The relevance of fire frequency for the floodplain vegetation of the Okavango Delta, Botswana

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Abstract

The study investigates the relevance of fire frequency for the floodplain vegetation of the Okavango Delta in Botswana, considering species composition, species richness, vegetation structure and tree density. Based on flood and fire frequency data derived from a series of satellite images, active and drying floodplains were separated and study plots were selected with fire frequencies up to ten burns between 1989 and 2003. Both for drying and active floodplains, no typical species assemblage could be associated with fire frequency. On drying floodplains, fire frequency showed no effect on species composition, but rather on vegetation structure. While small woody species showed higher cover values on high fire frequency, large trees showed significantly lower cover values on high fire frequency. For active floodplains, a significant response to fire frequency, both positively and negatively could be determined for specific species. But as almost none of these species appear at low or high frequency only, no differences in species composition could be associated with fire frequency. Rather flood frequency and specific annual flood cycles could be described as the determining factors for the vegetation on active floodplains.

Key words: fire ecology, plant diversity, savanna, southern Africa, vegetation structure, wetland

Résumé

Cette étude a analysé la pertinence de la fréquence des feux dans la végétation de la plaine inondable du Delta de l'Okavango, au Botswana, compte tenu de la composition des espèces, de leur richesse, de la structure de la végétation et de la densité des arbres. En se basant sur les données concernant les inondations et les feux dérivées d'une série d'images satellite, on a séparé les plaines inondables actives et desséchées et on a sélectionnés des plots d'étude avec des fréquences de feux allant jusqu'à dix entre 1989 et 2003. Que ce soit pour les plaines inondables actives ou pour celles qui se desséchaient, aucun assemblage d'espèces ne pouvait être associé à une fréquence de feux. Dans les plaines desséchées, la fréquence des feux n'a révélé aucun effet sur la composition des espèces mais plutôt sur la structure de la végétation. Alors qu'en cas de feux fréquents, les petites espèces ligneuses présentaient des valeurs de couverture supérieures en cas de feux fréquents, les grands arbres présentaient des valeurs de couverture significativement plus basses. Pour les plaines inondables actives, on a pu déterminer une réponse significative, positive ou négative, de la part d'espèces spécifiques. Mais presque aucune de ces espèces n'apparaît à faible ou forte fréquence de feux uniquement, et on n'a pu lier aucune différence de la composition des espèces à la fréquence des feux. Ce sont plutôt la fréquence des inondations et les cycles d'inondation annuels spécifiques qui seraient les facteurs déterminants de la végétation des plaines inondables.

Introduction

Vegetation fires are considered natural phenomena in many parts of the world and are shaping the landscape for millennia across entire continents (Bond & Van Wilgen, 1996). Fire is hence an important determinant of plant diversity and vegetation structure in regions where it occurs (Bond, 1997; DeBano, Neary & Folliott, 1998). As anthropogenic burning has become predominant (Frost & Robertson, 1985; DeBano *et al.*, 1998), the ecological impact of certain fire regimes is the subject of intense

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discussions. Nevertheless, relatively few studies try to identify the effects of certain fire regimes on vegetation (e.g. Russell-Smith *et al.*, 1998; Uys, Bond & Everson, 2004; Watson & Wardell-Johnson, 2004) and many of these studies show conflicting results because of the variety of the investigated vegetation types and fire regimes. Therefore, given the interaction between people, fire and vegetation in most parts of the world, studies considering local fire regimes on certain vegetation types are required to fully understand the ecological implications of a specific burning regime (Bond & Van Wilgen, 1996; Uys *et al.*, 2004).

The focus of the present study is on the relevance of fire frequency for the floodplain vegetation of the southern Okavango Delta wetland in Botswana in southern Africa. Recent studies of grasslands in southern Africa and Australia have shown only minor effects of fire frequency on species composition because of the general dominance of fire-tolerant species and the loss of disturbance-intolerant species in the flora (Morgan, 1999; Uys *et al.*, 2004). Although this trend towards disturbance-adapted vegetation might also be expected for the fire-prone floodplains of the Okavango Delta, studies on the vulnerability of wetland vegetation to fire are sparse, as the issue of fire in wetlands has been widely ignored so far.

The generally accepted trend of the structural response of vegetation to fire frequency is that the more frequent the fire, the greater the herbaceous component, and the less frequent the fire, the more abundant the woody component (Booysen & Tainton, 1984). The suppression of woody species by high fire frequency is described as the 'Gulliver effect' (Bond & Van Wilgen, 1996; Higgins, Bond & Trollope, 2000), with Gullivers being stunted multi-stemmed shrubs, which could come to dominance as adults but struggle to emerge from the herbaceous layer as juveniles because of regular fire events in this layer. However, high fire frequency can also reduce the mortality of large trees because of lower fire intensity and therefore flame heights, because of lower amounts of accumulated fuel loads (Trollope, 1980). According to these models, high fire frequency lead to the occurrence of many small shrubs and few large and intermediate-sized trees above the flame height.

Material and methods

Study area

The Okavango Delta in north-western Botswana, southern Africa, is a vast tropical wetland located in the centre of
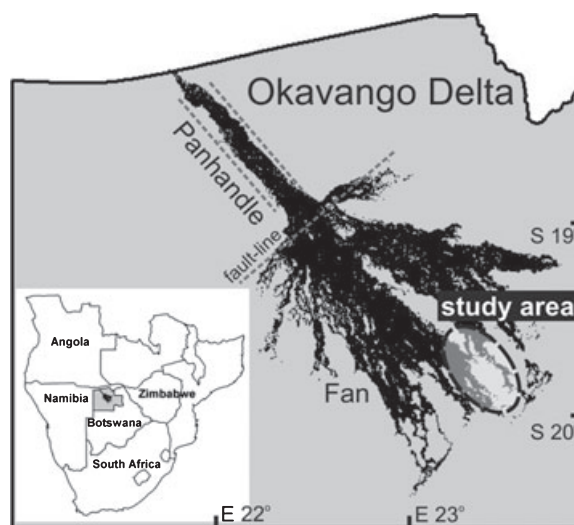

Fig 1 Location of the study area in the southern floodplains of the Okavango Delta wetland in northern Botswana

the Kalahari region. The wetlands of the world's largest RAMSAR site are supplied by the Okavango River, which has its catchment in the highlands of Angola. They form a mosaic of temporal, seasonal and permanent wetland habitats and drylands over an area of approximately 15,000 km^2. The Okavango Delta is an alluvial fan with a very low gradient of roughly 1:3300 (McCarthy *et al.*, 2000) divided by geological fault lines into the northern Panhandle and the unconfined Fan in the south-east (Fig. 1). The Panhandle region can be described as a permanent swamp, bounded by south-easterly striking fault lines, with water supply throughout the year. It is characterized by extensive mono-dominant *Cyperus papyrus* L. stands. With the drop of the confining fault lines, the water of the Okavango River spreads and forms the Fan of the Okavango Delta. Because of the missing confinement, the intensity of the flooding decreases to the distal reaches, so that the permanent swamps are replaced by seasonal swamps and floodplains.

The extent and duration of the flooding in the Okavango Delta show typically strong fluctuations. These fluctuations are caused by the irregular amount of inflow through the Okavango River into the Okavango Delta (approximately 10^{10} m^3 mean annual inflow), which is caused by the highly variable rainfall pattern both in the catchment of the Okavango River and over the Okavango Delta. The periodic summer rainfall occurs typically from October to April, with approximately 490 mm mean annual rainfall

over the Okavango Delta (McCarthy *et al.*, 2000). The consequence of these fluctuations in water supply is a small-scale pattern of temporal habitats and associated vegetation types, which are highly dependent on the flooding regime.

An extensive ecological zoning based on the flooding pattern of the Okavango Delta was done by SMEC (1989). According to the classification of this study, the focus area in the southern floodplains of the Okavango Delta is comprised of floodplains characterized by 'being subject to inundation on a seasonal basis in some years, but not in most years or only during higher floods'. These floodplains are basically dominated by grasses, with some sedges and occasional woody species, but the specific species composition is highly dependent on the flooding regime inside the floodplain category. Wetter sections of the floodplains, which are subject to longer and deeper floods are dominated by the tall sedges *Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J. Raynal and *Cyperus articulatus* L., and the grasses *Oryza longistaminata* A. Chev. & Roehr and *Leersia hexandra* Swartz on the floodplain fringes (Bonyongo, Bredenkamp & Veenendaal, 2000). The occurrence of *Panicum repens* L. or *Setaria sphacellata* (Schumach.) Moss indicates lower flood intensities, and dry floodplain fringes are typically dominated by *Cynodon dactylon* (L.) Pers. Occasionally flooded or drying floodplains with single woody species [e.g. *Acacia tortilis* (Forssk.) Hayne, *Combretum imberbe* Wawra, *Pechuel-loeschea leubnitziae* (Kuntze) O. Hoffm.] are usually dominated by *Urochloa* sp., *Eragrostis* sp. or *Aristida* sp. (Ellery & Ellery, 1997). The predominant soils in this region are bright, well-drained sands or loamy sands (Haplic Arenosols) and dark greyish brown, poorly drained sandy loams or clays (Eutric Gleysols) (De Wit & Nachtergaele, 1990).

All these floodplains are subject to inundation on a seasonal basis and therefore also experience periods when they are dry and not inundated. These are the periods when the floodplains are most susceptible to fire. Recent studies showed a high correlation between flood frequency and fire frequency: Floodplains that get inundated about every second year show the highest fire frequency and a mean fire return interval of about 5 years. Both drier and wetter sections of the floodplains showed mean fire return intervals of about 7–8 years (Heinl *et al.*, 2006).

Nowadays, most of the fires in the Okavango Delta have an anthropogenic origin (Cassidy, 2003; Heinl *et al.*, 2007). The reasons for burning are various, and include land clearing for cultivation, stimulating grass growth for grazing animals, hunting or to improve access to fishing grounds. Accidental fires may for example be caused by camp fires or fish-smoking. As these fires spread uncontrolled over the floodplains, they usually extend over many square kilometres.

Selection of study sites

The selection of specific study sites was based on the evaluation of a series of 98 Landsat satellite images from 1989 to 2003 (Heinl *et al.*, 2007). Burned and flooded areas were extracted from a 40-class unsupervised classification (ISODATA) of the georeferenced satellite images. Three bands, representing the mid-, near- and thermal infrared wavelengths (Landsat TM bands 4, 7 and 6, respectively) were included into the classifier, as they showed the best results in preliminary assessments. The image analyses provided data on fire occurrences and inundated areas for the southern floodplains of the Okavango Delta, which were then used to identify target study areas based on their fire and flood history in a geographic information system (GIS).

As the focus of the present research was on fire frequency and floodplain vegetation, areas with a specific fire frequency needed to be determined and floodplains needed to be specified. For the present study, all areas that were recorded as flooded at least once during the investigated period from 1989 to 2003 were considered as floodplains. This definition is in line with SMEC (1989), characterizing floodplains as subject to inundation on a seasonal basis or only during higher floods. However, the category still consists of a variety of habitats dependent on a flood frequency gradient, and includes almost permanently inundated regions as well as areas that were not flooded for more than 10 years. In order to consider this gradient and to differentiate clear habitats for the investigation, study sites were only selected for drying and active floodplains. Drying floodplains were defined for this study as not inundated for more than 10 years, while active floodplains were defined as flooded at least every second year. For the selection of specific study sites inside these floodplain categories, additionally both the time elapsed since the last flood and since the last fire event was considered. This led to the identification of comparable study sites and allowed to assign differences in the vegetation more clearly to fire frequency.

Finally, based on these criteria, the specific study sites on drying floodplains were limited to regions which were

not inundated for more than 10 years (since 2003), but flooded at least once between 1989 and 1992 (drying floodplains), and were burned in 2000, but not after 2000. In contrast, the study sites on active floodplains were limited to regions which were recorded as flooded at least every second year (active floodplains) and flooded and burned in 2003, but not after 2003. Specific threshold values (years) for the criteria were needed to establish a set of study sites with exactly the same flood history and time since the last fire event for each floodplain type, while covering a wide range of fire frequencies. Both the sites on drying and on active floodplains include areas with fire frequencies from 0 to 10 burns between 1989 and 2003. For comparative vegetation analyses, the fire frequency was grouped into low, mid- and high fire frequency (0–2, 3–5 and 6–10 burns between 1989 and 2003, respectively).

Sampling methods and analyses

The vegetation survey was performed in February 2004. A total number of 169 study sites were selected based on the criteria mentioned above and on accessibility, and were located by global positioning system (GPS). For active floodplains, 95 sites were investigated, of which 46 sites represented low fire frequency, 16 mid-fire frequency and 33 high fire frequency. On drying floodplains, 74 sites were investigated, of which 25 sites represented low, 24 mid- and 25 high fire frequency.

On each 10 m × 20 m site, cover and abundance were measured for each woody species as well as for three height classes: tree layer S (all woody species <1.5 m), tree layer M (1.5 m–3.0 m), tree layer L (>3.0 m). In one corner of each site, a quadratic 4-m^2 study plot was investigated, for which species and cover values after Londo (1984) were recorded. Above-ground living and dead biomass were sampled on 50 × 50 cm subplots and weight after drying for 48 h at 80°C. (Nomenclature of plant species is after Germishuizen & Meyer 2003; see Table 1 for the authority of the scientific plant names).

Statistical analyses were performed using PC-ORD 4.26, SPSS 12.0 and the statistical software R. The nonparametric Mann–Whitney test (U-test) was used for assessing the significance of differences in the investigated parameters (e.g. species number) for high and low fire frequency. In case of correlation between fire and flood frequency, those significant parameters were additionally tested by generalized linear models (GLM) with Poisson errors to determine whether fire or flood frequency explains more

variance in the data. The selection of study sites on active and drying floodplains was based solely on flood and fire frequency data derived from satellite images. The utility of this *a priori* approach was tested by using detrended correspondence analysis (DCA).

Results

Species assemblage

Detrended correspondence analysis of the data showed a clear separation of the plots on active and drying floodplains according to the species cover values (Fig. 2). The investigated plots were grouped along a flood frequency gradient (first axis) with no overlap. Compared with flooding, fire frequency played a marginal role in the species assemblage.

Further DCA were carried out separately for drying and active floodplains to investigate the relevance of fire and flood frequency for species assemblage. For drying floodplains neither the flood frequency nor the fire frequency showed a significant effect on species assemblage (Fig. 3). The gradient that is represented by the species grouped along the first axis is therefore difficult to assess, especially without further secondary environmental variables. But information from literature on the ecology of the species (Gibbs-Russell *et al.*, 1990; Oudtshoorn, 1999; RBG Kew, 2004) indicates that most likely soil texture and soil moisture are responsible for the species assemblage, with *Eragrostis rigidior*, *P. repens* or *Cyperus esculentus* repre-
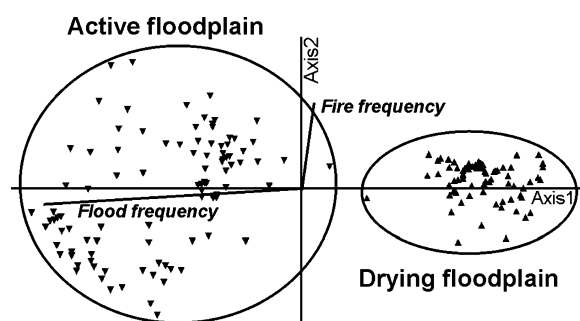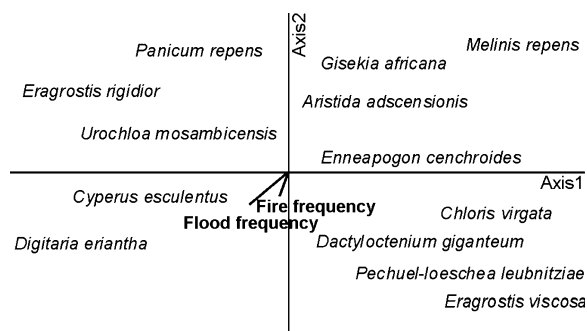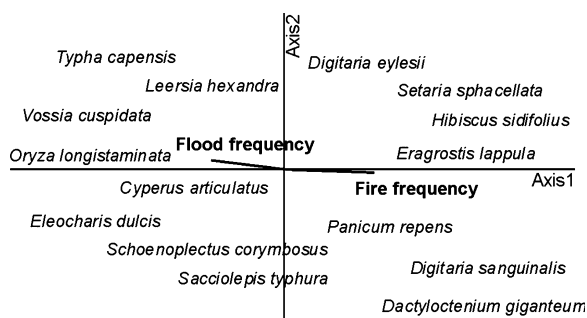

Fig 2 Detrended correspondence analysis (DCA-biplot) of the investigated study plots on active and drying floodplains. The flood frequency shows a high correlation with the first axis ($r^2 = 0.902$), with the first axis explaining 42.0% of the variance in the data. Fire frequency shows only a weak correlation to the second axis ($r^2 = 0.215$), with the second axis explaining only 4.4% of the variance in the data

Fig 3 Detrended correspondence analysis (DCA-biplot) showing selected species on drying floodplains. The flood frequency and the fire frequency show a very low correlation with the axes ($r^2 = 0.085$ and $r^2 = 0.067$, respectively), with the first axis explaining 41.8% and the second axis 12.0% of the variance in the data

senting species on moist, loamy sites (left side on Fig. 3), and *Chloris virgata*, *Melinis repens* or *Eragrostis viscosa* representing species on dry sandy soils (right side on Fig. 3).

On active floodplains, the species were grouped both along a flood frequency and fire frequency gradient on the first axis (Fig. 4). The negative correlation found between fire frequency and flood frequency on active floodplains, which is due to fire suppression by the flooding, has already been documented in previous studies (Heinl *et al.*, 2007). The effects of fire frequency on the species assemblage on active floodplains can therefore not clearly be separated from the effects of flood frequency. But when analysing the species representing this gradient and their

Fig 4 Detrended correspondence analysis (DCA-biplot) showing selected species on active floodplains. The flood frequency and the fire frequency show a slight correlation with the first axis ($r^2 = 0.282$ and $r^2 = 0.341$, respectively), with the first axis explaining 50.4% and the second axis 10.5% of the variance in the data

ecology, an obvious separation of species from drier and wetter habitats can be determined, with for example *Typha capensis*, *Vossia cuspidata* or *O. longistaminata* representing the wet wing (left side on Fig. 4), and *Eragrostis lehmanniana*, *Hibiscus sidifolius* or *Dactyloctenium giganteum* representing the dry wing (right side on Fig. 4). The species assemblage on active floodplains is therefore obviously determined by the flood frequency, while the fire frequency is in principle simply negatively correlated to the flood frequency.

Species composition

Within the investigated plots, a total number of 112 plant species were recorded, of which 82 could be identified. On drying floodplains 50 species were recorded, while on active floodplains 79 species were encountered. The active floodplains therefore showed higher plant species numbers than drying floodplains; however, more sample plots were considered for active (95) compared with drying floodplains (74). The mean number of species was 7.5 and 6.9 for active and drying floodplains, respectively.

The species composition on drying floodplains differed clearly from the one on active floodplains. Differentiator scores were calculated to show the principle occurrence of the plant species on the floodplain habitats (Table 1). Almost all species could clearly be assigned either to drying or to active floodplains.

The statistical analyses on species cover in relation to fire frequency revealed a significant response to the burning for individual species (Table 1). As for active floodplains a negative correlation between fire and flood frequency was encountered, these significant differences in species cover could not be clearly assigned to fire frequency. GLM analyses, however, indicate for *C. articulatus* and *Eclipta prostrata*, a significant negative response to high fire frequency and for *Cyperus denudatus*, *Eragrostis lappula* and *S. sphacellata*, a significant positive response to high fire frequency. For drying floodplains *C. dactylon* showed significantly lower cover values on high fire frequency (Table 1).

Vegetation structure

On active floodplains, only the structural response of the herbaceous layer was investigated, as no woody species occurred because of frequent flood events. The active floodplains showed, for low fire frequency, significantly

Table 1 Identified species and their frequency (number of records) on drying floodplains (FPd) and active floodplains (FPa)

Species	FPd	FPa	DS	RESP
Schoenoplectus corymbosus (Roem. & Schult.) J.Raynal	0	68	−68	n.s.
Eragrostis lappula Nees[F]	0	51	−51	+***
Panicum repens L.[W]	7	55	−48	+***
Cyperus articulatus L.[F]	0	45	−45	−***
Leersia hexandra Swartz[W]	0	45	−45	−***
Cyperus denudatus L.f.[F]	0	42	−42	+***
Setaria sphacellata (Schumach.) Moss[F]	0	33	−33	+***
Sacciolepis typhura (Stapf) Stapf	0	29	−29	n.s.
Oryza longistaminata A.Chev. & Roehr[W]	0	26	−26	−***
Acroceras macrum Stapf	0	25	−25	n.s.
Eleocharis dulcis (Burm. f.) Henschel[W]	0	23	−23	−***
Oldenlandia corymbosa L.[F]	0	21	−21	−**
Rhynchospora holoschoenoides (Rich.) Herter	0	19	−19	n.s.
Eclipta prostrata (L.) L.[F]	0	18	−18	−***
Ludwigia stolonifera (Guill. & Perr.) Raven[W]	0	18	−18	−***
Fimbristylis complanata (Retz.) Link	0	16	−16	n.s.
Miscanthus junceus (Stapf) Pilg.	0	12	−12	n.s.
Alternanthera sessilis (L.) DC.[W]	0	11	−11	−**
Kyllinga erecta Schumach.[F]	0	9	−9	−*
Digitaria eylesii C.E.Hubb.	0	8	−8	n.s.
Echinochloa jubata Stapf	0	8	−8	n.s.
Sphaeranthus flexuosus O.Hoffm. ex de Wild	0	6	−6	n.s.
Paspalum scrobiculatum L.[W]	0	5	−5	+*
Persicaria limbata (Meisn.) Hara	0	5	−5	n.s.
Potamogeton thunbergii Cham. & Schltdl.	0	5	−5	n.s.
Sida cordifolia L.	0	5	−5	n.s.
Sopubia mannii Skan[F]	0	5	−5	+*
Crotalaria sp.	1	5	−4	n.s.
Nymphoides indica (L.) Kuntze	0	4	−4	n.s.
Crotalaria sphaerocarpa Perr. ex DC.	0	3	−3	n.s.
Cyperus esculentus L.	2	5	−3	n.s.
Hibiscus sidiformis Baill.	0	3	−3	n.s.
Amaranthus thunbergii Moq.	0	2	−2	n.s.
Cyperus longus L.	0	2	−2	n.s.
Digitaria sanguinalis (L.) Scop.	0	2	−2	n.s.
Echinochloa stagnina (Retz.) Beauv.	0	2	−2	n.s.
Fuirena stricta Steud.	0	2	−2	n.s.
Heliotropium ovalifolium Forssk.	0	2	−2	n.s.

Table 1 (Continued)

Species	FPd	FPa	DS	RESP
Ludwigia leptocarpa (Nutt.) Hara	0	2	−2	n.s.
Typha capensis (Rohrb.) N.E.Br.	0	2	−2	n.s.
Cycnium tubulosum (L.f.) Engl.	0	2	−2	n.s.
Eragrostis lehmanniana Nees	0	1	−1	n.s.
Evolvulus alsanoides (L.) L.	0	1	−1	n.s.
Fuirena pubescens (Poir.) Kunth	0	1	−1	n.s.
Gomphocarpus fruticosus (L.) Aiton	0	1	−1	n.s.
Sesbania microphylla Phill. & Hutch.	0	1	−1	n.s.
Sesbania sesban (L.) Merr.	0	1	−1	n.s.
Tephrosia sp.	0	1	−1	n.s.
Vossia cuspidata (Roxb.) Griff.	0	1	−1	n.s.
Acacia erioloba E.Mey.	1	1	0	n.s.
Eragrostis viscosa (Retz.) Trin.	1	0	1	n.s.
Lonchocarpus capassa Rolfe	1	0	1	n.s.
Nidorella residifolia DC.	2	1	1	n.s.
Schmidtia pappophoroides Steud.	1	0	1	n.s.
Colophospermum mopane (Kirk ex Benth.) Kirk ex Leonard	3	1	2	n.s.
Digitaria eriantha Steud.	15	13	2	−*
Pogonarthria squarrosa (Roem.& Schult.) Pilg.	2	0	2	n.s.
Sesamum triphyllum Welw. ex Asch.	3	1	2	n.s.
Combretum imberbe Wawra	3	0	3	n.s.
Dactyloctenium aegyptium (L.) Willd.	3	0	3	n.s.
Eragrostis cilianensis (All.) Vignolo ex Janch.	3	0	3	n.s.
Cenchrus ciliaris L.	4	0	4	n.s.
Hibiscus calyphyllos Cav.	5	0	5	n.s.
Aristida adscensionis L.	7	0	7	n.s.
Aristida stipitata Hack.	7	0	7	n.s.
Ipomea coptica (L.) Roth. ex Roem. & Schult.	8	1	7	+*
Corchorus trilocularis L.	16	7	9	n.s.
Eragrostis rigidior Pilg.	9	0	9	n.s.
Eragrostis trichophora Coss. & Durieu	10	0	10	n.s.
Aristida stipoides Lam.	13	0	13	n.s.
Cynodon dactylon (L.) Pers.	16	1	15	−***
Dactyloctenium giganteum Fischer & Schweick.	17	1	16	+*
Indigofera sp.	20	2	18	n.s.
Stipagrostis uniplumis (Licht) De Winter	18	0	18	n.s.
Pechuel-loeschea leubnitziae (Kuntze) O. Hoffm.	19	0	19	n.s.
Melinis repens (Willd.) Zizka	25	0	25	n.s.
Chloris virgata Swartz	27	0	27	n.s.
Vernonia glabra (Steetz) Vatke	31	2	29	n.s.
Enneapogon cenchroides (Roem. & Schult.) Hubb.	30	0	30	n.s.

Table 1 (Continued)

Species	FPd	FPa	DS	RESP
Gisekia africana (Lour.) Kuntze	33	1	32	+*
Tragus berteronianus Schult.	57	1	56	n.s.
Urochloa mosambicensis (Hack.) Dandy	66	1	65	n.s.

Species are sorted by differentiator scores (DS), which are calculated as the difference of FPa and FPd. Negative DS indicate a general occurrence on active floodplains, positive DS indicate the occurrence on drying floodplains.

The response to high fire frequency (RESP) is indicated as positive (+) or negative (−) with significance levels (*U*-test: *$P < 0.05$; **$P < 0.005$; ***$P < 0.001$; n.s., not significant).

The superscript letter indicates fire frequency (F) or flood frequency (W) as the determining environmental parameter for the species cover on active floodplains after generalized linear models (GLM).

higher mean cover values of the herbaceous vegetation and also higher above-ground biomass values, both for living and dead material. However, fire frequency and flood frequency are negatively correlated, and GLM analyses revealed that the higher cover and biomass values are again rather due to high flood frequency than to low fire frequency.

On drying floodplains, significant response of the vegetation structure to fire frequency was found for woody species. At high fire frequency a significantly lower number of woody species were found, as well as lower cover and abundance values for large trees (tree layer L). Cover values of *C. imberbe* also showed a significant negative response to high fire frequency. The data therefore imply a negative impact of high fire frequency on the occurrence of larger trees on drying floodplains.

Discussion

The relevance of fire frequency for the vegetation of drying floodplains

Detrended correspondence analysis of the study plots on drying floodplains based on the species cover indicated neither a flood nor a fire frequency gradient in the data (cf. Fig. 3). Hence, no significant effect of fire frequency on the species assemblage could be derived. The overall missing effect of fire frequency on species cover on drying floodplains is most likely due to their adaptation to frequent fires as typical savanna species.

The main response of drying floodplains to fire frequency was found for cover and abundance of woody species. Generally, the abundance of woody species shows high tree mortality for all fire frequency classes (Fig. 5). Large trees (tree layer L) account for only about one-tenth of the abundance of small trees (tree layer S), independent of fire frequency.

In contrast to the almost parallel decline of the abundance of woody species with size through all fire frequency classes, the cover values differ clearly between high fire
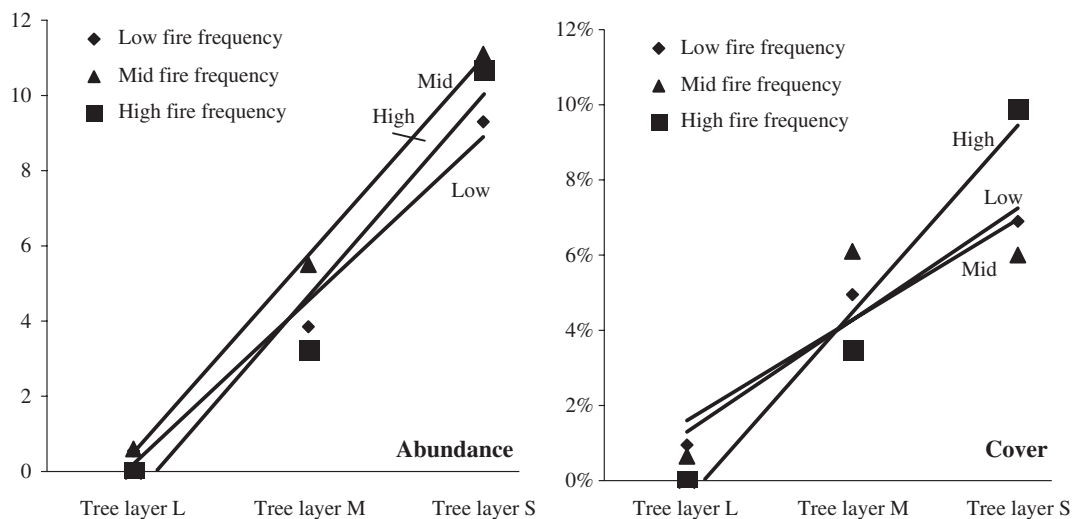
Fig 5 Mean abundance and cover values of the investigated tree layers S (small), M (medium) and L (large) for low, mid- and high fire frequency

frequency and the other fire frequency classes (Fig. 5). For small trees (tree layer S) higher cover values are observed at high fire frequency compared with mid- and low fire frequency. As abundance values are almost similar through all fire frequency classes, small woody species at high fire frequency tend to have higher cover values per individual than at other fire frequency. This wider growth of small woody species at high fire frequency is most likely due to lateral, basal regrowth after frequent disturbance events like fire. The ability of basal resprouting can be observed frequently in the study area, in particular for *Colophospermum mopane* and *P. leubnitziae*, the most common woody species in the study area.

In contrast to small woody species, larger trees (tree layer L) show comparatively low cover values at high fire frequency (Fig. 5). In combination with the low abundance values for larger trees at high fire frequency, an overall negative impact of high fire frequency on large trees is indicated. However, it is suggested that high fire frequency is not responsible for killing large trees, as flame heights of a burning grass layer are usually too small, but rather suppresses the recruitment of small individuals to the canopy layer.

These findings are very much in line with the phenomenon described as the Gulliver effect (Bond & Van Wilgen, 1996; Higgins *et al.*, 2000). Regular fires in the grass layer lead to a constant defoliation of small trees inside the grass layer and induce a lateral, basal regrowth that is responsible for higher cover values of these trees. The higher the fire frequency, the more difficult it is then for these woody species to emerge and to escape from the fire. Therefore, large trees are scarce under high fire frequency.

In addition to these findings of a negative impact of high fire frequency on the occurrence of larger trees, significantly fewer woody species numbers were recorded at high fire frequency and a significant decline of *C. imberbe* was observed. The high fire frequency, with fires occurring more than every third year, is therefore considered as too high to sustain a diverse savanna structure on drying floodplains in the Okavango Delta.

The relevance of fire frequency for the vegetation of active floodplains

In contrast to drying floodplains, the DCA of the study plots on active floodplains based on the species cover revealed, for both flood and fire frequency, a gradient along the first axis (cf. Fig. 4). However, the analyses revealed that species assemblage and vegetation structure on active floodplains are in principle determined by the flood frequency. Because of an observed negative correlation between fire and flood frequency, fire frequency can also be correlated with species assemblage and structure, but most likely does not affect them significantly.

Analyses of the cover values revealed for single species a highly significant decline on high or low fire frequency, showing an impact of fire frequency on specific species (Table 1). However, as the number of these species is low and as almost none of the species appear at low or high frequency only, no differences in species composition are ascribable to fire frequency on active floodplains.

The missing significant response of active floodplains to fire frequency, especially in terms of species composition, can be explained by considering the typical flood cycle in the study area. These floodplains in the southern Okavango Delta experience a period of short drought after the rainfall in February/March, followed by flooding around July and then a period of receding floods shortly before the next rainfalls. Fire in this region usually occurs during the drought between rainfall and the flooding, i.e. around June (Heinl *et al.*, 2007). During this period, plant species are well protected against fire, as most of the plant species, usually tall perennial sedges or grasses, are dormant. They spread and regrow by rhizomes, like *C. articulatus*, *S. corymbosus*, *O. longistaminata* or *P. repens* (Gibbs-Russell *et al.*, 1990; Oudtshoorn, 1999; RBG Kew, 2004) and these rhizomes are usually covered under a layer of accumulated biomass during this period. This thick organic layer of dead leaves and stems is not utilized by herbivores or termites because of the unpalatability and remains wet long after the rainfall, especially in combination with the high water-holding capacity of the upper organic layer in the soils of these floodplains. Fire temperatures are hence reduced by the moisture in the fuel and overall, the pre-fire vegetation appears well protected against fire.

Hence, changes in plant species composition with fire are only likely to happen if space and time is provided for new species to establish. Usually, the fire event does provide open space by removing most of the vegetation and litter (Bond & Van Wilgen, 1996; Heinl, Sliva & Tacheba, 2004). But the time-span for the establishment of new, e.g. pioneer species, is extremely short because of the impending flood. Water levels rise quickly and small species not capable of surviving under water are expected to

drown. In combination with the fast recovery of the established highly competitive species in the active flood-plains, the survival of new species after a fire event in the active floodplains and hence a change in species composition related to fire is therefore expected to be difficult and unlikely.

Acknowledgements

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