Fire and its influence on microbial community structure and soil biochemical properties in the Okavango Delta, Botswana

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The influence of wild fires on microbial community structure, soil organic matter, sulphur oxidising and nitrifying microbial populations in the floodplains of the Okavango Delta of Botswana was assessed. Microbial community structure was assessed by phospholipids ester-linked fatty acids (PLFA) quantification while microbial sulphur oxidisers were assessed by Most Probable Number (MPN). Community structure assessment showed that burning shifted the microbial community structure from single cellular bacteria being the dominant groups to filamentous fungi and actinomycetes being the most dominant groups. Generally burning increased the fungal component (18:2 ω6) matrix from 3.40 to 8.35 while the actinomycetes and sulphur reducing bacterial (10 Me 16:0) component also increased from 1.02 to 1.70 mostly in the floodplains. Generally, the organic matter content declined with burning. However, the influence of burning on soil pH was non conclusive. Soil microbial biomass carbon increased slightly after the fire. The number of heterotrophic and nitrite-oxidizing and sulphur reducing bacteria increased. Overall, these results indicate that burning significantly alters the microbial community structure as large above ground losses of nutrients during and after burning often results in low quantities of nutrients released into the soil.

Key words: Okavango Delta, Botswana, fire, soil microorganisms; organic matter, PLFA and nitrogen.

INTRODUCTION

The Okavango Delta, which is an inland alluvial fan, serves as the major source of water for flora and fauna in semi-arid north western Botswana. The Delta water originates from equatorial Angola as the Cuito and Cubango rivers which converge in Namibia as the Okavango River. In a given year, the intensity of floods in the Delta depends on the magnitude of the annual floodwater from Angola and the amount of local rainfall. The Delta comprises of three hydrologically defined ecological zones, which are; the permanently flooded areas, the seasonally inundated floodplains and higher dry lands (Omari et al., 2004; Bonyongo and Mubyana, 2004). The floodplains may further be divided into three zones namely; primary floodplain, which is regularly inundated in a year of average flood, secondary floodplain, which is inundated less frequently in a year of average flood; and the rarely flooded tertiary floodplain. Although the soils are sandy and have a low nutrient content (Bonyongo and Mubyana, 2004), seasonal patterns of drying and wetting result in changes in flora and fauna population and diversity, as quantities of nutrients are discharged through the system and deposited on the seasonal floodplains.

The high floral diversity of the Delta is dominated mostly by grass populations which are highly susceptible to wild fires during the dry season. Because of the seasonality most of the fires are caused by human interventions, through either carelessness when in transit or intentional. Fires may be beneficial in some ecosystems such as in the Pine Barrens where pitch pines grow on nutrient poor soils. Pine Barrens have adaptations that permit them to survive or regenerate well after fire. Thus

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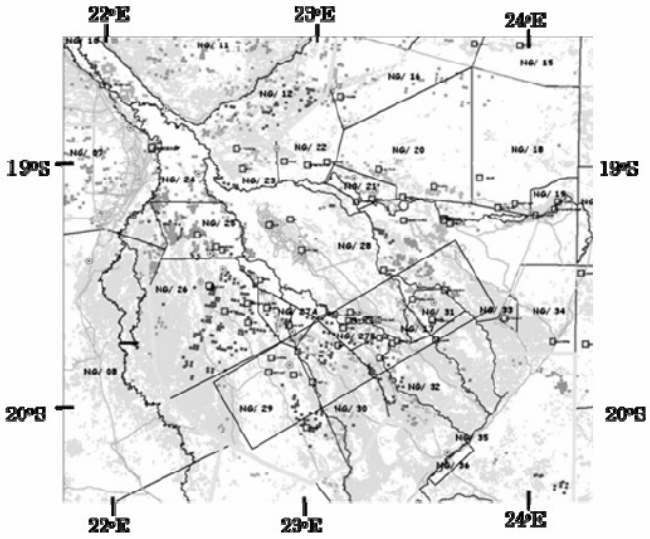

Figure 1. Map of the Okavango Delta showing mapped fire sites since 2000. Rectangular block indicates sampling site.

fire is beneficial to them as it protects them from invasion by woody species which are not adapted to fire (Hendler and Simonelli, 2004). However, fires have been reported to have a negative effect on vegetation in other areas (Prieto-Fernadez et al., 1998). In the Okavango Delta with its high animal population and diversity, these fires are not only detrimental to the vegetation but can also have traumatizing effects on the animals.

Depending on their intensity and frequency, fires may have an affect on soil microorganisms and soil biochemical properties. Soil microorganisms are a critical agent in relation to soil fertility and plant growth, mostly due to their participation in nutrient cycling. Other microbiota such as fungi and actinomycetes not only play major roles in decomposing organic residues arising from the high grasslands and other vegetation, but are also important in soil aggregate stabilization (Parkinson, 1984). Although there have been some studies on fire in relation to above-ground fauna and flora in the Okavango Delta, none has addressed their effect on soil microbial community structure and other below ground parameters. Thus based on data from other areas it can be assumed that depending on the fire intensity, soil microbiota and their activities could be affected and in turn affect soil fertility.

Ways of studying the influence of fire on microbial communities range from assessing the cell component of the population such as phospholipid ester-linked fatty acids (PLFA), enzyme assays which assess microbial activities to simple methods such as plate counts of soil microorganisms. Polar lipids in soil microbes are primarily phospholipids. Thus determination of PLFA can provide a quantitative measure of microbial biomass. With the use of specific markers, PLFA analysis can provide information on community structure composition. The use of PLFA analysis to assess microbial community composition has been used in rhizosphere, clinical sediments and biofouling studies (Horwath and Paul, 1994). Until 2000, fires in the Okavango were not monitored and neither were their effects. Thus the main objective of this ongoing study is to assess the effect of Okavango Delta fires on soil microorganisms and nutrient cycling with the immediate objectives being to study the effects on microbial community structure using the PLFA analysis, soil respiration and soil properties such as organic matter content, total nitrogen and pH.

MATERIALS AND METHODS

Site and Sampling

Sampling for microbial community and soil properties was undertaken in the floodplains at Nxaraga and also along the Boro route to the Okavango Delta (19° and 20°S and 23° and 24°E) (Figure 1). The plots at Nxaraga were burnt in June 2002 by a human induced fire. The Boro route plots were included in the study because they were located in former floodplains that bordered riparian woodlands, and so is very fire susceptible due to their dryness when compared to the more active floodplains. The

Table 1. Markers employed for the studies.

	Marker for	Reference
18:2ω6	Fungi	Wilkinson et al. 2002, White et al. 1996
18:1ω7, 16:1ω9, 18:1ω9, 17:1ω8c, 16:1ω7c, 16:1ω5, 16:1ω7t	Typical of Gram -negative bacteria	Borga et al. 1994 Zelles, 1997
20:4	Microeukaryote	White et al. 1996
i14:0, i16:0, i17:0, 17:1, a17:0, i15:0	Typical of Gram-negative and anaerobic bacteria	Wilkinson et al. 2002
15:1	Bacteria such as *Desulfobolus spp*	Baath & Anderson,2003
14:0, 15:0, 16:0, 17:0, 18:0	Common to all bacteria	White *et al.* 1996
cy19:0, cy17:0	Typical of Gram-negative, made in stationary phase	Zelles, 1997
10me16:0, 10me18:0	Typical of Actinomycetes and sulfate- reducing bacteria	Baath & Anderson, 2003 Wikinson et al. 2002

Boro route plots also have a documented history of burning since 2000. The most dominant grass species in the studied floodplains were *Setaria sphacelata*, *Panicum repens* (L.), *Paspalidium obtusifolium* (Delile N. D. Simpson), *Imperata cylindrica* (L. Raeusch), *Eragrostis inamoena* (K. Schum) and *Miscanthus junceus* (Stapf Pilg). These grasses are found throughout the Delta depending on the flood regime (Bonyongo and Mubyana, 2004). The vegetation along the Boro route consists mostly of secondary and scattered tertiary floodplain grasses. In some plots, there are isolated Mopane trees (*Colophospermum mopane*) which increase with distance away from the floodplain.

Microbial community structure by PLFA analysis, soil respiration and soil nitrogen were investigated at Nxaraga since this site experienced both frequent and intermittent flooding, unlike the Boro route where only the primary floodplains were flooded in that year.

To investigate the effect of fire on microbial community structure, soil samples were collected from the burnt plots and adjacent unburnt plots. Three replicates (consisting of five sub samples 30 cm apart) per plot were collected from the A_1 horizon using an undisturbed auger fitted with an end sterilized with 70% ethanol between the samples. Each sample (approx. 400 g) was put into a separate sterile zip lock bag. The sample bags were placed in cooler boxes and transported to the laboratory the same day. Moisture contents of the soil samples were determined gravimetrically immediately on arrival at the laboratory (Anderson and Ingram, 1993). The samples for PLFA analysis were lyophilized immediately on arrival at the laboratory. The samples for the determination of soil organic matter, nitrogen, pH and texture were air dried.

Soil respiration

Soil respiration was measured in the field at each sampling spot using a portable 12 V battery driven infrared gas analyzer (model EGM–3. PPS Systems) equipped with a data-logger, integral pump, an environmental sensor for soil temperature probe and a soil respiration chamber. The chamber, which enclosed a surface area of 7 x 10^{-3} m^2, had a small low speed fan for mixing the air in the chamber. During measurement the chamber was placed tightly onto a PVC collar on the soil surface and then allowed to stay in position for 120 seconds, or until a constant reading was obtained. This was when soil surface CO_2 was proportional to the rate of change of CO_2 concentration (Blanke, 1996). Soil temperature in the upper layer (5 cm) was measured using the temperature probe on the gas analyzer. For both soil respiration and temperature readings, each replicate reading consisted of five sub readings.

Microbial community structure using phospholipid fatty acid (PLFA) profiles

The extraction of phospholipid fatty acids was based on the method outlined by White and Ringelberg (1998). Briefly, the lyophilized soil sample was extracted in a single phase mixture of chloroform: methanol: acetone (1:2:08, v/v/v). The lipids were then separated into neutral lipids, glycolipids and polar lipids (phospholipids) on a silicic acid column after the extraction. The phospholipids were methylated and separated using a gas chromatograph equipped with a flame ionization detector. Methyl nonadecanoate fatty acid (19:0) was added as the internal standard before the methylation step. The peak areas were then quantified. The standard markers used in these studies were as given in Table 1. Fatty acid analysis was carried out using a Hewlett Packard HP5890 Gas Chromatograph equipped with a Hewlett Packard Ultra 1 capillary column (50 m x 0.20 mm i.d. x 25 mm film thickness). A splitless injection was employed. Injector temperature was maintained at 300°C and the oven temperature at 60°C for 1 min after injection. The oven temperature was then increased to 150°C at 30°C per min and held for 4 min followed by an increase to 250°C at 4°C per min and held for 15 min. Finally the oven temperature was increased to 300°C at 25°C per min and held for 6 min. The transfer line was held at 280°C throughout. Helium was used as the carrier gas (0.8 ml per min).

The fatty acid nomenclature employed was as follows; total number of carbon atoms: number of double bonds, followed by the position (ω) of the double bond from the methyl end of the molecule. The cis and trans configurations were indicated by c and t respectively, while Br and xi were used to indicate a branched fatty acid with unknown branching configuration and an unidentified fatty acid respectively. Cy denotes cyclopropane fatty acids. Anteiso- and isobranching were denoted by the prefix a or i. The sum of the following PLFAs was used as a measure of bacterial biomass 18:1ω7, 16:1ω7t, 18:1ω9, 17:1ω8c, 16:1ω7c, 16:1ω5, 14:0, 15:0, 16:0, 16:1ω9, 20:4, i14:0, cy17:0, 10me16:0, 10me18:0, i16:0, i17:0, 17:1, a17:0, i15:0, 15:1, 17:0, 18:0, and cy19:0. The PLFA 18:2 ω6 was used as a measure of fungal biomass (Baath and Anderson, 2003).

Sulphur oxidizers

Sulphur oxidizing populations in the soil samples were estimated by using the most probable number (MPN) of sulfur oxidisers (Hines et al. 1995). Replicate 10 g soil portions were used to make soil dilutions (10^{-3}-10^{-8}) in 0.2% NaCl solution. The dilutions were then plated onto 5 well series MPN plates containing sulphur media

Table 2. Probability levels for statistical significance for effect of burning on different parameters

Variable	*P*
Nxaraga site	
Soil respiration	**
Soil respiration X moisture regime	***
Soil nitrogen	ns
Soil nitrogen X moisture regime	***
Fungi:bacteria PLFA ratio	**
Moisture	
pH	ns
Boro Site	
Organic matter	**
Organic matter X vegetation	***
Soil Nitrogen	ns
Soil nitrogen X moisture regime	***
pH	ns
pH X Vegetation	ns
Sulphur oxidisers	*
Sulphur oxidisers X vegetation	*

*, **, ***, Statistical significance: at $P<0.05$, < 0.01 and < 0.001 respectively, ns = non significant

prepared as outlined by Hines et al. (1995). The MPN plates were incubated at 25°C for 3 weeks before reading. The data were interpreted using the MPN table for use with 5-tube dilutions.

Soil organic matter, total nitrogen and pH determinations

Soil organic matter levels, total nitrogen and pH measurements were all determined on air dried soils sieved through 2 mm sieves. Organic matter content was estimated indirectly from organic C. Organic C was determined by oxidation of organic matter with a hot mixture of $K_2Cr_2O_7$ and H_2SO_4 using the Walkley-Black procedure (Anderson and Ingram, 1993). The amount of organic carbon was then determined by titration with 0.05 N $FeSO_4$ following the procedure outlined by Nelson and Sommers (1982). The organic matter content was obtained by multiplying the organic C content with the factor 1.729 (Nelson and Sommers, 1982).

Total N was determined using an automated N analyser (LECO Model FP 328). Ethylene diaminetetraacetate, (EDTA), was used as the standard in the determination of the %N. Active soil acidity was determined in a 1:2 soil: water suspension as outlined by Anderson and Ingram (1993). The pH in 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.

RESULTS

Table 2 shows the overall effect of burning on the different soil parameters at the two study sites. The influence of burning on the dominant soil PLFA groups is given in Table 3. The influence of burning in the floodplains was pronounced in both bacteria and fungi PLFA composition, although the influence of moisture was also

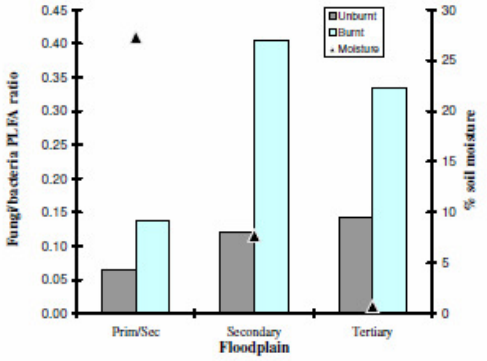

Figure 2. Fungi: bacteria PLFA ratio in the floodplains.

pronounced. The PLFA compositions of bacterial origin including 14:0, 15:1, 16:1ω7c and i15:0 decreased in the burnt plots. On the contrary, fungal and actinomycetes PLFA increased significantly with burning as indicated by an increase in 18:2ω6 and 10me16:0. The FAME 10me16:0, which is indicative of sulphur reducing bacteria, may also indicate an increase in the population of these soil microorganisms. Unlike fungi and aerobic bacterial, FAME of anaerobic bacteria did not seem to be significantly influenced by burning (Table 3). The fungal: bacterial ratio also indicates a significant increase in fungal populations in all the floodplains (Figure 2).

Significant variations in MPN sulphur oxidizing populations between the burnt and unburnt plots were also observed in the study plots (Figure 3). The MPN sulphur oxidizers in plots 1(03), 2(03) and 4(03) were significantly higher in burnt plots compared to their unburnt counterparts. Except for one plot 5(03) all the other burnt plots had higher MPN of sulphur oxidizers when compared to their unburnt counterparts. Thus although there was no significant difference in some plots (Figure 3), both in the grassland and Mopane woodland plots MPN of sulphur oxidizers in the burnt plots was always higher.

Analysis of soil respiration results showed that it varied with the floodplain as a consequence of the moisture regime (Table 4). Statistical analyses showed that the effect of moisture regime on soil respiration was more pronounced than the effect of burning. Thus there was a sequential decline in soil respiration in both the burnt and unburnt plots as distance from the riverbed increased. In the drier moisture regimes (secondary and tertiary floodplains) burning significantly decreased soil respiretion (Table 4).

Although variations in total soil nitrogen were observed in all the floodplains there were no significant differences

Table 3. The influence of burning on the dominant PLFA groups

Treat't	Floodplain	14:00	16: 1ω5	15:01	17:1ω8c	16:1ω7c	i15:0	15:00	18:2ω6	cy19:0	10me16:0	i17:1	a17:0
Unburnt	1°/2°	1.7230	4.2179	1.1468	3.0751	4.7690	8.3796	0.9816	2.3634	7.0423	0.8832	1.1622	4.7140
Unburnt	2°	1.6938	1.2487	1.4312	0.7434	2.0566	6.0208	0.8886	3.3636	6.2422	0.9699	1.2806	6.1550
Unburnt	3°	0.9725	3.5645	0.9742	1.1901	3.6687	5.2488	0.4575	4.4923	7.2330	1.2078	1.1283	6.9422
Burnt	1°/2°	1.2998	3.2654	1.5417	0.8654	4.3373	6.0610	0.6766	4.5104	8.0122	1.0602	1.1521	5.4358
Burnt	2°	1.4143	0.7199	0.6476	0.8376	1.0774	4.2212	0.7309	10.3894	9.5315	1.0686	1.2128	5.2334
Burnt	3°	0.7302	1.7502	0.1000	0.4446	1.7857	2.6040	0.0859	10.1582	11.6924	2.9857	2.4803	8.7455

1°/2° Primary/Secondary transition floodplain, 2° Secondary floodplain, 3° Tertiary floodplain
14:00 General bacteria; 16:1ω5 G negative; 15:01 General bacteria; 17:1ω8c G negative; 16:1ω7c G negative; i15:0 G positive; 15:00 General bacteria; 18:2ω6 Fungi; cy19:0 Stationary phase; 10me16:0 Actinomycetes, SRB, G negative; i17:1 G positive, Anaerobes; a17:0 G positive, Anaerobes

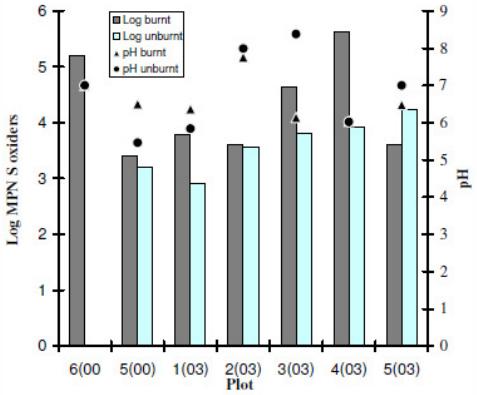

Figure 3. MPN sulphur oxidizers along the Boro route.

Table 4. Mean soil moisture, respiration and total nitrogen at Nxaraga

Floodplain	% moisture		Soil respiration (mgC/100g soil)		% Total Nitrogen	
	Burnt	Unburnt	Burnt	Unburnt	Burnt	Unburnt
Primary/Secondary	27.34	32.65	4.068	2.491	0.103	0.104
Secondary	7.70	1.71	1.707	2.753	0.130	0.105
Tertiary	0.70	0.78	1.992	2.440	0.026	0.012

between the burnt and unburnt plots (Table 4). The differences in total soil nitrogen were least in the primary floodplains (wetter regimes). However slight but non significant differences were observed in the drier moisture regimes of the secondary and tertiary floodplains.

The influence of burning on soil organic matter content varied between plots depending on vegetation cover (Figure 4). Plots with predominantly isolated Mopane tree vegetation (6(00), 5(00) and 1(03)) had significantly lower organic matter than grassland plots (2(03), 3(03), 4(04) and 5(03). However, the influence of burning was more pronounced in floodplain grasslands plots than in the Mopane tree vegetation plots. Lower soil organic matter content was recorded in burnt grassland plots when compared to unburnt plots. Variations in soil pH were observed between burnt and unburnt plots at both Nxaraga and along the Boro route. However, these differences could not be linked to the burning pattern. In this study, no significant variations in soil pH could be attributed to burning (Figure 4).

DISCUSSION

The increases in fungal PLFA observed in the burnt plots could mostly be attributed to increases in fungal population. Fire consumes aboveground litter and so relatively increases the amount of root litter C and N in the soil detritus pool (Ojima et al., 1994). After burning, most of the below ground root mass dies due to temporal reduction in photosynthesis. These then serve as a substrate to the soil organisms involved in decomposition. Both fungi and actinomycetes play a major role in decomposition of organic residues high in cellulose and lignin (Parkinson, 1984). Thus with the increase in dying root mass available for decomposition, there is highly likely to be an increase in these populations' substrates. Pietikainen et al., (2000) also in their forests studies observed a variation in the PLFA profile proportions at the burnt site. Increases in the PLFA cy19:0 made by Gram-negative bacteria in the stationary phase (Zelles, 1997) were also observed in burnt plots (unburnt, 6.86 and burnt, 9.75) at Nxaraga (Table 3). Low moisture level is an important factor that may cause microorganisms to enter the stationary phase (Zelles, 1997). The low soil moisture content arising from the burning may have exerted an additional stress on the bacteria, thus forcing them into the stationary phase. The increases in sulphur reducing bacteria PLFA (10me18:0) observed may be attributed to increases in soil ash content associated with burning. Burning produces ash which could be reduced to generate sulphur in the presence of water, hence providing available substrate for the sulphur reducing bacteria (SRB). With the flooding that is characteristic of these flood plains; this sulphur may serve as a substrate for the sulphur reducing bacteria. Previous studies on diazotrophs in the same floodplains have also reported increases in nitrogen fixing sulphur-reducing bacteria (Omari et al., 2004). The ash produced during burning could serve as a substrate for sulfur oxidizers. The increase in the PLFA profile for SRB in previously burnt plots during flooded periods may thus be attributed to the burning. In shifting cultivation systems, the most commonly observed change in soil following slash and burn clearing of tropical forest, is a short-term increase in nutrient availability of elements such as sulphur. Shifting cultivation studies also commonly cite the incorporation of nutrient rich ash from consumed above ground biomass into soil as the reason for this change (Giardina et al., 2000). These results are also in accordance with Klamer and Baath, (1998), who state that initially after a fire, microbial biomass picks up because of increased substrate.

The low organic matter content in burnt grassland plots (2(03), 3(03), 4(03) 5(03)) as opposed to the unburnt (Figure 4) can be attributed to losses of above ground

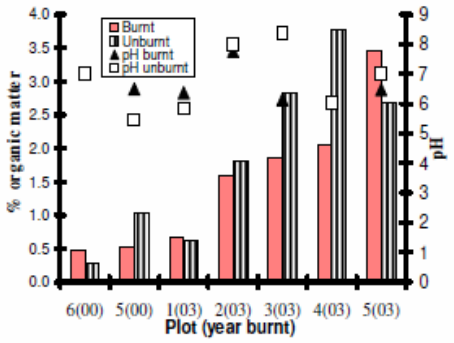

Figure 4. Soil organic matter content and pH along the Boro route.

vegetation due to fire. Above ground vegetation losses due to fire in grasslands can be massive as only root biomass is returned to the soil to contribute to soil organic matter formation. Depending on the frequency of fires, this could negatively affect levels of soil organic matter and eventually nutrient holding capacity. These soils are highly sandy (>85% sand; Bonyongo and Mubyana, 2004), thus most of their CEC is due to organic matter. Because of the role organic matter plays in nutrient holding, reductions in organic matter can result in low nutrient holding capacity, which could affect plant growth, especially in the dry season when there is no nutrient replenishment from floods.

Although in this study no significant changes in soil pH were detected between burnt and unburnt plots, it is highly likely that with frequent burning sulfur oxidizers will increase which could result in an increase in soil acidity.

Increases in the PLFA 10me18:0, indicative of actinomycetes, may well be attributed to increases in actinomycetes. Actinomycetes degrade resistance plant residues such as lignin and cellulose at high temperatures, typical characteristic of the Okavango Delta (day temperature >40^{0}C in dry season). Their hardiness allows them to survive under low moisture levels, which may follow burning.

The reductions in soil respiration in the burnt plots observed in this study could be attributed to reductions in soil microbial populations, especially general bacteria, as fire has been shown to put a stress on microbial activities such as reproduction (Ojima et al., 1994). This may in turn result in low overall microbial populations and thus the low soil respiration observed in the burnt plots. The low soil respiration also coincided with the low PLFA indicators for general bacterial observed in the burnt plots (Table 3). Although soil texture may influence soil respiration, it was not an important parameter to consider in this study, as all the soils studied were sandy (82-85 % sand).

The non significant influence of burning on soil nitrogen observed in this study could be attributed to the flood pattern of these soils. The Okavango Delta soils nitrogen is mostly of floodwater origin as moisture content is positively collated with soil N levels (Omari et al., 2004). In this study, total soil nitrogen was more associated with moisture than with burning (Table 2). Seasonal flooding in the Okavango Delta arises mostly from the inflow originating from the Angolan highlands streams which converge to form two major tributaries (Cuito and Cubango) that merge into the Okavango River, later flowing into the Delta. Debris, sediments, and chemical elements from the riverbanks upstream are hydro-logically transported to the floodplains through surface and ground water flow and with additions from precipitation (McCarthy et. al., 1991). It is therefore likely that even if there are losses of soil nitrogen due to burning, they will not be detected because of the nitrogen replenishment by floodwater.

Conclusion

The results of this study indicate that fire changes the soil microbial community structure. These changes are mostly expressed as increases in soil fungal and actinomycetes populations. Bacteria are highly likely to experience stress after burning as reflected by the increase in stationary phase PLFA. Overall, microbial population is reduced as reflected by decreases in soil respiration in the burnt plots. The influence of burning on soil organic matter content depends on the type of vegetation cover as soils dominated by Mopane woodland seemed to have been least influenced by fire. However, soils covered by grasslands showed significant decreases in soil organic matter with burning. In the floodplains, the effect of burning on organic matter is more pronounced in the primary floodplain with more grass cover than the tertiary floodplain with less grass.

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