Vegetation changes after single fire-events in the Okavango Delta wetland, Botswana

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A comparative study on burned and unburned areas has been conducted for the south-eastern floodplains of the Okavango Delta wetland, Botswana to assess differences in vegetation composition and structure after single fire-events. Main findings on plant traits and species occurrences supported the theory of only slight vegetation changes after fire in fire-prone environments. No specific plant trait was found to be favoured by the fire-event and only *Urochloa mosambicensis* showed a highly significant correlation to burning. Main changes were observed in vegetation structure, e.g. height and cover of the herb layer or biomass production. Interestingly, no main trends regarding how vegetation structure is generally affected by fire-events were deriv-able. Detailed analyses of five derived habitat types clearly showed different and contradictory responses to burning. This variability of vegetation response to fire-events, dependent on the habitat, was explained along a productivity gradient from active floodplains to dry Mopane woodlands. While floodplains showed an obvious decrease of standing biomass after the fire-event, an increase of biomass was observed for the Mopane woodlands. The nutrient pulses often described after fire-events, therefore seem to improve nutrient conditions best in poorer habitats, while for more productive sites, the enhanced nutrient availability after burning seem to be minor. Nomenclature: Arnold and De Wet (1993).

Introduction

Fire in southern African savannas is often described as a natural phenomenon. For hundreds of thousands of years fire has played an essential role in determining the savannas in a complex and dynamic interaction with climate, soils, geomorphology and herbivory (Bond and Van Wilgen 1996, Scholes 1997). The outcome of the combination of these factors in most of the tropical and subtropical environments of southern Africa is an open mosaic of trees and grasses, where none of the components is dominant. As simple as it is to define savannas roughly as tree-grass co-dominated vegetation types in the tropics (Scholes 1997), it is difficult to explain the reasons for this co-occurrence. Many studies have been published concerning tree-grass interactions in savannas, describing different hypotheses, models or recipes (Bond and Van Wilgen 1996, San Jose and Montes 1997, Scholes 1997, Scholes and Archer 1997, Jeltsch *et al*. 1999, Higgins *et al*. 2000), but they are often just based on case studies ending with a statement about savannas being notoriously complex and too unpredictable to identify, isolate or quantify the key determinants of savanna structure (Bond and Van Wilgen 1996, Scholes 1997). An approach to start untangling this complex web of interactions is to focus on one single factor, e.g. fire.

When fire is described as a natural phenomenon, it becomes part of the ecology of savannas. Species occurring in these fire-prone environments are therefore highly adapted to the fire occurrences and the post-fire environment. Species not escaping the fire in space or time, or not being able to resist the fire, or to recover, or re-grow quickly after the fire, are usually rare in savannas as they are out-competed by more fire tolerant species (Booysen and Tainton 1984, Bond and Van Wilgen 1996). Fire tolerance does not imply specific adaptations to fire (e.g. fire stimulated flowering, seed-release or germination), which is actually seldom found in savannas (Bond and Van Wilgen 1996, Bond 1997), but refers to the general ability to survive this kind of disturbance.

All these findings stress the importance of fire in savannas as an ecological factor, determining the typical plant species composition and vegetation structure through a permanent reoccurring disturbance. Different studies on post-disturbance species compositions have shown that the species assemblage of a community that experienced a certain, regular disturbance regime over a long period of time, does not

alter further after disturbance events, as a result of the loss of disturbance intolerant species in the flora (Días *et al.* 1999, Lavorel *et al.* 1999). Morgan (1999) even states that all species present pre-fire are also present post-fire in fire-prone environments.

Nevertheless fire can alter the vegetation, this not only where fire occurrences are rare events but also in the frequently burned savannas. Many findings have been published describing the relation between tree densities and fire frequency (Booysen and Tainton 1984, Walker 1985, Trollope *et al.* 1998), the effects of season of burning on species composition (Walker 1985, Frost *et al.* 1986) and the varying destructiveness of different fire intensities (Morgan 1999). Although the relative importance of fire frequency, intensity and season to the species composition and vegetation structure is still discussed, it is commonly accepted that for example annually burned sites are different to sites burned every ten years. Hence, effects of fire on vegetation also have to be considered in the long-term, by the so-called fire regime (Bond and Van Wilgen 1996).

The status of the fire as a natural phenomenon therefore has to be relativised: considering a single fire-event in general, it can always be seen as part of the ecology of the system, but putting this fire into a concrete broader context of a certain fire history, it can become a quite unusual or unnatural event. Therefore, especially for the assessment of the ecological consequences of fire, it is important not only to consider the immediate ecological settings at the fire-event, but additionally the ecological conditions during the previous years. However, to work with the pre-fire history of a site is a big and yet unsolved challenge, both in terms of assessing the fire-events for the past and in terms of handling the fire-occurrences. Fires happen, if not managed, chaotically and show no systematic reoccurring pattern (e.g. every second year in October) as managed systems do, and vary therefore highly in season, intensity and frequency. The combination of these factors, for the prevous decades, without knowing about the relative importance of each of the factors, leaves an unsolvable puzzle. More studies on the importance of these fire-regime parameters and their combinations should therefore be conducted to be finally able to describe the key factors of the fire history.

Detailed studies on the fire history of the previous decades for the 'Okavango Delta' study area using remote sensing techniques are in progress but not applicable yet. Before gathering these long-term fire data, a primary field study was carried out to investigate the immediate effects of fire on vegetation after single fire-events. The study is based on the above stated conclusion, that under a regular fire regime no significant species shifts occur after a single fire and that only changes in the regular fire regime will alter the vegetation. As fire-events in the Okavango Delta have been totally uncontrolled for decades, and no regular fire-regimes exist, shifts in species composition should be expected with every single fire-event. Thus, the main aim of this study is to prove the hypothesis that vegetation changes after single fire-events in the Okavango Delta.

The Okavango Delta in Botswana was chosen as a study site, because of rising anthropogenic pressures during the last decade and expected high changes in the spatial and temporal distribution of fires. The present study is part of an international research initiative on fire and ecological consequences for the Okavango Delta region, which should ultimately lead to a better understanding of ecological interactions between fire and vegetation and to new approaches in dealing with fire in this extraordinary valuable landscape.

Study area

The Okavango Delta is situated in north-western Botswana in southern Africa approximately between E22°–E24° and S18°–S20° (Figure 1). This vast wetland, protected by the RAMSAR convention, lies in the central Kalahari with a mean annual rainfall of about 490mm, which falls mainly during the rainy season from November to April (McCarthy *et al.* 2000).

The Okavango Delta is an alluvial fan with a very low gradient (app. 1:3 300 (McCarthy *et al.* 2000)) over the whole extension of roughly 20 000km², forming a widespread wetland composed of a pattern of channels, lakes, floodplains and slightly elevated dry islands. It is supplied by the Okavango River, with its catchment in central Angola, and enclosed by different geological fault-lines, which divide the Okavango Delta into two main parts: the northern 'Panhandle', confined by a north-westerly striking graben and the 'Fan', confined by south-westerly striking fault-lines, probably extensions of the Great Rift Valley (Scudder 1993). With the drop of the confining major fault-lines at the south-eastern end of the 'Panhandle', the water spreads out and forms the 'Fan' of the Okavango Delta. In this region, because of the missing confinement, the intensity of the flooding decreases to the distal reaches, where the perma-
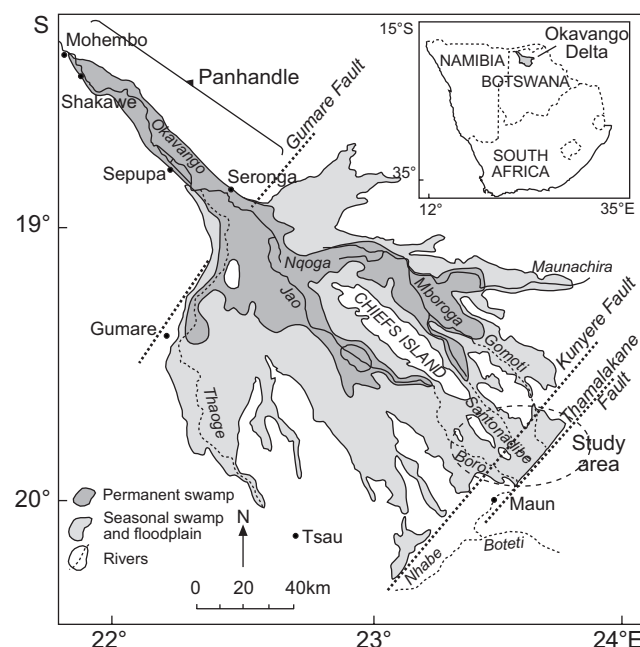

Figure 1: Location of the study area in the Okavango Delta (map according to Ellery and Tacheba 2003, modified)

nent swamps change to seasonal swamps and irregularly inundated floodplains. The water inflow into the Okavango Delta system through the Okavango River as well as the annual amount of rainfall shows typically high variations. As a consequence of these variable water amounts every year, there are strong annual shifts in the water distribution. Dry areas become inundated or swamps desiccate regularly as a part of this dynamic.

Fire-use in the Okavango Delta region

The Okavango Delta region, situated in the Kalahari, can be described as semi-arid savanna and is therefore fire-prone, as are most parts of southern Africa. Although the extensive flooding is the dominating ecological factor of the Okavango Delta that makes it incomparable to the typical savannas in southern Africa, fire is a common phenomenon for the Okavango Delta as for its surroundings. Most of these fires are man-made (Barbosa *et al.* 1999) and the majority of savanna fires are lit by people in the context of land clearing, livestock management and protection of property (Andersen *et al.* 1998). Discussions with local people and scientists confirmed these statements. So today almost all fires in the Okavango Delta region can be characterised as man-made.

The purposes for setting fires are quite varied, but they have not changed that much over the millennia. For thousands of years people have burned for cultivation, land clearing and to attract game to the palatable, nutritious flush after the burn (Booysen and Tainton 1984). Whereas the latter was used just for hunting in the past, nowadays game is also attracted for tourism and safari activities. Possibly because of this 'new source' of fire ignition, local scientists hypothesise that the number of fire occurrences in the Okavango Delta rose during the last decades. Although this could have grave ecological consequences for the whole region, no scientific research or administrative monitoring has been done on this topic yet. This paper therefore provides the first scientific insight into correlations between fire and vegetation for the Okavango Delta.

Materials and Methods

The present study aims to compare burned and unburned areas during the fire season 2000/2001, with respect to the effect of fire on vegetation diversity and the vegetation structure. As up to now no appropriate reports or data about fire occurrences in the Okavango Delta exist, LANDSAT 7 satellite images were used to map recent fire scars. Four images between August 2000 and February 2001 (09.08.2000, 25.08.2000, 10.09.2000 and 17.02.2001) were available to document the 2000/2001 fire season. Fire scars were detected manually by their colour and shape in combination with personal knowledge of burned areas by local researchers.

The study area was restricted to the south-eastern part of the Okavango Delta, consisting basically of seasonal floodplains and encompassing about 1 200km^2 (see Figure 1). This area was chosen because of regular fire occurrences, a relatively homogenous landscape and the accessibility of the study sites. Within this area 149 plots of 3m x 3m size

were selected arbitrarily, knowing that the plot either burned (n = 77) or did not burn (n = 72) during the preceding months. The co-ordinates of the plots can be made available on request. All plots were investigated between 15 March and 9 April 2001 at the end of the rainy season.

For each plot, all species were recorded. Each species was described in terms of coverage, phenology, plant type, life form, growth form, hairiness of the plant and leave characters. Phenology was classified in juvenile/sterile, fertile/in flower and ripe/with seeds. The plant type distinguishes grass, sedge, herb, shrub and tree, with trees per definition being woody species higher than 2m. Life form was noted following the classification by Raunkiaer (1934), distinguishing phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes. Growth form was described as reptant (creeping), caespitose (tufted) or scapose (single stemmed). Concerning the leaves, their form (entire or compound/lobed) and their size was described in three classes: small (<1cm^2), medium (1–25cm^2) and large (>25cm^2). Additionally presence or absence of waxes on the leaves and succulence was noted as well as the hairiness of the species, which was described in terms of presence or absence of clearly visible hairs.

Other parameters estimated at each plot were the mean height of the herb layer as well as the cover of living plants, of dry litter and of bare soil. Finally, within a sub-plot of 0.5m x 0.5m, the above ground living biomass was clipped at each plot. The biomass was dried for 48h at 80°C, weighed and calculated to gram per square metre (g m^{-2}). Grazing was assessed subjectively for each plot by looking for presence/absence of bitten-off culms.

Around each plot, a 50m x 50m quadrat was laid out to characterise the habitat in which the plot was located to allow a classification into broad habitat types. Within these quadrats only woody species taller than 0.5m were recorded and their cover was estimated.

For statistical analysis on correlations between the fire-event and the occurrence or failure of certain plant species, plant traits or site characteristics, bivariate analyses (Mann-Whitney test; U-test) using SPSS 11.0 were applied. Multivariate analyses (Detrended Correspondence Analysis (DCA)) using PC-ORD 4.0 was applied to find species assemblages related to the fire-event. For the determination of the habitat types cluster analyses were used.

Data Analyses and Results

As one of the main purposes of the present study was to find differences in species composition following a single fire-event, in a first step DCA analyses were used to measure the importance of the fire parameter for the species assemblage. For the analysis all 149 plots were included. The results show that the importance of the fire occurrence for the species composition regarding the whole data set of 149 plots is quite negligible. The first axis explains only 19.1% of the variance of the species data (see Figure 2 for r^2-values of the axis) and the maximum correlation of fire is with the third axis on a very low level of r^2 = 0.015.

The main factors determining the species assemblage derivable from the data are the cover of the herbaceous
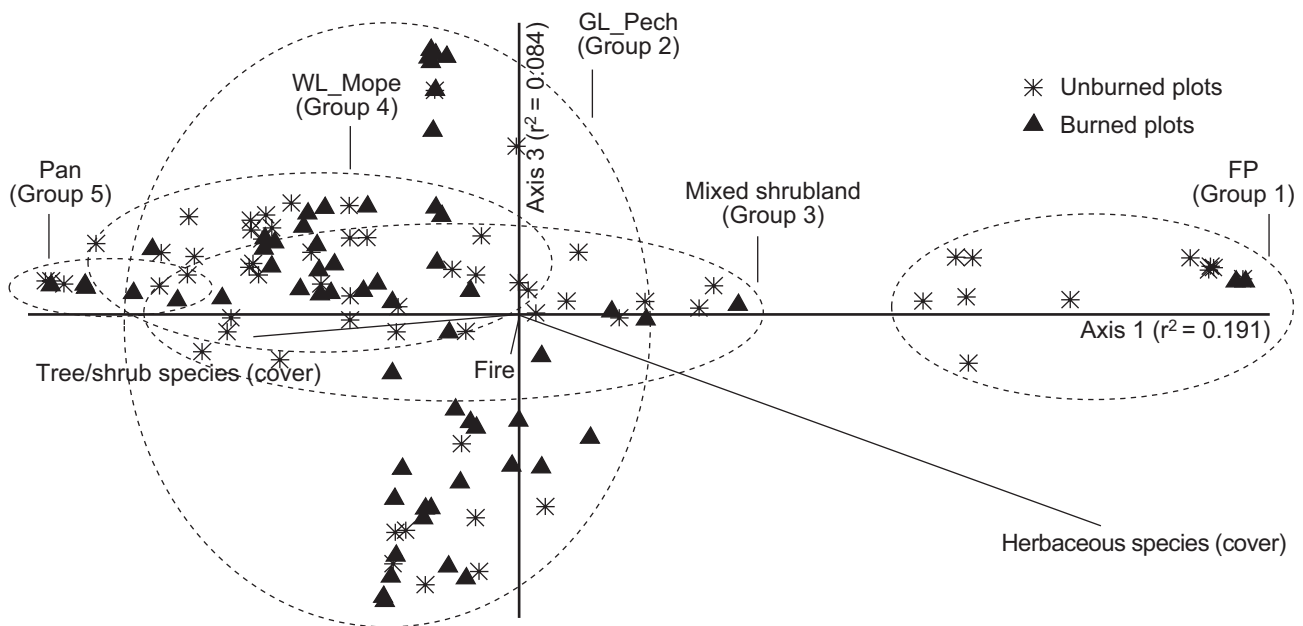
Figure 2: Graph plotted according to Detrended Correspondence Analyses (DCA) showing burned ($n_0 = 77$) and unburned ($n_1 = 72$) plots based on their similarities in species composition. The dotted ellipses summarise the plots grouped into one habitat type (see text for explanations and abbreviations). Note the clear separation of pans (Group 5) and floodplains (FP; Group 1) along the first axis

species (grasses, sedges and herbs) (correlation with first axis: $r^2 = 0.241$) and the cover of trees and shrubs ($r^2 = 0.109$). Although these parameters are not true 'environmental variables', they were included into the analysis because they indirectly reflect the time since the last flooding and the flood frequency. These parameters could not be considered directly because of missing data, but also could not be neglected because of the most likely superior ecological impact water has on the species distribution in the Okavango Delta. The two negatively correlated parameters as shown in Figure 2 reflect a flooding (moisture) gradient from active floodplains, with typically high cover of herbaceous species (mainly sedges) and no woody species to woodlands, with low cover of herbaceous species. Hence, along this gradient the whole data set can be split into several habitat types based on the cover of the woody species independently of the fire-event, as the cover of the woody species showed no correlation to fire (Figure 2).

For the cluster analysis (Relativized Euclidean Distance and Ward's Method as group linkage method) only cover values of the most dominant woody species of the study area were used, i.e. *Colophospermum mopane*, *Pechuel-loeschea leubnitziae* and *Acacia* species as well as a cumulative class for all other woody species. The cluster analysis split the data set into four groups (Table 1).

After the analysis, the treeless Group 0 was separated into two obviously different habitat types floodplains (Group 1) and pans (Group 5) because of their extremely different site conditions and species composition (cf. Figure 2).

Following the cluster analyses, the presence/absence of just two main plant species was found sufficient to describe the groups (habitat types) and their position along the described gradient: On the one hand *Colophospermum*

mopane (Mopane), typically the dominant tree species on arid sites in the vicinity of the Okavango Delta (Scholes 1997) unaffected by the flooding of the Okavango River, and on the other hand *Pechuel-loeschea leubnitziae*, a suffruticose *Asteraceae* showing pioneer character with high seed production and good resprouting capacities, and highly intolerant of flooding. It is therefore expected that a successional process on drying floodplains is roughly indicated by a reduced cover of sedges and first appearance of *Pechuel-loeschea leubnitziae*, followed by increasing *Colophospermum mopane*. Finally the derived habitats are therefore (see also Figure 2 and Table 1): (i) active floodplains (FP, n = 28), with no woody species, dominated by sedges or *Panicum repens* (Group 1), (ii) *Pechuel-loeschea* grasslands (GL_Pech, n = 61), with *Pechuel-loeschea leubnitziae* and no *Colophospermum mopane* trees and just single other woody species (Group 2), (iii) mixed shrublands with about similar covers of *Pechuel-loeschea leubnitziae* and *Colophospermum mopane* (Mop_Pech, n = 24), both having higher cover values than 5% (Group 3), (iv) Mopane woodlands (WL_Mop, n = 27), on sites unaffected by the flooding, with *Colophospermum mopane* as the dominating woody species with just single individuals of other woody species or *Pechuel-loeschea leubnitziae* (Group 4) and (v) pans (Pan, n = 9) with no woody species and in contrast to floodplains with totally different dominant species, e.g. *Sporobolus ioclados*, *Sporobolus spicatus* (Group 5).

This division of habitat types primarily based on the cover of woody species was also legitimated by further analyses of vegetation parameters (discussed in detail later, cf. Table 3). Significant differences for burned and unburned plots were found only for the cover of the herb layer (including grasses, sedges and herbs) while no differences were found for the

Table 1: Mean cover values and standard deviation (in brackets) for four groups after cluster analyses of the plots (using Relativized Euclidean Distance and Ward's Method as group linkage method). The analysis was based on the cover values of *Colophospermum mopane*, *Pechuel-loeschea leubnitziae*, *Acacia* species and a cumulative class for all other woody species

	Colophospermum mopane	*Pechuel-loeschea leubnitziae*	*Acacia* sp.	others
Group 0	0.0	0.0	0.0	0.0
Group 2	0.0	16.8 (±8.0)	0.9 (±1.5)	1.3 (±2.3)
Group 3	8.1 (± 2.4)	10.6 (±3.9)	0.1 (±0.3)	0.4 (±0.7)
Group 4	20.6 (±15.0)	0.3 (±0.7)	0.0	0.9 (±1.6)

cover of trees and shrubs. This indicates the independence of the tree cover on the fire-event. On the other hand, tree cover is most likely dependent on flooding and water fluctuations or long-term fire regimes. As these environmental parameters are not applicable but highly determine the habitat conditions and species composition, the tree cover was chosen to substitute these variables.

The DCA for the separate habitat types also showed no indications on fire determining the species composition. Thus, the Mann-Whitney-Test (U-test) was used to test the significance of differences in mean values for the measured plant attributes on burned and unburned plots on the bivariate level. Significant differences were found for sedges, grasses, perennial grasses, hemicryptophytes, hairiness of the plant and leaf size (Table 2). All remaining traits investigated (cf. Materials and Methods) showed no significant reaction to the fire disturbance. Significant differences between burned and unburned areas valid for all plots, were only found for hemicryptophytes favoured on unburned plots. All other responses were valid for certain habitat types only (Table 2).

Results on structural parameters of the vegetation, grazing evidence and biomass are presented in Table 3. Significant differences were found for height and cover of the herb layer (i.e. cover of grasses, herbs and woody species smaller than 0.5m), cover of the litter layer and bare soil. The evidence of grazing and biomass production also showed significant differences on burned and unburned plots. Interestingly, the median values calculated for all plots barely reflect the reaction of single habitat types, which show a variable and sometimes also contradictory response to fire dependent on the habitat. No significant differences were found in tree/shrub cover and height as already mentioned above, and in the mean number of species per plot.

Finally, species cover was analysed to detect certain species favoured or suppressed by the single fire-event (Table 4). Only eight species out of the 109 species recorded showed significant differences in cover on burned and unburned plots. Five of them showed significant differences not only for certain habitats but also for all plots. This could be interpreted as a general trend on how these species are affected by fire, independent of the habitat type. Nevertheless, *Sporobolus ioclados* showed different response to fire for the habitat types. Obvious dependence (P < 0.001) between the cover values and the fire-event was found for *Urochloa mosambicensis*, which seems to be highly favoured after the fire, especially on mixed shrublands (Mop_Pech) and on Mopane woodlands (WL_Mop).

Discussion

Many of the plant traits recorded and analysed have not been further described in the results. This is not only because of the missing significant difference of these attributes for burned and unburned plots, but also because during the survey several traits appeared less useful for further evaluation. For example phenology of the species varied widely during the three weeks period. Thus, the phenology could not reflect the effect of fire, as this was masked by the strong influence of the fast development of the plants. The hairiness of the plants showed high variability through the individuals of one species, not allowing a clear prediction on the species level. Leaf characteristics, e.g. a waxy surface or succulence, could not be considered because of a too rare occurrence for statistics.

As important, the division of the habitat types for analysing the effects of the fire-event on vegetation has to be stressed. The results vary widely dependent on the habitat and show partially contradictory development after fire, e.g. for grass cover on pans or on *Pechuel-loeschea* grasslands (GL_Pech) (Table 2). But before further interpretations on the traits can be done, the significant differences of certain plant traits related to fire have to be relativised. This is because all plant traits (Table 2) showed the same response to the fire-event as the general cover of the herb layer (Table 3), i.e. if a higher/lower cover of the herb layer was observed on, for example, unburned plots, the plant traits also seem to be favoured/suppressed on unburned plots. (The exception of the habitat type 'pan' will be discussed later.) This indicates that the higher values for certain plant traits are just because of the higher vegetation cover values on the plots. Therefore the significant differences between burned and unburned plots for certain traits are most likely not related directly to the fire-event itself, but only to different cover values after the fire-event. These traits are presumably, therefore, the ones that dominate the vegetation in general, independent of the fire-event both on burned and unburned plots. This was found looking at the example of hemicryptophytes, which account for 91.3% and 87.0% of the vegetation cover on unburned and burned plots, respectively, or grasses, which account for 92.4% and 97.2% of the vegetation cover on unburned and burned plots, respectively. Recognising this effect, the importance of the species groups or traits was calculated in relation to their relative cover values, i.e. instead of the plot size, the total vegetation cover within the plot was set to 100%. Using this relative value, for example, the significance of differences of hemicryptophytes on burned and unburned plots on flood-

Table 2: Median values for selected plant types, life forms and other plant traits on burned and unburned plots of the habitat types. See text for explanations on the abbreviations of the habitat types

	treatment	all plots n = 149 n_u = 72 n_b = 77	Pan n = 9 n_u = 3 n_b = 6	FP n = 28 n_u = 17 n_b = 11	GL_Pech n = 61 n_u = 25 n_b = 36	Mop_Pech n = 24 n_u = 12 n_b = 12	WL_Mop n = 27 n_u = 15 n_b = 12
sedges	unburned	ns	4.0*	ns	ns	ns	ns
(cover [%])	burned		0.0				
grasses	unburned	ns	38.0	ns	61.5*	ns	ns
(cover (%))	burned		66.5*		44.3		
perennial grasses	unburned	ns	ns.	ns	58.0**	ns	ns
(cover (%))	burned				41.8		
hemicryptophytes	unburned	57.8*	ns.	87.5***	60.5**	ns	ns
(cover (%))	burned	43.5		63.0	43.8		
plant hairy	unburned	ns	37.5	ns	58.0*	ns	ns
(cover (%))	burned		66.0*		42.0		
leaves <1cm²	unburned	ns	4.0*	ns	ns	ns	ns
(cover (%))	burned		0.0				
leaves 1–25cm²	unburned	ns	38.0	87.5**	ns	ns	ns
(cover (%))	burned		66.5*	63.0			

* indicates the significance of the difference of the values (* = P < 0.05, ** = P < 0.01, *** = P < 0.001)
ns = no significance
n = total number of plots investigated for each habitat, n_u = number of unburned plots, n_b = number of burned plots

Table 3: Median values for selected vegetation parameters on burned and unburned plots of the habitat types. See text for explanations on the abbreviations of the habitat types

	treatment	all plots n = 149 n_u = 72 n_b = 77	Pan n = 9 n_u = 3 n_b = 6	FP n = 28 n_u = 17 n_b = 11	GL_Pech n = 61 n_u = 25 n_b = 36	Mop_Pech n = 24 n_u = 12 n_b = 12	WL_Mop n = 27 n_u = 15 n_b = 12
herb layer	unburned	ns	63.3	80***	ns	80.0*	ns
(height (cm))	burned		66.7*	33.3		70.0	
herb layer	unburned	63.3*	33.3	63.3*	63.3**	51.7***	23.3
(cover (%))	burned	50.0	63.3*	66.7	50.0	46.7	31.7*
litter layer	unburned	8.1***	5.3*	40.0***	5.3***	ns	ns
(cover (%))	burned	1.0	0.2	1.0	0.8		
bare soil	unburned	33.3	66.7*	13.3	33.3	40.0	ns
(cover (%))	burned	50.0**	36.7	33.3***	46.7**	50.0***	
biomass	unburned	418.5**	262.7	858.3***	418.5**	ns	85.3
(g m⁻²)	burned	285.2	361.1*	307.4	324.1		157.3**
grazing	unburned	low	low	low	ns	ns	high*
evidence	burned	high**	high*	high***			low

* indicates the significance of the difference of the values (* = P < 0.05, ** = P < 0.01, *** = P < 0.001)
ns = no significance
n = total number of plots investigated for each habitat, (n_u) = number of unburned plots, (n_b) = number of burned plots

plains dropped from P = 0.001 to P = 0.796. To test these findings the general ratios between grasses and herbs and between annual and perennial species were analysed. No significant differences were found for both ratios analysed either for all plots or for each habitat type. All these analyses led finally to the assumption that none of the investigated plant traits was favoured or suppressed specifically by the fire-event. The plant traits present and characterising the burned plots seem to endure for longer periods and not to be directly dependent on single fire-events.

As indicated above, the habitat type 'pan' represents an exception, as the described parallels between the cover of the herb layer and the cover of the plant traits could not be found. Unfortunately this habitat type is only represented by nine plots and the contradictory results could also be because of statistical deficits. Nevertheless, the cover of the herb layer showed higher values on burned plots, which is already unusual for the data set, but which will be discussed later. Parallel to these values, grasses also showed significant higher cover values on burned plots (Table 2), following

Table 4: Mean cover values for selected plant species on burned and unburned plots of the habitat types. See text for explanations on the abbreviations of the habitat types

	treatment	all plots n = 149 n_u = 72 n_b = 77	Pan n = 9 n_u = 3 n_b = 6	FP n = 28 n_u = 17 n_b = 11	GL_Pech n = 61 n_u = 25 n_b = 36	Mop_Pech n = 24 n_u = 12 n_b = 12	WL_Mop n = 27 n_u = 15 n_b = 12
Aristida congesta ssp. *congesta*	unburned	0.6**	ns	ns	0.2*	ns	ns
	burned	0.0			0.0		
Dactyloctenium giganteum	unburned	1.1	ns	ns	3.2	ns	ns
	burned	2.6**			5.7*		
Pogonarthria squarrosa	unburned	0.6	ns	ns	ns	ns	1.1
	burned	3.0**					4.8*
Schoenoplectus rowlei	unburned	ns	ns	0.0	ns	ns	ns
	burned			0.6*			
Sporobolus africanus	unburned	0.1*	0.5*	ns	ns	ns	ns
	burned	0.0	0.0				
Sporobolus ioclados	unburned	ns	37.5	ns	8.2*	ns	ns
	burned		62.5*		1.4		
Tragus berterionanus	unburned	ns	ns	ns	ns	0.1	ns
	burned					0.7*	
Urochloa mosambicensis	unburned	5.3	ns	ns	ns	0.1	0.5
	burned	11.3***				17.7***	11.0***

* indicates the significance of the difference of the values (* = P < 0.05, ** = P < 0.01, *** = P < 0.001)
ns = no significance
n = total number of plots investigated for each habitat, (n_u) = number of unburned plots, (n_b) = number of burned plots

the same trend as described above. But in the case of this habitat type, the relative cover values for grasses also showed significant differences (P < 0.05) on burned and unburned plots, indicating a general trend not only to absolutely but also to relatively more grasses on the burned plots. On the other hand sedges showed both significantly higher absolute and relative cover values on unburned plots, even despite a lower herb layer cover on these plots. This implies that for the habitat type 'pan', sedges decline immediately after the fire-event and become replaced by grasses, while with time sedges recover and become more abundant relative to grasses. As no such phenomenon could be found for the other habitat types, one cannot expect or derive a general fire-sensitivity of sedges. This trend is probably highly dependent on the specific species found around the pans of the Okavango Delta.

The analysis of the species level led to a much higher variability in response to fire than was found for the traits. This is most likely because the level of detail of the regarded unit is in the case of species, much higher than that for the traits (e.g. just five categories for life form). So the observed dependence of the absolute cover values of the plant traits on the cover values of the herb layer was not repeated for the species cover values. This implies true responses of the species to the fire-event. However, the observed significant correlations presented in Table 4 have to be relativised. Many of the species show very low mean cover values. The mean cover values for *Aristida congesta* spp. *congesta*, *Schoenoplectus rowlei*, *Sporobolus africanus* and *Tragus berterionanus* were below 1% and those for *Dactyloctenium giganteum*, *Pogonarthria squarrosa* were around 5%. In combination with weak significance values (P < 0.05) a clear

trend for those species is not derivable. For *Sporobolus ioclados* clearly higher cover values could be recorded for pans on burned plots (Table 4). But the dependence of higher species cover values on higher total vegetation cover (described above) can be observed here as well. *Sporobolus ioclados* is the dominant plant species on pan depressions in the Okavango Delta and is most likely independent of the fire-event, as the relative cover values for *Sporobolus ioclados* are 87% on unburned and 91% on burned plots (P > 0.05). Similarly, for *Pechuel-loeschea* grasslands (GL_Pech), relative cover values showed no significant differences for *Sporobolus ioclados* on burned and unburned plots. The only obvious correlation between the fire-event and one single species was found for *Urochloa mosambicensis*. For all plots surveyed and for mixed shrublands (Mop_Pech) higher cover values of *Urochloa mosambicensis* were found on burned plots at a very high significance level (P < 0.001) even against the trend of higher vegetation cover on unburned plots for these habitat types. Although the higher cover of *Urochloa mosambicensis* on Mopane woodlands (WL_Mop) on burned plots could be related again to the higher vegetation cover after fire, this does not contradict the finding of *Urochloa mosambicensis* being favoured after a fire-event. A good recovery and dominance after fire was also reported for *Urochloa mosambicensis* for northern Australia (Falvey 1979, FAO nd). This perennial grass requires relatively high soil fertility on lighter soils and rainfall of more than 600mm a^{-1} over 3–4 months and is highly palatable. Under these conditions burning might therefore be a tool to provide good grazing grass, but besides more detailed studies on the positive correlation of *Urochloa mosambicensis* to fire, additional investigations on

side effects (e.g. overgrazing, species diversity) are necessary.

The investigations finally give the impression that almost no changes can be found on burned and unburned plots after single fire-events, comparing either all plots or just certain habitat types. Comparable results for fire or other kinds of regular disturbances are cited in the literature (Días *et al.* 1999, Lavorel *et al.* 1999, Morgan 1999). Nevertheless all these findings contradict common disturbance theories or succession models (e.g. Margalef 1968), which describe an initial colonisation of the post-disturbance environment, characterised basically by less competition, more light and higher nutrient availability (Bond and Van Wilgen 1996), thus by a few annual, fast growing species, with high seed production, that are then out-competed during the successional process. But, as differences on burned or unburned plots could not be found for the present studies, neither on species composition nor on herb/grass or annual/perennial ratios, this general successional pathway cannot be supported, despite finding the typical post-fire environment with a reduced litter layer, less vegetation cover and more bare soil on burned plots (Table 3). A theory for this missing linear succession after the fire-event has already been developed by Bond and Van Wilgen (1996). It describes a fire succession not dependent on a competitive hierarchy but on the timing of life-history events in relation to disturbance, indicating high species numbers after the fire and a successive elimination of species determined by the relative longevity of the species. The dominance of each species is therefore transitory as it ages and dies and re-establishes after the disturbance event. Following this argument, the missing differences on burned and unburned plots found for the present investigation would lead to the assumption that for the study area the inter-fire interval is very low, and allows all species to re-establish in short intervals.

Another explanation for the missing differences on burned and unburned plots could simply be the independence of the species establishment on the fire-event. As in fire-prone environments most species are adapted to the fire-event, one can assume that most perennial species manage to survive the fire, e.g. by protected growing points or resprouting. Annual species will most likely die-off but will not only find good conditions for regrowth immediately after the fire, but also during the inter-fire intervals as light and space are not limited in general for savannas. The low values for the vegetation cover of usually less than 60% support this theory (Table 3).

Despite the missing differences on burned and unburned plots related to plant traits and species composition, structural changes could be found highly dependent on the habitat type. This was already indicated above, since certain habitat types show higher herb layer cover values for burned plots and others for unburned plots (Table 3). The interesting phenomenon of the habitat types not showing the same response to fire can be explained along a rough productivity gradient of the habitats, described by the measured above ground living biomass on unburned plots. The gradient shown on Figure 3 ranges from highly productive, inundated active floodplains on organic rich soils (FP), to drying floodplains on loamy sands (Mop_Pech, GL_Pech), to pans and

Mopane woodlands (WL_Mop) on poor sands. With regard to the burned plots and the differences between the burned and unburned plots, a contrary development was observed. Biomass production increases against the productivity gradient, at least relative to the quantities of biomass on the unburned plots of the same habitat (see trend on Figure 3). The habitat types Pan and Mopane woodlands (WL_Mop) show even higher biomass values on burned than on unburned plots.

To explain these trends, the productivity of each habitat type has to be considered separately. The inundated floodplains (FP) experience a permanent nutrient and water supply throughout the dry-season, as flooding is most intense during the dry period for the Okavango Delta. With a fire, the biomass of a certain site is reduced almost to zero, while the unburned sites remain undisturbed. Due to the high productivity of the habitat, both on the burned and on the unburned plots, there is a steady parallel increase of biomass leaving significant differences between the two treatments shown in Figure 3.

The drying floodplains, i.e. mixed shrubland (Mop_Pech) and *Pechuel-loeschea* grassland (GL_Pech), in contrast experience the dry season without water supply and all herbs and grasses die off. After a fire that occurs during the dry season, similar conditions exist on burned as well as on unburned sites at the beginning of the rains. Pans and Mopane woodlands (WL_Mop), on sites with poor nutrient conditions, show a very low cover of the herb layer around 30% on unburned plots and significantly higher values for
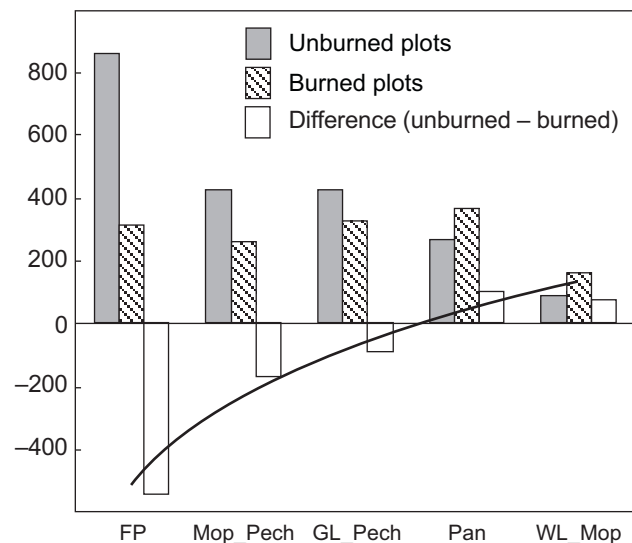

Figure 3: Median values for the above ground living biomass (g m^{-2}) on the five habitat types differentiated into burned and unburned plots. The trend, derived from the differences between the biomass on burned and unburned plots, shows the decline of the differences between burned and unburned plots and the change to more biomass on burned plots for pans and Mopane woodlands (WL_Mop). FP: active floodplains; Mop_Pech: mixed shrubland (*Colophospermum mopane*, *Pechuel-loeschea leubnitziae*); GL_Pech: *Pechuel-loeschea* grassland; WL_Mop: Mopane woodlands

burned plots (cf. Table 3). They probably experience a nutrient pulse after a fire that can lead in the short-term to a higher biomass production than on unburned sites. These nutrient pulses after a fire, also described by DeBano *et al.* (1998), probably happen in other habitat types too, but the improvement of the nutrient condition is most likely observable on the poorest sites. Long-term studies would be required to see how often these 'pulses' can be repeated before soil depletion takes place. In the context of variable response of fire for each of the habitat types, the evidence of grazing is also interesting to discuss (cf. Table 3). All habitat types without woody species, i.e. pans and floodplains (FP), were grazed after fire-events, while all unburned plots of these habitats remained ungrazed. In contrast, most of the plots (80%) with woody species, i.e. on *Pechuel-loeschea* grasslands (GL_Pech), mixed shrublands (Mop_Pech) and Mopane woodlands (WL_Mop), were ungrazed and this effect is obviously independent of the fire-event, as both grazed and ungrazed 'woody plots' were about equally affected by fire. Grazers probably avoid these 'woody areas' in general, as they do not provide open view and terrain to see and escape predators. In contrast, the open grasslands seem to be generally favoured by grazers and burned ones even more preferred, presumably due to the fresh young grasses growing immediately after the fire (Booysen and Tainton 1984, Bond and Van Wilgen 1996). This nutrient pulse after the fire is therefore most likely also the reason for the light grazing evidence in the open Mopane woodlands (WL_Mop) (cf. Table 3), where higher biomass production could be described after the fire.

Conclusion

After a single fire-event, the comparison of burned and unburned areas in the Okavango Delta region showed almost no differences in species composition and the cover of specific plant traits. However, differences were found in vegetation structure.

Interestingly, the defined habitat types varied considerably in their response to fire. In active floodplains (FP) with the highest observed biomass production and vegetation cover (Table 3), fire opens space in the dense stands with up to 100% vegetation cover, and most likely enhances the habitat and species diversity slightly due to the reduction of the dominance of a few highly competitive species, e.g. *Panicum repens.* Hence, fire on active floodplains should show high effects on vegetation through structural changes by biomass reduction (Figure 3) and should lead to a diversification of the vegetation. In contrast, for drying floodplains, i.e. *Pechuel-loeschea* grasslands (GL_Pech) and mixed shrublands (Mop_Pech), the effects of single fire-events seem to be weak, as vegetation tends to recover quickly after the fire, getting close to the pre-burn conditions (Figure 3). On pans and Mopane woodlands (WL_Mop) on poor sites with little cover of the herb layer, fires are followed by a short nutrient pulse, which enhances nutrient availability and productivity. These effects are most probably not repeatable in high intervals, as soil-nutrients are limited. Fire in Mopane woodlands (WL_Mop) and pans hence have clear effects on the herbaceous vegetation and should run on low frequencies to avoid soil-depletion.

The assessment of effects of single fire-events on vegetation could only give an insight into what happens immediately after the fire and most of the slight changes are not expected to be observable for the following vegetation period after the next drought. Long-term assessment of fires, i.e. working with the fire-regime of the area, would probably provide more detailed results and a better understanding of the ecological processes determining the vegetation of the Okavango Delta.

References

Andersen AN, Braithwaite RW, Cook GD, Corbett LK, Williams RJ, Douglas MM, Gill AM, Setterfield SA, Muller WJ (1998) Fire research for conservation management in tropical savannas: Introducing the Kapalga fire experiment. Australian Journal of Ecology **23**: 95–110

Arnold TH, De Wet, BC (1993) Plants of Southern Africa: Names and Distribution. Memoirs of the Botanical Survey of South Africa No. 62, Botanical Research Institute, Pretoria

Barbosa PM, Stroppiana D, Gregoire J-M, Pereira JMC (1999) An assessment of vegetation fire in Africa (1981–1991): Burned areas, burned biomass, and atmospheric emissions. Global Biogeochemical Cycles **13**: 933–950

Bond WJ (1997) Fire. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 421–446

Bond WJ, Van Wilgen BW (1996) Fire and Plants. Population and Community Biology Series 14. Chapman & Hall, London

Booysen PdV, Tainton NM (1984) Ecological Effects of Fire in South African Ecosystems. Ecological Studies 48. Springer-Verlag, Berlin

DeBano LF, Neary DG, Folliott PF (1998) Fire's Effects on Ecosystems. Wiley and Sons Inc., New York

Días S, Cabido M, Zak M, Martínez Carretero E, Araníbar J (1999) Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. Journal of Vegetation Science **10**: 651–660

Ellery WN, Tacheba B (2003) Floristic diversity of the Okavango Delta, Botswana. In: Alonso LE, Nordin LA (eds) A Rapid Biological Assessment of the Aquatic Ecosystems of the Okavango Delta, Botswana: High Water Survey. RAP Bulletin of Biological Assessment 27. Conservation International, Washington, DC, pp 69–96

Falvey L (1979) Establishment of two Stylosanthes species in a Urochloa mosambicensis-dominated sward in the Daly River basin. Journal of the Australian Institute of Agricultural Science **45**: 69–71

Food and Agriculture Organization (FAO) (nd) Grassland Index. http://www.fao.org/WAICENT/FAOINFO/AGRICULT/AGP6/agpc/doc/GBASE/data/pf000337.htm

Frost P, Medina E, Menaut J-C, Solbrig O, Swift M, Walker B (1986) Responses of savannas to stress and disturbance. Biology International, Special Issue 10

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology **88**: 213–229

Jeltsch F, Moloney K, Milton SJ (1999) Detecting process from snapshot pattern: Lessons from tree spacing in the southern Kalahari. Oikos **85**: 451–466

Lavorel S, McIntyre S, Grigulis K (1999) Plant response to distur-

bance in a Mediterranean grassland: How many functional groups? Journal of Vegetation Science **10**: 661–672

Margalef F (1968) Perspectives in Ecological Theory. University of Chicago Press, Chicago, Illinois

McCarthy TS, Cooper GRJ, Tyson RD, Ellery WN (2000) Seasonal flooding in the Okavango Delta, Botswana — recent history and future prospects. South African Journal of Science **96**: 25–32

Morgan JW (1999) Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology **144**: 127–144

Raunkiaer C (1934) The Life Forms of Plants. Oxford University Press, Oxford

San Jose JJ, Montes RA (1997) Fire effect on the coexistence of trees and grasses in savannas and the resulting outcome on organic matter budget. Interciencia **22**: 289–298

Scholes RJ (1997) Savanna. In: Cowling RM, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 258–277

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**: 517–544

Scudder T (1993) The World Conservation Union (IUCN) Review of the Southern Okavango Integrated Water Development Project. IUCN, Gland

Trollope WSW, Trollope LA, Biggs HC, Pienaar D, Potgieter ALF (1998) Long-term changes in the woody vegetation of the Kruger National Park, with special reference to the effects of elephants and fire. Koedoe **41**: 103–112

Walker BH (1985) Determinants of Tropical Savannas. IRL Press Limited, Oxford