

# DETERMINANTS OF TROPICAL SAVANNAS

Presentations made by savanna researchers  
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## CHAPTER 5 - FIRE THE ECOLOGICAL EFFECTS OF FIRE IN SAVANNAS P.G.H. Frost and F. Robertson

### 1. INTRODUCTION

Regular fires are one of the characteristic features of tropical savannas. While some are still caused by lightning (Kcmarek, 1972; West, 1972) the main source of ignition for the past tens of thousands of years has been man, for hunting, preparing land for cultivation, improving the quality of grazing for livestock, and controlling the spread of woody plants (West, 1972). This use has been so pervasive that some authors suggest that most savannas are anthropogenic systems derived from deforestation and repeated burning (Rawitscher, 1948; Budowski, 1956; Clayton, 1961; Singh et al., 1985). Although such 'derived' savannas are widespread in the tropics, particularly in the higher rainfall zones, fire is now generally recognized to be only one of a number of interacting factors affecting savanna dynamics (Huntley and Walker, 1982; Bourliere, 1983; Sarmiento, 1984; Tothill and Mott, 1985). Nevertheless, it is one of the few determinants which can be readily manipulated and, as such, is an important variable in any management programme.

In this chapter we emphasize the composite nature of fire as an ecological factor. Fire behaviour, timing, intensity and frequency of occurrence all vary somewhat independently of each other and affect both the environment and the biota in a number of direct and indirect ways. Fires reduce plant biomass and litter, thereby altering energy, nutrient and water fluxes between the soil, plants and atmosphere. These changes in turn may affect the long-term nutrient status and productivity of the system.

Fires also kill individual organisms, damage or destroy unprotected living tissues, modify growth and reproductive rates, change the availability and use of resources and alter competitive and other relationships between organisms. The effects of these impacts depend largely on the recent history of a site, the physiological and developmental state of an organism at the time of burning and the occurrence of future events such as rainfall, drought or herbivory. In the longer term, these effects may result in changes to the productivity and population structure of a species, the composition of communities and, ultimately, the probability and characteristics of future fires (see recent reviews by

Centinho, 1982; Trollope, 1982, 1984a; Gillon, 1983; Hodgkinson et al., 1984).

The effective use of fire as a management tool requires a thorough understanding of this complexity of interaction and response. Even though considerable practical knowledge is available on the application of fire in savanna management, much still needs to be learnt about its different effects and how these interact with other ecological processes to influence savanna dynamics. In this chapter we review some of the ecological effects of fire in savannas, in the context of the following questions:

1. What are the ecologically important characteristics of savanna fire regimes?
2. To what extent does fire influence the environment of savannas and, in particular, the fertility of savanna soils?
3. How does fire affect the composition, structure, and productivity of savanna plant communities?
4. To what extent are these patterns influenced by interactions between fire and other ecosystem components?

## 2. SAVANNA FIRE REGIMES

The type and intensity of fire, its seasonal occurrence and periodicity make up the fire regime of an area. These vary considerably across the range of savanna types. In the moist savannas, fires generally occur during the dry season or early wet season, at intervals of 1 - 5 years (Huntley, 1982; Trollope, 1982, 1984a; Hodgkinson et al., 1984). Most dry-season fires are ignited by man but lightning becomes important at the beginning of the rains (Romarek, 1972; West, 1972). In the more arid savannas, the interval between successive fires is much longer, 5 - 50 years, depending on fuel loads and therefore on the occurrence of periods of above-average rainfall (Siegfried, 1981; Hodgkinson et al., 1984; van der Walt and le Riche, 1984). Because of the general aridity of these savannas, fires can occur at almost any time, provided that there is a source of ignition. However, most occur at the beginning of the wet season when the frequency of lightning is highest (Siegfried, 1981; Hodgkinson et al., 1984).

The majority of savanna fires are surface fires, burning through the herbaceous layer. Flame heights are generally low, the mean flame-length of experimental head and back fires in a savanna grassland averaged 2.8 m (1.2 - 5.0 m) and 0.8 m (0.5 - 1.5 m) respectively (Trollope, 1978). Plant matter occurring above 3 - 4 m height is therefore not

normally ignited, though it can be severely scorched.

The rate of spread of savanna fires is highly variable, even in a single fire, reflecting differences in wind speed, topography and the amount and moisture content of the fuel. Recorded mean values for rates of spread range from 0.02 - 0.67 m/s (Gillon, 1972; Trollope, 1978; Gandar, 1982; Griffin and Friedel, 1984a). Head fires, burning with the wind, move faster than fires burning against the wind, and this affects both the temperature and duration of fire at a point and thereby fire intensity (Trollope, 1978).

Fire intensity also depends on the amount and type of fuel, its moisture content, and prevailing climatic conditions, principally air temperature and relative humidity. Since savanna fires are fuelled largely by grass, fire intensities vary considerably between seasons, landscape units and vegetation types. Communities in which there is a high biomass of grass, such as in valley bottoms or on floodplains, generally experience the most intense and uniform fires. In contrast, in woodlands and shrublands, where there is generally a lower grass biomass and more uneven distribution of fuel, fires tend to be less intense and burn more patchily.

Measured fire line intensities, calculated as the product of the amount of fuel present (or, more correctly, the amount of fuel actually consumed), its heat yield, and the rate of spread of the fire front, range from 104 - 770 kJ/s/m in *Acacia aneura* shrublands and open woodlands in arid central Australia (Griffin and Friedel, 1984a) to more than 5000 kJ/s/m in mesic, open woodlands on porous sands in South Africa (Trollope and Potgieter, 1983). Even higher intensities can be expected in the tallgrass savannas of the tropics.

Classifying fires in terms of the rate of release of heat energy does not provide sufficient information on the duration of the heat pulse at different points in the system. Yet both the magnitude and duration of the heat pulse affect the survival of organisms and their propagules, as well as the amounts of nutrient release and volatilization, and changes in soil properties. More biologically meaningful indices of fire intensity need to be developed.

### 3. EFFECTS OF FIRE ON THE ENVIRONMENT

The direct effects of fire on the environment centre on the rise in soil and atmospheric temperatures during the fire, and on the reduction of organic matter and release of elements. Fire also affects the environment indirectly by removing or reducing plant and litter cover, thereby modifying both the post-fire microclimate and the activity of the soil biota.

#### 3.1 TEMPERATURES DURING FIRE

There is considerable variation in the temperatures recorded during savanna fires. The fires are generally hottest at, or just above, the soil surface, ranging from  $< 70^{\circ}$  -  $> 800^{\circ}\text{C}$  at ground level to  $200^{\circ}$  -  $800^{\circ}\text{C}$  at 1 m (Cook, 1939; Pitot and Masson, 1951; Ramsey and Rose-Innes, 1963; Hopkins, 1965; Gillon, 1970; Harrison, 1976; Sweet, 1982; Trollope, 1978, 1984b; Trollope and Potgieter, 1983). Back fires are generally hotter than head fires at the soil surface, though there are exceptions. In savanna grasslands, some head fires exceed  $500^{\circ}\text{C}$  whereas under similar conditions back fires seldom exceed  $400^{\circ}\text{C}$  (Trollope, 1978). Above 1 m, head fires are almost always hotter than back fires. Temperatures though are generally much lower than those closer to the ground and decrease sharply with increasing height. At 4 m, for example, temperatures hardly reach  $100^{\circ}\text{C}$  and then only for very brief periods (Figure 5.1).

The temperature increases are transient, lasting a few minutes at most (Cook, 1939). In two experimental fires in Brazilian cerrados, surface soil temperatures were above  $50^{\circ}\text{C}$  for about 215 and 75 s, respectively (Coutinho, 1978). In another series of experiments, temperatures at ground level remained above  $50^{\circ}\text{C}$  for 50% longer under back fires (257 s) than under head fires (171 s) (Trollope, 1978). The differences in residence time at higher temperatures were even more pronounced (e.g. 270% at  $120^{\circ}\text{C}$ ). Conversely, at 1 m above grass canopy height (0.34 m) air temperatures of back and head fires remained above  $50^{\circ}\text{C}$  for 47 s and 115 s, respectively (Trollope, 1978).

Soil has a low thermal conductivity. Temperatures recorded at 2 cm below the surface seldom exceed  $35^{\circ}\text{C}$ , while at 5 cm depth there is almost no rise in temperature (Cook, 1939; Pitot and Masson, 1951; Ramsey and Rose Innes, 1963; Gillon, 1970; Coutinho, 1978). Higher soil temperatures than these can be expected under burning logs and other smouldering vegetation, but even then only a small fraction of the heat produced is likely to be transferred to the soil.

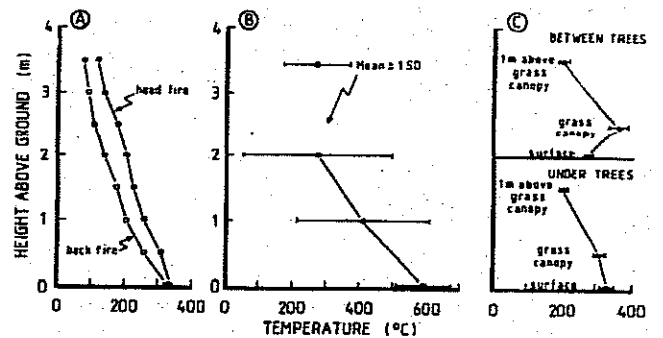


Fig. 5.1. Vertical temperature profiles of some savanna fires. A. *Acacia nigrescens*-*Seleznayia caffra* wooded savanna, Kruger National Park, South Africa (Potgieter 1974, in Trollope, 1984b); B. *Acacia nigrescens*-*Commersonia aculeolata* tree savanna, Botswana (Sweet, 1982); C. various savanna communities, Kruger National Park, South Africa (Trollope and Potgieter, 1983).

The rate of heat transfer is higher in moist than in dry soils, though temperatures at a given depth normally cannot rise above  $100^{\circ}\text{C}$  until all the moisture there has been evaporated (Raison, 1979).

These patterns of fire behaviour are broadly similar to those in other biomes, but they come from a very limited data base. In order to have a better understanding of the links between the various components of a fire regime, the behaviour of given fires, and their short- and long-term effects on the environment and biota, more studies of fire regimes and fire behaviour in savannas are needed.

#### 3.2 ALBEDO AND THE POST-FIRE ENERGY BALANCE

Fire causes a decrease in the reflection coefficient (albedo) of the soil surface, resulting in greater absorption of solar radiation (Figure 5.2). This in turn leads to soil surface temperatures being higher during the day and lower at night, and hence to greater daily surface temperature fluctuations (Raison, 1979; Savage, 1980; Cass

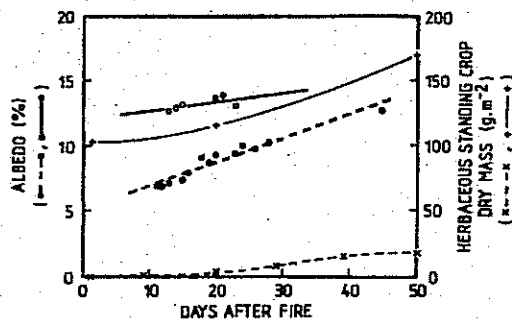


Fig. 5.2. Changes in the reflection coefficient (albedo) and in herbaceous standing crop after fire (albedo: solid circle burnt ground,  $\circ$  unburnt ground; herbaceous standing crop:  $\times$  burnt,  $+$  unburnt). Data from Harrison (1978).

et al., 1984). The extent of these changes depends on the thermal conductivity of the soil and on the partitioning of the additional energy between latent energy used in evaporating water, energy used by plants during photosynthesis, and sensible heat transfer to both the soil and atmosphere (Savage, 1980).

These changes persist until sufficient plant cover develops to intercept the incident radiation during the daytime and reduce radiative heat loss at night (Figure 5.2). Low rainfall, extreme temperatures and herbivory all tend to slow down the rate of plant recovery and thereby the increase in albedo.

### 3.3 SOIL PHYSICAL PROPERTIES

Savanna fires are generally not hot enough to cause direct changes in soil physical properties. However, in the longer term, soil bulk density and porosity can be adversely affected by the reduction in plant and litter cover, changes in microclimate, an increase in the rates of organic matter mineralization, and changes in soil fauna activity. Increases in surface soil bulk density (Trappnell et al., 1976; Webber, 1979; Brookman-Amisah et al., 1980), and reductions in moisture holding capacity (Cook, 1939) have been recorded on

annually burnt plots when compared with adjacent unburnt areas. The greatest increases occurred in plots burnt during the late dry season. Other studies though have shown no differences (Cass et al., 1984).

### 3.4 SOIL MOISTURE DYNAMICS

A number of studies have demonstrated lower soil moisture levels on burnt plots compared with levels on adjacent unburnt areas (Cook, 1939; San Jose and Medina, 1975; Savage, 1980; Gandar, 1982). The soil moisture balance on burnt ground is affected by a number of factors including (i) a reduction in plant and litter cover and subsequent exposure of the soil surface for a variable period of time after fire, leading to increased evaporation; (ii) the physical characteristics of the soil and its susceptibility to structural collapse; (iii) the timing and intensity of subsequent rainfall, and (iv) the rate of vegetation recovery.

Infiltration rates on sites burnt annually for many years can be much slower than on adjacent unburnt sites, largely as a result of changes in soil surface structure (Cass et al., 1984). These are probably caused by a decrease in soil organic matter levels and a consequent reduction in soil aggregate stability leading to individual soil particles becoming detached during rainfall. The particles block soil pores and form a surface crust which inhibits infiltration and increases runoff. The distillation of aliphatic hydrocarbons from litter and soil organic matter during fire, and their subsequent condensation on the soil particles, also leads to the formation of water-repellent surfaces, even on sandy soils (Cass et al., 1984).

### 3.5 EROSION

The risk of increased soil loss from an area laid bare by fires is a major concern in savanna management. Since soil nutrients are concentrated in the surface soil, extensive erosion may result in a significant depletion of the nutrient status of the soil, as well as in a reduction in soil depth and water holding capacity. Despite this concern, there is little quantitative information on the extent of soil loss in burnt savannas and on the factors which influence this (Cass et al., 1984; O'Connor, 1985). Some of the factors which increase the risk of erosion include reductions in soil surface stability, lowered infiltration rates and corresponding increases in runoff, topographic position and soil type. Sites on steep slopes with friable, clayey soils are particularly susceptible.

### 3.6 LITTER REDUCTION

In African savannas, fires consume around 70-90% of the herbaceous standing crop and grass litter, 20-50% of woody plant leaf litter, 12-58% of twigs, bark and woody fragments, and up to 20% of standing dead wood (Collins, 1977; Isichei and Sanford, 1980; Villecourt et al., 1980; Frost, 1985 and in prep.). The fuel loads in these studies varied from 4200-9000 kg/ha, with 48-63% of this being consumed by fire on each occasion. Comparable figures have been obtained from moist savannas in Central America (62-84% reduction; fuel loads 6740-13800 kg/ha; Kellman et al., 1985) and in arid central Australia (17-64% reduction; fuel loads 2500-7400 kg/ha; Griffin and Friedel, 1984a).

Some of the variation in the amount of material that is burnt depends on when litter falls in relation to the time of annual fires. In many West African savannas where the rainfall is bimodal, litter falls either during the short dry season or at the end of the long dry season after burning has taken place (Isichei and Sanford, 1980). Other sources of variation include the kind and intensity of fire. Back fires generally consume more of the herbaceous standing crop and leaf litter than do head fires (Trolllope, 1984b).

### 3.7 SOIL ORGANIC MATTER AND SOIL CARBON

The recorded effects of savanna fires on soil organic matter and soil carbon levels are inconsistent. Lower levels of organic carbon have been measured in the surface soils of annually burnt plots (White and Grossman, 1972; Brookman-Amisshah et al., 1980; Abbadi, 1983), and in plots burnt during the late dry season compared with early-burn and unburnt areas (Moore, 1960; Oguntala, 1980). In these latter experiments the levels of soil carbon were higher in the early-burn than in the unburnt plots. This has been attributed to the more vigorous root growth on the early-burn plots, especially by grasses (Kadeba, 1982). Higher levels of soil carbon have also been recorded in annual-, biennial- and triennial-burn plots than in unburnt plots or plots burnt only every 4 and 5 years. This is thought to be due to charcoal accumulation on the more frequently burnt plots (Sweet, 1982).

In other studies, the differences in soil organic matter levels between treatments have not been significant (Cook, 1939; Harrington, 1974; Harrington and Ross, 1974; Griffin and Friedel, 1984a), even between unburnt plots and

those burnt annually for 23 years (Trapnell et al., 1976). In this last experiment, wood and litter harvesting termites were more active on unburnt plots where they accumulated organic matter and nutrients in their mounds, thereby reducing the overall levels of soil organic matter (Trapnell et al., 1976).

### 3.8 CATION EXCHANGE CAPACITY

Since organic matter contributes greatly to the cation exchange capacity of many savanna soils, changes in SOM can be expected to result in parallel changes in CEC. In only one of the studies showing a difference between treatments in SOM was cation exchange capacity also measured and the change paralleled the change in SOM (Moore, 1960). In those studies where only minor differences in soil organic matter content were detected, CEC did not differ significantly between treatments (Coutts, 1945; Harrington, 1974; Harrington and Ross, 1974; Trapnell et al., 1976; Griffin and Friedel, 1984a).

### 3.9 RELEASE OF NUTRIENTS

Burning oxidizes organically bound elements in the vegetation and litter and releases them in forms available to plants. The intensity and duration of a fire, the amount of material which is consumed, and its nutrient content, all determine the quantities of nutrients released. Some of the elements, mainly nitrogen, carbon and sulphur, but including to a lesser extent phosphorus and potassium, are volatilized and may be lost to the atmosphere. Material which is not volatilized is either deposited on the soil surface or, in lesser amounts, is removed as particulate matter in smoke or ash. Material that is deposited on the ground either re-enters the soil, or is redistributed by wind or through surface runoff. The extent of this depends on topography, the length of time the soil remains bare after fire, and on the timing, amount and intensity of subsequent rainfall. The loss of nutrients through volatilization and export in ash during savanna fires has seldom been measured satisfactorily. Given the amount of organic matter that is burnt, considerable losses might be expected. However, in most cases, significant differences in nutrient concentration between fire treatments have been limited to the upper 0 - 5 cm of the soil.

The release of nutrients by fire differs markedly from the relatively slow, weakly pulsed decay of organic matter by micro-organisms in unburnt savannas. After fire,

the concentration of plant available nutrients in the soil solution increases sharply by amounts which broadly correspond to those released from the vegetation and litter (Cavalcanti, 1978 (quoted by Coutinho, 1982); Kellman et al., 1985). The increases are largely confined to the surface layers of the soil and are maintained for up to a month after fire. However, the initial peak in concentration declines rapidly, suggesting that free ions are soon adsorbed onto the exchange complex. Despite deep percolation of rainwater, leaching losses appear to be minimal (Kellman et al., 1985).

### 3.10 NITROGEN

Significant losses of nitrogen through volatilization during fires occur at temperatures above 400°C (Cass et al., 1984). How significant this is in the overall dynamics of nitrogen in savanna ecosystems is difficult to assess. Most of the published estimates of nutrient loss through volatilization and up-draught during fires are probably not accurate (Raison, 1979). However, they serve as a guide.

The reported losses due to volatilization in savanna fires vary between 4 and 33 kg N ha<sup>-1</sup> (Table 5.1). Regular losses of this magnitude might be expected to result eventually in lower levels of nitrogen in the soil. The recorded changes in soil nitrogen due to fire parallel the findings for changes in soil organic matter, described earlier, and are not repeated here.

In addition to the loss caused by volatilization, losses may also occur as a result of increased mineralization and the subsequent leaching of nitrates beyond the rooting zones of plants. Nitrification rates are initially reduced by fire but soon increase above levels recorded on adjacent unburnt plots, probably as a result of higher soil temperatures, and remain significantly higher for up to 3 months afterwards (Adedeji, 1983). Nitrate ions are highly mobile and increased concentrations have been recorded in water draining out of the topsoil of burnt plots (F. Meredith, pers. comm.). However, losses of nitrate through leaching are likely to be limited to porous, sandy soils in regions of high rainfall.

The limited data available on annual inputs of nitrogen in rainwater and through microbial fixation suggests that, at least in some cases, they are sufficiently large to balance the estimated losses due to volatilization and leaching (Table 5.1). However, there is no reason to suppose that the inputs from the atmosphere differ markedly from

SAVANNA LOCALITY	MEAN ANNUAL RAINFALL	LOSSES (kg N ha <sup>-1</sup> ) FIRE	GAINS (kg N ha <sup>-1</sup> a <sup>-1</sup> ) RAINFALL INPUT	N-FIXATION	TOTAL	REFERENCE*
High grass savanna (Andropogonae) (Bjura, Ghana)	1500	(20) <sup>a</sup>	(6)	(39)	(47)	10
Aeropus-Leptacoryphium seasonal savanna (Barinas, Venezuela)	1350	(15)	(5)	(12)	(17)	13
Trachypogon savanna (Calabozo, Venezuela)	1100	11.5 9-12	1.5	-	-	7, 8
Loudetia-Andropogon "derived" savanna (Lomé, Ivory Coast)	1730	10-23	19	9-12	23-33	1, 13
Guinea savanna (Kouliko, Nigeria)	1000	12-15	3-7	3-9	6-16	2, 5, 6
Monsoonal tall-grass savanna (Katherine, Australia)	950	8-10	1	2-3	3-4	9
Durbae-Brogosstic woodland (Hyleley, S. Africa)	630	33	1-5	30	31-35	3, 4
Sabel-Sudanian savanna transition (Hino, Mali)	580	4	3	4	7	11

\* 1. Abbadie (1984, 1984); 2. Adeniyi, quoted by Sanford (1982); 3. Frost (in prep.); 4. Rte (1981); 5. Isichei (1980); 6. Isichei and Sanford (1981); 7. Medina (1982); 8. Medina et al. (1978); 9. Moram and Wetzel (1960) quoted by Mott et al. (1985); 10. Nye and Greenland (1962); 11. Penning de Vries and Djiteye (1982); 12. Sarriente (1984); 13. Villecourt et al. (1986).

<sup>a</sup>) Estimated values in parentheses

Table 5.1. Calculated losses of nitrogen in savanna fires, and measured or estimated gains in rainfall and through microbial fixation of nitrogen.

those in unburnt savannas. Only if there is a higher rate of N-fixation on frequently burnt areas will the losses due to fire be counterbalanced. There is little information in this regard. It is worth noting though that the incidence of legumes, including those known to be nodulated and therefore potential N-fixers, is often higher on frequently burnt plots compared with unburnt ones (see data in Isichei, 1979 [quoted by Sanford, 1982]; Edroma, 1984; P.G.H. Frost, personal observation).

### 3.11 PHOSPHORUS

Phosphorus can be volatilized at temperatures above 500°C though this is only likely to be significant under complete combustion (Raison, 1979). The low solubility of P

and its tendency to form complexes with Al and Fe in acid soils, or with Ca in alkaline soils, makes it less vulnerable to leaching. Higher levels of extractable P have been recorded in the surface soils of annually burnt savannas compared with unburnt plots (Harrington, 1974; Trapnell et al., 1976; Afolayan, 1978; Brookman-Amisshah et al., 1980; Sweet, 1982). There is a slight positive relationship with frequency of burn (Sweet, 1982) and with season (intensity), since plots which have been subjected to more intense, late dry season fires have higher levels than either early-burn or no-burn plots (Trapnell et al., 1976; Oguntala, 1980). The increase in extractable P levels in the surface soil of regularly burnt areas suggests that fire promotes a more rapid cycling of phosphorus through the vegetation and soil, in contrast to unburnt areas where P is retained for longer by the vegetation.

A number of studies have shown no significant difference in the levels of extractable P between different burning treatments (Moore, 1960 [cf. Oguntala, 1980]; Harrington and Ross, 1974; Griffin and Friedel, 1984a; Kellman et al., 1985). To what extent these results reflect differences in the methodology of extracting phosphorus, as opposed to differences in process, is not clear.

### 3.12 SULPHUR

Like nitrogen, sulphur is readily volatilized during fire. Frequent burning therefore could result in a decrease in sulphur levels in the soil. This may be one of the reasons why Cerrado soils in Brazil are deficient in sulphur (McClung and de Frietas, 1959). In central Australian arid woodlands, no significant differences between treatments in extractable S were recorded (Griffin and Friedel, 1984a).

### 3.13 EXCHANGEABLE BASES

Sweet (1982) has recorded an increase in total exchangeable bases with increasing burning frequency. In other cases, a decline in TEB has been noted, usually in situations where the vegetation has been exposed to hot fires for many years (Moore, 1960; White and Grossman, 1972; Strang, 1974). These declines are probably the result of fire intensity rather than fire frequency. Moore (1960) demonstrated higher levels of TEB in plots exposed to cooler, early dry-season fires (which had the lowest TEB). However, the lack of replication in these experiments makes it difficult to assess their significance. In cases where declines have been observed, the prime cause of the reduction is thought to be the removal of ash by surface wash. In this

case though, the nutrients are being redistributed spatially within the system rather than being lost outright (Kellman et al., 1985). More intensive sampling would probably reveal increases in exchangeable bases at sites receiving the run-off.

The effects of long term burning on individual elements are variable. Sodium is very mobile but has not often been measured. White and Grossman (1972) noted an apparent decline on plots burnt annually for 38 years, but Kellman et al. (1985) detected no changes in plots burnt a number of times over a 7-year period. Potassium is also highly mobile and is readily leached from the vegetation and litter. This may explain in part the variable results which have been obtained. Most studies have shown no significant differences between treatments (Harrington and Ross, 1974; Trapnell et al., 1976; Griffin and Friedel, 1984a; Kellman et al., 1985). In other studies, higher levels of exchangeable-K have been found in annually burnt compared with unburnt plots, with early-burn having more than late-burn plots (Moore, 1960; Harrington, 1974; Afolayan, 1978; Brookman-Amisshah et al., 1980; Oguntala, 1980; Sweet, 1982). It is not clear to what extent these are site or sampling effects, as opposed to treatment effects, perhaps reflecting higher concentrations of potassium in plant tissues at the start of the dry season. Two studies have recorded lower amounts of exchangeable-K in annually burnt plots, possibly as a result of the removal of ash by surface wash (White and Grossman, 1972; Strang, 1974).

Calcium and magnesium are less soluble than K or Na and are also not readily volatilized. In most cases, a change in one of the elements is paralleled by a change in the other, though Griffin and Friedel (1984a) noted an increase in exchangeable Ca in open woodland sites after dry-season fires which was not matched by any increases in the other cations. It may be significant that these were the only sites where woody plant densities were markedly reduced (Griffin and Friedel, 1984b). In general, higher levels of exchangeable Ca and Mg are found in annually burnt plots compared with unburnt areas (Harrington, 1974; Trapnell et al., 1976; Afolayan, 1978; Sweet, 1982; Kellman et al., 1985). In some cases either no difference between treatments (Harrington and Ross, 1974), or a reduction on annually burnt plots has been recorded (White and Grossman, 1972; Strang, 1974). The response to season and intensity of fire is more variable. Plots subjected to more intense late dry season fires can have higher levels of exchangeable Ca and Mg than plots burnt during the early dry

season (Trapnell et al., 1976), or lower levels (Moore, 1960; Oguntala, 1980). In some cases, there have been no differences (Harrington, 1974; Afolayan, 1978).

#### 3.14 SOIL REACTION (pH)

The input of base-rich ash after fire can cause a short term increase in soil pH. The extent of the increase depends on the amount and composition of the ash, and on the buffering capacity of the soil (Cass et al., 1984). Longer term changes arising from exposure to different fire regimes tend to parallel the changes in exchangeable bases. There is a slight increase in pH with increased frequency of burning on soils derived from acid, igneous parent material (Sweet, 1982), between annually burnt and unburnt plots (Cook, 1939; Harrington, 1974; Trapnell et al., 1976; Afolayan, 1978), and between early-burn and both late-burn and unburnt plots (Moore, 1960; Brookman-Amisshah et al., 1980). In all cases, the changes have been less than 1 pH unit, an amount which is unlikely to greatly affect plant nutrient availability.

Thirty years of annual burning of a grassland firebreak in Zimbabwe resulted in a lower pH in the surface soil compared to that of an adjacent woodland, matching the recorded decline in total exchangeable bases (Strang, 1974). However, in another case where apparently significant declines in both the concentrations of exchangeable cations and percentage base saturation occurred, there was no corresponding decrease in pH (White and Grossman, 1972). No significant differences in soil pH have been noted in other studies (Harrington and Rose, 1974; Oguntala, 1980; Griffin and Friedel, 1984a), but in these cases the amounts of exchangeable bases also did not differ between treatments.

#### 3.15 SOIL BIOTA

The effects of burning on the composition and activity of the soil biota depend upon factors such as the kinds of organisms involved, fire intensity, and the extent to which burning alters the post-fire environment. Most savanna fires are not sufficiently intense to have a marked direct effect on the soil biota. The changes that do occur, even under relatively intense fires, are small, temporary, and usually confined to the top few centimetres of the soil surface (Nye and Greenland, 1961; Meiklejohn, 1955; Cass et al., 1984). Populations also tend to recover rapidly, often to levels above those in unburnt soil, though this depends largely on environmental conditions at the site, particularly soil moisture levels and the extent to which fire has modified

soil chemistry (Raison, 1979).

The change in environmental conditions can also affect community composition. Short-term increases in the numbers of nitrifying bacteria have been recorded in some cases (Dommergues, 1954; Adedeji, 1983), though not in all (Meiklejohn, 1955). The rise in pH and a higher concentration of soluble sugars in the soil solution may make conditions more favourable for bacteria than for fungi (Raison, 1979). In the longer term, frequent burning affects the soil biota by altering the amount and nature of organic matter inputs to the soil. For example, annual burning apparently reduces the activity of surface foraging, wood- and litter-eating termites (Trapnell et al., 1976). Similarly, in the monsoonal tallgrass savannas of northern Australia, the numbers of arthropod detritivores declined in frequently burnt areas, whereas other epigeic invertebrates were not permanently affected (Greenblade and Mott, 1983).

#### 4. EFFECTS OF FIRE ON PLANT SPECIES COMPOSITION

Plants differ widely in their tolerance of fire and in their capacity to recover afterwards. As a result, recurrent fires have considerable potential to influence the structure and composition of vegetation. The extent to which this occurs depends not only on differences in sensitivity between species but also on the type, frequency and intensity of fire, and on the physiological and developmental states of individuals at the time of burning. Events occurring in the interval between fires also influence the eventual outcome. Drought, above-average rainfall and herbivory affect fuel loads, and thereby fire intensity, as well as the condition of individual plants and their degree of recovery. The effects of fire regime on species composition therefore cannot be seen in isolation from the influence of these other factors. This complicates the interpretation of the results of most of the experiments on fire in savannas (van Wyk, 1972; O'Connor, 1985).

##### 4.1 FIRE TYPE AND PATTERN

Fire-sensitive woody species are widespread in the savanna biome (see Trapnell, 1959; Hopkins, 1965; West, 1972; San Jose and Farinas, 1983; Frost, 1984, for examples). In some cases they form the dominant component of the vegetation, despite recurrent fires (e.g. *Brachystegia* and *Julbernardia* spp. in Central African miombo: Trapnell, 1959). To survive and grow under these conditions individuals need to escape the full effects of



fire for long enough to enable them to pass through the vulnerable sapling stage and reach the more fire-resistant mature tree stage. Irregular fires in space and time produce the necessary circumstances for this to happen.

Most savanna fires burn patchily as a result of varying wind speeds, topography and fuel loads. The uneven distribution of herbaceous biomass in particular, resulting from differences between sites, suppressed grass production by trees, or the localized impact of herbivores, affects the likelihood of a plant being damaged or killed. The regular occurrence of fire-sensitive woody species in savannas suggests not only that patchiness is a characteristic of most savanna fires but also that the spatial pattern is relatively predictable. However, apart from the studies by Hopkins (1965) and Braithwaite and Esthergs (1985), the pattern of savanna fires has not been analysed. It remains to be seen how consistent the pattern is from one fire to the next.

The spatial scale and uniformity of burning also tend to define the nature and extent of certain post-fire interactions. For example, large herbivores are attracted to burnt areas by the flush of vegetation after fire and tend to concentrate at higher densities in areas which are patchily burnt or comprise only a relatively small proportion of the total. This can lead to heavy, localized use of the vegetation and possibly to changes in species composition, as well as to a lower probability of the area supporting another fire in the short-term. This interaction between the size of areas burnt, herbivore densities and subsequent vegetation change has not been thoroughly investigated, though it is probably an important factor affecting the changes in grass species composition on experimental fire plots in the Kruger National Park (van Wyk, 1972).

#### 4.2 FIRE FREQUENCY

Fire frequency determines the length of time that a plant has to recover before the next fire occurs. The slower the rate of recovery, the more likely it is that the structure and composition of the vegetation will be altered, particularly where fires occur frequently. The rate of recovery depends on (i) the extent of damage sustained by the plants; (ii) the method of regeneration, and (iii) the favourableness of the post-fire environment for establishment and growth, particularly the amount and temporal distribution of rainfall, and the extent and intensity of herbivory. Plants growing on moist, nutrient rich soils could therefore

be expected to be more tolerant of frequent fires than plants growing in less favourable environments.

Species which are tolerant of fire and regenerate vegetatively generally recover their pre-fire status in the community more rapidly than species which only regenerate from seed. For populations of these latter species to survive recurrent fires, they must be able to establish, grow and reproduce in the interval between successive fires. The high fire frequency in moist savannas is one of the main factors selecting against such species, particularly among woody plants.

Frequent fires reduce woody plant densities in moist savannas, primarily by killing or suppressing individuals in the smaller size classes (Trapnell, 1959; Charter and Keay, 1960; Hopkins, 1965; Geldenhuys, 1977; Brookman-Amisshah et al., 1980; San Jose and Farinas, 1983). Fire is relatively selective in this respect, with some species disappearing at a faster rate than others. Lianas appear to be particularly fire-tender (Trapnell, 1959; Malaisse, 1978). Protection from fire results in an increase in tree density, particularly of these fire-sensitive species. In the high rainfall savannas of the savanna/forest transition-zone, the species which establish are often evergreen forest species (Charter and Keay, 1960; Lawton, 1978) but elsewhere they are typical savanna species (Menaut, 1977; Trapnell, 1959; Brookman-Amisshah et al., 1980; San Jose and Farinas, 1983).

The dominant woody plants in arid savannas appear to be more fire-sensitive than most of the plants occurring in moist savannas, despite generally lower fire intensities. However, fires are infrequent and normally only occur after periods of exceptional rainfall, although when they do occur they can cause considerable mortality. Under these circumstances the affected plant populations rely almost entirely on post-fire regeneration from seeds for re-establishment (e.g. *Acacia aneura*, *A. deanei*, *Callitris columellaris*, *Cassia nemophila*, *Bremophila latrobei* and others in central Australia (Hodgkinson, 1979; Walker et al., 1981; Griffia and Friedel, 1984b); *Acacia erioloba* in southern Africa (van der Walt and le Riche, 1984)).

This relationship between seedling establishment and adult mortality means that these arid savanna communities are particularly susceptible to changes in species composition. Events such as intense herbivory, heavy rains or drought, occurring after a fire during the period of seedling establishment, can differentially affect the

survival of seedlings of the different species. This can lead to sudden, unexpected shifts in the composition of the post-fire community (Griffin and Friedel, 1985).

Where fires in arid savannas occur relatively frequently (usually under experimental conditions) they are seldom intense enough to kill established woody plants, though canopy cover is often sharply reduced. Woody plant density may even increase as a result of increased recruitment from seeds stimulated to germinate by fire (Sweet, 1982; Hodgkinson et al., 1984; Griffin and Friedel, 1985). Establishment is often aided by the adverse effects of fire on the herbaceous layer, particularly in years of low rainfall (Gertenbach and Potgieter, 1979).

Savanna herbaceous communities are less affected by fire than are the woody communities. The most obvious changes occur at the extremes of fire frequency (annual burning vs no burning). For example, in south and east African savannas, annual burning generally favours species such as *Themeda triandra*, *Digitaria pentzii*, *Pogonathria squarrosa* and *Heteropogon contortus* whereas less frequent burning favours species such as *Cymbopogon plurinodis*, *Strobolus fimbriatus* and forbs (Davidson, 1953; van Wyk, 1972; Harrington and Ross, 1974; Robinson et al., 1979; Edroma, 1984).

However, rainfall variability is a confounding factor (Kennan, 1972; Gertenbach and Potgieter, 1979; O'Connor, 1985). For example, *Themeda triandra* is susceptible to drought, and although it increases under frequent burning and decreases if fire is excluded (Davidson, 1953; Harrington and Ross, 1974; Robinson et al., 1979; Edroma, 1984), this only happens under average or above-average rainfall. The combination of frequent burning and low rainfall causes *T. triandra* to decline. In semi-arid regions therefore, the species is most successful under less frequent burning or even under complete protection (Theron, 1937 [quoted by Tainton and Mentis, 1984]; Kennan, 1972). Annual burning in these areas leads to an increase in annual and pioneer species (e.g. *Aristida barbicollis*, *A. scabrivalvis*, *Urochloa bulbodes*, *U. mosambicensis*; Kennan, 1972; Harrington and Ross, 1974; Gertenbach and Potgieter, 1979; R.I. Yeaton, personal communication).

Protection from fire results in an increase in mesic, shade-loving grasses such as *Panicum maximum* (Harrington and Ross, 1974), *Andropogon tectorum* (Brookman-Amisah et al., 1980), *Crasspedorhachis africanus* (Strang, 1974), and forest species (e.g. *Onlismenus* and *Lasiacis*; San Jose and Farinas, 1983; P.G.H. Frost, personal observation). However, some of

these species may be responding more to changes in tree density and associated microclimate than directly to the absence of fire, since the removal of woody plants is known to influence herbaceous composition and production (Dye and Spear, 1982; O'Connor, 1985).

Fire may also mediate competitive interactions between species. For example, in South America, frequent burning favours species such as *Trachypogon plumosus* and *Axonopus canescens*, which are subdominant in unburnt savannas, whereas protection favours their competitor, *Trachypogon montufari* (San Jose and Medina, 1975).

#### 4.3 SEASON AND INTENSITY OF FIRES

The time of burning interacts with plant phenology and post-fire weather conditions to affect plant survival and reproduction. In most savannas, the season of burn is a relatively predictable component of fire regime since most fires occur during the dry season. It is this within-year predictability which enables many species to avoid fire by being dormant during the main fire season.

Fire intensity is a function of fuel type, fuel load, moisture content, and atmospheric conditions at the time of fire, and therefore is linked to both the seasonality and frequency of burning. The longer the interval between fires the greater the fuel load and therefore the more intense the fire. Fire intensity exerts differential effects on the survival of plants and their propagules, and stimulates the germination of seeds of different species to various degrees. Intensity also variously affects the physical and biological environments of each species, making conditions sometimes more, sometimes less, suitable for establishment and growth.

The late dry season in Africa is a period of nutrient translocation and rapid growth by woody plants, and fire at this time is considered to be very damaging (West, 1972; Kennan, 1972). Woody plant density is lowest and grass production highest under a late dry season fire regime. Fires during the late dry season, when the grass is driest and the conditions are hottest, are more intense than early dry season fires (Sanford, 1982; Edroma, 1984).

In moist savannas, frequent late dry season fires destroy young trees and shrubs, or their aboveground parts, so preventing the development of taller, more fire-resistant size classes. Although woody plant growth may be further inhibited by browsing ungulates, fire alone is sufficient to promote a lower woody plant density. Conversely, with longer intervals between fires, woody plant density

increases to a point where there is insufficient grass to fuel a fire intense enough to affect woody plants. Beyond this point, other factors such as soil texture and depth, and soil water and nutrient availability become key determinants of grass:woody biomass ratios.

Alternatively, fires in the middle of the wet season in Africa are seldom damaging to woody plants because the burns are cool and patchy (Trollope, 1984a). The majority of trees and shrubs in South American humid savannas are evergreen, but grow and change their leaves during the dry season (Medina, 1982). In contrast to Africa, Sarmiento and Monasterio (1983) consider that fires during the season of growth in South America are not particularly damaging, because they simply stimulate new buds. It is fires during the wet season in South America that cause most damage to woody plants because this is not a growth period and no new leaves are produced. In Australia midsummer (wet season) fires generally decreased the density of *Acacia harpophylla* suckers, while dry season fires increased sucker density (Johnson and Purdie, 1981).

Head fires are most damaging to woody plants because maximum heat release occurs well above the soil surface, nearer the terminal buds, while back fires are most damaging to grass because fire intensity is highest at ground level (Trollope, 1984a). Most savanna grasses are capable of surviving burning during the dry season by being dormant and having their tiller initials protected by persistent leaf bases. However, the plants are much less tolerant of burning during the wet season even though fire intensity is lower, because they are physiologically active at the time. (West, 1965; Trollope, 1984).

There is very little quantitative information available on the effect of season of burn on herbaceous layer composition. Those effects that have been noted are frequently confounded by grazing and rainfall variability (van Wyk, 1972). Species such as *Themeda triandra* become dominant in swards burnt during the late dry season (Davidson, 1953; Trollope, 1982) whereas species such as *Cymbopogon plurinodis* decrease.

Conversely, *Themeda* declines in swards burnt during the late wet season and in unburnt areas. Burning during the middle of the wet season, at a time when plants are physiologically active, can have a marked adverse effect (West, 1965; Trollope, 1984). Burning during a mid-wet season drought indicates that this effect depends on the physiological state of the plant rather than on the season per se.

Differential growth and mortality of grass species depends partly on the degree of protection of tiller primordia. Species such as *Themeda triandra* elevate their tillers during the late dry season and so become very sensitive to damage by fire and herbivory. In other species, such as *Heteropogon contortus* in Africa and Australia, and *Hyparrhenia filipendula* and *H. hirta* in Africa, the tillers remain protected throughout the dry season and are not elevated until well into the wet season (Booyesen et al., 1963; Stocker and Mott, 1981; Mott et al., 1985). This accounts for the differences in productivity of these species and for the shifts in species composition which can occur under early, and late dry season fire regimes.

In central Australian rangelands, species such as *Enneapogon polyphyllus*, *E. avenaceus* and *Aristida contorta* are maintained under a regime of dry season fires, but are significantly reduced by wet season fires and replaced by forbs such as *Calocephalus platycephalus*, *Helipterum tietkenni*, *H. chersleyae*, *Brachycome ciliaris* and *Senecio magnificus* (Griffin and Friedel, 1984a).

Late dry season fires promote the growth and development of perennial grasses while early burning reduces perennial grasses and encourages annuals (Aclayan, 1978). Since most of the annuals have already set seed by that time, they are less adversely affected by fires occurring then than are perennials, which are generally still physiologically active. Consequently, a regime of regular early dry season fires tends to favour the development of an herbaceous community dominated by annual grasses. Sanford (1982), however, states that there is little evidence of any influence of time of burning on the relative success of annuals and perennials. This is an issue which requires more research.

#### 4.4 REGENERATION OF WOODY VEGETATION

Fire has much more of an effect on woody plant composition, though isolating the effects of season from those of intensity is difficult because the two variables are interrelated. Woody plants tend to be more susceptible in the late dry season when fires are generally more intense because at that time the initial temperature of plant tissue is higher and closer to lethal limits. The moisture content of the plant is also higher, resulting in a higher thermal conductivity and more rapid transfer of heat to the interior of the plant. Consequently, the proportion of woody plants in the community declines as fire regimes become

progressively hotter. In addition, many woody plants produce new leaves before the start of the rainy season and so have depleted reserves at that time. Since new leaves are also more susceptible to damage by fire, burning at the start of the wet season forces the plant to draw on already depleted reserves in order to replace those consumed in the fire (West, 1965; Kennan, 1972). Fire tends to favour those woody species having protected meristems and other fire-resistant above-ground structures (for example, thick bark); the capacity to resprout from below-ground meristems on rootstocks, lignotubers etc.; or seeds that can survive fire and in which heat triggers germination.

The development of adventitious buds from vascular cambium is a feature of savanna trees and shrubs (Sarmiento & Monasterio, 1983). This adaptation permits both the regrowth of branches after canopy damage and sprouting from underground parts if the aboveground shoots are removed. Most woody regrowth in the humid and subhumid savannas of Australia (Mott *et al.*, 1985), South America (Eiten, 1972; Medina, 1982) and Africa (Lawson *et al.*, 1968; Boaler 1966; Jackson, 1974) arises vegetatively from material remaining in the soil after disturbance. The most vigorous shoots are produced by plants with large belowground organs (Trapnell, 1953; Fanshawe, 1959).

Even where disturbance is sufficiently severe to remove large rootstocks, suppressed seedlings may remain in large numbers. After 15 years of hoe cultivation, 3,500 to 11,500 small woody plants per hectare remained in fields derived from *Combretum* spp. woodland in Malawi (Robertson, 1984). These suppressed seedlings, or seedling suffrutices (Boaler, 1966), whose belowground parts may be years older than the shoots which are regularly destroyed by fire, are also a feature of *Brachystegia* woodland (Boaler and Sciwale, 1966; Strang, 1974). Spontaneous dieback to ground level as reported by Trapnell (1959) and Boaler (1966) is probably rare unless the shoots are killed by fire, although partial dieback during the dry season is common (personal observation). The root:shoot ratio of young plants is high (Rutherford, 1982; Menaut and Cesar, 1982) and although the above ground parts may be killed, suffrutices persist despite burning. Burning becomes less effective in preventing regeneration in the drier subhumid savanna types with their lower grass biomass and greater number of fire-resistant species. Regular burning may reduce the number of suffrutices in humid savannas, but many still remained after thirty-six years of annual late burns in Zambian *Brachystegia* woodland (Mansfield *et al.*, 1976). Burning is not recommended in some

Australian *Acacia* savannas because scarification by fire permits imbibition and extensive regeneration of woody species (Leigh and Noble, 1981). In the same region, isolated large *Eucalyptus* trees may release large quantities of seed in response to heat stimulation by fire (Johnson and Purdie, 1981).

Regeneration in the humid savannas at the forest/savanna boundary is dependent both on sprouting and suckering and on seedling establishment. A favourable microhabitat provided by standing trees may be necessary for the germination and establishment of woody seedlings and in fact few seedlings establish in the grass patches in West African Guinea savanna even in the absence of burning (Menaut and Cesar, 1982). The canopy species of *Brachystegia* woodland seldom establish in open grassland probably because of the alternation between cool moist weather which stimulates germination and hot dry conditions which kill emergent seedlings (Strang, 1966). Seedlings are more common under savanna trees than in open grassland in woodland savanna in Belize (Kellman and Miyanishi, 1982) and *Trachypogon* savanna in Venezuela (San Jose and Farinas, 1983), perhaps through local nutrient enrichment or suppression by grass competition. Grass competition has been shown to prevent establishment of *Acacia* spp. seedlings in a well developed *Cenchrus ciliaris* sward in South Africa (Knoop and Walker, 1985). Regeneration of fire-sensitive *Callitris columellaris* in Australia is restricted to clumps of adult trees where grass growth is suppressed and fires infrequent, although regeneration will extend beyond the clumps if protected from fire (Stocker and Mott, 1981).

In the derived savanna zone of West Africa forest may regrow if the fire-sensitive forest species regenerate rapidly from sprouts and seed (Hopkins, 1983). However, if savanna grasses invade before the woody vegetation is established hot fires are likely and the grassland may then be invaded by the woody species characteristic of savanna. The dry dipterocarp forests of South-East Asia share a common flora with the derived savannas (Blasco, 1983). Here there is no invasion but an impoverishment of the original forest flora brought about by felling, cultivation and fire.

The effect of fire on tree regrowth is strongly influenced by stem diameter and height, but not in any consistent way. Seedlings and saplings are generally at greatest risk (Rutherford, 1981; Pellet, 1983; Griffin and Friedel, 1984b), but in some species, mortality appears to be highest in intermediate height classes (e.g. *Acacia karroo*: Trollope, 1974). In contrast, in *Acacia erioloba*,

mortality of mature trees was more than 7 times higher than that of saplings (van der Walt and le Riche, 1984) (Figure 5.3).

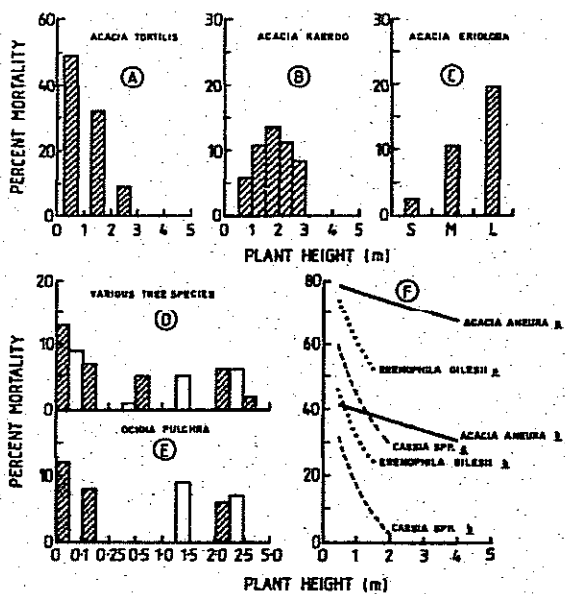


Fig. 5.3. Percent mortality caused by fire in various savanna woody plants. A. *Acacia tortilis* (Pellew, 1983); B. *Acacia karoo* (Trollope, 1974); C. *Acacia erioloba* (van der Walt and le Riche, 1984); D. various tree species, and E. *Ocotea pulchra* (shaded columns represent plants killed by a slow moving fire; clear columns, plants killed during a fast moving fire; Rutherford, 1981); F. various tree and shrub species (lines calculated from regression equations linking mortality to fire line intensity (I) and plant height class: a. I = 770 kJ/m; b. = 104 kJ/m (data from Griffin and Friedel, 1984b).

In the humid Guinea savanna zone at Olokemeji in Nigeria, the chances of stem survival increased considerably with increased size and basal area (Hopkins, 1965). Less than 25% of trees under 3 m in height survived 5 years of severe annual fires. Greater size was associated with apical buds borne above flame height and thicker bark which protected the cambium. Early cool fires in subhumid *Brachystegia* woodland kill stems below 0.5 cm in diameter while hot fires kill stems up to 5.0 cm (Ball, 1981a). The critical height for fire mortality among *Acacia tortilis* regrowth in the Serengeti woodlands is 3.0m (Pellew, 1983).

Although survival is usually high, fire often severely damages the aboveground parts of plants, particularly in individuals smaller than 2-3 m (Figure 5.4). The percentage topkill of *Acacia karoo* (as opposed to mortality shown in Fig. 5.3) was strongly associated with fire intensity in stems between 0.5 to 2.0 m in height (Trollope, 1984a). Stems less than 0.5 m tall were killed irrespective of fire intensity, while few stems exceeding 2 m in height were killed even if fires were very intense. This reverses the normal progression from the smaller to taller height classes as individuals age. Frequent reversals of this sort eventually result in distorted size distributions in which most of the population is confined to the smaller height classes (Figure 5.5).

Fire probably cannot prevent woodland regeneration after clearing in areas where conditions are particularly favourable for woody plant growth, such as areas of high annual rainfall with permeable soils and high infiltration rates. Annual burning was shown to hold regrowth at the open tree savanna stage following clear-felling in the humid Southern Guinea savanna zone, but under an annual early burning regime woody regrowth was almost as fast as that under complete protection, and the plots developed into forest (Rose Innes, 1971). In the subhumid Northern Guinea savanna zone even early burning prevented satisfactory tree growth (Brookman-Amisshah et al., 1980). Clear-felled plots in *Brachystegia* woodland at Ndola in Zambia developed only a few small trees and shrubs after 11 years of late burning, but early burned plots showed clumped coppice regrowth 4.5 m to 6 m tall (Trapnell, 1959). At a slightly lower rainfall, even annual late burns were insufficient to prevent the regrowth of clear-felled *Brachystegia* woodland in Zimbabwe (Barnes, 1965). Woodland species regenerate under an early burning regime whereas frequent late dry season fires destroy a woodland canopy and reduce it to coppice (Trapnell, 1959; Charter and Keay, 1960; Brookman-Amisshah et al., 1980).

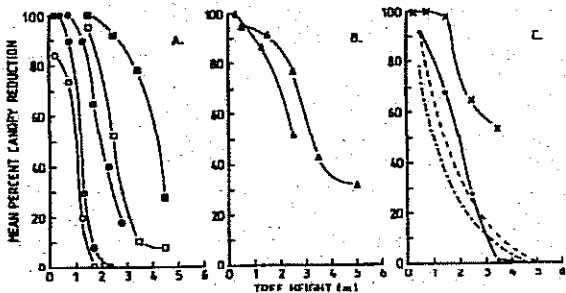


Fig. 5.4. Percentage reduction in tree canopy volume caused by savanna fires of differing intensities. A. *Acacia karroo*: open and half-open circles low intensity fires, solid circle high intensity fire (Trollope, 1984a); *Acacia karroo*: open square low intensity fire, solid square high intensity fire (Maddox, 1982, in Frost, 1984). B. *Acacia tortilis*: open triangle (Pellé, 1983), solid triangle (Sweet and Tacheba, 1985). C. *Ochra pulchra*: - - - - - 'slow' burn, - - - - - 'fast' burn (calculated from regressions given by Rutherford (1981)); various species: + (Herlocker, in Norton-Griffiths, 1979), x (Sweet and Tacheba, 1985). Recalculated from original data sources using midpoints of tree size and damage class intervals.

Complete protection from fire results in an increase in tree density, particularly of fire-sensitive species, leading to the establishment of woodland in many savanna areas, and to the development of forest in the high rainfall areas of the transition zone from savannas to forest (Trapnell, 1959; Eiten, 1972; Menaut, 1977; Brookman-Amissh et al., 1980; San Jose and Farinas, 1983).

Fire exclusion is the most effective method of encouraging woody regrowth. However, complete protection from fire may be unattainable because of the high incidence of man-made fires and the probability of lightning fires, which are common in Africa (West, 1972) and Australia, although not reported in South America (Coutinho, 1982). The intensity of accidental fires will increase with each year of protection owing to the accumulation of moribund grass. Annual early

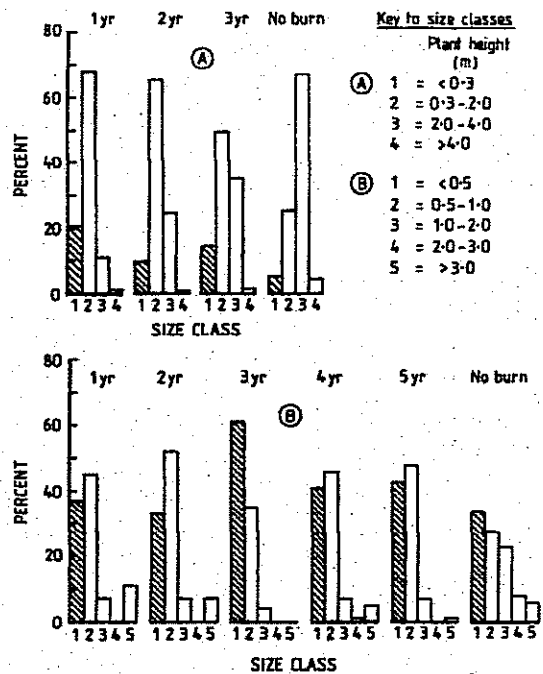


Fig. 5.5. Size distributions of trees in savannas burnt at different frequencies. A. *Brachystegia spiciformis-Julbernardia globiflora* woodland, Zimbabwe (Boulton and Nudel, 1981); B. *Acacia nigrescens-Combretum spicilatum* tree savanna, Botswana (Sweet, 1983). The smallest size class is shaded for emphasis.

burning is used in Zimbabwean *Brachystegia* woodland to prevent fuel accumulation after canopy removal by elephant, and also in forestry areas (Fanshawe, 1959). Fire intensity (determined by air

temperature, relative humidity, windspeed and grass fuel load) must be such that the woody plant biomass lost does not exceed the increment made during the previous wet season. Complete protection for some years is necessary if the woody plants are very slow-growing or unusually fire-sensitive, e.g. the canopy species of *Baikaea* woodland in Africa (Geldenhuys, 1977) and *Callitris* spp. in Australia (Leigh and Noble, 1981).

Woody plant regeneration may be encouraged by fire protection in humid savannas, allowing the germination and subsequent establishment of fire-sensitive forest species. In subhumid savannas regeneration is plentiful unless the disturbance has been very severe, but may be improved if a few canopy trees are left and stumps are not removed. Late hot fires in *Brachystegia* woodland where trees have been felled by elephant burn the trunks of even the largest fallen trees to 30 cm or more below ground level. This destroys the root-collar junction where the majority of adventitious buds arise and the trees seldom sprout again. In arid savannas fire may encourage regeneration through seed, but only if followed by favourable circumstances. Where grass growth is very high, such as in valley situations, fires will be very intense and so be able to trap woody plants in an early growth stage. All other things being equal, the ratio of grass to woody plants will be highest under a regime of predominantly late-dry season fires and least under a regime of late-wet season or early-dry season fires.

#### 4.5 SEED AND SEEDLING DYNAMICS

Fire creates opportunities for enhanced reproduction by removing plant cover and reducing competition from established plants. The increase in nutrients is also a potential factor. Fire directly and indirectly stimulates germination in a number of species (*Heteropogon contortus* (Shaw, 1957; Tothill, 1969, 1977); *Themeda triandra* (Lock and Milburn, 1971; Trollope, 1984a); *Cassia nemophila* and *Acacia aneura* (Moore, 1973; Hodgkinson, 1979). This effect can come about both by the direct effect of heat on the seeds, causing abrasion in hard-seeded species, and increased soil temperatures resulting from the reduction in plant and litter cover (Tothill, 1977).

In some annual grass communities, particularly in areas of high and reliable rainfall, germination at the start of the wet season exhausts the seed store in the soil. Since these communities depend on a continued input of viable seed in order to persist at a site, they are particularly vulnerable to any factors, such as early wet season fires or

heavy grazing, which might limit seed set (Mott and Andrew, in press). For example, in northern Australia, the seeds of the annual grass *Sorghum intrans* germinate soon after the first rains. Burning during dry intervals in the early wet season causes a marked change in the composition of communities dominated by this species because the developing plants are killed before they are mature and set seed (Smith, 1960; Stocker and Mott, 1981). In contrast, dry season fires have little effect on composition, although plant density decreases because the harsher physical conditions of burnt sites result in higher seed mortality and lower seedling establishment.

## 5. PLANT PRODUCTIVITY AND QUALITY

### 5.1 PLANT PRODUCTION

A range of conceptual and methodological problems surround the measurement of plant production (Sarmiento, 1984). The most commonly used methods involve destructive sampling of plant biomass at regular intervals during the growing season, with production being calculated either as the sum of all positive biomass increments or as the difference between the seasonal peak and trough of biomass. Differences in the timing of growth between species are usually ignored, as is growth after the time of peak biomass. Contemporaneous flows to decomposers and to herbivores are often neglected. In most cases, only the biomass of aboveground parts is measured; belowground production and the transfer of material to and from roots and underground storage organs is seldom taken into account, even though such transfers are an essential part of plant functioning. Since defoliation usually results in a temporary cessation or reduction in root growth, any apparent increase in aboveground production may be more than offset by lowered belowground production. In view of these deficiencies in method, the following discussion is focused primarily on changes in aboveground yield rather than in net production. Most of the applicable studies have been concerned with changes in grass yield.

In perennial grasses, fire removes moribund material and old leaves, thereby allowing more light to reach the younger, photosynthetically more efficient tillers at the base of the plant. The number of tillers often also increases as a result of the removal of apical dominance. The higher daytime temperatures and increased net radiant flux density of burnt areas generally produce more

*taurinus* which congregate on recently burnt areas once the grass begins to grow. (In contrast, dry season fires can reduce the availability of browse and cause browsing animals to move elsewhere [Bell and Jachmann, 1984]. This may increase browsing pressure on trees in unburnt areas [Harrington and Ross, 1974].)

Heavy grazing, particularly if the interval between the start of regrowth and subsequent defoliation is short, can limit the rate of recovery and reduce the standing crop of grass carried over into the dry season. This decreases the likelihood of the area sustaining fire the following year. Fire can even be excluded in the longer term, provided that the grazing pressure remains high. In this case, woody plants are able to invade, especially when the competitiveness of the grass layer is reduced by heavy grazing, drought, or both. If this encroachment is not checked subsequently by fire or browsing, thickets and woodland may eventually re-establish (Norton-Griffiths, 1979; Feliew, 1983).

Fire-maintained grasslands occur mainly in areas where drainage is restricted. In these areas, the grasses are usually too fibrous to support anything other than large-bodied grazers such as buffalo *Syncerus caffer* and elephant. As a result, the grass biomass is seldom reduced sufficiently to exclude fire (Bell, 1981). Invasion by woody plants under these conditions is difficult and only likely to occur if the area is protected for long enough from fire (San José and Farinas, 1983).

#### 7. DISCUSSION

Much of the current knowledge of fire and its effects on savanna structure and functioning has come from general observation supplemented by information derived from a limited number of experiments, most of which have been in existence for many years. This is unusual, for most ecological experiments tend to be of relatively short duration. Consequently, one might expect that over the years a significant body of understanding has been built up from the results of these experiments. Is current understanding sufficient to allow the effects of fires to be predicted? This review suggests not.

There are still a number of areas where our understanding of the ecological effects of fire is poor. These include information on the spatial aspects of fire behaviour, the degree of heterogeneity that results, what causes this, and what the consequences are for plant recruitment. Few studies have investigated the effects of

fire on single species, particularly the ways in which fire affects individuals and how this varies with the age, size and physiological condition of the individual and with the type, timing and intensity of the fire. In this respect, we need to know if plants which are drought-stressed, or recovering from herbivory, are likely to be more or less affected by fire. More consideration needs to be given to the possible contingency of effects, not only on the intensity, timing and frequency of fire, but also on the state of the organisms at the time, as well as on subsequent interactions with herbivores, rainfall, drought, and other fires.

The following hypothesis is relevant in this regard: the main determinant of the effect of fire on population structure and community composition in savannas is the interaction with future events, such as rainfall, drought, or herbivory, occurring during the recovery phase. Obviously, the more severe a fire is, in terms of mortality or degree of topkill, the longer the recovery phase and the greater the potential for interaction with other events. Populations which have to recover from seeds will be more susceptible to change than those whose members recover by resprouting. The rate of recovery is also affected by the favourableness of conditions for regrowth, especially the adequacy of water and nutrient supply. Therefore, as a corollary, we suggest that the less favourable the environment, the slower the recovery phase will be, and that this increases the likelihood of subsequent events affecting the eventual outcome. We also predict that the effects of fire will be less pronounced on sandy than on clayey soils because (i) the effect of exposure of the soil surface is less severe on sandy soils (there is less erosion, less compaction, and better infiltration resulting from single-grain structure of these soils), and (ii) the higher infiltration rates on sandy soils promote a more rapid recovery of the plants because more of the rainfall becomes available for their growth.



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