The Effects of Soil Cover on Soil Respiration and Microbial Population in the Mopane (*Colophospermum mopane*) Woodland of North Western Botswana

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**ABSTRACT**

Soil cover influences soil biological and chemical processes in various ways. The effects of soil cover (bare soil without litter, litter cover, Mopane tree canopy and grass cover) on soil respiration and microbial population at four sites in the Mopane woodland of north western Botswana were investigated. Soil respiration rates were measured using an infrared gas analyzer. Nitrifying bacterial populations were quantified by MPN on ammonium and nitrite carbonate media, oligotrophs on 1% nutrient agar, actinomycetes on starch casein agar, bacteria in the soil homogenate by MPN on sodium chloride agar baited with *Escherichia coli*. Fungal biomass carbon using buried slides were also determined. Soil respiration in different habitats was significantly influenced by type of cover, diurnal temperature variations and soil moisture. Soils under cover showed significantly higher soil respiration than the bare soils. Autochthonous bacterial populations in the Mopane woodland soils consisted mostly of oligotrophs which varied insignificantly between seasons. Fungi were the most dominant microorganisms in all the Mopane woodland soils, with biomass of 102.05 to 282.14 µg C/g in the wet season and 11.84 to 44.16 µg C/g soil in the dry season. Microscopic observation of buried slides revealed that fungi play a vital role in holding soil particles together in these soils. The results showed a strong positive relationship between changes in fungal biomass and fluctuation of soil respiration. However, no clear correlation was observed between the variation of soil respiration and other microbial populations (oligotrophic bacteria, actinomycetes, and nitrifying bacteria). Overall, these results indicate that in soils under Mopane tree canopy, fungi contribute significantly to soil structure and soil respiration. Other microbial populations consist mostly of oligotrophs which show minimal seasonal variations. Soil moisture significantly influences seasonal fluctuation in soil respiration.

**Keywords:** biomass, fungi, habitats, Maun, nitrification, oligotrophs

**INTRODUCTION**

Mopane woodland soils of north western Botswana are part of the larger Kalahari Sando Region which stretches from the central part of Congo Brazzaville, running through the south eastern part of the Democratic Republic of Congo, the north western part of Angola, the south western part of Zambia, the northern western part of Namibia, the northern, and southern parts of Botswana and the northern tip of South Africa (Steffen 2000). These soils are highly sandy (>85% sand) with a very low moisture holding capacity (Benyengo and Mubyana 2004). The soils also receive very low annual rainfall of approximately 450 mm (Rugrose 1999) usually between the months of December and March. Most of the year these soils are exposed to extremely dry conditions with mean maximum relative humidity of 64% and minimum of 20% (Blakota 1987). Apart from the Okavango Delta and the immediate vicinity with a very high plant diversity and density due to flood waters (Musama et al. 2004), Mopane woodland soils which are further from the Delta are very rarely if at all influenced by the Delta water. This gives rise to a vegetation type of low plant diversity and low density during the dry season (May to September) which is dominated by Mopane trees (*Colophospermum mopane*) and shrubs (*Ximenia calytra*) in these Mopane woodland soils (Ellery and Ellery 1997). During the rainy season, few annual grasses germinate but these usually dry out shortly. Tropical forest such as the Mopane woodland though dry and with little plant diversity are of great environmental significance in the regions they occur, as they are important in the carbon cycling budget of those areas (Mellilo et al. 1992; Lloyd and Taylor 1994; Veenendaal et al. 2003).

Among the components of carbon balance from the Mopane woodland is soil respiration. Soil respiration is the release of carbon dioxide (CO₂) from soils by living soil biota and roots respiration, and to a lesser extent, chemical oxidation of carbon compounds (Holt et al. 1990; Lloyd and Taylor 1994). Soil respiration is the main mechanism of carbon transfer from soil to the atmosphere (Larsen et al. 1998; Yiqing et al. 2005). Understanding the relationship between soil respiration and the influencing factors is as important as quantifying the amount of CO₂ released from the soil (Fang et al. 1998). Although there have been studies on soil CO₂ efflux beneath forest canopy (Fang et al. 1998, Yiqing et al. 2005), the results vary between regions due to variations in environmental factors. Factors such as season, precipitation, temperature, topography, soil properties and soil organic matter due to their influence on soil microbial population and soil cover, may influence soil respiration (Holt et al. 1990; Fang et al. 1998; Ryan and Law 2005).

Despite the abundance of soil respiration data, global coverage is poor with arid and tropical regions having received the least attention (Yiqing et al. 2005). Until this study, no measurements of CO₂ efflux had been undertaken in the tropical Mopane woodland soils of north western Botswana. This study was set up to determine spatial variation of CO₂ efflux on the forest floor of the Mopane woodland in Maun during different seasons. The variation was determined in four different habitats (spatial variation);
soils without litter cover (bare soils), soils with cover i.e., soils with dead litter cover (litter cover), soils with grass cover (grass cover) and soils directly under mopane trees canopy (tree canopy). The study also aimed at relating the variability to soil moisture content and soil temperature to soil respiration. Furthermore, the study attempted to determine the variability of some selected microbial populations (fungi, chlorophytes, bacteria, fungi, actinomycetes, and protozoa) between different habitats and possible relationship to soil respiration. The study's specific objectives were to assess (i) the influence of seasonal variations i.e., soil moisture content, soil temperature and effect of time of day on soil respiration, (ii) the variability of soil respiration between different habitats and (iii) the effect of different habitats on selected microbial populations.

MATERIALS AND METHODS

Site description and sampling

The study was conducted in the mopane woodland about 10 km east of Mabula, Botswana (23° 33' E, 19° 54' S), 960 m above sea level (Egbersmale et al. 1996). The area is also the surroundings of the carbon flux tower in the region (23° 33'08" E, 19° 54' 52" S). Four sites were randomly selected around the tower area at 10, 30, 50 and 70 m away from the tower. The sites were chosen because they had the best combinations of the four habitats closest to the tower with existing environmental data. At each site four habitat samples were taken: i) bare soil without litter cover, ii) bare soil with litter cover, iii) soil under grass cover and iv) soil under mopane trees canopy. Each habitat had three replicates.

Sampling was carried out in August and October 2004, and January and May 2005. Based on the rainfall patterns in the study area, October to January were selected as the wet season and the May to August as the dry season. Soil samples were collected from the A0 horizon at each sampling spot using a disturbed auger. Each 500 g soil sample collected was put in a separate sterile plastic bag. The soil samples were placed in a cooler box and transported to the laboratory for analysis. Once in the laboratory, the samples were partitioned according to use. The soil samples for microbiological analysis were analysed immediately upon arrival at the laboratory. Whenever it was not possible to perform microbiological analysis immediately upon arrival at the laboratory, the samples were refrigerated at 4°C and analysed within 2 days. The soil samples were then stored at room temperature.

Soil respiration determinations

Soil respiration was measured using a portable 12V battery driven soil respiration system consisting of an infrared carbon analyser (model EGM-3. PP Systems) with a data-logger and integral pump, an environmental sensor for soil temperature (temperature probe) and a soil respiration chamber (PP Systems-Infrared Gas Analyser (EGM-3). The chamber enclosed a surface area of 7 x 10-4 m2 and was equipped with a small low speed fan for mixing the air in the chamber. To avoid disturbance during repeated measurements and to ensure consistency at different locations, 48 polyvinyl chloride (PVC) collars with sharpened edges (150 mm tall, wall thickness 3 mm) were installed to exactly fit the chamber's outer diameter.

The collars were hammered 100 mm into the forest floor 3 days before the first measurement at each habitat. For measurement, the chamber was placed tightly onto the PVC collar on the forest floor surface. During the measurement, air was drawn from the chamber through a filter into the analyser at intervals of 120 sec. Forest floor CO2 was regarded as being proportional to the rate of change of CO2 concentration in the chamber (Baldwin 1990). Four replicate measurements were taken between 08:30 hrs and 11 hrs and another 48 between 13 and 18:30 hrs. Each time the soil respiration was measured, soil temperature at the A0 horizon (5 cm) was also measured using the temperature probe of the EGM-3. PP System.

Microbial soil analyses

Fungal biomass carbon determination using the Roscoy-Cholodny slide technique

Fungal biomass carbon was determined in situ using the Roscoy-Cholodny slides technique (Roscoy et al. 1936, Parkinson et al. 1971, Franklin 1975, Parkinson and Paul 1984; Atlas and Barth 1993). The technique assumes that the glass slide surface is non-selective and acts like the surface of mineral particles in soil. Thus organisms that adhere to the slide can be considered representative of that soil community in general (Atlas and Barth 1993).

Two slides (rocked to and fro) were buried vertically in the soil at each habitat. After 7 days, the slides were removed by agitating them from side to side and slowly pulling them out of the soil. Each slide was best fixed and stained with Methylene blue (1 g 50%). Methylene blue dissolved in 0.1 g NaCl solution in water for 1 min. The stain was then washed off under a gentle running tap water and allowed to air dry. The slides were examined under a compound microscope (Zeiss, Germany GZN) and fungal hyphal lengths were measured (using a calibrated eyepiece micrometer) at 400X magnification. Four hyphal lengths in 15 fields of view per slide were measured and recorded. Mycelial hyphae then were expressed in μg C/g soil biomass carbon using the following assumptions: Fungal hyphae mean diameter is 3-4 μm, density 1.0 μg/cm, dry weight 28%, carbon content 52% on dry weight basis and 1 m mycelium contains approximately 1 μg carbon (Roscoy et al. 1936, Parkinson et al. 1971; Franklin 1975; Parkinson and Paul 1984).

Microbial diversities were determined using plate count technique on solid agar media and MPN. Serial dilutions of soil in sterile tap water were prepared up to 10-8 to plot different solid agar media. Total bacteria populations were determined by spread plating the serial soil dilutions on Tryptone soy broth (BIOMAX 1-28/300) amended with 15 g/l agar (High Media MS90). Oleaginous bacteria were enumerated by plating 0.1 ml dilutions of the 10-2-10-8 on to nutrient poor solid media consisting of soil extract agar amended with 1% nutrient broth (Wallim 1982).

Actinomycetes populations were estimated by spread plating serial soil dilutions on starch casein agar (Williams and Wellman 1982) and then incubating at 25°C for 14 days, to obtain actinomycetes colonies typical of actinomycetes. The colonies were counted using a colony counter and recorded for each habitat. The most probable number (MPN) of bioplastic proteobacteria was determined using the baited plate technique as outlined by (Gupta and Germain 1988). Soil dilutions (10-2 to 10-5) were plated onto the 24 multi-well MPN plates containing 0.8% NaCl solid 15% agar and over laid with 0.5 ml of concentrated cell suspension of Escherichia coli as prey. The plates were incubated at room temperature and microscopic observations of protozoa were made from 6 to 14 days. To verify the method, control samples were made using soils obtained from the Biological Sciences Nature Reserve in Gabarone with known populations of soil protozoa. The MPN of predatory protozoa were determined with reference to the table of Cowan (1950) for use with 10-fold dilutions and 5 replicates per dilution.

MPN of nitrifying bacteria were estimated on ammonium-molybdate carbonate medium and nitrite-calcium carbonate media for ammonium oxidizers and nitrite oxidizers respectively. Soil aliquots (0.33 ml) of 0.1 g soil (10-2 to 10-5) were plated out on to MPN plates containing the media as outlined in the procedure by Schmid and Belser (1989). The plates were incubated in the dark at room temperature for 4 weeks and then tested for the presence of nitrite using Green loriw reagent and for nitrite oxidizers using Zn-MnO4 medium (Schmid and Belser 1989). The MPN of nitrifying bacteria was also calculated using Cochrane's (1950) table for a 10-fold dilution series for 5 replicates per dilution.
Determination of soil characteristics

Soil pH was determined in a 1:2 soil:distilled water suspension (active acidity) and 1:2 soil:0.01 M CaCl₂ (potential acidity) and then measured using a Corning scale pH meter electrode (model 215). Soil texture (%sand, silt and clay) was determined by the hydrometer method (Bouyoucos method). The soil texture class was also determined by using the International classification (Anderson and Ingram 1993). 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 organic matter content was determined using the Walkley-Black method (Walkley 1947).

Statistical analysis

Analysis of variance was performed using the SPSS 10.0 package. Post hoc analyses were performed using the Tukey Test. In the analysis, group separation was based on habitat (bare soils without litter cover, soils with litter cover, grass cover and soils directly under Mopane tree canopy), season, time of the day and the parameter studied.

RESULTS

Effect of environmental factors on soil respiration

The Mopane woodland soils studied were found to be highly sandy with 95% sand and 1.4% silt in all the habitats from which samples were collected. These Mopane woodland soils were found to be slightly acidic with pH values ranging from 5.59 to 6.40. The pH values did not vary significantly between habitats and between seasons (Table 1). The differences in active and potential acidity were also minimal. Generally, the soils had very low organic matter of less than 1% in all the habitats. Total nitrogen levels in these soils were also very low and were always below 0.01% in all the habitats. None of the soil physical characteristics varied with season. Statistical analyses of the data obtained showed that not all factors studied significantly influenced soil respiration (Table 2). Only soil moisture content, temperature, habitat, and fungal biomass were observed to influence soil respiration.

Soil respiration at different habitats differed with season, with higher rates recorded in the wet season than the dry season (Table 3). There were significant differences (P < 0.05) in soil moisture content between the seasons, with the wet season having significantly higher soil moisture content than the dry season. Although there were significant differences in soil moisture content between the two seasons, no significant differences were observed between habitats within the same season. In this study, soil respiration also differed with season (Table 3). Generally higher rates of mean daily respiration (0.24 to 0.65 g CO₂/m²/hr) were observed during the wet season with high soil moisture content (2.01% to 2.99%), while relatively low soil respiration rates (0.05 to 1.2 g CO₂/m²/hr) were recorded during the dry season when soil moisture was very low (0.6% to 0.88%) (Table 3). Within each season the bare habitat (bare soils without litter cover) showed significantly lower soil respiration than habitats with cover (bare soils with dead litter cover, soils with grass cover and soils directly under Mopane tree canopy). The rate of the day did not seem to significantly influence soil respiration within each habitat as there were no significant differences in soil respiration rates between the mornings and afternoons (Table 3). Among the different habitats both in the mornings and afternoons, soil respiration rates did not differ significantly between the three habitats with cover. However, soil respiration rates in the bare soil without cover was significantly lower (P < 0.05) than habitats with cover.

Although there were no significant differences in soil temperatures between the wet and dry season, there were soil temperature variations with time of the day. Afternoon soil temperatures were generally higher than the morning temperatures (Table 4). Soil temperature across the seasons did not differ significantly; therefore it had no observable influence on seasonal variation in soil respiration. Soil temperatures also did not significantly differ between the habitats within each season although they were observed to be
Table 4 Effect of mean soil temperature and time of the day on the mean soil respiration in the different habitats during the dry and wet seasons

<table>
<thead>
<tr>
<th>Soil habitat</th>
<th>Morning Temp (°C)</th>
<th>Respiration (g CO₂/m²/h)²</th>
<th>Afternoon Temp (°C)</th>
<th>Respiration (g CO₂/m²/h)²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>22.4 ± 2.0</td>
<td>0.24 ± 0.07</td>
<td>40.5 ± 2.7</td>
<td>0.49 ± 0.14</td>
</tr>
<tr>
<td>Litter cover</td>
<td>26.9 ± 1.0</td>
<td>0.62 ± 0.48</td>
<td>38.1 ± 5.0</td>
<td>0.58 ± 0.12</td>
</tr>
<tr>
<td>Grass cover</td>
<td>27.2 ± 1.3</td>
<td>0.55 ± 0.30</td>
<td>38.4 ± 4.9</td>
<td>0.65 ± 0.20</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>20.8 ± 1.4</td>
<td>0.04 ± 0.4</td>
<td>57.3 ± 5.3</td>
<td>0.53 ± 0.11</td>
</tr>
<tr>
<td>Dry season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>25.3 ± 4.4</td>
<td>0.05 ± 0.3</td>
<td>31.7 ± 3.7</td>
<td>0.08 ± 0.03</td>
</tr>
<tr>
<td>Litter cover</td>
<td>28.7 ± 4.5</td>
<td>0.09 ± 0.02</td>
<td>33.7 ± 4.3</td>
<td>0.09 ± 0.04</td>
</tr>
<tr>
<td>Grass cover</td>
<td>31.9 ± 5.8</td>
<td>0.08 ± 0.03</td>
<td>34.0 ± 4.3</td>
<td>0.09 ± 0.04</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>28.3 ± 5.0</td>
<td>0.11 ± 0.02</td>
<td>26.7 ± 4.7</td>
<td>0.12 ± 0.03</td>
</tr>
</tbody>
</table>

Table 5 Seasonal variation in microbial populations in the different Mopane habitats

<table>
<thead>
<tr>
<th>Soil habitat</th>
<th>Log 10 CFU/g soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet season</td>
<td></td>
</tr>
<tr>
<td>Bacteroidetes</td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>6.46 ± 0.37</td>
</tr>
<tr>
<td>Litter cover</td>
<td>6.90 ± 0.32</td>
</tr>
<tr>
<td>Grass cover</td>
<td>6.62 ± 0.20</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>6.91 ± 0.25</td>
</tr>
<tr>
<td>Actinomycetes</td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>4.84 ± 0.21</td>
</tr>
<tr>
<td>Litter cover</td>
<td>4.77 ± 0.11</td>
</tr>
<tr>
<td>Grass cover</td>
<td>4.77 ± 0.15</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>4.80 ± 0.21</td>
</tr>
<tr>
<td>Dry season</td>
<td></td>
</tr>
<tr>
<td>Bacteroidetes</td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>4.56 ± 0.07</td>
</tr>
<tr>
<td>Litter cover</td>
<td>5.64 ± 0.90</td>
</tr>
<tr>
<td>Grass cover</td>
<td>4.64 ± 0.07</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>4.75 ± 0.24</td>
</tr>
<tr>
<td>Actinomycetes</td>
<td></td>
</tr>
<tr>
<td>Bare</td>
<td>4.64 ± 0.17</td>
</tr>
<tr>
<td>Litter cover</td>
<td>4.86 ± 0.18</td>
</tr>
<tr>
<td>Grass cover</td>
<td>4.79 ± 0.19</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>4.80 ± 0.19</td>
</tr>
</tbody>
</table>

Fig. 1 Soil respiration in the different habitats in the wet and dry seasons.

Fig. 2 Effect of time of day on soil respiration.

slightly higher in the wet season. Instead they differed with time of the day. In all the results indicated that soil respiration was higher in the wet season in comparison to the dry season (Fig. 1). Mean morning soil respiration was also always lower than afternoon soil respiration (Fig. 2).

Microbial diversity in the habitats

Microbial diversity studies in the different Mopane woodland soils habitats showed that soil bacterial populations were generally low. Total bacterial counts enumerated on full strength nutrient agar were low most of the times, especially during the dry season where they were below 10² CFU/g soil (Table 5). However, bacteria enumerations on 1/10 strength nutrient agar revealed that there were oligotrophic bacterial populations in the Mopane woodland soils. Although not significantly higher (<1 log₁₀ unit), generally the oligotrophic bacterial populations in the habitat without cover (bare) were lower than in habitats with cover in both the wet and dry season (Table 5). No detectable differences in oligotrophic populations between the seasons were observed. Thus the influence of season on the oligotrophic bacterial population was non-significant, as the populations in the different habitat did not differ with season (Table 5).

Actinomycetes were also found to occur widely in all the Mopane woodland soil habitats both in the wet and dry season. However, the effect of habitat on actinomycetes populations was not significant. The actinomycete populations did not seem to be influenced by the seasons as there were no significant differences in the actinomycete populations between the wet and dry seasons. Samples from the Mopane woodland soils did not show any bactericorecorcorporated protozoa, however the control samples from the Biological Science Nature Reserve in Gaborone indicated those samples to contain at least 10² MPN protozoa per gram soil.

Nitrifying bacteria (ammonium and nitrite oxidizers) populations in the Mopane woodland soils were fairly high and varied with season and habitat. However, because of major variations between replicates, these variations were not statistically significant and did not show a specific pattern as such could not be correlated with soil respiration (Table 6). It was also observed that ammonium oxidizers were significantly higher during the wet season. In addition no significant difference in the populations of ammonium oxidizers at bare habitats without litter was observed between the seasons.

Soil fungal biomass carbon as determined using the Rosso-Cholodny method varied between habitats (Table 7). In both seasons, fungal biomass carbon did not vary between sampling times within the seasons. However between seasons, the wet season had significantly higher fungal biomass carbon than during the dry season (Table 7). The wet season was characterised by high fungal biomass carbon which coincided with high soil respiration. On the contrary,
Table 6: The influence of season on the Most Probable Number of nitri-
ifers in the different Mopane habitats

<table>
<thead>
<tr>
<th>Soil habitat</th>
<th>Wet season</th>
<th>Dry season</th>
<th>Wet season</th>
<th>Dry season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base</td>
<td>783</td>
<td>681</td>
<td>159</td>
<td>552</td>
</tr>
<tr>
<td>Litter cover</td>
<td>1119</td>
<td>600</td>
<td>134</td>
<td>218</td>
</tr>
<tr>
<td>Grass cover</td>
<td>781</td>
<td>750</td>
<td>204</td>
<td>676</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>1318</td>
<td>630</td>
<td>204</td>
<td>149</td>
</tr>
</tbody>
</table>

*Most Probable Number per gram soil

Table 7: Seasonal variation in fungal biomass carbon (µg C/g soil) in dif-
ferent habitats.

<table>
<thead>
<tr>
<th>Soil habitat</th>
<th>Wet season</th>
<th>Dry season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Base</td>
<td>153.19 a</td>
<td>11.84 a</td>
</tr>
<tr>
<td>Litter cover</td>
<td>266.09 b</td>
<td>23.99 b</td>
</tr>
<tr>
<td>Grass cover</td>
<td>285.14 b</td>
<td>34.00 b</td>
</tr>
<tr>
<td>Tree canopy</td>
<td>162.01 a</td>
<td>44.16 b</td>
</tr>
</tbody>
</table>

lower fungal biomass carbon was recorded in the dry season. During the wet season, the difference in fungal biomass in habitats with cover and those without cover were not always statistically significant, but they were always lower in the habitat without cover.

**DISCUSSION**

**Effect of abiotic factors on soil respiration**

The Mopane woodland soils of northern west Botswana were found to be highly sandy with most habitats having sand contents above 95% (Table 1). As such, these soils have an inherent low moisture and nutrient holding capacity. With the rains in the wet season, soil moisture increased. However, soil moisture content variation within seasons was minimal: 2.01 to 2.69% in the wet season and 0.68 to 0.88% in the dry season (Table 3). The increased soil moisture content in the wet season coincided with the increase in soil respiration as the wet season showed significantly higher soil respiration than the dry season (Table 3). In this study, the effects of soil moisture content on soil respiration within seasons were minimal. Variation in soil respiration within each season was not significantly correlated with soil moisture content. However, significant variation in soil moisture content existed between seasons (Table 2). This variation coincided with fluctuation in soil respiration, suggesting a strong link between variation of soil respiration and soil moisture between seasons. A strong seasonality in soil respiration is highly pronounced in areas with a sea-
sonal pattern of rainfall (Cuevas 1995). Thus seasonality in soil respiration in the Mopane woodland was linked to the seasonal pattern of rainfall in the area. These results also agree with observations by other researchers that an in-
crease in water potential coincides with increased microbial respiration and the resultant soil respiration (Moore 1980).

Soil moisture also plays a significant role in soil respiration as observed in Australian tropical semi-arid woodland where soil moisture content was observed to be the major factor controlling soil respiration (Holt et al. 1990). Furthermore, fluxes of CO₂ have been found to show a general increase with soil moisture content in a range of soils (Howard and Howard 1993). When the relationship between seasonal variation of soil respiration, soil moisture and soil temperature were explained by multiple linear regression analysis, soil moisture accounted for 82% of the variance, with temperature accounting for only 7% in the dry tropics in eastern Australia (Holt et al. 1990). In the pre-
sent study the regression equation employed for the three variables (habitat, soil moisture content and soil tempera-
ture), showed that these explained over 76% of the variance. Soil moisture alone accounted for 73% of the variance with temperature and habitat providing only 48% of the variance. Litter in most forest soils has a signif-
inant role in soil moisture between seasons in the Mopane wood-

land was strongly associated with the seasonality of the soil respiration.

Increase in soil temperatures have been shown to result in increased soil respiration when moisture is not a limiting factor in a range of soils (Howard and Howard 1993). Other studies have shown that although temperature has some in-
fluence on soil respiration it only exerts a decisive influence when there is sufficient soil moisture (Lloyd and Taylor 1994). In the Mopane woodland soils studied, soil tempera-
ture did not differ significantly between seasons. The mean daily temperatures ranged from 32.1 to 33.9°C in the wet season and 27.5 to 32.9°C in the dry season. Therefore it was not easy to link variation of soil respiration between seasons to soil temperature. Meanwhile the temperatures varied from 25.3 to 31.9°C in the mornings and from 26.7 to 40.5°C in the afternoons (Table 4). The effects of morn-
ing and afternoon temperatures differed significantly in the Mopane woodland. Lower temperatures recorded in the mornings coincided with lower soil respiration rates. The afternoons with higher temperatures were characterized by higher rates of soil respiration. This therefore suggested a positive relationship between the diurnal soil respiration rate and soil temperature in these soils (Fig. 2). This relationship has not been observed in all ecosystems (Holt et al. 1990) however, it has been reported in some (Blankes 1998, Fang et al. 1998).

Other studies have shown diurnal soil respiration to be controlled by soil temperature and independent of diurnal soil moisture content in a range of soils (Parker et al. 1983). Possibly because an increase in soil temperature leads to an increase in the pool size of carbon respired by soil microbes (Zogg et al. 1997). This increase in substrate pool size at higher temperatures results in a shift in the microbial commu-

nity position associated with soil warming as dominant communities at higher temperatures have the ability to meta-

bolize substrates not used by members of microbial community dominant at low temperatures (Zogg et al. 1997). This may be the case in the Mopane woodland soils of Main.

**Effect of biotic factors on soil respiration**

In this study different rates of soil respiration were recorded in different habitats. The bare habitat had significantly lower rates of soil respiration compared to habitats with cover. Habitats under Mopane tree canopy recorded the highest rates of soil respiration (Tables 3 and 4) irrespective of variations in temperature and moisture. This was evident in mornings as well as afternoons and in the overall respiration recorded during the two seasons. These findings are comparable to the results obtained in a pure plantation where soil respiration under palmetto was significantly higher than that from open floor in slash pure plantation (Fang et al. 1998).

In this study, fungal biomass carbon was higher in soils under cover than those under cover. A link exists between basal respiration and macrofungal biomass and organic carbon; as some researchers have observed maximum microbial populations in forest soils with high litter fall and the lowest population when litter fall was minimal (Yonge et al. 2005). The influence of cover has also been noted in earlier studies in the same region. Mulyacas John et al. (2007) showed that soils under grassland cover had higher organic matter and higher microbial biomass than Mopane woodland soils in the same region. Thus the Mopane woodland soils were characterized by higher mic-

robial activity in habitats with litter cover giving rise to higher rate of soil respiration. Valentini et al. (2000) also suggested that habitats with cover are highly likely to have a higher soil respiration and that the major contributors to soil respiration in forest soils such as Mopane woodland soils are root and mycorrhizal. In bare habitat soils with no litter cover the contributors to soil respiration are mostly...
likely to be chemical oxidation and minimal contribution arises from microorganisms and soil fauna (Ryan and Law 2005). Since there were very few or no fine roots in bare soils, soil respiration may have originated mainly from microbial respiration especially fungi. Burned root and root slides in bare soils without litter cover showed presence of less fungal hyphae when compared to habitats with cover. This provides additional evidence of microbial activity in these habitats and their possible contribution.

This study also showed that in Mopane woodland soils, habitat can be used as a predictor of variations in soil respiration. The linear regression model showed that 36% of the time, habitat alone accounted for the variation in soil respiration. The regression coefficient also showed that the effect of habitat was significant (p < 0.05). One way ANOVA with habitat as an independent and soil respiration as the dependent factor, showed the effects of habitat on morning, afternoon and mean daily soil respiration to be significant at p < 0.05.

In the Mopane woodland soils studied, total bacterial counts were very low. However, oligotrophic bacterial populations ranged from 3.1 x 10^7 to 2.1 x 10^8 g^-1 soil in the dry season and 1.2 x 10^7 to 3.0 x 10^7 g^-1 soil in the wet season (Table 5). The Mopane woodland soils of Maun are an extension of the Okavango delta soils. However, irrespective of having similar physical soil characteristics, these soils harbour lower bacterial populations than similar woodland soils closer to the Okavango Delta (Mubanya et al. 2003). This was attributed to declining moisture content, resulting in very little vegetation and soil organic matter as distance from the Delta increases. When compared to other regions, these populations are also slightly lower than what was observed by Otia and Hatori (1985) in their study using two types of soils. A comparison of microbial populations of oligotrophic bacteria were observed to vary from 3.9 x 10^5 to 6.5 x 10^6 g^-1 soil, and from 7.2 x 10^5 to 3.3 x 10^6 g^-1 soil even drier matter of sands denoted as sand A and sand B respectively. Moisture content in the Mopane woodland soils had been accounted for 55% of the variance, while all other microorganisms accounting for only 30.3% of the variance. The regression coefficient revealed that the effect of fungal biomass was significant whereas the effect of microorganisms was not significant. This suggests that fungi have a more significant influence on variations of soil respiration compared to other microorganisms studied in the Mopane woodland soils. This study confirms Yung (2005) findings who observed that CO_2 tends to show a positive correlation with fungal biomass.

In this study (Table 6) ammonium oxidizers were generally higher in the wet season. During this season there is a lot of microbial activity and mineralization releases ammonium ions from ammonium compounds and these serve as substrates for ammonium oxidizers. Nitritification of ammonium compounds such as ammonium sulphate has been observed to proceed more rapidly at 25°C at different moisture content levels. However, it is also inhibited at very low or very high moisture content and soil temperatures (Causon and Mann 1980); characteristic of these Mopane woodland soils where the moisture contents are very low in the dry season. In bare soils, nitrate formation was generally lower than in habitats with cover especially in the dry season as indicated by the high population of NO_3 oxidizers. Presence of nitrifying bacteria in dry Mopane woodland soils is also indicative of their adaptation to the soil climate.

In the Mopane woodland soil fungal biomass carbon varied significantly with season in all habitats (Table 7). These variations seemed to be soil moisture content dependent and fungal biomass was affected more than the biomass of other microorganisms studied. Fungal biomass carbon ranged from 102.0 to 282.14 mg C g^-1 soil in the wet season and from 11.84 to 44.16 mg C g^-1 soil in the dry season (Table 7). Fungal populations, like all microbial populations, show a positive response to increasing water availability (Cuevas 1993). Moreover observations of higher fungal populations in the wet season than in the dry have been recorded in the Okavango region as well as in other parts (Banda 2004). In this study the wet season was characterized by high fungal biomass carbon coinciding with high soil respiration rates. Similarly the very low fungal biomass carbon observed in the dry season corresponded to very low soil respiration rates. The high soil respiration in the wet season observed in this study was due to increased root exudates which serve as microbial substrates. The fungal biomass fluctuations may be associated with low below ground plant biomass during the dry season which may serve as a substrate as opposed to the wet season with high plant biomass (Bonyongo and Mubanya 2004). Mellilo et al. (1992) also noted that in the wet season, favourable moisture which permitted flourishing ground vegetation in turn added fresh substrate to the soil in the form of leaf litter and root. These conditions may have accounted for an elevation in fungal biomass carbon during the season. The biomass decline to very low levels in the dry season must have been due to deficiencies in moisture. Generally higher levels of fungal biomass carbon were recorded in habitats with cover, this was more pronounced in the dry season. This may explain the higher activity observed in these habitats as reflected by the respiration rates thereof. The close relationship between high fungal biomass carbon, high moisture content and high plant litter indicates fungal as the major decomposers in these soils probably because fungi are more active at lower soil water potential than bacteria (Bandu 2004). Moreover direct microscopic observation has shown that in the upper soil horizon a blend of bacteria, mycelium, hyphae and yeast cells usually form 90-95% of the biomass (Zvyagintsev 1995).

When the relationship between variation of soil respiration and oligotrophic bacteria, actinomycetes, nitrifying bacteria and fungal biomass carbon were explained by a linear regression analysis, the equation explained at least 54% of the variance. Fungal biomass alone accounted for 55% of the variance, while all other microorganisms accounting for only 30.3% of the variance. The regression coefficient revealed that the effect of fungal biomass was significant whereas the effect of microorganisms was not significant. This suggests that fungi have a more significant influence on variations of soil respiration compared to other microorganisms studied in the Mopane woodland soils. This study confirms Yung (2005) findings who observed that CO_2 tends to show a positive correlation with fungal biomass.
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