

The Influence of Range Fire on Soil Fungi, Microbial Activity and Soil Properties along the Boro Route of the Okavango Delta

Agripina Banda • Tabo Mubyana-John* • Joanne E. Taylor

Department of Biological Sciences, University of Botswana, P/B 0022, Gaborone, Botswana

Corresponding author: * mubyanat@mopipi.ub.bw

ABSTRACT

The influence of burning on soil microbial dehydrogenase activity, nitrogen content and fungal population along the Boro route in the Okavango Delta was assessed in the flood and dry seasons. Soil samples from the burnt plots and the adjacent control un-burnt plots were cultured on agar plates using dilution methods. *Fusarium* spp. were dominant while *Aspergillus* species were low in burnt plots. The other fungi such as *Drechslera* sp., *Exophiala jeanselmei*, *Penicillium compactum* and *Chrysosporium merdarium* were only in the burnt plots as compared to unburnt control plots. However, fungal diversity and soil dehydrogenase activity reduced after 6 months of burning showing significant increase in *Chrysosporium merdarium* in almost all the burnt plots. The influence of burning on soil nitrogen was insignificant instead flooding had a stronger influence on nitrogen content than burning. The results indicate that burning increased fungal diversity and biomass, however reduces overall microbial enzyme activity after burning without influencing soil nitrogen and pH.

Keywords: burning, fungal diversity and density, microbial biomass, dehydrogenase

INTRODUCTION

Sometimes fire has been described as an essential factor for the maintenance of savannas and their typical appearance (Vijver *et al.* 1999; Govender *et al.* 2006; Aleper *et al.* 2008; Peterson and Reich 2008). Although fire may have some desired effects such as clearance of unwanted vegetation, it also has negative transient effects such as changing the vegetation diversity by favouring species which are resistant and those with early post recovery (Paul and Clark 1996; Heintz *et al.* 2007b). Burning lowers species richness and diversity of plants (Heintz 2001). Burning of vegetation deprives the soil organisms of the much needed organic material required to form organic matter (Certini 2005) which influences nutrient mineralization and in turn plant nutrient uptake (Paul and Clark 1996; Raynaud *et al.* 2006). Fire may negatively affect soil microbial biomass and soil microorganisms' capacity to carry out many of their nutrient cycling activities (Giardina *et al.* 2000; Jensen *et al.* 2001; Michelsen *et al.* 2004; Chu and Grogan 2009) and also influences nutrient cycling through their enzyme activities. Decomposition of organic residues in soil involves many reactions among which is dehydrogenation, a process catalysed by the dehydrogenase enzyme mostly of microbial origin and is an integral part of the microbial community structure (Ceasar-TonThat and Cochran 2001; Mubyana-John *et al.* 2007). Any disturbance in the soil microbial community is likely to influence the dehydrogenase activity of the soil and its activity is an indicator for microbial activity (Ross 1971; Skujins 1973; Tabatabai 1994; Araújo *et al.* 2009). Thus, soil fungi concentrate in the subsoil and play a major role in organic matter buildup by decomposition and degradation of resistant organic components such as cellulose, lignin, keratin and chitin (Kara and Bolat 2007). They also participate in the stabilization of soil aggregates due to their filamentous nature and thus may prevent soil erosion (Packham *et al.* 2002; Osono *et al.* 2003).

The Okavango Delta, in northwestern Botswana, a semi arid to arid country with very low rainfall, serves as the

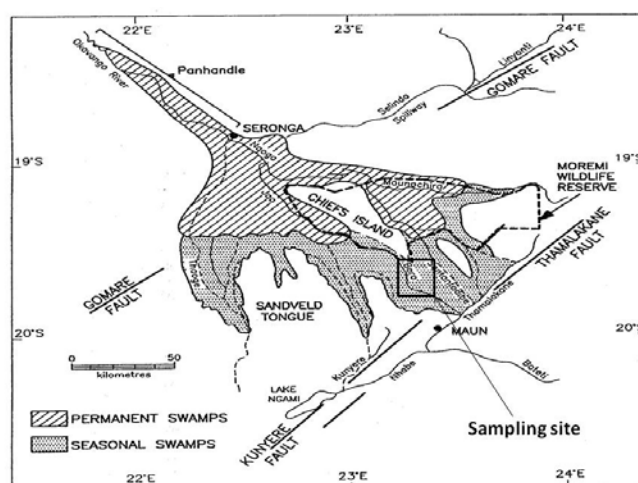


Fig. 1 Map of the Okavango Delta in north-western Botswana, sampling area indicated by a square. Source Harry Oppenheimer Okavango Research Centre, Cartographic unit. Maun, Botswana.

major source of water for flora and fauna in the area. Although the Delta is a protected area, wild fires do occur there. These fires may be caused by lightning or by human activities (Heintz 2001; Kgathi *et al.* 2005; Heintz *et al.* 2007a). The Okavango Delta has a savanna biome with occasional swamps in the floodplains, Mopane and shrub woodland type of vegetation as distance from the riverbed increases. In the floodplains although sedges and grasses form the main vegetation layer they are extremely effective at suppressing regeneration of other growth forms (Ellery and McCarthy 1998). The grasses exhibit rapid growth after sprouting at the onset of floods and rains and they become highly flammable due to human activities and veld fires after the floods recede. There have been several studies conducted in the Delta on the effects of fire on vegetation and wildlife. However, very few documented studies address the

Table 1 Location of the sampling plots in the Okavango Delta.

Plot	GPS coordinates	Vegetation	Burning history
6b	34K0742339 (7804766)	Short Mopane and grass	Burnt in 2000
6ub	Adjacent to above	Short Mopane and grass	Unburnt
6(01)b	34K0742806 (7804507)	Short Mopane and grass	Burnt in 2001/2
51ub	34K0743743 (7805587)	Short Mopane and grass	Unburnt control for 6(01)b
03(1)b	34K0747118 (7805803)	2° floodplain grassland	Burnt July 2003
03(1)ub	Adjacent to above	2° floodplain grassland	Unburnt
03(2)b	34K0738281 (7807176)	3° floodplain mostly <i>Cynodon dactylon</i>	Burnt July 2003
03(2)ub	Adjacent to above	3° floodplain mostly <i>Cynodon dactylon</i>	Unburnt
03(3)b	34K0737916 (7807693)	2° floodplain mostly <i>Panicum repens</i>	Burnt August 2003
03(3)ub	Adjacent to above	2° floodplain mostly <i>Panicum repens</i>	Unburnt
03(4)b	34K0737260 (7808591)	2° floodplain grassland	Burnt August 2003
03(4)ub	Adjacent to above	2° floodplain grassland	Unburnt
03(5)b	34K0736861 (7809169)	2° floodplain grassland	Burnt August 2003
03(5)ub	Adjacent to above	2° floodplain grassland	Unburnt

b: burnt, ub: no record of burning since 2000, 1° - primary, 2° - secondary, 3° - tertiary

effect of fire on below ground microbial communities, nutrient cycling and other activities. The main objective of this study was to assess the effect of burning on soil microbial activities as reflected by microbial enzyme, fungal density and diversity.

MATERIALS AND METHODS

Site and sampling

Sampling was undertaken along the Boro route in the Okavango Delta (23 24°E, 19-24°S) (Fig. 1). The plots (Table 1) were located in the floodplains and bordering riparian woodlands, as these are the areas most susceptible to fire. The selected plots had documented history of burning since 2000. Adjacent unburnt plots were used as controls. The floodplains were dominated by grasses such as *Panicum repens*, *Setaria sphacelata* in the lower flood plains and *Cynodon dactylons* in higher floodplains bordering the Mopane riparian woodlands. The riparian woodlands consisted mostly of scattered Mopane (*Colophospermum mopane*) with patches of grasses.

Sampling was carried out in September 2003, less than 2 weeks after the onset of fire season in the Delta and also in February 2004. September is characterised by dry soil spells in the tertiary floodplains and the riparian woodlands. While in February, the soils are mostly wet from the surface floods characteristic of the Okavango (Ellery and McCarthy 1998). For each plot, three replicate soil samples located at least 20 m apart and each consisting of 5 sub-samples of approximately 30 cm apart were collected from seven burnt plots and their corresponding unburnt control plots. The samples were taken from the A1 horizon (about 5 cm deep) using a clean core borer. Representative samples of approximately 500 g each were then transferred into four polyethylene bags with Ziploc closure. In all a total of 42 samples each composing of five sub samples were collected at each sampling time. These were packed in cooler boxes and transported to the laboratory immediately.

Fungal density and diversity

Fungal populations in the soil samples were estimated by plate count method by making soil dilutions in sterile physiological solution (8.0 g NaCl/L) and then plating out on malt extract agar (MEA, Oxoid medium CM57, Oxoid Ltd. Basingstoke, Hampshire UK) amended with 0.3 mg/L streptomycin sulphate (Parkinson and Paul 1982). Three replicates per sample were made. The agar plates were incubated at 30°C for a week. Population counts and diversity were determined and corrected for moisture content in order to express them on dry weight basis. The given percentage values were calculated from the total number of fungal species isolated from the burnt and unburnt plots. After isolation different fungi were purified by transferring mycelia disks from the different colony types on to fresh MEA amended with streptomycin sulphate. Identification of the isolates was based on macroscopic fungal colony morphology and microscopic reproductive features

as described by Domsch *et al.* (1993) and other reference books (Ellis 1971, 1976; Carmichael *et al.* 1980; Sutton 1980; Hanlin 1990; Klich 2002). *Fusarium* spp. were identified according to Nelson *et al.* (1983) and Domsch *et al.* (1993). For sterile fungi, sporulation was induced by growing them on water agar supplemented with carnation leaves (Fisher *et al.* 1982; Kirk *et al.* 2001) and incubating the plates under ultra-violet light (short wave length-340 nm) at 25°C until the fungi sporulated. When induction of sporulation was not successful, isolates were recorded as 'un-identifiable sterile mycelia'.

Dehydrogenase activity

Dehydrogenase activity was determined using the method outlined by Tabatabai (1994) and Friedel *et al.* (1994). Replicate 20 g portions of air-dried and soil sieved through a 2 mm sieve, samples were extracted with methanol and colorimetric determination of 2,3,5-triphenyl formazan (TPF) produced by reduction of 2,3,5-triphenyl tetrazolium chloride (TTC) by the soil enzyme. The red colour intensity developed by the TTC was measured at 485 nm using a spectrophotometer (Spectronic instrument 20D+) and TPF was used as a reference standard.

Microbial biomass

The fumigation re-inoculation method was used to determine microbial biomass carbon (Jenkinson and Paulson 1976; Parkinson and Paul 1982). To differentiate soil fungal biomass from bacterial biomass selective inhibition technique (Anderson and Domsch 1978; Baath and Anderson 2003) was used. The method involved substrate-inhibition respiration using antibiotics selective against bacterial or fungal respiration. Streptomycin sulphate (2%) plus chlorophenicol (1%) were used to inhibit bacterial respiration while cyclohexamide (0.05%) was used to inhibit fungal respiration. Triplicate 100 g fresh soil samples were used in the determination of CO₂ evolved (Parkinson and Paul 1982). Controls consisted of soils to which no inhibitor had been added. Microbial biomass was calculated by subtracting CO₂-C evolved from amended samples from the non-amended and then dividing by 0.5. The factor 0.5 used was based on the calculated fraction of biomass C mineralised to CO₂ over the 10-day incubation period (Jenkinson and Paulson 1976; Bailey *et al.* 2002b).

Soil properties

Soil moisture content was determined gravimetrically from weight loss after 10 g of each soil sample was oven dried at 105°C overnight (Anderson and Ingram 1993). Soil texture (% sand, silt and clay) was determined by the hydrometer (*Bouyoucos* method) (Anderson and Ingram 1993). The soil textural class was then determined by using the soil textural triangle (Anderson and Ingram 1993). The other soil was air dried and passed through a 2 mm mesh sieve to determine total N using an automated N analyser (LECO Model FP 328). Ethylenediaminetetraacetate (EDTA) was used as the standard. Active soil acidity was determined in a soil:

Table 2 Fungal species isolated from the unburnt and burnt plots of the Okavango Delta soils in September 2003. (Values given are means of three replicates)

No. of Genera	Fungal genera/species	CFU/g soil in unburnt plots	CFU/g soil in burnt plots
1	<i>Absidia corymbifera</i>	10	4
2	<i>Acroconidiella tropaeoli</i>	0	1
3	<i>Alternaria alternata</i>	5	3
4	<i>Aspergillus candidus</i>	0	1
	<i>Aspergillus clavatus</i>	146	2
	<i>Aspergillus flavus</i>	1	0
	<i>Aspergillus fumigatus</i>	18	31
	<i>Aspergillus japonicus</i>	1	6
	<i>Aspergillus niger</i>	10	7
	<i>Aspergillus parasiticus</i>	0	27
	<i>Aspergillus wentii</i>	98	213
	<i>Aspergillus</i> spp.	137	122
5	<i>Chalara elegans</i>	2	3
6	<i>Chlamydomyces palmarum</i>	1	0
7	<i>Chrysosporium merdarium</i>	0	5
8	<i>Cochliobolus lunatus</i>	0	68
	<i>Cochliobolus sativus</i>	1	4
9	<i>Drechslera</i> sp.	0	15
10	<i>Exophiala jeanselmei</i>	0	7
11	<i>Fusarium equiseti</i>	11	246
	<i>Fusarium oxysporum</i>	3	8
	<i>Fusarium</i> sp.	0	4
12	<i>Mucor</i> sp.	0	2
13	<i>Oidiodendron echinulatum</i>	2	4
	<i>Oidiodendron</i> sp.	1	0
14	<i>Penicillium brevicompactum</i>	0	1
	<i>Penicillium compactum</i>	0	2
	<i>Penicillium funiculosum</i>	7	1
	<i>Penicillium rugulosum</i>	0	9
	<i>Penicillium spinulosum</i>	0	1
	<i>Penicillium steckii</i>	74	13
	<i>Penicillium vulpinum</i>	1	2
	<i>Penicillium</i> spp.	58	171
15	<i>Pithomyces</i> sp.	1	1
16	<i>Phoma medicaginis</i>	14	5
17	<i>Pseudeurotium zonatum</i>	9	0
	<i>Pseudeurotium</i> sp.	11	0
18	<i>Rhizopus oryzae</i>	1	0
	<i>Rhizopus stolonifer</i>	1	1
19	<i>Sporothrix schenckii</i>	13	6
20	<i>Stachybotrys chartarum</i>	25	0
21	<i>Trichocladium asperum</i>	4	0
22	<i>Trichoderma</i> sp.	7	7
23	<i>Verticillium</i> sp.	2	0
	Unidentified fungi	276	169

water (1: 2) suspension as outlined by Anderson and Ingram (1993). The pH of the supernatant was measured using an Accumet®/Fisher Scientific Model 50 pH meter (London, UK) with a combination glass electrode and readings were recorded to two decimal places.

Statistical analysis

Analysis of variance was performed using the SPSS 11.0 package. *Post Hoc* analyses were performed using Tukey's test ($P \leq 0.05$) (Elston and Johnson 2008). In the analyses group separation was based on burning history, habitat (whether grassland or riparian woodland).

RESULTS

Fungal diversity

In all there were 23 different genera of fungi consisting of many species isolated from the Boro region of the Okavango Delta (**Table 2**). There were many unidentifiable species i.e., more than 35 species isolated from both the burnt

Table 3 Fungal species isolated from the unburnt and burnt plots of the Okavango Delta soils in February 2004. (Values given are means of three replicates)

No. of genera	Fungal genera/species	CFU/g soil in unburnt plots	CFU/g soil in burnt plots
1	<i>Absidia corymbifera</i>	3	7
2	<i>Alternaria alternata</i>	0	4
3	<i>Aspergillus fumigatus</i>	130	92
	<i>Aspergillus japonicus</i>	1	12
	<i>Aspergillus niger</i>	11	10
	<i>Aspergillus parasiticus</i>	31	71
	<i>Aspergillus wentii</i>	175	127
	<i>Aspergillus</i> spp.	113	136
4	<i>Chalara elegans</i>	16	1
5	<i>Chrysosporium merdarium</i>	0	19
6	<i>Cochliobolus sativus</i>	2	7
7	<i>Fusarium equiseti</i>	9	217
	<i>Fusarium oxysporum</i>	3	21
	<i>Fusarium</i> sp.	14	3
8	<i>Mucor</i> sp.	9	2
9	<i>Penicillium brevicompactum</i>	3	0
	<i>Penicillium steckii</i>	19	1
	<i>Penicillium vulpinum</i>	18	0
	<i>Penicillium</i> spp.	16	8
10	<i>Pithomyces</i> sp.	0	2
11	<i>Phoma medicaginis</i>	12	2
12	<i>Rhizopus oryzae</i>	7	7
	<i>Rhizopus stolonifer</i>	1	1
13	<i>Sporothrix schenckii</i>	1	9
14	<i>Trichoderma</i> sp.	1	1
	Unidentified fungi	45	8

and the unburnt plots during the first sampling period. Although there were many genera isolated from the burnt plots, many could not be identified to species level. In all, the burnt plots had more unidentifiable species. There were also many unidentifiable fungal colonies, of which 13% were from the unburnt plots and 8% were from the burnt plot (**Table 2**). Macroscopic and microscopic observations revealed that there were usually few of each species among the unidentifiable. *Aspergillus* and *Penicillium* spp. comprised the major genera and made up 39 and 16% of the total isolates, respectively. Only about 0.7% of the total isolates were *Fusarium* species isolated from the unburnt plots, while 12% of the isolates from the burnt plots were *Fusarium* species.

During the second sampling, in February, only 14 genera consisting of 19 known species were isolated from the unburnt and the burnt plots (**Table 3**). The total number of isolates from the second sampling was much lower than those obtained from the first sampling. Unidentifiable fungi from the unburnt plots made up 3% of the total isolates and only 0.6% of the total isolates could not be identified in the burnt plots. However, species diversity was slightly, but non significantly, higher in the burnt plots during both sampling periods.

Figs. 2 and 3 show fungal population in the plots in September shortly after burning and in February. Only six plots were sampled during the second sampling period. Of these four burnt plots all of which were under grassland indicated a higher population than that of the control plots. The increase in fungal population observed in grassland was not observed in Mopane riparian woodland plots. The earliest burnt plot, 6, and the latest burnt plot, 03(5), showed a slightly lower population than that of the unburnt plots. The February sampling i.e., 6 months after the fire results indicated non significant differences in fungal population due to burning. Also there were no differences between the riparian woodland (6b, 6ub, 51ub) plots and the floodplain grassland plots (03). Results from the first sampling showed that the fungal population in the burnt plots were slightly higher or equal to that in the unburnt plots in five of the seven sampled plots. A slightly lower population

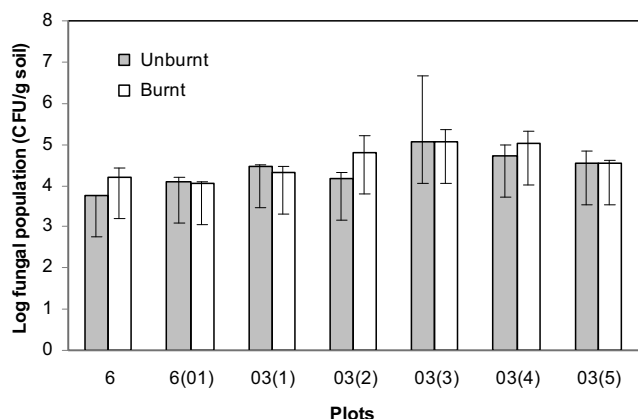


Fig. 2 Soil fungal populations in September 2003.

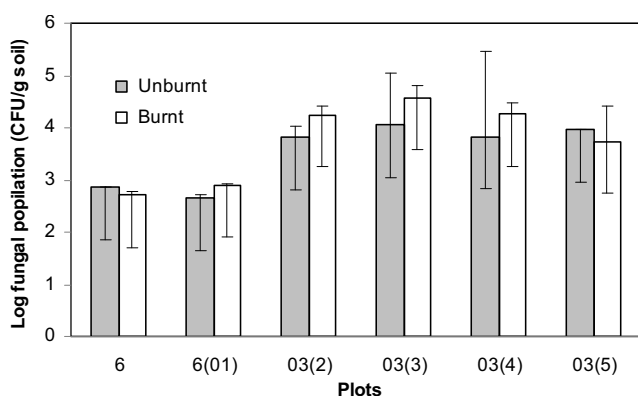


Fig. 3 Soil fungal population in February 2004.

than that of the unburnt plots was observed in plots 6(01) and 03(1).

Fungal and bacterial biomass

The results from the first sampling showed a fungal biomass which ranged from 98.27 mg C/g soil to 167.20 mg C/g soil in the burnt plots, while that in the unburnt plots ranged from 67.47 mg C/g soil to 167.93 mg C/g soil. Significantly higher fungal biomass in burnt plots than in

the respective controls plots were recorded in five plots during the first sampling period. After 6 months from the last burning, the fungal biomass in the burnt plots ranged from 56.47 mg C/g soil to 168.67 mg C/g soil, while fungal biomass in the unburnt plots ranged from 60.13 mg C/g soil to 127.60 mg C/g soil (Tables 4, 5). Riparian woodland plots (6, 6(01)) generally had lower fungal biomass compared to grassland plots (03). There was variability among plots on the influence of burning on bacterial biomass C as some plots indicated an increase while others did not. Immediately after the fire there was an increase in bacterial biomass C (Table 4), however, this increase was not maintained but declined after 6 months (Table 5). Overall, bacterial biomass C was higher immediately after the fire in September than in February in both the burnt and unburnt plots.

Tables 6 and 7 show total soil nitrogen levels in the burnt and unburnt plots in September and February. In all the studied plots there was no significant difference in total soil N content between the burnt and unburnt plots. The active soil pH of the plots ranged from 5.8 to 8.4 but did not differ significantly between the burnt and unburnt plots (Tables 6, 7). Soil texture also did not differ between the burnt and unburnt plots at both sampling times (Tables 6, 7).

Dehydrogenase activity

Soil dehydrogenase activity during the first sampling period ranged from 132 to 241 µg/g soil in the burnt plots (Tables 6, 7). Much wider variations were recorded in the unburnt plots (112 to 281 µg/g soil). In four of the plots, the dehydrogenase activity was significantly higher compared to the corresponding unburnt plots, the other three plots showed a dehydrogenase activity, which was lower than the unburnt adjacent plots. Similar results were obtained during the second sampling, except for the 03(5) plot in which the dehydrogenase activity was almost the same as that of the control (Table 7).

DISCUSSION

The soils of the Okavango Delta along the Boro route showed high fungal diversity. In all, in the unburnt plots they were more than 35 fungal species, which could be identified. These belonged to more than 23 different genera. Burning influenced fungal genera diversity more than it influenced fungal population (Table 2; Figs. 2, 3). There was also a shift in fungal diversity with burning.

Table 4 The influence of fire on fungal/bacterial biomass C ratio in soil sampled from unburnt and burnt plots along the Boro route in the Okavango Delta in September 2003. (Values given are means of three replicates).

Plots	Fungal biomass C (mg C/100 g soil)		Bacterial biomass C (mg C/100 g soil)		Fungal/bacterial biomass	
	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt
6	67.47 ± 27	98.23 ± 33	15.04 ± 2.3	22.00 ± 1.9	4.38	4.47
6(01)	129.80 ± 20	104.87 ± 40	22.30 ± 4.1	2.20 ± 0.3	5.82	47.67
03(1)	111.47 ± 25	167.20 ± 12	27.10 ± 3.0	37.40 ± 3.2	4.11	4.47
03(2)	105.60 ± 19	109.27 ± 25	17.80 ± 1.9	81.40 ± 5.2	5.93	1.34
03(3)	132.73 ± 34.9	139.33 ± 22	19.10 ± 2.1	24.20 ± 1.9	6.95	5.76
03(4)	167.93 ± 8	151.07 ± 9	28.60 ± 2.6	28.60 ± 1.9	5.87	5.28
03(5)	145.93 ± 27	163.53 ± 17	25.10 ± 2.1	30.80 ± 2.4	5.81	5.30

Table 5 The influence of fire on fungal /bacterial biomass C ratio in soil sampled from unburnt and burnt plots along the Boro route in the Okavango Delta in February 2004. (Values given are means of three replicates).

Plots	Fungal biomass C (mg C/100 g soil)		Bacterial biomass C (mg C/100 g soil)		Fungal/bacterial biomass	
	Unburnt	Burnt	Unburnt	Burnt	Unburnt	Burnt
6	93.87 ± 30	86.53 ± 19	20.53 ± 1.8	9.53 ± 2.7	4.57	9.08
6(01)	60.13 ± 22	56.47 ± 13	41.80 ± 4.8	12.10 ± 3.6	1.44	4.67
03(2)	112.20 ± 20	88.73 ± 15	6.60 ± 0.7	22.00 ± 2.9	17.00	4.03
03(3)	119.53 ± 8	168.67 ± 16	15.40 ± 1.2	17.60 ± 5.2	7.76	9.58
03(4)	127.60 ± 23	140.80 ± 12	6.60 ± 0.9	1.30 ± 0.2	19.33	108.31
03(5)	121.00 ± 23	151.80 ± 14	3.20 ± 0.1	2.20 ± 0.5	37.81	69.00

Table 6 Soil dehydrogenase activity, total nitrogen, active acidity and texture in unburnt and burnt plots along the Boro route of the Okavango Delta in September 2003.

Plot texture	Treatment	Dehydrogenase ($\mu\text{g TPF/g soil}$)	Total soil N (%)	Active acidity (pH)	Soil class
6	Unburnt	112 \pm 56	0.01 \pm 0.01 *	7.00 \pm 0.00	S
	Burnt	206 \pm 10	0.03 \pm 0.00	7.00 \pm 0.00	S
6(01)	Unburnt	169 \pm 29	0.00 \pm 0.00	5.96 \pm 0.09	S
	Burnt	144 \pm 21	0.00 \pm 0.00	6.50 \pm 0.26	S
03(1)	Unburnt	152 \pm 38	0.24 \pm 0.05	5.84 \pm 0.20	SL
	Burnt	148 \pm 19	0.29 \pm 0.01	6.37 \pm 0.33	SL
03(2)	Unburnt	189 \pm 51	0.05 \pm 0.01	7.99 \pm 0.92	S
	Burnt	222 \pm 13	0.12 \pm 0.02	7.76 \pm 0.38	S
03(3)	Unburnt	281 \pm 16*	0.11 \pm 0.02***	8.38 \pm 0.11 ***	SL
	Burnt	132 \pm 30	0.36 \pm 0.01	6.14 \pm 0.01	SL
03(4)	Unburnt	209 \pm 25	0.39 \pm 0.02	6.02 \pm 0.06	SL
	Burnt	241 \pm 11	0.39 \pm 0.04	6.04 \pm 0.09	SL
03(5)	Unburnt	173 \pm 63	0.11 \pm 0.02	7.00 \pm 0.00	S
	Burnt	174 \pm 2	0.11 \pm 0.01	6.48 \pm 0.26	S

Values given are means of three replicates; ψ S = Sandy, SL = Sandy loam

Significance is indicated by asterisks: *, $\alpha < 0.05$; **, $\alpha < 0.01$; ***, $\alpha < 0.001$; where α is the probability of type I error; blank = not significant.

Table 7 Soil dehydrogenase activity, total nitrogen, active acidity and texture in unburnt and burnt plots along the Boro route of the Okavango Delta in February 2004.

Plot texture	Treatment	Dehydrogenase ($\mu\text{g TPF/g soil}$)	Total soil N (%)	Active acidity (pH)	Soil class
6	Unburnt	98 \pm 6 **	0.03 \pm 0.01	6.24 \pm 0.07 ***	S
	Burnt	151 \pm 7	0.34 \pm 0.15	7.00 \pm 0.00	S
6(01)	Unburnt	123 \pm 17	0.02 \pm 0.00	6.35 \pm 0.07 **	S
	Burnt	112 \pm 11	0.01 \pm 0.00	5.82 \pm 0.02	S
03(2)	Unburnt	157 \pm 2 *	0.05 \pm 0.01 ***	8.00 \pm 0.69	S
	Burnt	198 \pm 13	0.12 \pm 0.00	7.00 \pm 0.00	S
03(3)	Unburnt	134 \pm 7 ***	0.38 \pm 0.01 *	5.84 \pm 0.08	SL
	Burnt	72 \pm 2	0.35 \pm 0.01	5.77 \pm 0.07	SL
03(4)	Unburnt	115 \pm 2	0.31 \pm 0.00	5.69 \pm 0.21	SL
	Burnt	149 \pm 14	0.30 \pm 0.00	5.70 \pm 0.15	SL
03(5)	Unburnt	137 \pm 23	0.21 \pm 0.01	6.17 \pm 0.42	S
	Burnt	137 \pm 4	0.20 \pm 0.01	6.02 \pm 0.09	S

Values given are means of two replicates; plot 03(1) not sampled; ψ S = Sandy, SL = Sandy loam

Significance is indicated by asterisks: *, $\alpha < 0.05$; **, $\alpha < 0.01$; ***, $\alpha < 0.001$; where α is the probability of type I error; blank = not significant.

Other researchers in the field have also observed a shift in soil fungal diversity due to burning (Suzuki and Bärlocher 2009). Burnt plots tended to promote higher species diversity. Species such as *Aspergillus wentii*, *Fusarium equiseti* and *Penicillium* spp. increased significantly in the burnt plots. On the contrary burning seemed to contribute to the disappearance of some species such as *Pseudeurotium* sp., *Pseudeurotium zonatum*, *Rhizopus oryzae*, *Stachybotrys chartarum*, *Trichocladium asperum* and *Verticillium* sp. while others such as *Aspergillus clavatus* and *Penicillium steckii* only declined. The burnt plots seemed to have a higher diversity of genera than the unburnt. Trappe *et al.* (2005) reported similar findings. Irrespective of having more genera there were fewer species per genus and fewer individuals per species in contrast to the unburnt plots where there were many species per genus and more individuals per species. Overall in September after burning the results indicated an increase in fungal diversity. Fungal diversity was generally low in the February sampling. Many species observed during the dry September sampling were not detected in the February samples irrespective of whether the plot had been burnt or not (Tables 2, 3). This was attributed to high moisture content during the February sampling, as the high floodwaters might have reduced soil oxygen available for microbial respiration (Trappe *et al.* 2005). Soil fungi are mostly aerobic and thus increased soil moisture may reduce their population.

In this study, fire may also have resulted in species dominance change as reflected by the appearance of new species in the burnt plots, a trend also observed by other researchers (Lygis *et al.* 2010). Species such as *Chrysosporium merdarium*, *Acroconidiella tropaeoli*, *Aspergillus candidus*, *Cochliobolus lunatus*, *Drechslera* sp., *Exophiala jeanselmei*, *Penicillium spinulosum* and *Penicillium rugulo-*

sum were observed in the burnt plots and yet none of these taxa were isolated from the unburnt plots. Some species were more affected by fire than others. Results from both sampling periods indicated that the genus *Aspergillus* was negatively affected by fire while *Fusarium* sp. showed an increase with burning initially as reflected by *F. equiseti* and *F. oxysporum* which still maintained increased populations in the burnt plots. Deka and Mishra (1984) also made a similar observation. Generally there was a return to original species composition after 6 months, an indication of recovery of species. Whether these species had become accustomed to the fire circle or reintroduced from surrounding unburnt areas was not clear. A shift in species diversity resulting in an increase in the *Fusarium* species may negatively affect the plant population in the burnt site as some *Fusarium* species are plant pathogens causing root and stem rot, vascular wilt, fruit rot or ear diseases (Domsch *et al.* 1993). These results are in accordance with other investigations that have also shown changes in the fungal species after fire (Yibarkuk *et al.* 2001; Wuthrich *et al.* 2002; Lygis *et al.* 2010).

The results from this study generally showed an increase in the fungal species and population in plots where grasses were the dominant vegetation as opposed to riparian Mopane woodland 6 months after the fire. This trend has also been observed in other areas (McMullan-Fischer *et al.* 2002; Mubyana-John *et al.* 2007), although shortly after the fire fungal population may decline as shown by Liu *et al.* (2001) who found a decrease in the soil fungal population one month after fire. Both heat and ash modify soil chemical and physical status (Diaz-Ravina *et al.* 1992; Certini 2005). With burning and death of the above ground matter in grasslands, there is usually a lot of below ground material that will likely die and serve as substrate for soil organisms

such as fungi and actinomycetes who play major roles in decomposition of organic residues. This has also been suggested as a possible explanation by other researchers (Vazquez *et al.* 1993; Liu *et al.* 2001). Fungi play a major role in decomposition of organic residues, thus on a short term basis, in grasslands it is likely there would be an increase in fungal activities due to increased substrate (Kara and Bolat 2007). Although fire may produce a sharp increase in soil microbial populations, the groups are affected differently. In this study however, soil bacterial biomass also showed significant increase shortly after burning but decreased 6 months later probably because of declining substrate levels. Increases in fungal biomass were also observed shortly after burning in the grassland plots indicating possibly the substrates were still available, as all the roots may not have been decomposed after 6 months. Young shoots will also result in more root exudates when compared to older plants.

Both fungal and bacterial biomass may have been temporarily higher in the burnt plots because of the readily available substrates. Michelsen *et al.* (2004) and Albrecht *et al.* (1995) also observed increased fungal biomass in burnt plots. Expectedly, fungal biomass was much higher than the bacterial biomass values as indicated by the high fungal/bacterial ratios as fungi play a much more active role in the degradation of organic residues, whereas bacteria are more involved in nutrient cycling. However, some authors have also indicated that the selective inhibition method may not be the best measurement for biomass, as it only provides information about respiratory activity of the fungal and bacterial components of the total biomass (Bailey *et al.* 2002a).

Plots with mostly Mopane (6b, 6b(01)) showed a decrease in fungal biomass with burning (Table 5). Generally the riparian Mopane plots had lower fungal biomass than the grassland plots. Grasslands are more susceptible to fires, even less intense fires, than riparian Mopane vegetation, thereby contribute more to below ground nutrients for the soil organisms. As such frequent fires may alter plant diversity due to the death of grasses but may leave tree species unaffected thus altering the structure of the ecosystem (McMullan-Fischer *et al.* 2002; McIver and McNeil 2006). The change in the structure of the ecosystem can decrease the range of substrates present. Frequent or repeated burning can result in less litter and less substrate for the soil organisms (McIver *et al.* 2007). The fungi community responds better to a wide range of substrates than a narrow range. The loss of substrates due to fire could be responsible for the low species diversity observed in the riparian Mopane woodland plots (plots 6 and 6(01)) (Packham *et al.* 2002; Mlambo *et al.* 2007; Siele *et al.* 2008).

Soil dehydrogenase assay indicated an increase in activity in some burnt plots and not others (Table 6). Within each plot, there were variations in soil dehydrogenase activity between the burnt and unburnt plots without any clear pattern. Six months after burning soil dehydrogenase activity values declined compared to shortly after the fire. The correlation factor between burning and dehydrogenase was very low indicating another factor probably influenced soil dehydrogenase activity more than burning (Hamman *et al.* 2008; Garcia-Villaraco Velasco *et al.* 2009). Based on this study we hypothesize that soil moisture was likely the factor that resulted in increased soil dehydrogenase activity as it coincided with the onset of the floods.

In this study, soil nitrogen levels (Tables 6, 7), did not seem to be influenced by burning probably because nitrogen in the Delta is mostly replenished by the floodwater (Omari *et al.* 2004).

CONCLUSION

Fires in the Okavango Delta, along the Boro route affected microbial populations differently. Changes took place in fungal diversity with many genera and species observed but with fewer individuals per species. This was however contrary to unburnt plots where there were few genera and species but with many individuals per species. Increases in fun-

gal biomass were observed 6 months after burning, but not immediately. This increase depended more on vegetation than any other factor as the effects were more pronounced in grassland than riparian Mopane woodland. The effect of burning on soil dehydrogenase showed a considerable variation possibly because the different microbial groups producing the enzyme were affected differently. So far burning did not seem to affect soil pH and nitrogen. The above results are based on short-term effects of fire; however, continued study may reveal long-term effects.

ACKNOWLEDGEMENTS

This work has been supported by funds from The Belgian Government through the University of Botswana Post Graduate Program in Environmental Microbiology.

REFERENCES

- Albrecht SL, Rasmussen PE, Skirvin KW, Goller RH (1995) Is burning an effective management practice for the Pacific Northwest cereal region? In: *Columbia Basin Agricultural Research Annual Report*, Special Report; Oregon Agricultural Experiment Station and USDA-ARS, Corvallis, Oregon **946**, 105-109
- Aleper D, Lye KA, Moe SR (2008) Response of *Acacia sieberiana* to repeated experimental burning. *Rangeland Ecology and Management* **61**, 182-187
- Anderson JM, Ingram JSI (1993) *Tropical Soil Biology and Fertility: A Handbook of Methods*, CAB International, Wallingford, UK, 340 pp
- Anderson JPE, Domsch KH (1978) A physiological method for the quantitative measurement of microbial biomass in soil. *Soil Biology and Biochemistry* **10**, 215-221
- Araújo AS, Leite LF, Santos VB, Carneiro RF (2009) Soil microbial activity in conventional and organic agricultural systems. *Sustainability* **1** (2), 268-276
- Baath E, Anderson TH (2003) Comparison of soil fungal/bacterial ratios in a pH gradient using physiological and PLFA-based techniques. *Soil Biology and Biochemistry* **35**, 955-963
- Bailey VL, Peacock AD, Smith JL, Bolton H Jr. (2002) Relationship between soil microbial biomass determined by chloroform fumigation-extraction, substrate induced respiration, and phospholipid fatty acid analysis. *Soil Biology and Biochemistry* **34**, 1385-1389
- Bailey VL, Peacock AD, Smith JL, Bolton H Jr. (2002) Fungal to bacterial ratios in soils investigated for enhanced C sequestration. *Soil Biology and Biochemistry* **34**, 997-1008
- Carmichael JW, Kendrick WB, Connors IL, Sigler L (1980) *Genera of Hyphomycetes*, University of Alberta Press, Alberta, Canada, 386 pp
- Cesar-TonThat TC, Cochran VL (2001) Role of saprophytic basidiomycete soil fungus in aggregate stabilization. In: *Sustaining the Global Forum, 10th International Soil Conservation Organisation Symposium on Soil Erosion Research*, Purdue University, USA, pp 575-579
- Certini G (2005) Effects of fire on properties of forest soils: A review. *Oecologia* **143**, 1-10
- Chu H, Grogan P (2009) Soil microbial biomass, nutrient availability and nitrogen mineralization potential among vegetation-types in a low arctic tundra landscape. *Plant and Soil* **329**, 411-420
- Deka HK, Mishra PR (1984) Effect of fuel burning on the microbial population of soil. *Folia Microbiologica* **29**, 330-336
- Diaz-Ravina M, Prieto A, Acea MJ, Carballas T (1992) Fumigation extraction method to estimate microbial biomass in heated soils. *Soil Biology and Biochemistry* **24**, 259-264
- Domsch KH, Gams W, Anderson T (1993) *Compendium of Soil Fungi* (Vols I, II), IHW-Verlag Eching, Germany, 860 pp
- Ellery WN, McCarthy TS (1998) Environmental change over two decades since dredging and excavation of the lower Boro River, Okavango Delta, Botswana. *Journal of Biogeography* **25**, 3611-378
- Ellis MB (1971) *Dematiaceous Hyphomycetes*, Commonwealth Mycological Institute, Kew, UK, 608 pp
- Ellis MB (1976) *More Dematiaceous Hyphomycetes*, Commonwealth Mycological Institute, Kew, UK, 507 pp
- Elston RC, Johnson WD (2008) *Basic Biostatistics for Geneticists and Epidemiologists. A Practical Approach*, John Wiley & Sons Ltd., UK, 373 pp
- Fisher NL, Burgess LW, Toussoun TA, Nelson PE (1982) Carnation leaves as a substrate and for preserving cultures of *Fusarium* species. *Phytopathology* **72**, 151-153
- Friedel K, Mülter K, Fischer WR (1994) Comparison and improvement of methods for determining soil dehydrogenase activity by using triphenyltetrazolium chloride and iodinitrotetrazolium chloride. *Biology and Fertility of Soils* **18** (4), 291-296
- Garcia-Villaraco Velasco A, Probanza A, Gutierrez Mañero FJ, Cruz Treviño A, Moreno JM, Lucas Garcia JA (2009) Effect of fire and retardant on soil microbial activity and functional diversity in Mediterranean pasture.

- Geoderma* **153**, 186-193
- Giardina CP, Stanford Jr. RL, Dokersmith IC, Jaramillo VJ** (2000) The effects of slash burning on ecosystem nutrients during the land preparation phase of shifting cultivation. *Plant and Soil* **220**, 253-255
- Govender N, Trollope WSW, Van Wilgen BW** (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* **43**, 748-758
- Hamman ST, Burke IC, Knapp EE** (2008) Soil nutrients and microbial activity after early and late seasons prescribed burns in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* **256**, 367-374
- Hanlin RT** (1990) *Illustrated Genera of Ascomycetes* (Vol 1), The American Phytopathological Society Press, Minnesota, USA, 263 pp
- Heinl M** (2001) Fire and its effects in the Okavango Delta of Botswana. Chair of Vegetation Ecology, Technische Universität München (TUM), 139 pp
- Heinl M, Frost P, Vanderpost C, Ciliva J** (2007) Fire activity on dry lands and in the floodplains in the Southern Okavango Delta, Botswana. *Journal of Arid Environments* **68**, 77-87
- Heinl M, Sliva J, Murray Hudson M, Tacheba B** (2007) Post-fire succession on savanna habitats in the Okavango Delta wetland, Botswana. *Journal of Tropical Ecology* **23**, 705-713
- Jenkinson DS, Paulson D** (1976) The effects of biocidal treatments on metabolism in the soil. *Soil Biology and Biochemistry* **8**, 167-177
- Jensen M, Michelsen A, Gashaw M** (2001) Responses in plant, soil, inorganic and microbial nutrient pools to experimental fire, ash, and biomass addition in woodland savanna. *Oecologia* **128**, 409-485
- Kara O, Bolat I** (2007) Soil microbial biomass C and N changes in relation to forest conversion in the North-western Turkey. *Land Degradation and Development* **19**, 421-428
- Kgathi DL, Mmopelwa G, Mosepele K** (2005) Natural resources assessment in the Okavango Delta, Botswana: A case study of some key resources. *A United Nations Sustainable Development Journal* **29**, 70-81
- Kirk PM, Cannon PF, David JC, Staplers JA** (2001) *Ainsworth and Bisby's Dictionary of the Fungi*, C.A.B. International, Wallingford, UK, 655 pp
- Klich MA** (2002) *Identification of Common Aspergillus Species*, Centraalbureau voor Schimmelcultuur, Utrecht, The Netherlands, 116 pp
- Liu FM, Toda H, Haibara K** (2001) Effects of clear cutting and burning on characteristics of nitrogen mineralization and microbes in the forest soil of *Pinus massoniana* plantation in southern China. *Ecological Research* **16**, 531-542
- Lygis V, Vasiliauskaitė I, Stenlid J, Vasaitis R** (2010) Impact of foreign fire on occurrence of *Heterobasidium annosum* S.S. wood rot and other wood inhabiting fungi in roots of *Pinus mugo*. *Forestry* **83** (1), 83-92
- McIver JD, James D, Ottmar R** (2007) Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in Northeastern Oregon. *Forest Ecology and Management* **238**, 268-279
- McIver JD, McNeil R** (2006) Soil disturbance and hill-slope sediment transport after logging of a severely burned site in Northeastern Oregon. *Western Journal of Applied Forestry* **21** (3), 123-133
- McMullan-Fischer SJM, May TW, Keane PJ** (2002) The macrofungal community and fire in a mountain ash forest in southern Australia. *Fungal Diversity* **10**, 57-76
- Michelsen A, Anderson M, Jensen M, Kjeller A, Gashaw M** (2004) Carbon stocks, soil respiration and microbial biomass in fire-prone tropical grassland, woodland and forest ecosystems. *Soil Biology and Biochemistry* **36**, 1707-1717
- Mlambo D, Mwenje E, Nyathi P** (2007) Effect of tree cover and season on soil nitrogen dynamics and microbial biomass in an African savanna woodland dominated by *Colophospermum mopane*. *Journal of Tropical Ecology* **23** (4), 437-448
- Mubyana-John T, Wutor VC, Yeboah SO, Ringrose S** (2007) Fire and its influence on microbial community structure and soil biochemical properties in the Okavango Delta, Botswana. *Scientific Research and Essays* **2** (2), 047-054
- Nelson PE, Toussoun TA, Marasas WFO** (1983) *Fusarium Species. An Illustrated Manual for Identification*, The Pennsylvania State University Press, University Park, London, 193 pp
- Omari K, Mubyana T, Matsheka M, Bonyongo C** (2004) Flooding and its influence on diazotroph populations and soil nitrogen levels in the Okavango Delta. *South African Journal of Botany* **70**, 734-740
- Osono T, Ono Y, Takeda H** (2003) Fungal growth on forest floor and decomposition needle litter of *Chamaecyparis obtuse* in relation to resource availability and moisture condition. *Soil Biology and Biochemistry* **35**, 1423-1431
- Packham JM, May TW, Brown MJ, Wardlaw TJ, Mills AK** (2002) Macro-fungal diversity and community ecology in nature and regrowth on wet eucalyptus forest in Tasmania: a multivariate study. *Australian Ecology* **27**, 149-161
- Parkinson D, Paul EA** (1982) Microbial Biomass. In: Page AL, Miller RH, Keeney DR (Eds) *Methods of Soil Analysis Part 2, Chemical and Microbiological Properties* (2nd Edn), American Society of Agronomy, Soil Science of America Publishers INC, Madison, Wisconsin, USA, pp 821-830
- Paul EA, Clark FE** (1996) *Soil Microbiology and Biochemistry*, Academic Press, London, 340 pp
- Peterson DW, Reich PB** (2008) Restoration and maintenance of oak savannas. *Natural Areas Journal* **6**, 6-36
- Raynaud X, Lata J, Leadley PW** (2006) Soil microbial loop and nutrient uptake by plants: A test using a coupled C:N model of plant-microbial interactions. *Plant and Soil* **287**, 95-116
- Ross DJ** (1971) Some factors influencing the estimation of dehydrogenase activity of some soils under pasture. *Soil Biology and Biochemistry* **3**, 97-110
- Siele MP, Mubyana-John T, Bonyongo MC** (2008) The effects of soil cover on soil respiration in the Mopane (*Colophospermum mopane*) woodland of Northwestern Botswana. *Dynamic Soil, Dynamic Plant* **2** (2), 61-68
- Skujins JJ** (1973) Dehydrogenase: an indicator of biological activity in arid soils. *Bulletin on Ecological Research Communication, NFR* **17**, 235-241
- Sutton BC** (1980) *The Coelomycetes*, Commonwealth Mycological Institute, Kew, UK, 696 pp
- Suzuki A, Bärlocher F** (2009) Editorial for the special feature: Propagation strategy of fungi. *Mycoscience* **50**, 1-2
- Tabatabai MA** (1994) Soil enzymes. In: Weaver RW, Scott A, Bottomley P, Bezdicsek D, Smith S, Tabatabai A, Wollum A (Eds) *Methods of Soil Analysis Part 2: Chemical and Microbiological Properties* (3rd Edn), American Society of Agronomy, Soil Science of America Publishers INC, Madison, Wisconsin, USA, pp 775-826
- Trappe JM, Claridge AW, Jumpponen A** (2005) Fire, hypogeous fungi and mycophagous marsupials. *Mycological Research* **109**, 516-518
- Vazquez FJ, Acea MJ, Carballas T** (1993) Soil microbial populations after wildfire. *Microbiology Ecology* **13**, 93-104
- Vijver CADM, Poot P, Prins HHT** (1999) Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil* **214**, 173-185
- Wuthrich C, Schaub D, Webber M, Marxer P, Conedera M** (2002) Soil respiration and soil microbial biomass after fire in a sweet chestnut forest in southern Switzerland. *Catena* **48**, 201-215
- Yibarkuk D, Whitehead PJ, Russell SJ, Jactson D, Godjuwa C, Fisher A, Cooke P, Choquenot D, Bowman DMJS** (2001) Fire ecology and Aboriginal land management in Central Arnhem Land, north Australia: A tradition of ecosystem management. *Journal of Biogeography* **28**, 325-343