

Description of a fire and its effects in the Nylsvley Nature Reserve: A Synthesis Report

M V Gandar

A report of the Savanna Ecosystem Project National Programme for Environmental Sciences

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO



Issued by
Cooperative Scientific Programmes
Council for Scientific and Industrial Research
P O Box 395
PRETORIA
0001
from whom copies of reports in this series are available on request

Printed in 1982 in the Republic of South Africa by the Graphic Arts Division of the CSIR

ISBN 0 7988 2608 8

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PREFACE

The Savanna Ecosystem Project of the National Programme for Environmental Sciences is one of several national scientific programmes administered by the CSIR. The National Programme is a cooperative undertaking of scientists and scientific institutions in South Africa concerned with research related to environmental problems. It includes research designed to meet local needs as well as projects being undertaken in South Africa as contributions to the international programme of SCOPE (Scientific Committee on Problems of the Environment), the body set up in 1970 by ICSU (International Council of Scientific Unions) to act as a focus of non-governmental international scientific effort in the environmental field.

The Savanna Ecosystem Project being carried out at Nylsvley is a joint undertaking of more than fifty scientists from the Department of Agriculture, the Transvaal Provincial Administration, the CSIR, the Transvaal Museum, and eight universities. As far as possible, participating laboratories finance their own research within the project. The shared facilities at the study area and the research of participating universities and museums are financed from a central fund administered by the National Committee for Environmental Sciences and contributed largely by the Department of Environment Affairs.

The research programme of the Savanna Ecosystem Project has been divided into three phases - Phase I (mid 1974 to mid 1976) - a pilot study of the Nylsvley study area, in particular the description and quantification of structural features of the ecosystem, Phase II (mid 1976-1979) - studies in the key components and processes including the development of mathematical models, and Phase III (1979-1984) - extension to other sites and the study of management strategies for the optimal utilization of Burkea savanna ecosystems.

The present report forms part of the study of the key components and processes of the ecosystem, concentrating on the behavioural characteristics of a savanna fire, its short-term effects on the various components of the ecosystem, and their responses to the stresses imposed by these effects. The report also forms part of the South African contribution to the international SCOPE mid-term programme on the ecological effects of fire.

ACKNOWLEDGEMENTS

This report is a synthesis of the research carried out by many of the participants in the Savanna Ecosystem Project and their contributions are gratefully acknowledged. In particular, I would like to thank Dr J J Bezuidenhout, Miss L Dempers, Mr P Ferrar, Mr D Grossman, Professor J O Grunow, Mr T D Harrison, Mr R H Munro, Dr M C Rutherford, Mr J Watson and Mr I Zimmerman for permission to use their unpublished data, and Mr B J Huntley who initiated and coordinated the research effort. Financial support was provided by the National Programme for Environmental Sciences of the CSIR, through Cooperative Scientific Programmes.

ABSTRACT

This report synthesizes information gained from a study of an experimental fire ignited in an 182 ha portion of the Savanna Ecosystem Project study area in early September 1978. Three smaller fires, each covering 1 ha within this area, were ignited immediately before the main fire so that the behaviour of the fire could be more readily assessed. This also provided an opportunity to study the effects of different rates of spread of the fire (and thus, indirectly, different fire intensities) on the woody vegetation and its subsequent recovery. Descriptions are also given of the postfire environment, the immediate and short-term effects of the fire on vegetation structure and on various animal populations, the postfire recovery of woody and herbaceous plants, and the responses of the animal populations to the fire and the postfire environment.

SAMEVATTING

Hierdie verslag is 'n samevatting van inligting verkry van 'n studie van 'n eksperimentele vuur in 'n 182 ha gedeelte van die studie area van die Savanne-ekosisteemprojek vroeg in September 1978. Drie kleiner vure, wat elk 1 ha binne hierdie area gedek het, is onmiddellik voor die hoofvuur aangesteek sodat die gedrag van die vuur beter bepaal kan word. Dit het ook geleentheid geskep om die uitwerking van verskillende tempo's van die verspreiding van die vuur (en dus indirek verskillende vuurintensiteite) op die houtagtige plantegroei en die daaropvolgende herstel, te bestudeer. Beskrywings van die na-vuurse omgewing word ook aangegee. Die onmiddellike en kort-termyn invloed van die vuur op plantegroeistruktuur en op verskeie dierebevolkings, die herstel van hout- en kruidagtige plante na die vuur en die reaksie van dierebevolkings op die vuur en die na-vuurse omgewing word ook beskryf.

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INTRODUCTION

The South African Savanna Ecosystem project is a multidisciplinary investigation of the structure, functioning and dynamics of an area of savanna in the Nylsvley Nature Reserve in the northern Transvaal. The project was initiated in 1974 and is planned to run until 1984.

The objective is to acquire the basic understanding of savanna to be able to predict the response to, and stability under, both natural and man-induced stresses. The stress imposed by fire is important for two reasons. Firstly, fire has always been a factor in savanna, to the extent that it should be regarded as an integral component of savanna functioning. Secondly, fire is a management tool that man can use or abuse in efforts to make the system suitable to his needs.

The land for the Nylsvley Nature Reserve was acquired in 1973 by the Transvaal Provincial Administration in order to establish a reserve. Prior to this it had been a cattle ranch and had been subjected to periodic burning. Unfortunately there are no records of fires, but the area was probably burnt on average every four or five years. The SASEP study area had not been burnt since the establishment of the reserve. On September 5 1978 Camp 2 of the study area was burnt. The reason for the fire was to maintain a fire regime similar to the one under which the system appeared to have developed.

This fire afforded the opportunity of studying the immediate effects of the fire and postfire responses of many components of the system. The work was aimed at answering the following questions:

- 1. What are the behavioural characteristics of fire in Burkea savanna?
- What are the causes of differences in vegetation structure under a uniform fire regime over a large area?
- 3. What are the influences of termitaria, selectively grazed areas, differences in fuel load, microtopography etc, on the effects of fire at a subhabitat level?
- 4. What are the immediate effects of fire on animal populations?
- 5. How do these effects vary between species in terms of mortalities, injuries, disruption or stimulation of reproduction, feeding, social or diurnal behaviour, changes in predator-prey relationships etc?
- 6. What are the immediate or short-term postfire responses of the various plant and animal groups in <u>Burkea</u> savanna?
- 7. How does fire response of plant species vary in terms of survival, pattern of vegetative growth, positions of lateral buds, pollination, seed production and dispersal, dormancy and germination?
- 8. What are the immediate postburn effects of fire on soil moisture status?

- 9. What are the immediate and short-term effects of fire on soil chemical properties in <u>Burkeas vanna?</u>
- 10. What are the immediate and short-term effects of fire on patterns of mineral release from both live and dead plant material?
- 11. What are the immediate and short-term effects of fire on soil respiration characteristics?
- 12. How does net primary productivity and biomass accumulation differ between burnt and unburnt Burkea savanna?

The extent to which these points were addressed and the depth of the investigations were limited by the number of SASEP research workers available at the time, and the extent of their commitments to other ongoing research. Thus, for many of the above points there are no or only incomplete answers. However, a number of fires are planned for the future, both to maintain the habitat in its present form and for research. This report synthesizes the information which was obtained from the first fire and identifies the areas where knowledge is lacking.

THE EXPERIMENTAL AREA

Camp 2 consists of 182 ha of mainly broadleafed <u>Burkea africana/Eragrostis pallens</u> savanna (hereafter referred to as <u>Burkea</u>) and <u>Acacia spp/Eragrostis rigidior</u> microphyllous savanna (referred to as <u>Acacia</u>). The relative areas of these habitats are given in Table 1.

Table 1. Areas of habitats in Camp 2 before and after a fire. (From Monro 1978)

		Before ha	e fire %	Afte ha	fire %
DITRUEA	Burnt			109	60
BURKEA	Unburnt	142	79	33	19
ACACIA	Burnt			19	10
	Unburnt	32	17	13	7
FIREBREA	K	8	4	8	4

The fuel load and moisture content of the herbaceous stratum a week prior to the fire was:

Grass biomass	$8,4 \text{ g m}^{-2} \text{ (dry mass)}$
Grass standing dead	73,7
Other spp biomass	1,3
Other spp standing dead	5,6
Total fuel load	89,1
Moisture content	4,2%

(Data from Grunow and Grossman 1978)

Leaf litter layers were sometimes up to 10 cm deep, especially under Ochna pulchra (Rutherford 1981).

Prefire climatic records are available. Rainfall is given in Table 2. A number of prefire animal censuses were made, and these will be reported on in detail in the discussions of the respective animal groups that follow.

Table 2. Pre- and postfire rainfall.

Date	Rainfall	Date	Rainfall
	mm	1978	mm
78.05.31	2,0	78.10.17	28,7
78.08.28	0,5	78.10.18	15,6
78.08.29	4,7	78.10.19	3,8
78.09.05	Fire)	78.10.30	16,7
78.09.08	1,0	78.11.2	7,7
78.09.13	22,0	78.11.3	23,3
78.10.04	0,5	78.11.8	0,7
78.10.05	2,0	78.11.21	15,5
78.10.13	0,7	78.11.24	8,3
78.10.14	17,0	78.11.25	2,4
78.10.16	19,7	78.11.26	2,5

Climatic conditions at the time of burning are given in Table 3.

Table 3. Weather conditions at the time of the fire, 5 September 1978.

Time SAST	Screen temperature oc	Screen relative humidity %	Screen vapour pressure humidity mb	Screen saturation vapour pressure deficit mb
1800	19,0	28	8,5	13,3
1900	17,2	33	6,4	13,1
2000	15,1	40	6,8	10,2
2100	12,7	49	7,1	7,5
2200	11,6	53	7,2	6,4
2300	10,7	55	7,0	5,8
2400	10,7	56	7,2	5,6

Mean wind speed at 2,0 m from 12h00 5 September 1978 to 07h00 6 September 1978 was 1,8 m s $^{-1}$.

METHODS AND RESULTS

Fire data

Maximum temperatures were recorded during the fire by Harrison (1978). These were recorded using Rockwell Tempil sticks. A tempil stick is designed to melt at a specific temperature. By applying sticks of different melting temperatures to the surface of a piece of metal and by observing which sticks melt, the maximum temperature attained by the metal can be estimated. Twelve different sticks were used, the lowest melting point being 260°C and the highest 816°C .

The woody species in which tempil plates were placed were <u>Burkea africana</u>, <u>Grewia flavescens</u>, <u>Ochna pulchra and Terminalia sericea</u>. Three tempil plates were positioned on the surface under each tree. A profile of plates at 0,2; 0,4; 0,7; 1,0; 1,5 and 2,0 m were attached to the trunk of the tree (or a vertical fencing dropper in the case of <u>G flavescens</u>). A further three tempil plates were exposed in the canopy. Air temperature profiles were taken above grass. Lastly, 29 plates were employed at the surface, mainly positioned over tufts of grass.

Surface temperatures under trees varied from under 260°C where fuel did not ignite to over 816°C under 0 pulchra and 0 flavescens. Under 0 africana and 0 serices no melting occurred over 0 m. Canopy temperature was probably well under 0 at one 0 pulchra site 0 order of 0 was measured at 0 m. In 0 flavescens temperatures of the order of 000 at 00 m were registered in two of the three shrubs monitored.

Temperatures in grass tufts ranged from less than 260°C in a tuft of Panicum maximum to over 816°C in a tuft of Elyonurus argenteus. 460°C. tuft temperature was The distribution of temperatures was bimodal with clusters at 350°C and at 600°C. high temperatures recorded were confirmed by visual observations during Several tufts were seen to glow orange/red after the flames had died down. From Wien's law the temperature of a body emitting in these wavelengths is about 4500°C. Temperatures in litter varied over the whole range but many sites registered temperatures in excess of 750°C. Detailed records are given by Harrison (1978).

Three 100 m x 100 m blocks of Burkea were burnt separately with a headfire just before the remainder of Camp 2 was burnt. The rates of spread of the flame front in the three blocks were: Block A 0,12 m s^{-1} , Block B 0,17 m s^{-1} and Block C 0,67 m s^{-1} . The fuel load in the herbaceous layer in Block B was 90 g m⁻² which is equivalent to approximately 1760 kJ m^{-2} . The power (ie energy released per second) per metre of flame front is given by the product of rate of spread and fuel load. Thus the power for Block B = 300 kW m^{-1} . that the initial flame front burns all the herbaceous material but nothing else. Neither of the assumptions is correct, but if the amount of herbaceous material which is not burnt immediately is approximately the same as the amount of litter and woody material consumed by the flame front (ie not including combustion after the flame front has passed), the calculated power is the correct value. In fact it is probably a slight underestimate.

The rate of spread of the fire in Block C was much faster than in the other two, flame heights were greater, higher temperatures were recorded and fuel combustion was more complete. Combustion continued for longer periods in Blocks A and B where a few slow burning backfires remained after the initial flame fronts had swept across the blocks.

If the fuel load in Block C was the same, the energy released per second would have been greater than in Block B by the ratio of 67:17. However, since the faster spread was probably related to greater fuel load, the power can be assumed to be have been greater than 1200 kW m $^{-1}$. Three air temperature profiles were taken in each of Blocks A and C. In the faster burning Block C, higher temperatures were recorded both at ground level and in the profile but the results were not suitable for statistical analysis.

Postfire energy balance

Harrison (1978) measured albedo and soil heat flux periodically after the fire on burnt and unburnt sites using a two channel recorder. The recorder was placed on the boundary of an open area of burnt grass and an adjacent unburnt area dominated by the grasses Schmidtia pappophoroides, Eragrostis pallens and E superba. Concurrent with the records being taken at the fire site, the amount of incoming solar radiation was recorded at the micrometeorological station approximately 1,5 km away.

From Table 4 it may be seen that the mean albedo of the unburnt site remained constant at 13 or 14%. When the albedo of the burnt site was first measured it was found to be 7%. A total of 23 mm of rain had fallen on two days after the fire and before the first albedo measurements. The albedo of the burnt area might therefore have been less than 7% immediately after the fire because the surface was blacker before the rain. The mean albedo of the burnt area rose to 8% by the 16th day after the fire. On the 24th day it was measured as 10% and on the 45th day it was measured as 12%.

Only one soil heat flux plate was used to record the soil heat flux. At the burnt site the plate was positioned between burnt grass tufts under black ash. At the unburnt site the plate was positioned between grass tufts under bare soil. At both sites the plate was positioned as close to the surface as possible. The amounts of energy being conducted into the soil at the two sites are similar (Table 4).

Initially the burnt and unburnt sites had albedos of 7% and 13% respectively. As both sites appear to have similar soil heat fluxes, the burnt site must transfer more energy to the atmosphere. A small part of the excess energy may go to latent heat of vaporisation as the soil on burnt sites dries out, and there will be slightly greater long wave radiation from the surface as it heats up. However, it is assumed that most of the extra solar energy absorbed by the burnt surface is transferred to the atmosphere by sensible heat flux.

Surface temperatures were not measured but they are known to be higher generally on blackened burnt surfaces (Vogl 1974). Typically they are 2 to 10 °C higher than those of unburnt areas (Phillips 1919; Daubenmire 1968). The failure to detect soil heat flux differences implies low thermal conductivity of the sandy soils at Nylsvley.

Postfire soil moisture

A neutron probe (Nucletronics BASC A18-14) was used to measure soil moisture at the surface, 30 cm and 45 cm depth. Probe tubes were sunk at two burnt sites and at two unburnt sites. These were all in open grass veld. Due to a defect in the neutron probe, measurements only commenced a month after the fire and from then were taken weekly for five weeks. Moreover, the probe was inaccurately calibrated but the results are still useful for comparative purposes even if actual percentages of moisture are unknown.

The surface was generally dry in all areas and no differences were detectable between burnt and unburnt areas. Differences between burnt and unburnt sites were apparent at 30 cm and 45 cm depth where the moisture content of soils under the burn was between 5% and 50% lower. The percentage difference varied with time, and the depth of maximum moisture difference was not consistent. For example on 13 October, the soils under the burn were 14% drier at 30 cm and about 50% drier at 45 cm. However, on 11 November they were 50% drier at 30 cm but only 8% drier at 45 cm. These sorts of fluctuation occurred throughout the monitoring period and did not appear to relate to previous rainfall patterns.

Table 4. Albedo and soil heat fluxes on burnt and unburnt grass sites. (Data from Harrison 1978)

Date	No of days after fire	Site	Mean albedo %	Incoming solar %	Maximum incoming solar W m ⁻²	Maximum reflected W m ⁻²	Maximum s h f W m ⁻²
78.09.16	11	burnt	7	_	1030	70	138
78.09.17	12	burnt	7	-	972	65	138
78.09.18	13	burnt	7	-	744	52	116
		unburnt	13	-	972	122	138
78.09.19	14	unburnt	13	24	972	124	199
78.09.20	15	unburnt	13	21	629	83	130
		burnt	7	17	858	63	147
78.09.21	16	burnt	8	17	915	72	137
78.09.23	18	burnt	8	20	801	74	157
78.09.24	19	burnt	9	17	915	79	147
78.09.25	20	burnt	8	17	629	59	104
		unburnt	13	16	915	124	127
78.09.26	21	unburnt	14	14	915	126	123
78.09.28	23	unburnt	14	16	629	81	98
		burnt	9	15	858	81	124
78.09.29	24	burnt	10	15	858	86	117
78.10.01	26	burnt	9	14	915	90	117
78.10.03	28	burnt	10	18	915	95	163
78.10.20	45	burnt	12	22	1118	142	231

Factors which tend to decrease soil moisture after a burn include increased insolation and reduced infiltration (Jansen 1959; West 1965). On Nylsvley's sandy soils, crusting of exposed soil is probably an important obstacle to infiltration. Phillips (1919) reports that infiltration may be higher immediately after a burn. On the other hand there is less interception and less transpiration after a fire, at least initially. Soil moisture in the lower horizons may even increase soon after a fire (Daubenmire 1968). This possibly occurred after the rain on 13 September (see Table 2) a week after the fire but before monitoring commenced.

Microbial activity in the soil

Steyn and Bezuidenhout (1979) monitored ATP content of the soil, propagule counts and $\rm CO_2$ production in the upper three cms of soil on burnt and unburnt sites in the <u>Burkea</u> area. Root and rhizosphere respiration was also measured. The techniques used are described by Steyn and Bezuidenhout (1979).

There was no significant difference in ATP content (proportional to bacterial biomass), CO₂ production (proportional to microbial activity) or propagule counts between sieved soil from burnt and unburnt sites. Soils incubated at 25°C generally showed an increase in microbial activity. If soil was dried, microbial activity dropped but if it was remoistened the activity increased for a while to a level higher than average. Dessication and warming of soil after a burn will have opposite influences on microbial activity. In this instance they may have approximately cancelled out one another. It has been shown in other grasslands that the substrate of organic C and N is not much affected by fire (Cook 1939; White and Grossman 1972). By using an enrichment technique it was concluded that the population of nitrifying bacteria was negligibly small in both soils.

Respiration of roots and rhizosphere

It was not possible to distinguish between root respiration and rhizosphere respiration. There was a small increase in the rhizosphere and/or root respiration from day five after the fire up to at least day 30. Translocation of materials from the roots for regrowth would increase root respiration. There may also have been some root die-back and subsequent fungal attack.

Aboveground biomass of the grass layer

This was monitored in the <u>Burkea</u> area by Grunow and Grossman (1978) for 60 days subsequent to the fire. A further sample was obtained at the end of March. Biomass was estimated from 50 quadrats (0,5 m²) clipped on burnt and control areas. The burnt areas were protected from postfire grazing by large and medium sized mammals by diamond mesh enclosures. They were not protected from insects or small mammals. Grasses and non-grasses were separated and sorted into live and dead.

Values of biomass and standing dead are given in Table 5. Immediately after the burn biomass was zero. Forbs were only noticed after 20 days (Table 6). On 26 October 1978, 52 days after the fire, flowering was noticed in the following grasses in the burnt area: Trachypogon spicatus, Elyonurus argenteus, Brachiaria serrata and Setaria perennis.

Mean biomass accumulation rate over the 60 day period after the fire was 0,29 g m $^{-2}$ day $^{-1}$ on burnt areas and 0,73 g m $^{-2}$ day $^{-1}$ on the unburnt control. The different rates are reflected in Figure 1.

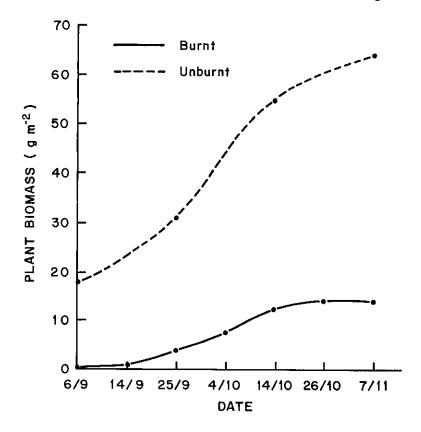


Figure 1. Accumulation of aboveground herbaceous biomass for burnt and unburnt areas, Nylsvley, September 1978 to November 1978.

The date of the fire was 5 September 1978.

The rate of biomass accumulation decreased in November especially in burnt areas. The rainfall during November 1978 was 63 mm compared to the November average of 100 mm and the grasses appeared to be under water stress at the time. Burnt veld is more susceptible to drought than unburnt (Theron 1937; Irvine 1943) and this probably accounted for the greater decrease in biomass accumulation on the burnt areas.

A final sample was taken at the end of March 1979 to check the effects of fire after a full season. The main points to emerge from this end of season sample are that fire

had no effect on the live grass biomass at the end of the season although it depressed the production of biomass initially;

- reduced end of season standing dead grass to less than half of that on unburnt areas;
- increased forb biomass.

Also in March, samples were taken from an area which had not been protected after being burnt (see final entry in Table 5). This shows that postfire grazing causes a marked reduction in both live and dead grass. However, in the unburnt <u>Burkea</u> area, grazing by large mammals does not affect the live biomass of grass in the short term (Gandar 1980). The interaction of burning and grazing is discussed in the next section.

In a separate investigation of the effects of fire in <u>Burkea</u> at Nylsvley, it was found that live biomass after a burn continued to rise erratically till it became equivalent to that on unburnt areas after about four months (D Grossman, personal communication, 1979), though total standing crop still lagged. It was evident too from this latter investigation that forage grasses (<u>Brachiaria nigropedata</u>, <u>Panicum maximum</u>, <u>Rhynchelytrum villosum</u>, <u>Brachiaria serrata</u>, <u>Setaria perennis and others</u>) recovered more quickly from burning than did nonforage grasses (<u>Eragrostis pallens</u>, <u>Aristida congesta</u>, <u>Aristida stipitata</u>, <u>Perotis patens</u>, <u>Urelytrum squarrosum etc</u>).

E pallens, an unpalatable grass co-dominant with Digitaria eriantha, was particularly slow to recover. E pallens is regularly one of the first grasses to flush at the beginning of a season. It had already begun its growth when the area was burnt on 5 September. At this time it would have depleted some of its reserves without having had time to replenish them and this may have delayed the postfire response. Daitz (1954), however, found that percentage carbohydrate in the roots could not explain the disappearance of Themeda triandra from lateburn plots. Untimely burning can also destroy tillers (Booysen et al 1963). D Grossman, personal communication, 1979, suggests that the slow recovery of E pallens may partly be a result of protection from fire over the previous six years and a lighter grazing load since cattle were removed in May 1977. There were signs that some unpalatable grass species were becoming choked with standing dead and becoming moribund so that reserves were probably deficient anyway. It is noticeable that on firebreaks which are burnt annually in winter E pallens flushes early and vigorously. This accords with both the above theories.

Protection from grazing, and postfire recovery of the grass layer

Grossman $\underline{\text{et}}$ $\underline{\text{al}}$ (1979) demonstrated that the postfire recovery of the grass layer, as reflected by the peak standing crop, was retarded by utilization by large herbivores after the fire.

Following the fire, 3 m x 3 m exclosures, made by winding black polythene strips around four corner posts, were erected as follows: 20 sites were chosen randomly in the open areas in an Acacia patch, and 20 sites randomly chosen in the canopied parts of a Burkea patch.

Table 5. Biomass, standing dead and standing crop dry masses $(g m^{-2})^a$ for burnt and unburnt areas in the grass layer of <u>Burkea</u> savanna, Nylsvley, September 1978 to November 1978. (Data from Grossman and Grunow 1978)

		Burnt					Unburnt			
Date Grass Live	Grass Dead	Forbs Live	Forbs Dead	Total St crop	Grass Live	Grass Dead	Forbs Live	Forbs Dead	Total St	
78.09.06	0	0	0	0	0	14,0	80,2	2,1	6,4	102,7
78.09.14	0,30	0	0	0	0,30					
78.09.25	3,90	0	0,17	0	4,07	28,6	81,0	2,4	3,2	115,2
78.10.04	7,10	0	0,56	0	7,66					
78.10.14	12,52	0	2,64	0	15,16	47,9	114,6	6,9	2,6	172,0
78.10.26	13,01	0	3,59	0	16,60					
78.11.07	13,69	0	4,38	0	18,07	56,1	83,3	7,7	2,8	149,9
79.03.20	52,2	17,4	19,0	3,7	92,3	53,7	43,7	9,2	1,3	107,9
Grazed	35,3	6,9	16,7	0,8	59,7					

^aMean of 50 quadrats

Table 6. Non grass dry matter as percentage of biomass, standing dead and standing crop in burnt and unburnt areas in the grass layer of <u>Burkea</u> savanna, Nylsvley, September 1978 to November 1978. (Data from Grossman and Grossman 1978)

		Burn		Control				
Date	Biomass	Standing dead	Standing crop	Biomass	Standing dead	Standing crop		
78.09.06	0	0	0	11,6	7,3	8,1		
78.09.14	0	0	0					
78.09.25	4,1	0	4,1	7,7	3,8	4,8		
78.10.04	7,3	0	7,3					
78.10.14	17,4	0	17,4	12,1	2,2	5,5		
78.10.26	21,6	0	21,6					
78.11.07	24,2	0	24,2	12,1	3,2	7,0		
79.03.20	26,7	17,5	24,6	14,6	2,9	9,7		

Four treatments, each replicated five times:

- 1. Protection from large herbivores for 29 days after fire 2. " " " 67 " " "
- 3. " " " " 101 " "
- Control (no exclosures erected)

were assigned randomly to the sites in both vegetation types. The exclosures were removed after the appropriate periods.

On 26 February 1979 one 2 m^2 quadrat was clipped per site. Harvested material was sorted into grasses and forbs, dried and weighed.

Standing crop for the different categories and treatments is presented in Table 7. The following points emerge from this:

- i. Acacia savanna: Whilst the grass standing crop harvested in the different treatments in the Acacia area did not differ significantly, due to the variability between replicates, a trend is nevertheless apparent. There is an increase in dry matter with increasing length of protection from large herbivores.
- There was almost no difference in end of season herbaceous ii. standing crop in the Burkea area between unprotected plots and plots which had been protected for 67 days. However, protection for 101 days caused standing crop to differ significantly $(P \angle 0,05)$ from all other treatments. inspection revealed that Hyperthelia dissoluta which formed 73% of the standing crop in the 101-day protection sites had not been eaten at these sites. In the unprotected sites, and those opened to herbivores at 29 and 67 days after the fire, this grass had been well utilized in the young growth stages. Sometime between 67 and 101 days after the fire the grass appears to have lost some of its palatability to large The fact that end of season herbivores when protected. standing crop was not noticably improved by protection for up to 67 days does not imply that postfire protection has no effect. For example, it would be interesting to examine the effect of protection on root reserves during future fires.

In general, the grasses in the <u>Burkea</u> area were well utilized while still young, but utilization of these areas decreased as the grasses matured. Forbs did not constitute the same high percentages of total standing crop in the <u>Burkea</u> area as in the <u>Acacia</u> areas, where <u>Solanum</u> panduraeforme is a major component of the herbaceous layer.

iii. A comparison between the two vegetation types reveals a lower standing crop in the <u>Burkea</u> than in the <u>Acacia</u> areas. Impala concentrated in the <u>Burkea</u> areas after the fire (Table 14) and these areas were heavily utilized. The total standing crop of between 5,4 and 8,9 g m-2 was recorded in those treatments opened up to herbivores 67 days and earlier after the fire. This is extremely low and probably reflects the heavy utilization.

In a nature reserve such as Nylsvley, where fire is used as a management tool, care should be taken to ensure that a sufficiently large area is burnt at any one time, to avoid the over-utilization which obviously occurred in Camp 2. At the same time though, the area being burnt should not be so large that it leaves the animal populations with reduced food supplies in the immediate postfire period.

Table 7. Phytomass (g m⁻²) of grass and forbs in two vegetation types and under four different postfire treatments and results of analysis of variance. (Data from Grossman et al 1979). All measurements were made in February 1979, five months after the fire.

	Unpro- tected	Protected for 29 days after	Protected for 67 days after	Protected for 101 days after	Level of significance for F test
CACIA					14-14-14-1-1
grass	7,2	11,0	15,8	23,3	NS
forbs	12,2	16,7	8,4	11,3	NS
Total	19,4	27,7	24,2	34,6	NS
BURKEA					
grass	8,3	5,0	5,8	25,2	P<0,05
forbs	0,6	0,5	2,6	0,5	NS
Total	8,9	5,5	8,4	25,7	P<0,05

Effects on woody plant component

Fire has been used as a management tool in savanna to control the woody component and it is generally accepted that late dry season fires are the most effective in this role. Rutherford (1981) has made a detailed study of the effects of the Nylsvley fire on survival, regeneration and leaf biomass of woody plants.

All the work on the woody plants was done in blocks A and C which were the blocks with the slowest and fastest fires respectively. Control measurements were made on plants in an unburnt area. Woody plants of various species, including standing dead trees, were labelled with numbered aluminium tags. Recordings were made at regular monthly intervals, with the most detailed measurements being made shortly before the burn, and after the completion of one season's growth but before leaf fall. The measurements, details of which are given by Rutherford (1981), were made to determine the mortality/survival of individual plants, the degree of canopy reduction, the destruction and degree of basal shoot regeneration, and the associated changes in leaf and twig biomass.

Mortality of woody plants was low. For tree species it was 1% in the control group, 2% on the faster burn and 5% (significantly greater than the control) on the slower burn. The difference is largely explained by the high mortality (about 10%) of Ochna pulchra plants smaller than 0,25 m high. Half of the seedlings of Burkea africana, less than 0,1 m high, were killed in both burns. Excluding Dichapetalum cymosum, the fire caused no mortality of multistemmed shrubs. The observations on D cymosum are difficult to interpret because of its suffrutex growth form. It is noteworthy that there was no mortality of Grewia flavescens, although it burnt the most fiercely and the aboveground parts were often entirely consumed by fire.

Canopy mortality was 43,2% on the faster burn and 23,5% on the slower burn, compared to 0,7% in the control group. Nearly all the canopy mortality occurred in plants under 2 m. No canopies above 5 m were killed. Canopy mortality of <u>Vitex rehmannii</u> was noticeably higher although no plants of this species died. Height, volume and leaf biomass of the canopies were also reduced. Estimates of what the leaf biomass would have been in the absence of fire were made by measuring stem diameters and using regressions of leaf biomass on stem diameter which were determined from unburnt trees. Reductions in canopy height, volume and leaf biomass were strongly dependent on plant height, being close to 100% for all plants less than 0,5 m tall and approaching 0% for plants over 5 m (See Figures 2 and 3). Percentage reduction in canopy was greater as a result of the faster burn than the slower. For trees greater than 2,5 m, 0 pulchra had greater canopy leaf biomass reduction than Terminalia sericea and B africana. There is evidence that in canopy damage and canopy mortality some southern African Acaciadominated communities are more susceptible to fire than the Burkea community at Nylslvey (Rutherford 1981). Work on B africana and other species in South West Africa (Geldenhuys 1977) and on Nigerian savanna (Kemp 1963) suggests that stem basal area is not reduced by regular burning. This implies that radial stem growth is not adversely affected despite loss of canopy to fire.

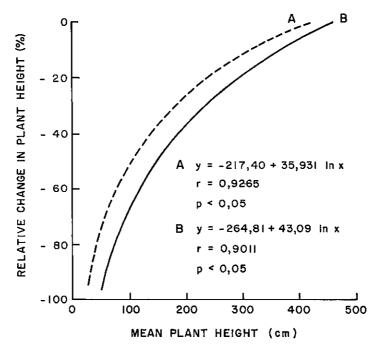


Figure 2. Relationships between mean plant height and relative change in plant height in Ochna pulchra subject to: A. a slow burn and B. a fast burn. (Data from Rutherford 1981)

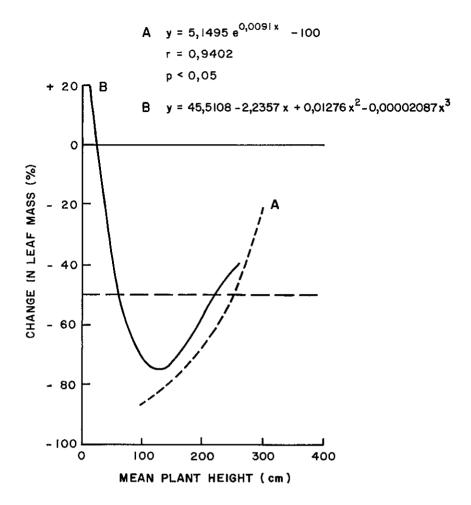


Figure 3. Relationship between mean plant height and change in canopy leaf mass (A) and change in total plant leaf mass (B) for Ochna pulchra in both burn intensities. The broken line indicates the points at which leaf mass is reduced by more than half of the total amount. (Data from Rutherford 1981)

Table 8. Mortality of basal shoots in the fire and subsequent regeneration. (Data from Rutherford 1981)

	Control	Slower burn	Faster burn	
Basal shoot mortality	14%	91%	100%	
No of new shoots per plant	0,09	2,42	4,55	

The mortality of basal shoots and the number of new shoots for tree species are given in Table 8. Both fires destroyed virtually 100% of the basal shoots of multistemmed shrubs. The number of new regenerative the basal shoots for each shoot destroyed was 1,88 for 0 pulchra and 1,30 for

B africana so there is a net increase in the number of shoots. T sericea had low basal shoot regeneration with only few small basal shoots, which carried low leaf biomass relative to twig biomass. The basal shoot regeneration:destruction ratio increases with increasing plant height although for small plants both the destruction and regeneration of basal shoots is greater than for large plants. Basal regeneration of burnt plants was more than ten times that of unburnt. It was greater on plants which had been severely or completely burnt, provided the plants were not killed, than those which were lightly burnt.

Basal regeneration increased with increasing canopy damage. For O pulchra, basal regenerative shoot biomass increased exponentially as the extent of reduction in canopy leaf biomass increased (Figure 4). Basal shoot regeneration varied parabolically with plant height and reached a maximum for plants about 1,5 m tall. The ratio of leaf mass to twig mass in basal regenerative shoots varied inversely with plant height.

When leaf biomass change (ie the algebraic sum of canopy leaf biomass loss and basal shoot regeneration mass) is plotted against tree height for <u>O pulchra</u> (Figure 3), the net loss is greatest for individuals between 1 and 1,5 m in height. Extrapolating this curve, it seems probable that very large trees exhibit no change in total leaf biomass, while the smallest plants may show a net gain.

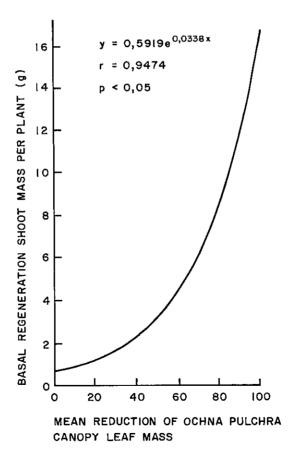


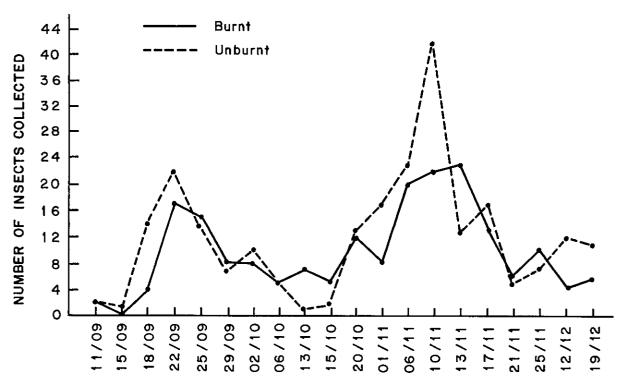
Figure 4. Relationship of reduction in Ochna pulchra canopy leaf mass and regeneration basal shoot mass per plant. (Data from Rutherford 1981)

Of the standing dead woody plants, 24% were felled by the fire and most of these were completely burnt. This compares with the 19% of individuals which fell over in the absence of fire. No individuals over 1,5 m tall were felled by the fire.

Regression equations have been determined for all relationships mentioned in this summary (Rutherford 1981).

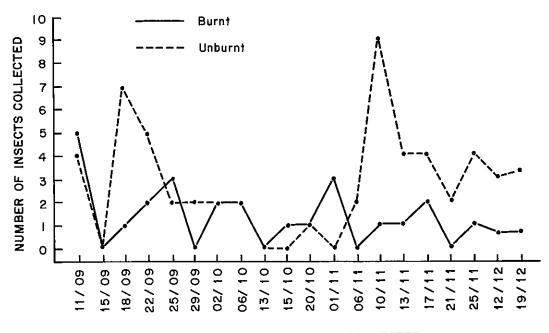
The emergence of adult Scarabaeidae and Curculionidae (Coleoptera) after the fire

Light-tight emergence traps were used. The traps were square frames covered with black PVC sheet. The base was $0.5~\mathrm{m}^2$. The only light entering a trap was through a small perspex window to which insects emerging from the soil under the trap were attracted and there caught in glycerine. The traps were painted white outside to prevent overheating. Fifteen were placed in unburnt <u>Burkea</u> areas and 15 in burnt <u>Burkea</u> areas. The traps were emptied, moved and reset twice per week. The numbers of <u>Scarabaeidae</u> and <u>Curculionidae</u> caught are shown in Figures 5 and 6 (Dempers 1978).



DATES ON WHICH INSECTS WERE COLLECTED

Figure 5. The emergence of beetles of the family Curculionidae on burnt and unburnt sites at Nylsvley after a fire on 5 September 1978.



DATES ON WHICH INSECTS WERE COLLECTED

Figure 6. The emergence of beetles of the family Scarabaeidae on burnt and unburnt sites at Nylsvley after a fire on 5 September 1978.

It is apparent that emergence is not greatly affected by the fire until two months after the fire (Table 9). Thereafter there is a significantly lower emergence rate in burnt areas.

Table 9. Numbers of beetles emerging after the fire. (Data from Dempers 1978)

	Scarabaeidae			Curculionidae		
	On burn	Off burn	Signif.	On burn	Off burn	Signif.
Up to two months	20	25	NS	84	91	NS
After two months	7	32	0,001	112	147	0,05
Total	27	57	0,01	196	238	0,05

This suggests that the larvae and pupae which live in the soil survive the fire. After a while changes in the soil subsequent to the fire cause a drop in the population. Depletion of food resources may have been a factor. The fire occurred just after the first signs of growth in some plant species during which there will have been a withdrawal of reserves from the roots, the main food item of the larvae. Then came heavy utilization by ungulates, particularly of regenerating <u>Burkea</u> areas. The net energy flow is probably upwards from the roots for some time after the fire. D Grossman (unpubl) has shown with potted grass that frequent defoliation causes a decrease in root biomass.

The two peaks in emergence apparent in Figures 5 and 6 were both preceded by rainfall (Table 2) which suggests that dessication may also inhibit emergence. Whether either depletion of food resources or dessication causes mortality is not known. If development were merely retarded there would still be a drop in emergence rate although numbers emerging would eventually catch up. If this were the case, the monitoring programme did not run long enough to pick up the delayed increase in emergence.

The response of termites to fire

The following observations on termites after the fire were made by P Ferrar (unpubl). There was little heating of the soil during the fire and there were probably few termites in the upper soil when the burn started. Most termites can move quite quickly along their galleries to lower levels. After the fire, soil was dug in a number of places and searched for dead termites but none were found. It is surmised that mortality in the soil is negligible, but that mortality of foraging termites would have occurred in wood, which was extensively burnt. Ahlgren (1974) reports that termites can survive a forest fire under charred boards. On the day after the fire Odontotermes were found foraging in leaf litter which had been scorched on top. There was one dead soldier with them that may have been killed by the heat of the fire the day before.

Postfire effects on termites include changes in food supply shelter, affecting mainly foraging species. The patchiness and low intensity of the fire meant that not all forage was destroyed though some nests may have had their entire foraging range burnt out. measure of termite foraging activity can be obtained by noting the percentage of toilet rolls placed in a grid in the field which are attacked by termites (Ferrar 1978). The number attacked during the first month after the fire was much lower than normal but thereafter it was typical of that observed in other Burkea areas. High surface temperatures on exposed soils may have curtailed the amount of time during a day in which termites could forage near the surface. on toilet roll baits by Microtermes were less than normal but the The dessication of the soil would have tended to reason is unknown. drive termites deeper and may also have reduced foraging activity.

It has been found elsewhere that humus in the top few millimetres of soil may be oxidised in a fire (Daubenmire 1968). However, observations of the surface layers in the <u>Burkea</u> area suggest that the organic content of the soil had not changed much after the fire, and the nests of humivorous <u>Cubitermes</u> seemed to be functioning normally.

Destruction of arboreal insects by fire

The insect fauna of two tree species, <u>Dombeya rotundifolia</u> and <u>Ochna pulchra</u>, were sampled before and after the fire. Trees were sprayed with insecticide and the insects were collected on a groundsheet placed under the canopy. Three trees of <u>O pulchra</u> and two of <u>D rotundifolia</u> were sprayed before the fire. This was repeated two days after the fire and again two weeks after the fire on different trees of the same species. The results are presented in Table 10 and Table 11.

Table 10. Number of insects on 3-4 m high <u>Dombeya</u> <u>rotundifolia</u> trees before and after the fire.

DATE	78.08.29 ^a		78.09.07 ^b		78.09.19 ^c	
	RE	PLICATE	REP	LICATE	REPL	ICATE
HEMIPTERA	1	2	1	2	1	2
Lygaeidae d	480	80	550	5	7	0
Pentatomidae	1	0	0	0	0	0
Cicadellidae	2	3	0	0	0	0
Pyrrhocoridae	0	3	0	0	0	0
Miridae	1	0	2	0	0	0
Homoptera (unidentified)) 3	5	0	0	0	0
COLEOPTERA						
Chrysomelidae	1	0	0	0	0	0
Coccinelidae	2	1	0	0	0	2
Nitidulidae	2	0	70	0	0	0
Curculionidae	2	5	0	0	0	0
Apionidae	10	2	18	0	0	0
Unidentified	14	4	10	1	0	0
LEPIDOPTERA						
Larvae (unidentified)	4	0	1	0	0	0
TOTAL	522	103	651	6	7	2

^aTrees in flower, ^bFlowers singed, ^cFlowers practically dead, ^dAll the Lygaeidae were Oxycarenus albipennis.

Table 11. Number of insects on 2 m high Ochna pulchra trees before and after the fire.

DATE	78.09.04		78.09.07		78.09.19ª		
	REPLICATE		REPLICATE				
	1	2	3	1	2	3	1
HEMIPTERA							
Cicadellidae	30	5	0	0	0	0	0
Pentatomidae	0	1	0	0	0	0	0
Unidentified	0	1	0	0	0	0	0
COLEOPTERA							
Chrysomelidae	3	0	0	0	0	0	0
Coccinelidae	0	0	1	0	0	0	0
Nitidulidae	0	1	1	0	0	0	0
Curculionidae	0	2	0	0	0	0	0
Unidentified	3	6	15	0	0	0	0
LEPIDOPTERA							
Unidentifed							
larvae	3	0	0	0	0	0	53 ^b
TOTAL	. 39	16	17	0	0	0	53

^aTotal of two trees

There was almost total destruction of the insect fauna on Ochna pulchra despite the fact that no tempil sticks melted in the canopy of any tree above two metres height. Smoke may have contributed to this destruction. It is not known whether eggs and pupae in protected sites survived, neither are there any data on the fate of larvae in galls, but it is expected that most or all of these survived.

bAll the Lepidoptera larvae found on 19 September 1978 were of the same species.

Orthoptera mortality and subsequent changes in population structure

The effect on Orthoptera, in particular grasshoppers, was studied in an area of <u>Burkea</u> in which the fire had been very patchy. Unburnt patches, some only two metres across, amounted to 21% of the area. A drop-tent of base 1 m² was used for sampling. This was cast from the end of a four metre pole. Only 30% of grasshopper biomass was lost in the fire. It is not known what percentage of the loss was mortality and what was flight. Mortality depends on several factors:

- i) Time of year. In early September the grasshoppers were mostly adults which would have been able to dodge the flames more effectively.
- ii) Patchiness of the fire. The path of the fire was sometimes uncertain and the fire front uneven. This is characteristic of grass fires generally (Vogl 1974). Mobile insects can escape through breaks in the fire front and shelter in unburnt patches.
- iii) Speed and intensity. D Gillon (1971) reports that mobile insects can flee in front of a flame front moving at 500 m hr⁻¹ (data from Ivory Coast savanna). Three measurements were made of rate of spread at Nylsvley and ranged from 440 m hr⁻¹ to 2400 m hr⁻¹. Gillon also reports that temperatures inside tufts may remain as low as 50°C and at this level fire is not necessarily destructive to insects. Harrison's measurements of tuft temperature were made just above the tufts, not within them. Only one tempil plate failed to reach the lowest melting temperature of 260°C. At least one nymph which was almost certainly too small to dodge the flames survived on a burnt patch. Reported nymphal mortalities range from 4,5% (Y Gillon 1972) in Ivory Coast savanna to 100% in rangeland in USA (Hunter 1905).
- iv) Time of day. Hunter (1905) states that grasshopper mortality is much greater in fires on cool windy nights when insects are less active and the fire front moves faster. The Nylsvley fire passed through the area being studied at about 2000 hours. Conditions are given in Table 2. Insect mortality also comes about through predation by insectivorous birds which are attracted to a fire where they catch fleeing insects on the wing (Komarek 1969; Y Gillon 1972). The forktailed drongo, Dicrurus adsimilis, is the commonest species at fires in the Nylsvley area (Paintin 1965; W Tarboton, personal communication, 1979). A night fire would protect grasshoppers from this source of mortality.

Egg pods of grasshoppers and stick insects (<u>Phasmidae</u>) in the soil survived the fire but the mortality of nymphs emerging onto the bare burnt areas in October was high.

Where there was a mosaic of burnt and unburnt patches, a very high concentration of grasshoppers occurred on the unburnt patches with negligible numbers on the burnt ones. The biomass on these patches was over three times prefire levels.

Table 12. The density and dry biomass of grasshoppers in the mosaic of burnt and unburnt patches of <u>Burkea</u> savanna.

Day	Treatment	No of Samples	Mean density (m ⁻²)	Mean biomass (g m ⁻²)	Standard error (biomass)
Prefire	Unburnt	56	0,52	0,0355	0,0072
Postfire					
5	Unburnt	35	1,97	0,1172	0,0199
23	Unburnt	46	1,17	0,0863	0,0135
42	Unburnt	45	1,76	0,0781	0,0121
78	Unburnt	30	1,80	0,0403	0,0095
127	Unburnt	34	1,29	0,0140	0,0041
Postfire					
2	Burnt	31	0,03	0,0003	
21	Burnt	40	0,18	0,0070	
35	Burnt	60	0,30	0,0072	0,0027
63	Burnt	50	0,58	0,0189	0,0068
126	Burnt	40	1,55	0,0156	0,0059
Postfire		,	·		
40	Unburnt ^a	57	0,74	0,0504	0,0152
130	Unburnt ^a	59	3,00	0,0355	0,0064

^aUnburnt <u>Burkea</u> savanna away from Camp 2 where the fire occurred.

Acrotylus diana and Acorypha pallidicornis were the first species to re-invade in the first week after the fire. A diana is a cryptically coloured grasshopper which favours open habitats. A pallidicornis is a mixed feeder (Gandar in press) eating grass, forbs and litter. On the burnt areas they fed regularly on ash. The crop of one specimen caught on the burn contained only ash. After about three weeks Pnorisa squalus, Dnopherula spp and Parga xanthoptera were also found on the burnt areas. Phaeocatantops decoratus and Catantops melanostictus followed in smaller numbers in mid October. These two species are forb feeders and it was at this time that forbs reappeared (Tables 5 and 6). There was evidence that grasshoppers fed less selectively on the burnt areas. Crop contents were examined using the method described by Gandar (in prep).

Immediately after the fire the average biomass for the entire burn mosaic was 70% of that of unburnt savanna. Instead of catching up, the grasshopper biomass on the burn mosaic was 44% of unburnt Burkea areas after six weeks and 42% after four months. The size structure of the populations in Camp 2, which was burnt, and in unburnt Burkea savanna was very different, indicating that the mortality of nymphs emerging on the burnt area was very high in the first month after the fire. Predation was probably also high as insectivores exploited the exposed situation of insects on the burn. There was an obvious concentration of grey hornbills, Tockus nasutus, which feed on grasshoppers, around the burn for a few weeks after the fire. There was a noticeable darkening of the cuticles of grasshoppers on the burn which may have offered some One specimen of \underline{P} <u>xanthoptera</u>, which is normally straw coloured, was completely black. The fire had occurred after the final moult so this was an actual darkening as opposed to the development of a new darker cuticle. The effect has been documented previously by Burtt (1951) and Hocking (1964).

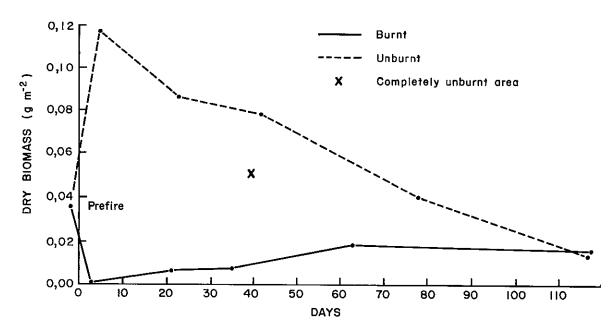


Figure 7. Grasshopper dry biomass in mosaic of burnt and unburnt areas after a patchy fire on day ß (5 September 1978) in Burkea savanna. A point showing the biomass on day 40 on a completely unburnt area of Burkea savanna is included for the sake of comparison.

Changes in the species structure of the small mammal population

Sherman traps were laid out on eight 10×10 grids with 10 m intervals between the traps. Seven grids were in <u>Burkea</u> areas and one in an Acacia area. The data below were collected by Watson (unpubl).

On every grid the trapping success was higher after the burn (January 1979) than before it (July 1978). This does not necessarily indicate an increase in population size since the shortage of food after the burn

may have made the bait in the traps more attractive. Also in June 1979, the trap success was even lower than in the prefire samples. It is also not possible to distinguish postfire changes from seasonal change. Of more significance are the changes which occurred in the structure of the rodent community.

Table 13. Numbers of small mammals trapped before and after the fire. Recaptures are excluded.

	Before (July 1978)	After (Jan 1979)	Significance
Tatera leucogaster	9	16	0,1
Dendromus melanotis	9	0	0,002
Saccostomus campestri	s 1	5	•
Mus munitoides	1	12	0,001
Aethomys chrysophilus	4	7	NS ·
Others	2	5	NS
Total	26	45	0,01
Trap nights	3800	3400	

Kern (1978) found that <u>Tatera leucogaster</u>, the bushveld gerbil, was dominant in the small mammal population after fire in Kruger National Park. It was restricted to areas of less than 70% cover and a little litter, and was replaced by other species as the area recovered from the burn. It was trapped more readily after the Nylsvley burn (Table 13) but the percentage <u>T leucogaster</u> in the total catch did not change. Evidently the prefire conditions were also suitable. Two <u>T leucogaster</u> which were trapped and marked before the fire were retrapped after the fire. This and <u>Saccostomus campestris</u>, the pouched mouse, which was also trapped more often after the fire, are mixed feeders eating mainly tree seeds (Temby 1977). These seeds survived the fire in partially burnt litter.

Dendromus melanotis, the black-eared climbing mouse, was not caught at all in January 1979. Temby (1977) reports that it lives in holes constructed by dung beetles and that it feeds mainly on grass seeds. It forages over large distances (Jacobson 1977). It might be assumed that it survived the fire but emigrated from the burnt areas in response to a shortage of food. In June 1979, nearly a year after the fire, two specimens of D melanotis were trapped on a grid near the edge of the burn. This may indicate that they are returning. Mus munitoides also increased on the burnt area. Like D melanotis it feeds mainly on grass seeds but will also feed on insects (Jacobson 1977) and may possibly have exploited this source after the fire. It increased most sharply on a grid in an area of mainly Setaria perennis, Elyonurus argenteus and Trachypogon spicatus which are amongst the first grasses to set seed.

Foraging range of the various rodents probably increased after the fire. One Aethomys chrysophilus moved 550 m in five days after the fire. However, the two \underline{T} leucogaster retrapped four months after the fire were caught within 70 m of the sites where they were trapped before the fire.

The response of impala to postfire conditions

Monro (1978) carried out prefire and postfire censuses by systematically walking transects through Camp 2. The mean numbers seen per census increased after the fire. Some large but incohesive groups formed after the fire although mean group size did not alter significantly (see Table 14).

Table 14. Numbers and group sizes of impala before and after the fire. (Data from Munro 1978)

	Before	After
Mean number seen per census	29	56
Maximum number seen per census	60	115
Maximum mixed group size	25	70
Maximum bachelor herd size	12	24

The sequence of events following the fire was:

DAYS AFTER FIRE	0 - 10:	Very few impala on the burnt areas and no grazing there. A few individuals remaining in unburnt areas but most moving to other parts of the reserve.
	11 - 20:	Increasing numbers of impala seen on burnt areas, but probably requiring forage from other areas for sustenance.
	21 - 30:	Peak numbers on preferred burnt areas forming large aggregations, but probably still requiring supplementary forage from other areas.
	31 ++ :	Gradually decreasing numbers on burnt areas. Density of animals on preferred burnt areas still relatively high after 90 days though.

The grass layer biomass increased rapidly between 10 and 40 days after the fire (Table 5).

There was a complete change of habitat preference from Acacia to Burkea areas. The area of Burkea most favoured after the fire was an open area with a large variety of grasses on the northern boundary. The grass Setaria perennis predominated and was one of the first to recover. Forage grasses generally recovered more quickly. Although grasses in the Burkea areas maintain lower protein levels through the winter than did those in areas of Acacia, crude protein content of the recovery

growth of spring burnt veld is high (Mes 1958; Tainton <u>et al</u> 1977), and possibly the plant diversity in <u>Burkea</u> area and the increase in forage grasses became the main determinants of habitat preference. Unfortunately no comparative data are available on the response to fire of grasses in the <u>Acacia</u> areas.

Carr (1976) found that in the absence of fire the preference shown by impala for $\underline{\text{Acacia}}$ areas is 13,9 times the preference for $\underline{\text{Burkea}}$ areas in September and October, dropping to a factor of 3,8 in November and December.

Table 15. Impala density in the various habitats in Camp 2 before and after the fire. Units are impala ha $^{-1}$. (Data from Munro 1978)

	Prefire	Postfire		
		burnt area	unburnt area ^s	
Burkea ^b	0,06	0,51	0,20	
Acacia ^b	0,39	0,02	0	
Firebreak ^c	1,07	0,02	0,3	

^aUnburnt area refers to parts of the area through which the fire passed but which were not touched by the fire.

Miscellaneous observations

The following casual observations were made but no quantified data were collected.

- i. Thysaneura (silver fish) were active in leaf litter shortly after the fire. The litter had been scorched on top.
- ii. Damage to new growth: many of the first grass leaves to appear after the fire became constricted at particular points along their lengths. The distal part of the leaf soon died and broke off at the constriction. In some areas this appeared to be the principal form of damage to new growth. A number of species of grass were affected, including Digitaria eriantha and Eragrostis pallens, the main species in Burkea areas. Grass on unburnt areas also suffered. The damage seemed less intense there, but this was not measured.

The constrictions resembled feeding effects caused by some sap suckers. Several Hemiptera were caught on the burn at the time. They were put in cages over undamaged grass but did not induce any effects.

bAreas of the above habitats are given in Table 1.

^CThe firebreak was burnt a few months before the September fire.

Solanum panduraeforme is a small woody plant very common in the Acacia patches. It is attacked by a rust, Puccinia agrophila, which may cause extensive damage to leaves (Rey 1978). It was very apparent that the degree of infection was much lower on the burnt areas. P agrophila is a fungus and many of its spores pass from one season to the next in leaf litter.

DISCUSSION

In terms of the twelve questions set out in the introduction, the following points emerge.

1. Behavioural characteristics

Three types of variation are involved. Firstly, there are variations between fires at different times in similar areas, as determined by parameters such as wind speed and the moisture content of the vegetation. This could not be examined in only a single fire.

Secondly, there is variation on a scale of tens to hundreds of metres. The patchiness of the fire on this scale was greater than anticipated and the three fire behaviour blocks did not adequately describe it. These showed rates of spread varying by a factor of four. It is evident that a mean value for rate of spread and rate of energy release would not be very helpful. Future fire behaviour research in such savanna types could more profitably focus on the scale, pattern and range of this variation and its underlying causes in terms of question 3 in the introduction.

Patches, amounting to 26% of Camp 2, were not burnt. Small back fires were burning twelve hours after the initial flame front had passed. It is noteworthy that 41% of the <u>Acacia</u> patches, which are intensively used by herbivores was unburnt, as opposed to 24% of lightly utilized <u>Burkea</u> patches.

The extent of this variation is probably the most important feature of fire behaviour. The fragmentation of the flame front leaves unburnt remnants which are of particular significance to arthropods (eg grasshoppers and termites). There is some evidence that it also affects small mammals. The importance of this variability in fire behaviour in maintaining a varied habitat is discussed below.

The third type of variation is on the microhabitat scale. For example, grass tuft temperatures varied from less than 260°C to over 816°C but no information was collected on the causes or effects of these differences.

2. Vegetation structure.

Structural changes in the vegetation induced by the fire varied with fire characteristics. For example in the faster burning Block C, there was greater canopy destruction than in Block A. There was twice as much basal regeneration induced by the fire in Block C. However, although temperatures in Block A were lower, the slower

fire and prolonged heating especially near the ground caused greater shrub mortality than on Block C. Thus where the fire is fast and hot, high canopy destruction, high basal regeneration and low shrub mortality can be expected. These three factors add up to a lowering of browse levels in areas of fast hot burns relative to areas of prolonged cooler burns.

Observations on the effects of a single fire do not necessarily indicate the long-term effects of fire. Although mortality of trees was low in the Nylsvley fire, it has been reported (Kennan 1971) that regular fires reduce tree density in <u>Burkea africana</u>-dominated savanna. Also, although <u>Ochna pulchra</u> showed low mortality in the Nylsvley fire, Geldenhuys (1977) has suggested that <u>O pulchra</u> is sensitive to regular burning in South West Africa.

Comparing the Nylsvley data with those of Kennan (1971) and Trollope (1974) in <u>Acacia</u> savannas, it appears that, although total plant mortalities may be low in both <u>Acacia</u> and <u>Burkea Ochna</u> savannas, <u>Burkea Ochna</u> Nylsvley woody plants are less susceptible to killing of canopies through fire than some <u>Acacia</u> plants (Rutherford 1981). The fire in the <u>Acacia</u> patches at Nylsvley appeared to be much less intense than in the <u>Burkea</u> woodland so possibly the opposite occurred at Nylsvley. The effects of fire on trees were not monitored in the <u>Acacia</u> patches.

Structural diversity in the herbaceous layer as a result of fire was not investigated. However, in <u>Burkea</u> areas, the percentage of forbs in the herbaceous biomass increased after the fire. This may have reduced structural diversity since it appeared from observation, rather than measurement, that the unburnt patches in the fire mosaic generally had a high percentage of forbs.

Although a start has been made on studying the effects of fire irregularities on vegetation structure, there are no Nylsvley data on the reverse relationship either at the subhabitat level or on a larger scale. Patterns in vegetation structure and fire behaviour may be mutually interactive, and future fire behaviour research at Nylsvley could probe this possibility.

3. Effects on animals

The effects of fire on animal populations (questions 3 and 4) were varied and sometimes serious, but generally it was not completely disastrous. Since fire is a basic component of savanna functioning it is to be expected that faunal groups would have evolved some means of resisting, avoiding, escaping and reinvading after fire.

Escape was used by large mammals and there was no evidence of any mortality. Adult grasshoppers, and possibly other mobile insects, were also able to escape the flames. Though, as mentioned earlier, the speed of the flame front will affect mortality. The ability of insects to flee is also affected by ambient temperature. Small mammals survived the fire but it is not known whether this was by fleeing the flame front or by sheltering in burrows. The uneven

nature of the flame front and the patchiness of the fire would assist the small animals to dodge the flames.

Animals may also survive the passage of fire by avoiding high temperatures. At least one grasshopper nymph did so, presumably in a tuft of grass. Small mammals and burrowing insects, for example, can probably survive in their burrows. In the soil itself beetle larvae, orthoptera eggs and termites were unaffected by the passage of fire. Animals may also shelter under stones, though in the burnt area there were very few stones which could have provided shelter.

Although some arboreal insects survived in canopies of <u>Dombeya rotundifolia</u> trees 3-4 m high, there was total destruction of insects in 2 m high <u>Ochna pulchra</u> trees. Generally speaking, these arboreal insects have mobile adult forms. Reinvasion was not measured but potentially it was rapid.

Gandar (in press) noted that grasshoppers at Nylsvley often have a large degree of asynchrony of breeding cycles even within a single species. There were also instances recorded of plasticity in breeding cycles. This has obvious adaptive value in an area such as Nylsvley which is subjected to sporadic fire and drought, both of which induce different mortalities on the different stages of the life cycle.

4. Responses of animals

Responses of animal groups in the immediate postfire period are very varied even within a defined group such as grasshoppers. They generally respond to one of the following factors:

- i) availability, visibility or nutrient content of food
- ii) changes in the structure of the habitat
- iii) changes in physical characteristics of the habitat.

Details of the responses of the different groups are given in the previous section of this report. Some examples to illustrate each of the above three principles will be given here.

Food:

The immediate effect of reduction of food supply on the burnt areas, particularly for animals feeding on the herbaceous layer, caused large mammals to leave the area altogether while insects congregated on unburnt patches in the mosaic. Insectivores such as the grey hornbill were attracted to the area by the exposed situation of their Young orthoptera nymphs emerging on burnt areas shortly after the fire generally did not survive. the first flush of grass, impala returned in large numbers to feed on the nutritious new growth. They shifted their preference from Acacia areas to the species rich, but normally nutrient poor, Burkea areas. It was found that grasshoppers on recently burnt Burkea fed less selectively than those on unburnt areas. Perhaps the flush of nutritious plant material enables animals to feed on a broader spectrum of plants thus enhancing the nutritional benefits. Insects became more common on the burnt areas with the flush of vegetation and the return of forbivorous grasshoppers coincided with the emergence of forbs.

Structure:

The species composition of the populations of grasshoppers and of small mammals on the burnt areas were very different from before the fire. While some of the change can be interpreted in terms of food supply, the main changes were the disappearance of those animal species favouring long grass and abundant cover, and the return of those favouring open areas.

Physical conditions:

Termite foraging activity decreased after the fire. While this may be a response to the reduction in food supply, P Ferrar (personal communication) suggests it was more likely because of high surface temperatures. Drying of the soil caused termites to descend deeper into the soil after the fire. Soil dessication is a probable explanation of why the emergence of adult beetles from soil-dwelling larvae suddenly dropped on burnt areas relative to unburnt areas, two months after the fire. Darkening of grasshopper cuticles in response to surface blackening after the fire was also noted.

5. Responses of plants

The only information relating to the fire responses of different species of plants (question 7) comes from Rutherford's work on trees described in the previous section.

The observation that palatable (to large herbivores) species of grass recovered more vigorously from the fire than unpalatable species, suggests that it may be worth examining the vigour of this response in relation to the previous degree of utilization. Alternatively, it suggests that the palatable species are adapted to defoliation, by way of having larger root reserves, than are the unpalatable and less utilized species.

6. Soils

The data on soil moisture (question 8) are incomplete, but do at least establish that under the circumstances of low rainfall that followed the burn, soil moisture is lower on burnt than unburnt areas to a depth of at least 45 cm. Increased absorption of solar energy on the blackened bare surface could account for some of the drying out of soil, but since soil heat fluxes on burnt and unburnt sites are very similar, it is unlikely to account for much more than surface drying. The reduction of infiltration is probably more important. Hoof action of the congregation of mammals on burnt areas may lessen the effect of soil capping.

There is evidence that the reduction in soil moisture after a fire affects soil arthropods, and increases susceptibility of grasses to drought. It is also one of the factors governing soil microbial activity. More information on soil moisture would be valuable. No information was obtained on the effects of fire on soil chemistry or on mineral release, transport or uptake (questions 9 and 10).

Soil respiration on burnt sites was not significantly different from unburnt sites (question 11) but in the absence of other soil data, this is difficult to interpret. In a previous section it was suggested that this result was due to coincidental balancing of opposing influences.

7. Primary productivity and biomass accumulation

Biomass accumulation was not greatly affected by fire directly. End of season herbaceous biomass was similar in burnt and unburnt Burkea areas provided it was not grazed. Fire appeared to affect herbaceous biomass more through indirect effects, such as increasing susceptibility to drought and by stimulating young growth which attracted high densities of large herbivores.

Leaf biomass of woody plants declined by about 40% but the net loss was smaller for larger trees. Despite this, there may not be much decrease in radial stem growth, though this has not yet been verified at Nylsvley.

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