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INTERACTION BETWEEN ANIMALS, VEGETATION, AND FIRE IN SOUTHERN RHODESIA

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On the wide savannas of the great tableland of eastern and southern Africa, as Huxley (1962) has described, there evolved during the Tertiary the most striking climax community to persist into modern times. Attempts are now being made to preserve at least parts of this unique ecosystem by the institution of a number of large game reserves scattered throughout the area.

Huxley refers to the scientific work already in progress on a number of different aspects of this game conservation, but it is apparent from the studies which he and others have described, that comparatively little attention has yet been given to the vegetation. Nor has it yet been generally appreciated that the wide diversity of game animals is not only reflected in, but also is dependent largely upon, an equal diversity of habitats.

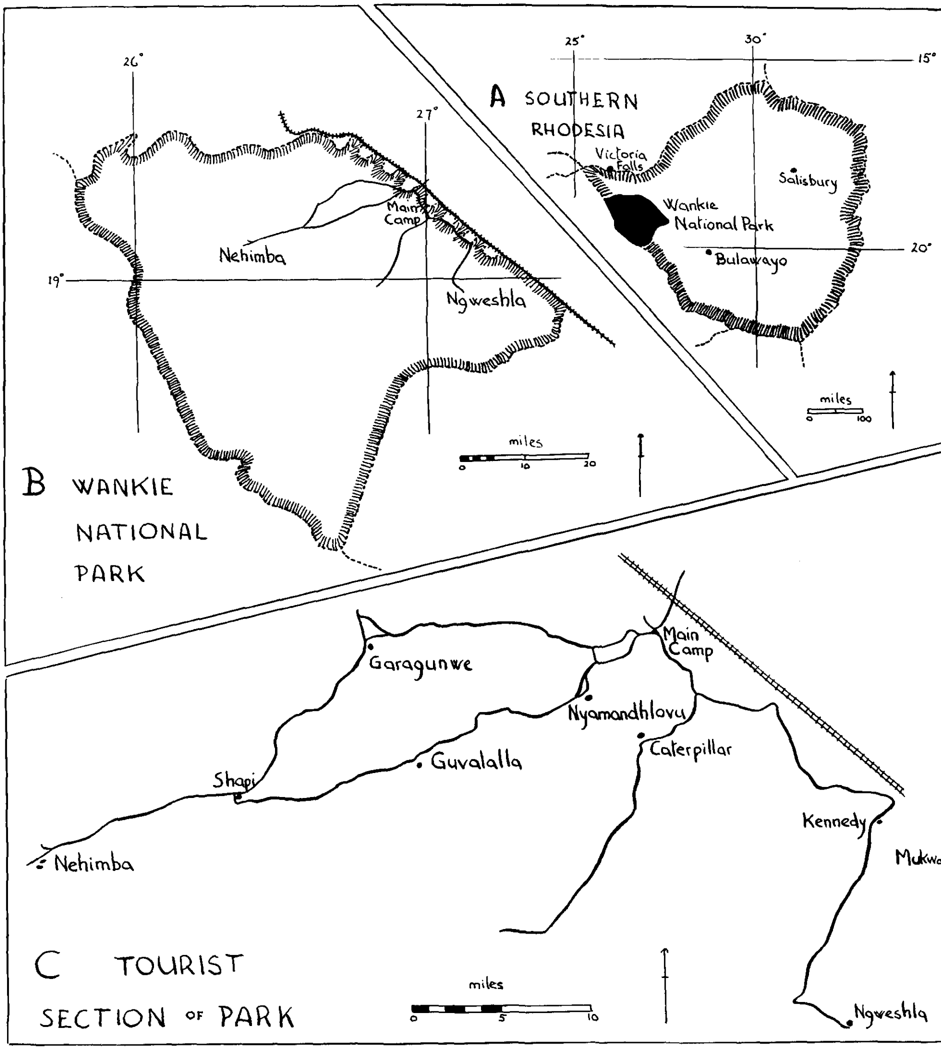
The Wankie National Park, in which the investigations described here were undertaken, is situated in the south-west of Southern Rhodesia (see map). In its northern and tourist section, where additional permanent sources of drinking water have been made available, this game reserve provides a unique opportunity for studies on the interaction between artificially high populations of the larger game animals and the natural vegetation.

The Park lies at about 3,500 ft altitude and is on the Kalahari Sands formation. This is an aeolian deposit up to 100 ft in depth, superimposed on Karroo sandstones and volcanics, extending northwards from Bechuanaland to the Congo River, and in southern Rhodesia reaching eastwards from the Victoria Falls to near Bulawayo. The Kalahari Sands were formed in the Late Tertiary, but were disturbed and re-deposited during the Pleistocene, in some instances being known to have covered human occupation sites, before the sand surface was again consolidated (Clark, 1959).

Summarized metereological data for the area are given in table 1. The annual rainfall recorded over the last 14 years varies from 19 to 37 inches, averaging approximately 24 inches. Although subject to high tropical temperatures in summer, frosts may occur in winter, more especially in June and July.

The Park was formally taken over for its present purpose in 1928 (Gale, 1963). The land around what is now the Main Camp had previously been farmed for some years on an extensive basis by Europeans, and other sections hunted over from time to time by both Europeans and Africans. It would appear that, while game concentrations have undoubtedly been present in the region for a very long time, protection from hunting, and, more especially, the provision of further permanent drinking supplies, have led to great increases in the numbers of game animals using the northern section, more particularly those of elephant, wildebeeste, zebra, and buffalo.

As described in another paper (Boughey, 1961), the undisturbed vegetation of the region in which the Park lies can be defined in terms of a catena type in which the better-drained flat or gently sloping land is covered by teak woodland, with a great abundance of Teak (*Baikiaea plurijuga* Harms). A timber company had operating rights for the extraction of Teak in the area before 1928. This



Map showing the location of: A, the Wankie National Park in southern Rhodesia; B, the position of the area of the Park investigated; C, the distribution of the various pans, drinking holes, and roads in the tourist section of the Park.

timber exploitation could partly or entirely explain the absence of tall Teak trees of an *emergent* form, and account for the fact that the vegetation here is of a *woodland* rather than a dry deciduous forest type. The effect of fire also has to be taken into consideration. According to Mitchell (1961a), a drastic reduction in the numbers of game which once inhabited the teak forests of the Kalahari Sands is responsible for the almost complete disappearance of those forests; the animals

TABLE 1

*Summarized metereological data from screen situated at 3,519 ft altitude, 18° 42′ S, 26° 56′ E, adjacent to main camp Wankie National Park**

1) *Amount of Annual Rainfall (July through June)*

Season	Total inches per annum	Number of rainy days	Season	Total inches per annum	Number of rainy days
1948/49	28.0	59	1955/56	21.9	78
1949/50	19.8	79	1956/57	18.2	68
1950/51	17.0	62	1957/58	39.5	88
1951/52	37.0	76	1958/59	27.9	80
1952/53	29.0	83	1959/60	25.8	58
1953/54	25.2	73	1960/61	28.2	85
1954/55	34.5	87	1961/62	19.2	72

2) *Average of mean monthly temperature 1951—1960.*

July (coldest month) 57.1 F (absolute min. 19F)
October (hottest month) 76.8F (absolute max. 102F)

3) *Average of mean monthly relative humidity 1951–1960.*
September (driest month) 37% (at 2PM 23%)
February (wettest month) 77% (at 6AM 94%)

*All figures are by courtesy of the Federal Metereorological Department.

prevented the accumulation of sufficient material from the usually sparse herbaceous cover to sustain a grass fire. Mitchell's general explanation cannot however be applied to account for the degradation of the teak forest to woodland in the northern part of the Wankie Park, for it would seem that animal populations here have always been fairly high. As will be discussed later, it must also be borne in mind that grass fires always have occurred over the elephant damaged Teak areas even before there was significant interference by man.

The catena pattern of plant communities in the northern section of the Park is illustrated diagramatically in figure 1. Degraded teak forests in the form of woodland occupy the upper sections of the gentler slopes and rises of the deeper sands, while the poorer drained shallower sands carry a mixed savanna woodland in which tree species such as *Lonchocarpus capassa* Rolfe, *Ziziphus mucronata* Willd., *Acacia galpinii* Burtt-Davy, *A. giraffae* Willd., *Combretum imberbe* Wawra,

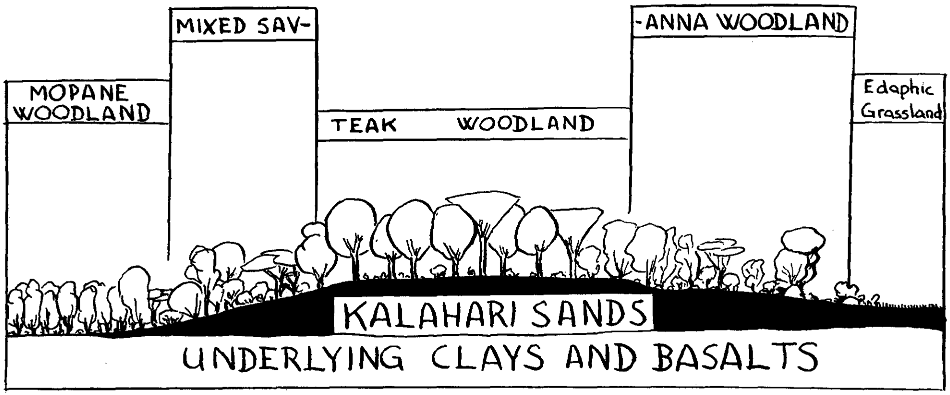


FIGURE 1. Diagramatic scheme illustrating the catena pattern of plant communities in the northern section of the Wankie National Park, and showing the relative positions of teak woodland, mixed savanna woodland, mopane woodland, and edaphic grasslands (vleis).

and *C. hereroense* Schinz are characteristic dominants. The clay depressions bare of Kalahari Sands which occur more especially west and north of Shapi Pan, and occupy the base of the catena pattern, develop what is called locally mopane woodland. This is a savanna woodland, closing locally to a woodland, composed almost entirely as a dominant of the Mopane tree, *Colophospermum mopane* (Kirk ex Benth.) Kirk ex J. Leonard.

The area of the northern section of the Park with a catena pattern formed principally of the three main plant communities, teak woodland, mixed savanna woodland, and mopane woodland, which was examined in the course of these studies, lies between the Main Camp and Nehimba Pan about 50 miles to the west, and the Main Camp and Ngweshla Pan 35 miles to the south. The work was carried out mainly in the course of visits to the area in January, July, and December 1960, and May and July, 1961. This area of the reserve was selected because of the high animal populations in the drought months of May to October, when drinking water is scarce or absent elsewhere in the park, and the animals have to congregate near permanent drinking holes. It was considered that under these extreme conditions ecological interactions would be heightened and the more readily identifiable. A secondary consideration was that this particular area is provided with a network of roads, so essential for access in the rainy season.

The procedure followed in the preliminary investigations described here was highly subjective. What was judged to be the least disturbed vegetation in each of the three plant communities recognized was located and examined. An attempt was then made to identify the progressive steps in its degradation and to record the game animals especially associated with each successive stage.

Vegetation was recorded in sample belt transects, 20 ft wide and 20, 40, or 60 ft, long according to the relative density of woody growth, laid down in representative portions of each community. The position, identity, height, and canopy spread of all woody plants in the transect were recorded. The profile diagrams and ground plans reproduced here as text figures are prepared from these data, as are the diagrams of hypothetical succession schemes.

The terms used for physiognomic types of vegetation are those recommended by the Yangambi ecological conference (C.S.A. 1956). Figures for distance, altitude, space, and height have been left in the original units of miles and feet in which they had to be measured, rather than converted to metric units.

SUCCESSIONAL RELATIONSHIPS—TEAK WOODLAND

Undisturbed Teak Woodland

Small areas of teak woodland, about 5 to 20 acres in extent, still occur in the area investigated, especially in the western and better-drained part; rather larger copses occur along the first portion of the road leading south to Ngweshla Pan. This teak woodland is composed of stands, often nearly pure, of Teak trees between 40 and 50 ft high (fig. 2). The commonest tree associates in these Teak stands are *Guibortia coleosperma* (Benth.), J. Léonard, and *Croton zambesicum* Muell. Arg., with on the rises *Mundulea sericea* (Willd.) Greenway and an undescribed form of *Pterocarpus angolensis* DC. Shrubby associates are *Baphia obovata* Schinz, *Diplorhynchus condylocarpon* (Muell. Arg.) Pichon subsp. *mossambicensis* (Benth.) Duvign., and *Bauhinia mendonçae* Torre & Hillcoat.

Such teak woodlands are visited throughout the year by older elephants either singly or in small parties, and seasonally from about June through November, by large breeding herds commonly up to 100 to 200 head strong. Few trees in the woodlands are without some scars of these visits. The most significant damage caused by the elephants at this stage is the stripping of bark from Teak trees in large sheets. While many trees successfully recover from this damage, those which have been completely girdled by the bark stripping eventually die. It is considered by the Park Wardens that the elephants do not strip off Teak bark to eat, indeed they have never been observed to do so, but are merely whiling away the time whilst sheltering in the woodland from the heat of the day, or resting at night.

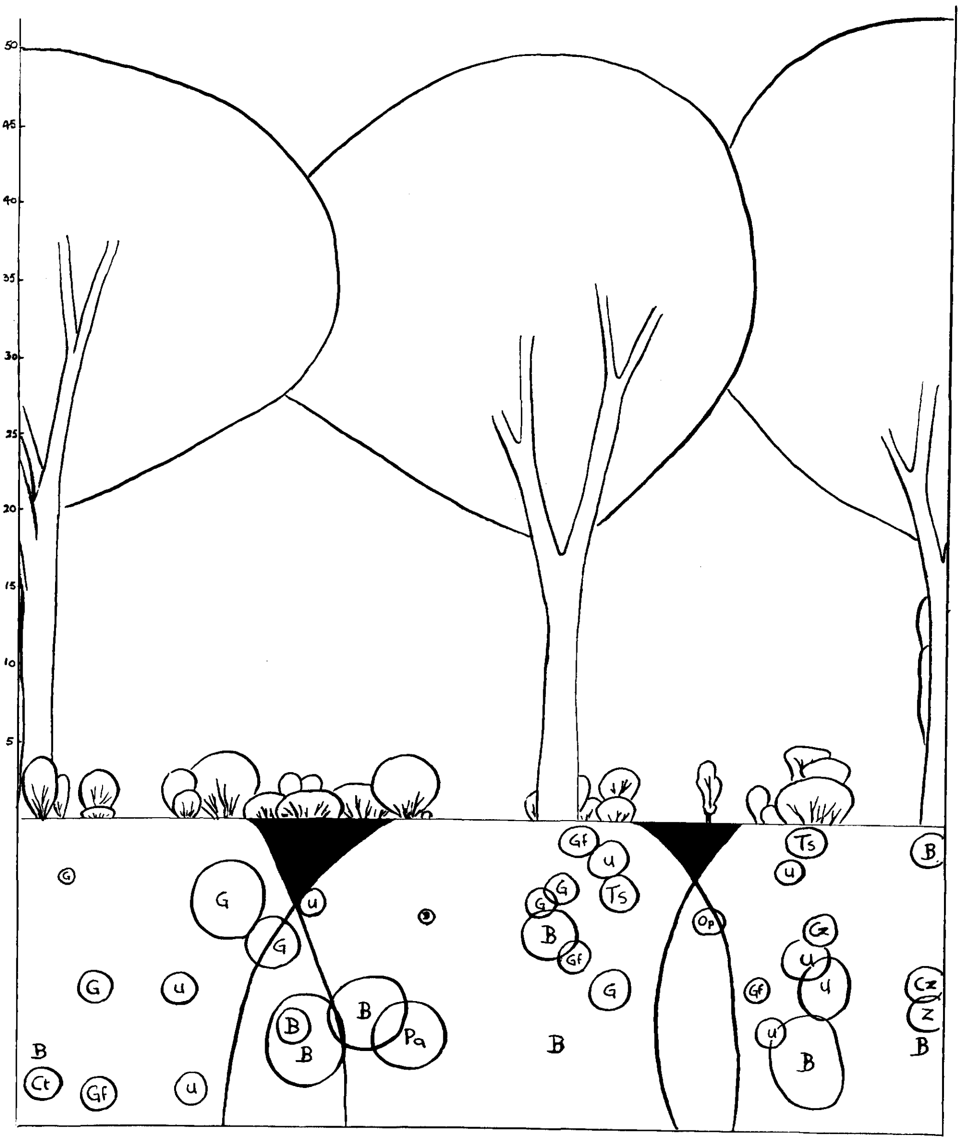


FIGURE 2. Profile diagram and ground plan of a portion of teak woodland, prepared from a transect taken some nine miles from Main Camp along the Guvalalla road.

Baikiaea—Terminalia Woodland

Gaps created in the teak woodlands by the death and eventual fall of ringed trees, and by the odd tree pushed over by elephants, are colonized by a number of invading tree species. Of these *Terminalia sericea* (aggregate) is by far the most abundant, with many Teak saplings, a little *Burkea africana* Hook., some

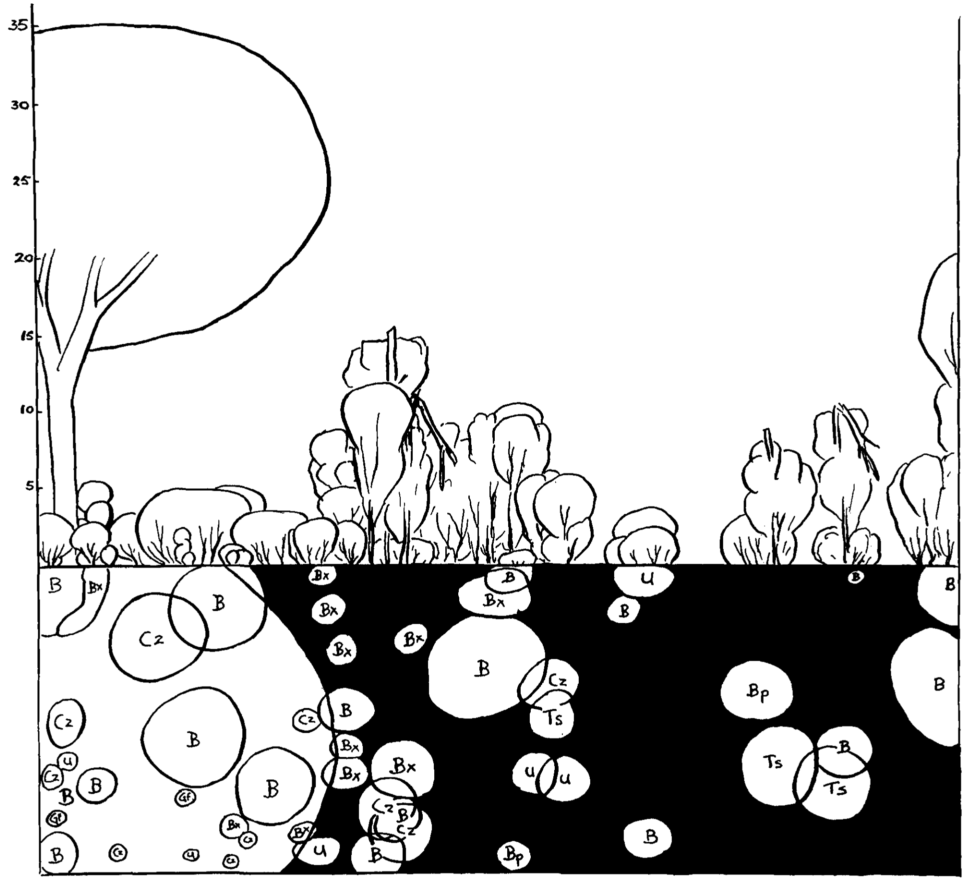


FIGURE 3. Profile diagram and ground plan of *Baikiaea—Terminalia* woodland, ravaged and opened up by elephants, prepared from a transect taken some 13 miles from Main Camp along the Guvalalla road.

KEY TO THE SYMBOLS FOR PLANT SPECIES EMPLOYED IN FIGURES 1–5

The scale shown on all profile diagrams is the same, figures indicating the height in feet. Each ground plan is 20 ft wide, and is composed of one, two or three 20 ft squares as the case may be. The area on the ground plan covered with a mechanical tint indicates in each case the extent of ground not directly shaded from above by woody plants, and is therefore some indication of the amount of grass cover in the community illustrated.

A —*Acacia galpinii*
Ag —*Acacia giraffae*
As —*Asparagus* sp.
At —*Acacia tortilis*
B —*Baikiaea plurijuga*
Bp —*Baphia obovata*
Bx —*Bauhinia mendoncae*
Bu —*Burkea africana*
Ch —*Combretum hereroense*
Ct —*Canthium* sp.
Cz —*Croton zambesicum*
D —*Dichrostachys cinerea*
Di —*Diplorhynchus condylocarpon*
Ea —*Erythrophlelum africanum*
G —*Grewia bicolor*
Gf —*Grewia flavescens*
Mc —*Maytenus cymosus*
Op —*Ochna pulchra*
Pa —*Peltophorum africanum*
R —*Rhus tenuinervis*
S —seedling of *Terminalia sericea*
Ts —*Terminalia sericea*
U —indet. sp.
Z —*Ziziphus mucronata*

Combretum sp., and an increase in *Baphia obovata* and *Bauhinia mendonçae* in the shrub layer (fig. 3). These younger and smaller invaders appear to be left relatively undisturbed for a time, while the elephants persist in the destruction of the remaining older and larger teak trees, but sooner or later they turn their attention to the young growth in the gap, and commence to break off the tops of the *Terminalia* and other tree species.

Burkea—Terminalia Savanna Woodland

By the time only a few old relict Teak trees survive, the original woodland has been opened up considerably, and the community is more properly now called

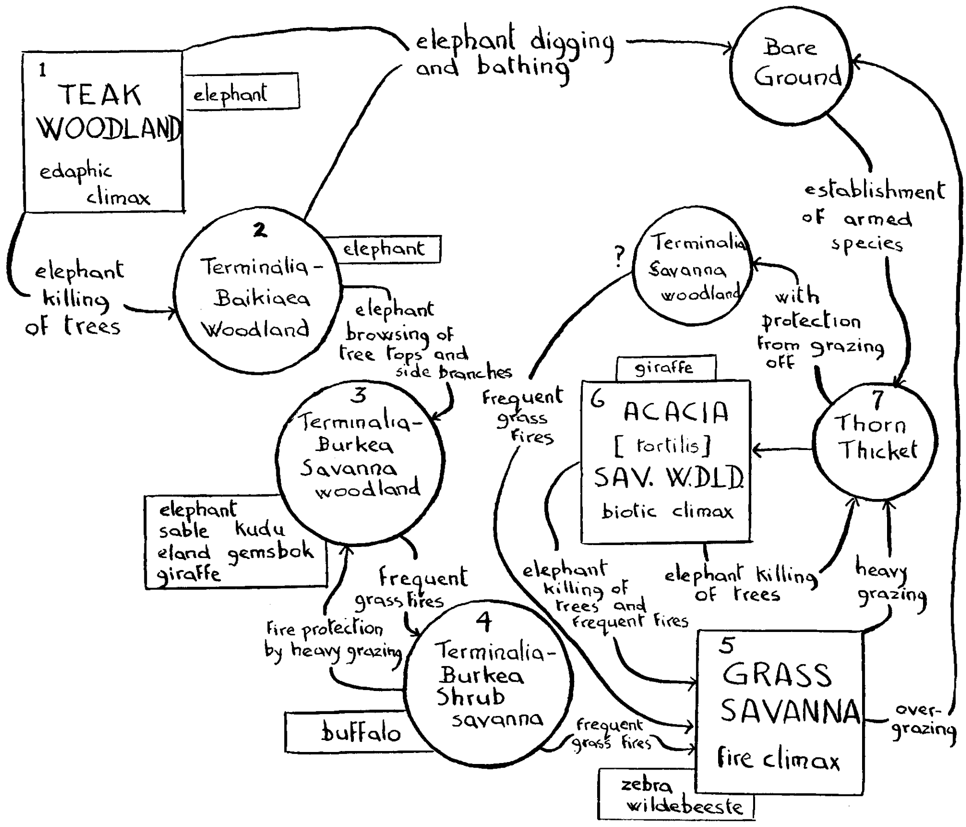


FIGURE 4. Diagramatic hypothetical scheme showing the various secondary communities derived from the teak woodland vegetation type on Kalahari Sands in the northern section of the Wankie National Park, the major ecological factors which operate in this ecosystem, and the larger game animals associated with particular plant communities.

savanna woodland. In these more open conditions there is a proportionally increased representation of the tree *Burkea africana*, and more dense stands of grass are established.

The foliage in an undisturbed Teak woodland is not only mostly unreachable, it is also apparently unpalatable. The presence of more plentiful grass and of palatable young tree browse within reach in the *Burkea—Terminalia* savanna woodland may have two direct and important consequences. For the first time large game animals in addition to elephant begin to feed extensively in the area; sable antelope, kudu, and less importantly gemsbok, were commonly observed here. The relative intensity and the time of year of the grazing, as opposed to browsing, which these animals do is of great ecological significance. If the animals mostly browse in the rainy season, and graze during the dry season, the grass will be favoured. Should the reverse occur, the woody vegetation will increase at the expense of the grass. In the first circumstance there may be an ample supply of flammable material remaining in October. If a grass fire is then started accidentally by some human agency, as frequently occurs in this area, most tree seedlings will perish. Although the thick bark of mature trees in this community

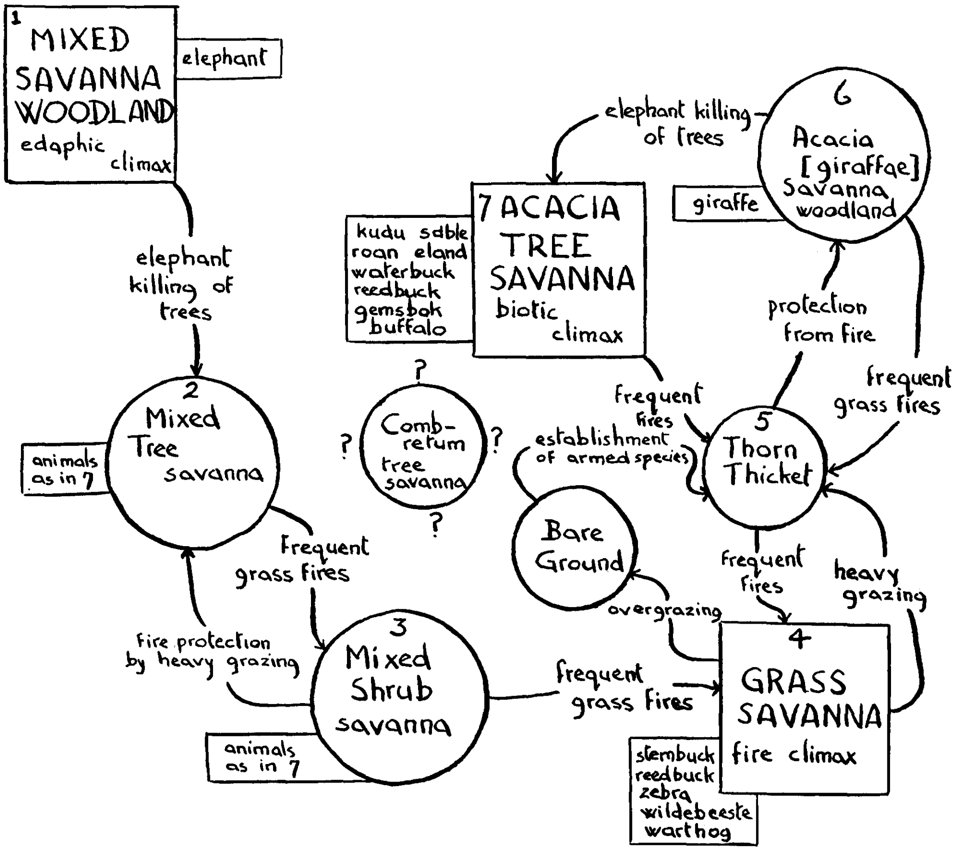


FIGURE 5. Diagramatic hypothetical scheme showing the various secondary communities derived from the mixed savanna woodland type of vegetation on Kalahari Sands in the northern section of the Wankie National Park, the major ecological factors which operate in this ecosystem, and the larger game animals commonly associated with particular plant communities.

usually insures their being fire resistant, saplings have not yet developed this and may be burnt to the ground, generally sprouting again from the burnt collars during the next rainy season.

Elephants are liable to grub for edible roots such as those of *Bauhinia fassoglossis* Kotschy ex Schweinf. and perhaps to dig for salt or water, in any of the types of woodland or savanna woodland so far discussed. At the beginning of the rainy season in November, the holes which they have dug fill with water and may be used as mud baths by the elephants. The vegetation around such holes is destroyed, leaving patches of bare ground. Thickets of thorny species, in particular *Dichrostachys cinerea* Wight and Arn. and *Acacia* sp. develop on these bare sites.

Elephants commonly browse on this *Burkea—Terminalia* savanna woodland and often "top" the trees at a height convenient for their reach, about 4 ft. Numerous giraffe also browse the tops of the trees, but seemingly without any significant ecological effect.

Burkea—Terminalia Shrub Savanna

As already noted, grass fires in the *Burkea—Terminalia* savanna woodland will kill most tree seedlings and burn tree saplings to the ground. From the latter a sprout growth develops, which may again be burned to the ground by a fire one or two years later. Ultimately all the mature trees, which have probably mostly been able to withstand the frequent fires but are relatively short-lived die out, leaving only a shrub savanna of sprout growth.

This is the stage which buffalo most seem to favor; they graze the grass between the shrub clumps and trample the area heavily. Such a grazing pressure may be maintained that fires do not occur for several years, and the sprout growths may get 3 or 4 ft high, but usually a fire eventually comes along and burns them down again.

Grass Savanna

Continued trampling of shrub savanna by buffalo combined with only moderate grazing pressure permits the survival of sufficient flammable material to provide for late (October, November) fires annually. This in a few years results in the

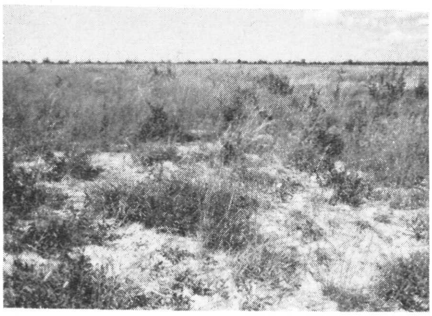


FIGURE 6. Sprout growth of original teak woodland species in the grass savanna surrounding Nehimba Pan.

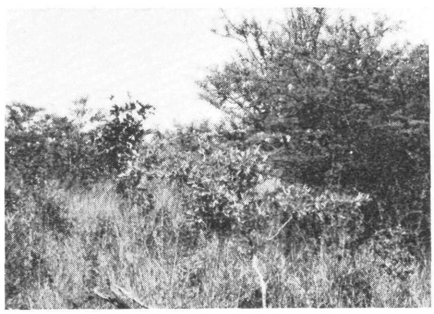


FIGURE 7. Saplings of *Terminalia sericea* growing within the protection of an *Acacia* savanna woodland.

complete suppression of all woody growth. The resultant grasslands come to support large herds of wildebeeste and zebra as well as smaller animals such as ostrich and stembuck.

A good example of such a grassland in course of formation in the northern section of the Park is to be seen at Nehimba Pan, which lies in the middle of a grass savanna about one mile across. Nehimba Pan provides a permanent water supply, due to seepage into it of water from the surrounding area, and it must have been visited by large concentrations of animals in the dry season before the game reserve was founded. Under present conditions something like two thousand buffalo come down to water between noon and dusk every day during the height of the dry season. Despite this large animal population using the drinking holes, Nehimba Pan plain does not appear to be heavily grazed, nor are large herds of wildebeeste or zebra in occupation of or visiting the area. As a consequence the flammable grass material which persists into the dry season each year is considerable, and the plain appears to burn annually. This frequency of burning is sufficient to keep in check the re-growth from such sprout clumps as have survived from the tree cover of the original savannas and teak woodland (fig. 6).

Not all grass savanna in this northern section of the park has been derived in this manner from the breakdown of teak woodland and savanna. Many of the smaller pans are surrounded by an edaphic grassland (fig. 1), or *vlei* as such vegetation is called locally; these grasslands are discussed later.

Acacia Savanna Woodland

With heavy grazing of grass savanna by wildebeeste and zebra herds, and the consequent disappearance or at least the infrequency of grass fires, various armed woody species such as *Acacia giraffae*, *A. galpinii*, *A. tortilis* (Forsk.) Hayne, *Dichrostachys cinerea*, *Dalbergia melanoxylon* Guill. & Perr., and *Maytenus cymosa* (Soland.) Exell, become established. Presumably these thorny species are able to invade such areas because their spiny shoots largely escape being grazed off. At least the young shoots are not bitten off wholesale, whereas the unprotected seedlings of unarmed tree species tend to be grazed right off.

As they mature, these *Acacia* savanna woodlands seem to be more frequently visited by giraffe than other plant communities in the area; giraffe browsing nevertheless would not appear significantly to affect the ecological succession described here.

Grazing pressure is relaxed in these developing *Acacia* savannas presumably because of their thorny nature; perhaps spines are liable to penetrate the feet of animals as well as to discourage them from grazing. In more open communities grass fires may therefore once more become frequent, and this vegetation can be reduced again to a grass savanna. The thorny tree species of this savanna woodland do not appear to have the vigorous sprouting abilities of the broad-leaved tree species of the original teak woodland, so that a shrub savanna is not formed as an intermediate degraded community.

The best examples of this biotic climax *Acacia* savanna woodland in which the dominant tree was *Acacia tortilis*, were seen in the area some 12 miles from the Main Camp along the road passing Caterpillar Pan. The low hill-tops here, which must once have been covered with teak forest, now carry mature *Acacia* savanna woodland. It has been shown experimentally (Boughey, 1963) that seedlings of *Acacia tortilis heteracantha* (Burch.) Brenan cannot germinate in the shade of the parent trees. If the trees in this instance, which appear to belong to *A. tortilis spirocarpa* (Hochst. ex A. Rich.) Brenan, behave similarly, these *Acacia* savanna woodlands will be unable to maintain themselves for more than one generation on a given site unless seedling reproduction again becomes established as the stand deteriorates. Certainly no seedlings or saplings of the dominant species were observed in the savanna woodlands.

The animal populations which must have been responsible for the break-down of the original teak woodland in this area beyond Caterpillar Pan no longer appear to be present in the same concentrations. Perhaps this once favoured area was deserted by the game when artificial drinking holes were established along the tourist roads a little to the north. There is some suggestion that in these circumstances seedlings of *Terminalia sericea* will invade the area and become established. Indeed young almost pure *T. sericea* savanna woodlands are very commonly to be seen in the area associated with *Acacia* savanna woodlands (fig. 7). It is possible that this *Terminalia* community takes over when the latter become overmature.

Thicket

Ground laid bare by over-grazing or by animal digging in any of the plant communities discussed is liable to be invaded by armed thicket-forming species: the most aggressive of these is *Dichrostachys cinerea*. It seems likely that the armed tree species cited as forming the principal dominants of *Acacia* savanna woodland become established first as a low-growing more or less open thicket. The longer-lived tree species such as *Acacia tortilis* eventually emerge above the shorter-lived, and in this area shrubby, species like *Dichrostachys cinerea*. As already stated, young plants of the broad-leaved tree species are protected from grazing-off when they become established in these thorny thickets and savannas, and such species as *Terminalia sericea* frequently constitute an important element of such vegetation.

SUCCESSIONAL SCHEME—TEAK WOODLAND

The successional inter-relationships of these several plant communities which arise with the degradation of teak woodland by animals and by fire, and the points at which these major ecological factors operate, are expressed diagramatically in figure 4. It is to be noted that with a continuing rise in the number of game animals in this area, many of the trends are at present unidirectional: this point will be discussed later.

SUCCESSIONAL RELATIONSHIPS—MIXED SAVANNA WOODLAND

Undisturbed Mixed Savanna Woodland

As is illustrated in figure 1, areas of the northern section of the park which occupy depressions in the Kalahari Sands, where drainage is poorer but not so seasonally impeded as to exclude tree growth altogether, could be expected to be covered with mixed savanna woodland. The principal tree dominants in this community are *Acacia giraffae*, *A. galpinii*, ***Lonchocarpus capassa***, ***Combretum imberbe***, ***C. hereroense***, ***Peltophorum africanum*** Sond., ***Rhus tenuinervis*** Engl., with most frequently on termite mounds, *Ziziphus mucronata* Willd. and ***Diospyros mespiliformis*** Hochst. ex A.DC. Around Mukwa Pan, in the east of the section, the palm ***Hyphaene crinita*** Gaertn. is associated with these last two species and largely confined to termite mounds (fig. 8).

In the northern section of the park however, because of the proximity of this type of vegetation to drinking holes, in no area has it remained even relatively undisturbed. As in the case of teak woodland, it is again elephants which are the main destructive agents. They strip the bark more particularly from the *Acacia giraffae* trees, in this instance apparently finding some nutritional need satisfied by it. Again trees are commonly killed by girdling (fig. 9), and whole trees may be pushed over and wrecked. Mixed savanna woodland therefore does not exist in the area of the park under consideration although it must have been the starting point for the successions described below, and it must exist elsewhere in the park.

Mixed Tree Savanna

Thinning out of the trees in a mixed savanna woodland by elephant produces a tree savanna, which is now the most conspicuous vegetation surrounding the pans and water-holes on Kalahari Sands in this northern section (fig. 10).

Digging by elephants may clear the ground, and thorn thickets usually develop on such bare areas as in the teak woodland succession. A number of other animals may also contribute to the laying bare of the ground, especially wart-hogs which closely graze the grass margins of pans during the rains, and grub there for edible roots in the dry season.

In some areas the mixed tree savanna may be replaced by a tree savanna or a savanna woodland in which the principal tree dominant is *Combretum hereroense*. In many instances, around the margins of the pans an invasion of broad-leaved species, and more particularly of *Terminalia sericea* occurs. A particularly striking example of this broad-leaved invasion was found at Mukwa Pan. Here *Terminalia sericea* and *Burkea africana* are colonizing the flat land between the termite mounds which was originally treeless, supposedly because of the former degree of seasonal water-logging in the area.

It would seem that as a pan providing a permanent source of drinking water develops, the removal of soil particles with the drinking water causes it to deepen until it has a significant effect on the local water-table. Weir (1961) in a paper on the evolution of drinking holes in the Wankie National Park, has remarked on the quantities of mud as well as water that drinking animals remove. He did not however continue the evolution of the pan to its logical end, when so much

FIGURE 8. The palm species *Hyphaene crinita* growing on termite mounds near Mukwa Pan.

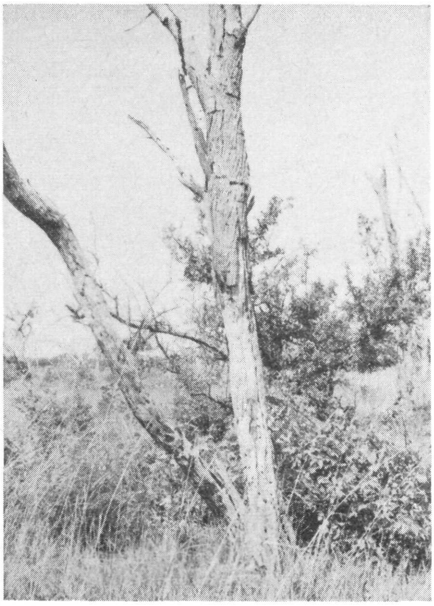


FIGURE 9. An *Acacia giraffae* tree completely ring-barked as a result of elephant bark-stripping activity.

sand has been removed with drinking water that the hole is so deep the water table of the surrounding soil has lowered beyond the point when it can be restored to the same level each year by rain falling on the surface of the surrounding soil. The hole then ceases to have available water in the dry season, and being no longer visited presumably rapidly fills up with blown or washed soil.

Mixed Shrub Savanna

As in the teak successions the occurrence of frequent grass fires at this point will prevent the survival of seedlings and will burn saplings down to sprout growth, resulting in the development of a shrub savanna formed mostly from the same species as the two previous communities. There is also a *Combretum hereoense* shrub savanna, and this is particularly conspicuous around several of the pans near the Main Camp.

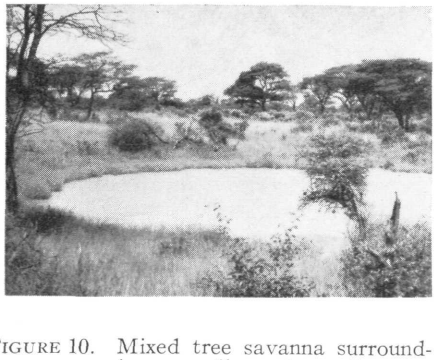


FIGURE 10. Mixed tree savanna surrounding a small pan two miles east of Guvalalla Pan.

Grass Savanna

Around a pan which dries out in the dry season, grazing pressure will not be sufficient to remove the vigorous grass growth which appears on these comparatively well-watered sites. Annual grass fires are then likely to occur, and these will gradually exhaust and eliminate the woody plants of the mixed shrub savanna, leaving a grass savanna remaining. Where drinking water is available all the year round however, the grass is grazed too short to provide flammable material. The woody species of the shrub savanna then persist and are supplemented by a further invasion of tree species.

Grass savanna resulting from degradation of the mixed savanna woodland is similar in appearance (fig. 11) to that derived from the teak woodland. Its specific composition, which is not considered in this paper, is however different, and in addition to herds of wildebeeste and zebra, it is frequented by animals which do not go too far from water like wart-hog (fig. 12), ostrich, reedbuck, and stembuck.

FIGURE 11. Zebra grazing a grass savanna derived from mixed savanna woodland; a thorn thicket is becoming established in the fore-ground.

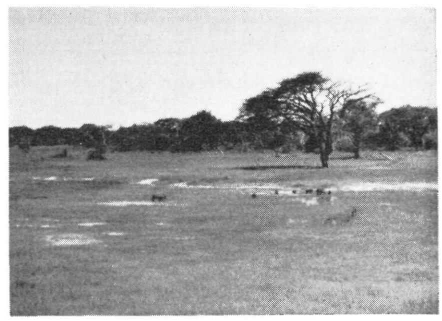


FIGURE 12. A warthog family rooting near a pan in the soil of a grass savanna derived from mixed savanna woodland.

Thorn Thicket

Where grazing activity around permanent water-holes is sufficiently intense to prevent the persistence of sufficient flammable material to support a grass fire, the woody tree species of the mixed savannas increase greatly, producing a thicket growth. The commonest species are *Acacia giraffae*, *A. galpinii*, *A. tortillis*, *Dichrostachys cinerea*, *Maytenus cymosus*, and *Dalbergia melanoxylon*, the same group of pioneer species in fact which are present in the thicket and savanna woodland of the teak woodland succession. All these species, as noted previously, are armed, and while this does not prevent their leaves being eaten, it is usually sufficient to ensure that whole shoots are not bitten off. The plants when merely defoliated can then grow a new set of leaves in the rainy season, when animals are more dispersed and the grazing pressure lighter. An illustration of the ability of these armed species to survive in even the most densely populated areas is given in figure 13.

Acacia Savanna Woodland

Although the pioneer thicket species are the same in both the teak woodland and the mixed savanna successions, the savanna woodland which emerges from the thicket appears to be formed of a different balance of species, and more particularly, of *Acacia* species. In the teak series it was *Acacia tortilis* which emerged as a single dominant; on these more poorly-drained Kalahari Sands of the mixed savanna succession, it is *A. giraffae* which assumes this dominant position. Such *A. giraffae* savanna woodlands are very conspicuous in the area round Kennedy; they are also very prominent adjacent to the Main Camp. In both areas these savanna woodlands may owe their survival to a reduced elephant pressure, for elephant herds devastate these savanna woodlands to which they may partly be attracted by their fondness for *A. giraffae* pods. As mentioned earlier, elephants will strip the bark from these acacias, wreaking incredible damage to the savanna woodland such as is illustrated in figure 14. Unless elephants avoid a particular savanna woodland because of lack of convenient drinking supplies, or dislike of the proximity of humans, it therefore has little chance of survival, and in fact in the northern area of the park, most of such communities have been broken down to tree savannas.

SUCCESSIONAL SCHEME—MIXED SAVANNA WOODLAND

The probable inter-relationships of these various secondary communities derive from mixed savanna woodland, and the principal ecological influences which effect them, are expressed diagramatically in figure 5.

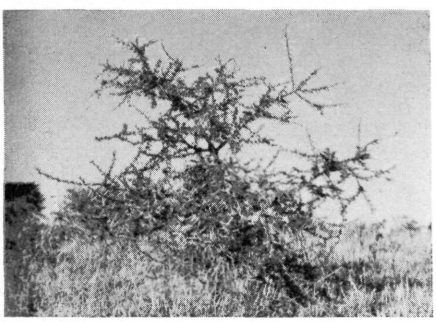


FIGURE 13. A thorny sapling of *Acacia tortilis* established in a heavily-grazed grassland.

FIGURE 14. Acacia savanna woodland devastated by elephants, which have killed most of the taller trees by bark-stripping.

SUCCESSIONAL RELATIONSHIPS—MOPANE WOODLAND

Mopane Woodland

This woodland, more correctly termed savanna woodland (Boughey, 1961), develops on the clay depressions which occur to the north and west of Shapi Pan, in the northern area of the Park under consideration. Undisturbed mopane savanna woodland here is comparatively rare, and only one example was found along the road between Shapi Pan and Nehimba Pan (fig. 15), although the road from Shapi Pan to Garagunwe Pan passes through some half-dozen such undisturbed mopane woodlands.

Such woodlands are inhabited especially and typically by herds of impala, which seem to require the browse provided by Mopane leaves when the predominantly annual grasses of this vegetation type have been entirely grazed off towards the close of the dry season. Other animals, particularly herds of sable antelope, were occasionally seen in mopane woodland, and herds of elephant are common in the dry season, although the clay is too soft for them to penetrate in the wet season. Elephants browse on the Mopane trees usually by pulling off side branches or tops, but occasionally they will push over a whole tree.

Mopane Shrub Savanna and Grassland

Around the pans and water-holes which are very common in the necessarily low-lying Mopane areas (fig. 1), trees are ravaged by elephant and other game, until they are little more than poles about 4 ft high, with stubby side shoots bristling out all round (fig. 16). Should such an area be left sufficiently lightly grazed to provide material for a grass fire, these stubby Mopane trees will be burned down to the ground and will sprout later. This is the typical appearance of Mopane in areas of high animal populations (fig. 17). This kind of shrub savanna is extremely widespread in the northern sections of the Kruger National Park, and also in remote areas of the Rhodesian low veld between this park and Wankie. It is sometimes maintained that frost-damage rather than grass fires are responsible for holding the Mopane in sprout form.

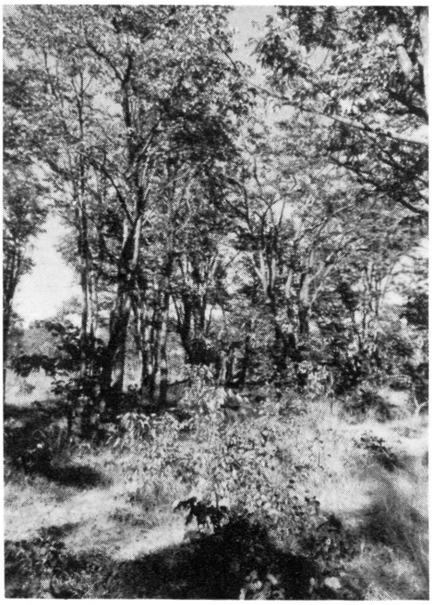


FIGURE 15. A little-disturbed *mopane* savanna woodland on basaltic clay bare of Kalahari Sand.

Repeated fires in the mopane shrub savanna will so weaken the Mopane stools that the plants eventually die out, leaving a grass savanna. Overgrazed areas of this grass savanna do not however appear to be invaded by armed woody species, as in the two previous successions. Possibly the seasonal water-logging in the rainy season which such plants would have to endure is sufficient barrier to invading species from the Kalahari Sands areas.

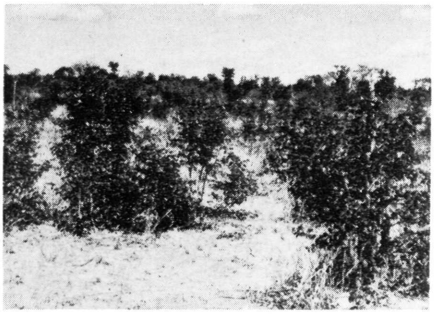


FIGURE 16. Mopane trees reduced to sprouting stumps by heavy elephant browsing near a water-hole.

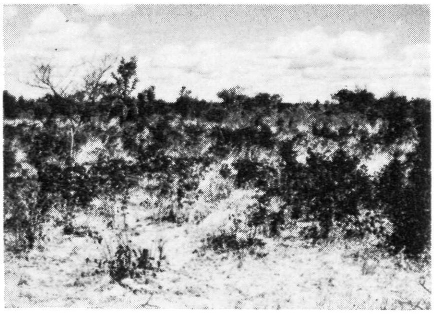


FIGURE 17. Sprout shoots of Mopane, all that now remains of a mopane woodland after heavy elephant browsing followed by grass fires.

DISCUSSION

It is concluded from these preliminary studies that most of the vegetation of the Wankie National Park, in so far as the northern areas studied are concerned, is composed of secondary communities. These secondary communities, whose nature is determined primarily by the intensity of biotic or fire factors, appear mostly to be much more suitable for game occupation than the undisturbed edaphic communities of the region. Each secondary community appears to have associated with it a particular group of game animals, making up a complex ecosystem.

The two predominant variable ecological factors in the ecosystem are elephant damage and burning by grass fires. The operation of both these factors and therefore the nature of the balance within the ecosystem, are clearly controllable, and can be brought within a game management policy. For the present the only control on elephant numbers exercised is an attempt to disperse them over a wider area in the dry season by the provision of additional permanent drinking holes. For nearly thirty years grass savannas adjoining the tourist roads near the Main Camp in the northern areas of the park described here were burnt annually, to provide an early crop of fresh grass which would bring the animals down where the tourists could see them from their cars. Latterly, with insufficient flammable material, it has only been possible to burn every other year. As grazing animals control the amount of such material remaining, control of species such as wildebeeste and zebra, which tend to occupy the same grasslands continuously throughout the year, offers scope for additional management practice.

The purely subjective conclusions of this preliminary study can be verified in two ways, by the laying down of permanent observation areas, and by statistical sampling. The first of these methods has already been adopted, and a permanent transect was laid down in 1960. Also a map of the principal vegetation types which he recognized in one small part of this area has been prepared by Mitchell (1961b). Over the years such records will provide an unchallengeable account of change. The statistical approach however offers promise of more immediate information.

The demonstrable existence of the various plant communities described in this paper may be determined by using as a criterion the degree of association between plant species. It is also possible to assess the relative extent of the various communities arranged on this basis. This statistical investigation has already been carried out in this northern area of the park, and the results will be described in a further paper. It should also be possible to correlate animal presence with plant species, so that the whole picture of the ecosystem is obtained.

More detailed information is required both as to the operation of the elephant damage factor and the influence of grass fires. The possible existence of these factors and of the secondary communities described in the less densely populated areas of the park must be investigated. It is certain that many of the changes recorded as uni-directional in the hypothetical schemes illustrated in figures 4 and 5 will be found to proceed also in the opposite direction in areas where game populations are smaller and more scattered.

The spread of plant species is obviously much dependent on animal activity. Elephants consume large quantities of *Acacia giraffae* pods, and seeds of this and numerous other flowering plant species may be recovered undamaged from elephant dung. In the rainy season dung beetles rapidly bury any fresh dung, so that great quantities of seed are in this manner inadvertently planted in an excellent seed-bed.

Until more detailed information of this nature can be obtained, management policies in this and other game parks can at best be based on *ad hoc* measures, decided by devoted officers forced to formulate some definite policy with only their long experience to guide them in their decisions. It is fortunate that this experience coupled with sound judgement has so far prevented disastrous upset in this finely balanced ecosystem.

ACKNOWLEDGMENTS

I wish to record my grateful thanks to Mr. T. E. Davison and Mr. B. Austen, the past and present Senior Wardens of the Wankie National Park respectively, for many discussions on the habits of game animals and for the excellent facilities and great encouragement given for work inside the park, for which thanks are also due to the Director of National Parks, Mr. R. E. Stewart.

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Summary of Oil and Gas Activity in Ohio During 1962. *Warren L. Calvert.* 1963. Ohio Geological Survey Report of Investigations No. 47. 125 p., 5 figs. Copies mav be obtained from The Ohio Division of Geological Survey, 1207 Grandview Ave., Columbus 12, Ohio. 97 cents plus 3 cents tax in Ohio.

Seventy-three percent of the 1,522 new wells drilled for oil or gas in Ohio during 1962 produced either oil or gas, or both, in varying amounts. Forty-seven old wells were reworked or drilled deeper. New gas pools were discovered in Athens, Auglaize, Morrow, Richland, and Washington Counties and a new oil pool in Morrow County. Almost half of the new wells were drilled to the "Clinton" sandstone in eastern Ohio. Considerable interest was shown in the older horizons in Ohio, especially in Morrow County, where 21 wells were drilled to Cambrian rocks and two in the basement complex. Some Cambrian correlations are discussed.

The report contains schedules listing all the wells drilled in Ohio by county and township with either oil or gas, or both, in varying amounts. Forty-seven old wells were reworked or drilled deeper, secondary recovery operations, brine wells, and wells abandoned. Tables summarize information on wells by producing horizons and by exploratory status. Petroleum geologists and oil and gas operators in Ohio will find these annual statistics useful.

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