more than 5 km long were measured. Small drainage ways, cattle trails and other minor obstructions formed innumerable fire-breaks in the savanna, limiting the extent of the burnt areas. The trade winds prevalent during the dry season, extended all fires in a southwest direction, making the measurements mentioned the longest direction in elongate-shaped areas.

In conclusion, it can be stated that precious little information exists on the effect of fire on the tropical vegetation of Latin America. Leaving the question of the role of fire in the origin of tropical American grasslands aside, it can be stated that under present conditions fire plays an important role in maintaining the existing grasslands in their present form. The principal use of these grasslands in their natural or semi-natural state is in raising livestock. This represents a sizeable industry and the effect of human actions on the basic food supply of this industry can be profound. With the importance of fire in the ecological balance of these grasslands, the control of fire, as opposed to its elimination, should be a basic subject for investigation. We know too little about the effect of season or interval of burning on such things as forage production, brush control, soil conditions and all the other factors which contribute to the ecological balance in producing grasslands. The studies done in other environments, with different species, provide an excellent guide
as to what results could reasonably be expected and what methods and designs could be adopted to carry out the studies, but the applicable knowledge must come from local studies. With the accumulation of data, the evidence on more basic problems can also be interpreted more intelligently and the general hypotheses can be based on firmer foundations.

LITERATURE CITED

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