

The structure of a grass community in *Burkea africana* savanna during recovery from fire

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Three adjacent sites, differing in their fire histories, in the *Eragrostis pallens*–*Digitaria eriantha* association of the *Burkea africana* savanna at Nylsvley, northern Transvaal were compared. One site has been burned annually while the second and third sites had last been burned 5 and at least 12 years previously. Grass species richness was highest on the annual burn and decreased with an increasing period of protection from fire. Total mean basal areas of the grasses increased by 78% from the annual burn to the protected site. The dominant grasses in this association, *Eragrostis pallens* Hackel and *Digitaria eriantha* Steudel, increased in abundance with protection from fire until they comprised approximately 97% of the total number of individuals and total mean basal area found at the protected site. Annual burning reduced the density and average diameter of individuals of *E. pallens*, allowing opportunistic species to colonize this association. Significantly more individuals of *E. pallens* were found in the 5-year burn. Its numbers declined in the protected site, presumably as a result of self-thinning. The number of tillers produced, the number that flowered and flowering phenology of *E. pallens* was similar in populations on the annual burn and in the protected site. On the burnt area after 5 years of protection, plants of this species produced significantly fewer tillers and the time of flowering was delayed compared with other treatments. Significantly more tillers of *E. pallens* were grazed upon on the sites protected for 5 and 12 years. In contrast, *D. eriantha* plants showed no increase in size from the annual to the protected site but their density did increase.

Drie aangrensende gebiede, met verskillende brandgeskiedenis, in die *Eragrostis pallens*–*Digitaria eriantha*-deelgenootskap van die *Burkea africana*-savanne is vergelyk. Een gebied is jaarliks gebrand terwyl die tweede en derde gebiede onderskeidelik 5 en 12 jaar gelede gebrand is. Die hoeveelheid grasspesies per steekproef was die hoogste in die jaarliks gebrande gebied, en het voortdurend afgeneem hoe langer die gebiede beskerm was. Totale gemiddelde basale oppervlakte van die grasse het van jaarlikse brand tot die beskermde gebiede met 78% toegeneem. Die oorheersende grassoorte in hierdie deelgenootskap, *E. pallens* en *D. eriantha*, het in voorkoms toegeneem as gevolg van beskerming teen vuur, totdat hulle ongeveer 97% van die totale aantal individue en totale gemiddelde basale oppervlakte in die beskermde gebiede beslaan het. Jaarlikse brand het die digtheid en gemiddelde deursnee van *E. pallens* individue verminder, met die gevolg dat opportunistiese spesies in hierdie deelgenootskap kon koloniseer. Beduidend meer individue van *E. pallens* is gevind by die tussentydse brand. Hul getalle het verminder in die beskermde gebied as gevolg van selfuitdunning. Die aantal uitlopers geproduseer, aantal uitlopers wat blom en blomfenologie van *E. pallens* was dieselfde tussen die bevolkings op die jaarliks gebrande en by die beskermde gebied. By die tussentydse brand was die aantal uitlopers deur hierdie spesie geproduseer beduidend minder en die blomtyd vertraag. Beduidend meer uitlopers van *E. pallens* is benut in die gebiede wat vir 5 en 12 jaar beskerm was. In teenstelling het *D. eriantha* geen toename in grootte getoon van die jaarlikse na die beskermde gebiede nie, maar die aantal individue het wel toegeneem.

Keywords: *Burkea africana*, *Digitaria eriantha*, *Eragrostis pallens*, fire, grassland structure

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Introduction

The effect of fire on the structure and functioning of grasslands and the herbaceous layer of savannas has been widely reported (Daubenmire 1968; Vogl 1974; O'Connor 1985). Common observations are that fire retards the establishment and growth of woody shrubs in such systems (Vogl 1974; Gillon 1983), enhances the vitality of grasses through the removal of ageing plant parts and of any possible growth inhibitors they might contain (Gillon 1983; Frost 1985), increases the nutritive values of plants (Gillon 1983) and results in the replacement of unpalatable species with more palatable ones (Grossman *et al.* 1981; Gandar 1982). Fire also acts as a natural selective force in the development of grassland species by synchronizing flowering and seed germination (Daubenmire 1968; Vogl 1974; Gillon 1983). In grasslands and savannas fire also retards the development of most grass species (Gillon 1983), accentuates the effects of seasonal drought (Daubenmire 1968; Gillon 1983; Frost 1985), and, in drier areas, reduces productivity (Vogl 1974).

Most studies of the effects of fire on grasslands and the herbaceous layer of savannas are concerned with the changes which occur immediately after a fire and in the

following 4–5 years (e.g. see the review of O'Connor 1985, and the references therein). Other studies have concentrated on the frequency of burning, again with intervals of up to 5 years between burns (Kennan 1972). Many of these studies have shown that annual burning results in an increase in the number of species in the herbaceous layer, due primarily to the invasion of opportunistic species, while areas burned at longer intervals have fewer species in the herbaceous layer (Vogl 1974; Gandar 1982). In addition, there is a change during this period in the stratification of the vegetation as taller-growing grasses shade out the smaller-growing ones and fire-adapted forms are replaced (Gillon 1983). Finally, grasslands and savannas, unburned for periods of 4–5 years, are often described as moribund (Grossman *et al.* 1981) and such areas are usually burned at that point (van Wyk 1972).

Few studies have placed emphasis on the changes occurring in grasslands and savannas during long-term recovery from disturbance by fire. Studies of this nature are necessary to understand the principles which govern the structure of savanna grasslands. Such studies allow us to see the process of species replacements occurring within that community in the absence of fire. In this study the structure of the *Eragrostis pallens*–*Digitaria eriantha* association after

annual burning, 5 years after a burn, and in an area protected for at least 12 years from fire is evaluated in order to establish the pattern of change in species composition, the changes in relative abundance of the component species, and some of the effects of protection from burning on the dominant grass species, *E. pallens* and *D. eriantha*.

Study area

The study area is located within the Nylsvley Nature Reserve, approximately 16 km south of Naboomspruit in the northern Transvaal, South Africa (24°40'S, 28°43'E). Mean annual rainfall, based upon 40 years of records for Mosdene, 10 km north-east of Nylsvley, is 640 mm, of which 80% falls from November through March (Huntley & Morris 1982). Mean daily air temperature ranges from 12° to 20°C in April through August, 14° to 22°C from September through October and 20° to 25°C from November through March (Huntley & Morris 1982). The soils in the study area are non-calcareous, well-drained sands of poor nutrient status (Grossman 1981). Fires are controlled within the study area by a series of firebreaks. Most of the camps within the study area are burnt on a 3–5 year rotation. A section of one camp has been protected from fire for at least 12 years. The study sites are lightly grazed by impala (*Aepyceros melampus*), Cape hare (*Lepus capensis*) and spring hare (*Pedetes capensis*) and were last used by cattle in 1977 (Grossman *et al.* 1981). The climate and soils of this region combine with the disturbance regime to support a semi-arid, dystrophic savanna (Huntley & Walker 1982).

The three sites studied are approximately 1 ha in area, are located on the Middleburg series of the Hutton soil form (Harmse 1977) and have been burned at various times in the past. One site, burned annually, is located in the firebreak at the top of a ridge while a second site is located adjacent to the firebreak in an area burnt 5 years previously. The third site is located about 1 km from the latter site in an area which has not been disturbed by fire for at least 12 years. These sites are referred to here as the annual burn, intermediate burn and protected site respectively. All three sites are situated in the *Eragrostis pallens*–*Digitaria eriantha* association of the *Burkea africana* savanna (Coetsee *et al.* 1976; Yeaton *et al.* 1986).

Methods

Ten randomly chosen line transects were established in unshaded habitats in each of the three study sites. A sample size of ten line transects per site was sufficient to show statistically significant differences in this vegetation type (Yeaton *et al.* 1986). Each line transect was 5 m long and each plant whose base was crossed by the line was identified and its basal diameter recorded. Basal diameters were measured to gain an approximation of each individual's ecological effect on neighbouring plants (Mack & Harper 1977; Newbery & Newman 1978; Waller 1981; Liddle *et al.* 1982; Firbank & Watkinson 1987). The basal diameters were converted to basal areas and summed for each species within each transect. The average values for the ten samples were calculated for each species and the relative abundance of each species calculated as a percentage of the total basal area recorded for that site. The comparison of the total basal areas of the three sites has been reported previously (Yeaton *et al.* 1986). The mean and standard error for the number of individuals and the diameters of individuals of *E. pallens* and *D. eriantha* and for all individuals of every species recorded were calculated at each site. *F*-tests followed by *t*-tests were utilized to determine differences in the variances and means of number of individuals and plant diameters between the three sites. *T*-tests, using logarithmic transformations of the data, were

run whenever significant differences in variances between sample sets were found (Steel & Torrie 1960).

The nearest-neighbour technique of Pielou (1960) was used to test for evidence of interactions between individuals of *E. pallens* at each site. In this method individuals of *E. pallens* are chosen randomly following the operational definitions of Yeaton & Cody (1976) and the distance between each individual and its nearest-neighbour and their sizes measured. A positive linear correlation between the sums of sizes for nearest-neighbour individuals and their distances apart indicates that competition is occurring (e.g. Fontyne & Marshall 1978; Yeaton *et al.* 1977). Pairs of correlation coefficients were tested (Steel & Torrie 1960) to determine whether differences in the intensity of competition occur between sites with time since the last burn. It can be assumed that higher correlation coefficients indicate stronger competitive interactions because the size attainable by the smaller individual as a function of its distance from its nearest-neighbour is more effectively restricted (Yeaton *et al.* 1985). In addition, nearest-neighbour measurements were obtained at the intermediate burn site for the interspecific pairing of *E. pallens* and *D. eriantha* and the intraspecific pairing of *D. eriantha* individuals to determine if competitive interactions were possibly occurring. These measurements were made only in the intermediate burn site where the density of *E. pallens* is highest and where the intensity of interactions are likely to be greatest. Correlation coefficients for intraspecific and interspecific nearest-neighbour pairs were compared statistically to determine if competitive interactions are weaker between different species than they are within a species.

Finally certain aspects (number of new tillers produced, phenology, and the number of stems removed by grazers) of the life history of the dominant species, *E. pallens*, were compared between the three sites. A sample of at least 21 individuals of different basal diameters was marked and monitored over a 2-month period (2/1/84–1/3/85) of growth. This time interval covered the period from the first flush of tillers on the plants until no new tillers were produced and when translocation of assimilates, as evidenced by browning of the stems, had begun. All live tillers, green and longer than 5 cm, were marked in waterproof red ink. The diameter of the plant at its base, the number of tillers marked and the number of tillers bearing flowers were recorded for each plant. At 2-week intervals any new tillers that had developed were marked and their numbers recorded and a recount was made of the number of flowering tillers. In addition, we counted the number of previously marked tillers whose tips had been removed by grazing animals in the interval since the last count. From these data the mean and standard error for the total number of tillers per cm of plant basal diameter was determined, as also was the percentage of tillers removed by herbivores over the 2-month period. At 2-week intervals the proportion of tillers which flowered was determined. In the first two categories sites were compared using *t*-tests with appropriate logarithmic or arc-sine transformations (Steel & Torrie 1960) while for the phenological data, comparisons were made between sites at 2-week intervals, again using *t*-tests on transformed data.

Results

The species composition and abundances, given as a percentage of the total mean basal area for the three sites are presented in Table 1. The number of species decreased from 11 in the annual burn to four in the protected site. The total mean basal area increased with time since the last burning, but only significantly so between the annual burn and the intermediate burn and the protected site (Yeaton *et al.*

Table 1 The species composition, average basal area (BA) and percentage basal area (%) of the *Eragrostis pallens*-*Digitaria eriantha* association for sites burned annually, protected from fire for 5 years (intermediate) and protected from fire for at least 12 years (protected). BA = basal area in cm²

Species	Annual		Intermediate		Protected	
	BA	%	BA	%	BA	%
<i>Eragrostis pallens</i>	208	35,8	1069	79,0	1570	82,8
<i>Rhynchelytrum repens</i>	167	28,8				
<i>Tristachya rehmannii</i>	59	10,2				
<i>Diheteropogon amplexens</i>	41	7,2	65	4,8		
<i>Schizachyrium jeffreysii</i>	38	6,5				
<i>Aristida mollissima</i> subsp. <i>argentea</i>	26	4,5				
<i>Digitaria eriantha</i>	25	4,4	169	12,5	266	14,0
<i>Pogonarthria squarrosa</i>	11	1,9				
<i>Eragrostis</i> sp.	3	0,5				
<i>Aristida stipitata</i>	1	0,1				
<i>Aristida congesta</i>	1	0,1				
<i>Elionurus muticus</i>			31	2,3		
<i>Panicum maximum</i>			18	1,4		
<i>Andropogon</i> sp.					49	2,6
<i>Themeda triandra</i>					11	0,6
Total	580	100,0	1352	100,0	1896	100,0

1986). Two species, *E. pallens* and *D. eriantha*, were common to all three sites. In each case *E. pallens* was the numerical dominant (Table 1). Together, *E. pallens* and *D. eriantha* comprised over 97% of the total number of individuals recorded at the protected site (Table 1). Similarly, these two species comprised nearly 97% of the total mean basal area of the grass community at the protected site. However, the mean number of individuals recorded per site and their mean diameters differed (Table 2). In general, the average number of individuals was greatest at the intermediate site and then decreased with time since the last burn while the mean diameter of individuals increased directly with time since the last burn. For *E. pallens* the average number of individuals was significantly greater by a factor of two after 5 years protection from fire than in the annual burn ($P < 0,01$) and in the protected site ($P < 0,01$). No significant difference in average number of individuals was found between the annual burn and the protected site. For *D. eriantha* a three-fold increase in the average number of individuals was recorded from the annual burn to the protected site but only the differences between the annual burn and the protected site were significant ($P < 0,01$). In contrast, the average diameter of an individual *E. pallens* increased with time since the last burn (annual versus intermediate, $P < 0,001$; intermediate versus protected, $P < 0,001$). No significant changes in mean plant diameter were recorded for *D. eriantha* between the three sites. Each species increased its proportional contribution to total basal area with time since last burning. Individuals of *E. pallens* were 55% larger in mean basal area on the intermediate burn than on the annual burn and 67% larger on the protected site than on the intermediate burn (Table 2). Similarly, individuals of *D. eriantha* were 62% larger in mean basal area on the intermediate burn than on the annual burn and 21% larger on the protected site than on the intermediate burn.

Positive linear regressions were found for all intraspecific and interspecific pairs of nearest-neighbours (Table 3).

Table 2 The mean (\bar{X}) and standard errors (SE) for numbers of individuals and their diameters for *Eragrostis pallens*, *Digitaria eriantha* and all species (including *E. pallens* and *D. eriantha*) recorded in the herbaceous layer of the *Burkea africana* savanna at sites that are burned annually or have been protected from fire for 5 or 12 years; n = the number of quadrats sampled in the section of the table dealing with number of individuals and = the number of plants recorded in the section dealing with plant diameters

	Number of individuals								
	<i>Eragrostis pallens</i>			<i>Digitaria eriantha</i>			All species		
	n	\bar{X}	SE	n	\bar{X}	SE	n	\bar{X}	SE
Annual burn	10	3,9	1,0	10	0,9	0,5	10	8,4	0,7
Intermediate burn	10	8,0	0,8	10	2,5	0,6	10	11,6	0,9
Protected site	10	4,6	1,4	10	2,9	0,4	10	7,7	0,4
	Plant diameters (cm)								
	<i>Eragrostis pallens</i>			<i>Digitaria eriantha</i>			All species		
	n	\bar{X}	SE	n	\bar{X}	SE	n	\bar{X}	SE
Annual burn	39	7,4	0,6	9	4,9	1,2	84	7,1	0,5
Intermediate burn	80	11,0	0,6	25	8,0	0,9	116	10,3	0,5
Protected site	46	19,1	1,4	29	9,0	1,1	77	15,3	1,1

Table 3 The regression equations and correlation coefficients for sums of sizes and distances apart of nearest-neighbour pairs of *Eragrostis pallens* on the three burn sites and for intraspecific and interspecific pairs of *Digitaria eriantha* on the site protected from fire for 5 years. Y = the sum of sizes in cm, X = the distance apart in cm, r = the correlation coefficient and n = the number of nearest-neighbour pairs sampled

Annual burn	<i>Eragrostis pallens</i> against <i>Eragrostis pallens</i> $n = 60$; $Y = 0,53 X + 8,9$; $r = 0,68$; $P < 0,01$
Intermediate burn	$n = 71$; $Y = 0,81 X + 1,9$; $r = 0,91$; $P < 0,01$
Protected site	$n = 60$; $Y = 0,82 X + 2,6$; $r = 0,85$; $P < 0,01$
Intermediate burn	<i>Digitaria eriantha</i> against <i>Digitaria eriantha</i> $n = 24$; $Y = 0,89 X - 0,4$; $r = 0,89$; $P < 0,01$
Intermediate burn	<i>Digitaria eriantha</i> against <i>Eragrostis pallens</i> $n = 52$; $Y = 0,80 X + 1,9$; $r = 0,84$; $P < 0,01$

Significant differences between the correlation coefficients for intraspecific pairs of *E. pallens* occurred for the annual burn versus the intermediate burn ($P < 0,001$) and for the annual burn versus the protected site ($P < 0,02$). On the intermediate burn no significant differences were found for the correlation coefficients between intraspecific nearest-neighbour pairs of *E. pallens* and *D. eriantha* and the interspecific pairings. Intraspecific nearest-neighbour pairs of *D. eriantha* were infrequent, comprising only 16,3% of the samples taken at this site.

Differences were found between populations of *E. pallens* on the three sites in the number of tillers produced, the timing of flowering and in the percentage of tillers removed by herbivores (Table 4). Significantly fewer tillers were produced per unit basal area in the population at the intermediate burn than in that of the annual burn ($P < 0,01$), while no significant differences were found between the populations of the protected site and the other two sites. No

Table 4 Some life history characteristics of *Eragrostis pallens* on sites protected from fire for various lengths of time. Numbers in parentheses are the numbers of individuals monitored. \bar{X} = mean and SE = standard error

	Annual (21)		Intermediate (24)		Protected (25)	
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
Number of tillers produced/cm of plant diameter	0,85	0,16	0,34	0,05	0,55	0,10
Percentage of tillers flowering on						
2/1/85	22,7	5,4	0	0	13,4	4,4
28/1/85	45,0	4,9	26,6	5,3	51,7	4,3
1/3/85	81,1	4,8	81,3	4,2	85,9	3,0
Percentage of tillers grazed	4,6	1,6	22,4	4,8	28,3	5,7

significant differences were found at the end of the growing season in the percentage of flowering tillers. However flowering was delayed at the intermediate site at the start of the growing season and flowering was still less productive 1 month into the following period (P ranging from $< 0,02$ to $< 0,001$). No significant differences were found at any point between the annual site and the protected site in the percentage of tillers flowering. Significant differences occurred between sites in the percentage of tillers grazed. Significantly fewer tillers were removed from the annual burn than from either the intermediate or protected site (annual versus intermediate, $P < 0,01$; annual versus protected site, $P < 0,001$).

Discussion

The changes observed in the *Eragrostis pallens*–*Digitaria eriantha* association over time follow the same general pattern reported for grasslands and savannas by previous authors (Daubenmire 1968; Vogl 1974; Gillon 1983; Grossman *et al.* 1981; O'Connor 1985 and references therein). There is a decrease in the number of species recorded while the total mean basal area of the grasses increases from the site burned annually to the protected site. Annual burning combined with the effect of fire on soil moisture availability keeps the individual plants small, leaving space for the colonization of opportunistic species such as *Rhynchelytrum repens*, *Schizachyrium jeffreysii*, *Pogonarthria squarrosa*, *Aristida mollissima* subsp. *argentea*, *A. stipitata* and *A. congesta*. It should be noted that these species are of poor fodder quality (Field 1976; Grossman *et al.* 1981).

Aside from the general trends in the organization of the grassland and savanna associations reported above, what changes are observed in the structure of populations of the dominant and subdominant species? *Eragrostis pallens* is the dominant species in the herbaceous layer of this dystrophic savanna, both in terms of numbers of individuals present and in total mean basal area. *Digitaria eriantha*, while reduced in numbers and in total mean basal area at sites burned annually, becomes a subdominant in the association after protection from annual burning. The smaller plant diameters found at the annual burn site are due to the reduction in size of *E. pallens* as aged plant parts are removed by fire. Grossman *et al.* (1981) also found a 53% decline in the percentage of basal cover for *E. pallens*, from 1,47% before a fire to 0,69% after a burn at Nylsvley. However, the statistical significance of this decline was not reported. The variance of plant diameters for *E. pallens* increased over time as a result of the recruitment of new

individuals from seed into the population. This recruitment is also shown by the greater number of individuals of *E. pallens* recorded on the intermediate burn. After at least 12 years of protection from fire, the number of *E. pallens* tufts began to decrease as a result of self-thinning. A comparison of the correlation coefficients obtained from the populations of nearest-neighbour *E. pallens* on the three sites suggests that the intensity of competition increases significantly from the annual burn to the intermediate burn and remains high on the protected site. Thus, self-thinning begins sometime in the 4-year period after a burn and is still continuing after 12 years of protection from fire. The average diameter of an *E. pallens* individual increases as a result.

In contrast, the population of *D. eriantha* increases in numbers more slowly, presumably as a result of competitive interactions with the numerically more abundant and larger individuals of *E. pallens*. No significant differences were found in comparisons of the correlation coefficient for the strength of interaction between the two species with either of the correlation coefficients for the intraspecific cases. This suggests that the intensity of competition is as great between these two species of grasses as it is between individuals of the same species and implies that these species are utilizing the same limiting resources (Yeaton *et al.* 1985). Hence, *E. pallens* and *D. eriantha* must be either replacing one another spatially over an environmental gradient or temporally by a successional process (Pickett 1980; Yeaton *et al.* 1980; Yeaton 1983). Since these two species are associated over a complex environmental gradient (Yeaton *et al.* 1986), the latter situation is more likely. The habit of *D. eriantha* of reproducing vegetatively from stolons may aid this species in dispersing to and successfully colonizing open microsites within the stand where interaction with *E. pallens* is reduced. Later, *E. pallens* may colonize sites occupied by *D. eriantha* and replace the latter species by outcompeting it. Thus, although *D. eriantha* is the subdominant species in this association, its persistence is dependent upon an ability to utilize microsites opened by small-scale disturbances within the stand.

The overall effects of frequent fire on the *Eragrostis pallens*–*Digitaria eriantha* association of dystrophic savanna appear to be negative. Most of the species that are promoted by annual burning are considered generally to be unpalatable while *D. eriantha*, a palatable species, is reduced in both number of individuals present and in its total mean basal area by frequent burning. *Eragrostis pallens*, the dominant but unpalatable species, produces more tillers and reproduces earlier on the annual burn site than in the intermediate burn. However, the vigour of *E. pallens*, as measured by the number of new tillers formed annually per unit basal area, is increasing after at least 12 years of protection from fire. Concurrently, *D. eriantha* increases in abundance, possibly as a result of increased shade from the growth of woody shrubs and trees. *Panicum maximum*, a palatable species which is present in shaded microhabitats in the *E. pallens*–*D. eriantha* association of the *Burkea africana* savanna, could also be expected to benefit from increased levels of shading (Kennard & Walker 1973).

It would appear then that effective management of this semi-arid, dystrophical savanna requires a strategy involving more than just burning every 3–5 years. A programme which reduces the density of *E. pallens* but not the palatable *D. eriantha* would seem to be more appropriate. Longer intervals between burns would increase the relative abundance of *D. eriantha*, increase the amount of shade necessary for the establishment of the palatable *P. maximum* and increase the number of tillers of *E. pallens* grazed by herbivores.

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