Influence of seasonal flooding on soil total nitrogen, organic phosphorus and microbial populations in the Okavango Delta, Botswana

Tabo Mubyana★*, Martin Krah†, Otlogetswe Totolo‡ & Mpaphi Bonyongo†

★ *Department of Biological Sciences, University of Botswana, Private Bag 0022, Gaborone, Botswana*
† *Harry Oppenheimer Okavango Research Centre, Private Bag 285, Maun, Botswana*
‡*Department of Environmental Sciences, University of Botswana, Private Bag 0022, Gaborone, Botswana*

(Received 22 July 2002, accepted 22 July 2002)

The effect of flooding on soil total nitrogen, phosphorus and microbial population in different vegetation zones (floodplain, island and woodland) and profile depth (0·1, 0·5, 2·0, 3·0, 4·0 and 5·0 m) of the Okavango Delta was studied from February to July 1999. Total nitrogen significantly differed with soil profile depth, moisture regime and months. In the woodlands, insignificant total nitrogen was detected at all depths except at 0·1 m, where 0·03% and 1·17% were detected in February and March, respectively. In the island samples, only 0·05% was detected at 4 m in February. Nitrogen in the floodplain samples was concentrated in the A1 horizon where 0·12%, 0·61% and 0·03% were detected in February, March, and May, respectively. Organic phosphorus significantly differed with vegetation zone but not with months and depth. Although organic phosphorus was low (0·02–0·52%) at all sites, it was liberally distributed throughout the profiles. On the island, actinomycetes were only detected up to 2 m in February and up to 3 m in July. Fungi concentrated in the top 0·5 m (10^3–10^5). In both the floodplain and island samples, bacteria concentrated in the upper 3 m. However, after May, populations decreased significantly. In the floodplain, significant actinomycetes populations were only detected in the upper 0·5 m. Generally, organic phosphorus showed positive correlations with fungal populations. This study indicates that these soils are low in total nitrogen and phosphorus.

Keywords: Okavango; Botswana; soil nitrogen; phosphorus; woodland; island; floodplain

*Corresponding author. E-mail: mubyanat@mopipi.ub.bw.

Introduction

The Okavango Delta of northern Botswana is an inland delta sustained mainly by rainfall in the Angolan highlands. The rainwater converges to form the major tributaries, which merge into the Okavango River. The latter flows through the Caprivi strip of Namibia and the Delta's panhandle region. Eventually, it spreads into numerous channels, temporary and seasonal swamps, supporting a highly diversified pristine ecosystem. Although high rainfall occurs in Angola in November–December, the annual floodwaters only reach the seasonal swamps of the Delta in June–September and thus coinciding with the dry season of the Kalahari desert, imbedding the Okavango Delta. The Okavango soils are highly sandy with a minimum of 85% sand. Therefore, they have been classified by FAO/UNESCO soil classification system as Fluvisols with a very low CEC (<5 meq $100\,g^{-1}$ soil) and thus have a low nutrient holding capacity (Staring, 1978). These soils also have a high hydraulic conductivity and low water holding capacity. The seasonal floods are most likely to leave these soils highly leached and thus low soil nitrogen and phosphorus content, with the phosphorus being subjected to both leaching and fixation by cations at most soil pH values (Moistafa, 1999). These soils are also very low in organic matter. Typical habitats consist of floodplains, woodlands and islands. Grasses and sedges characterize the floodplain. Riparian vegetation and palm trees characterize the woodland, while the islands are mostly bare with little to no vegetation cover at all. Micro-organims play a major role in mineralization of organic P to available P, which is later used by both the soil flora and fauna (Currie & Kalff, 1984; Gachter *et al.*, 1988; Richardson, 1994). They also play a major role in soil nitrogen transformations such as fixation, nitrification and denitrification (Hart *et al.*, 1994; Smith, 1994). Soil moisture controls microbial activity through its influence on oxygen and water availability. An understanding of the influence of seasonal flooding on microbial activities and levels of major nutrients such as nitrogen and phosphorus may lead to better understanding of interactions between the different habitats and vegetations types of the seasonal swamps. Therefore, the main objective of this study was to first obtain data on the influence of flooding on the predominant habitats (vegetation zones), which are floodplains, islands and the riparian wood fringe (woodland) on the islands.

Methods and materials

Site and sampling

The Harry Oppenheimer Okavango Research Centre (HOORC) field site in Nxaraga, located at the southern tip of the Moremi Game Reserve (Fig. 1), was selected for the study due to its high annual variations in soil moisture content. The flood season commences in June and terminates in October–November, flooding the seasonal floodplains and raising the water table of the adjacent wood fringe and islands. The flood season is followed by a dry season (November–May) with very low soil moisture and declining ground-water table.

Soil samples were collected monthly from the floodplain, woodland and island at different profile depths (0·1, 0·5, 2·0, 3·0, 4·0 and 5·0 m) from February to July/August 1999. These months represent the most drastic soil moisture fluctuations between the dry and flood months (Heemstra, 1976). Due to waterlogging in the floodplains, samples were only collected from February to May. A depth marked undisturbed soil auger was used for soil sampling. To investigate the influence of flooding on microbial populations, total nitrogen, organic and available phosphorus,

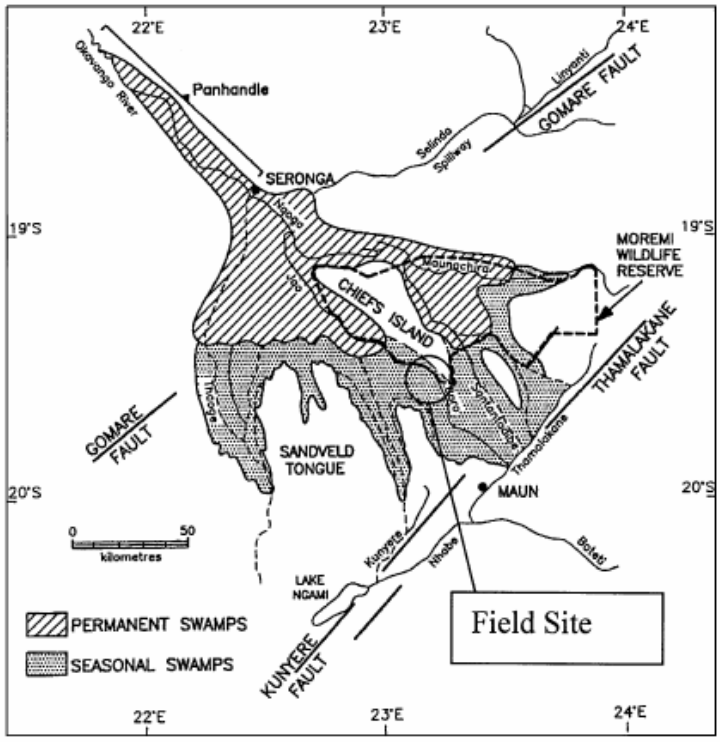

Figure 1. The Okavango Delta in Northern Botswana, the Harry Oppenheimer Okavango Research Centre field site is located at the southern tip of Chief's island within the seasonal swamps.

five samples were collected from each depth using an undisturbed auger fitted with a 70% alcohol sterilized end. Samples were then put into sterilized zip bags and brought to the lab and mixed to create a composite sample for the profile. Three profiles (replicates) were sampled per vegetation zone (habitat). The soil samples for nutrient analyses were air-dried, sieved through a 2 mm sieve and stored at room temperature until analyses.

Microbial populations

Samples for microbial population counts were moisture re-equilibrated to 60% moisture holding capacity for 48 h by adding sterile distilled water prior to the determination of microbial populations. Microbial populations were determined by plate count techniques using the following solid agar media. Bacteria populations were determined by spreadplating serial soil dilutions on trypticase soy broth (BIOMERIEUX Y42830) amended with 15 $g l^{-1}$ agar (High Media M290). Most probable number (MPN) estimates of total bacteria enumerated on 0·3% (w/v) trypticase soy broth (Lawrence & Germida, 1988) were used to verify bacteria spread plate counts. The MPN estimates of total bacteria were determined by reference to the table of Cochran (1950) for use with ten-fold dilutions and five tubes per dilution. Fungi populations were estimated by spreadplating serial soil dilutions on malt extract agar (MEA, Oxoid medium CM57, Oxoid Ltd., Basingstoke, Hampshire, UK). While actinomycetes populations were estimated by spreadplating serial soil dilutions on starch casein agar (Kurster & Williams, 1964; Williams & Wellington, 1982).

Anaerobic bacteria populations were determined by plate count methods as above but incubated in anaerobic gas chambers (Gerhardt *et al.*, 1981).

Determination of total nitrogen and phosphorus

Total N was determined using an automatic N analyser (EA 1100, ThermoQuest). The system was calibrated using EDTA as a standard.

Soil organic P content was calculated from ignited (550°C) and unignited samples after extraction with 1 N H_2SO_4 (Wanatabe & Olsen, 1965; Olsen & Sommers, 1982). Available P in the soil samples was determined using the Bray P-1 method (Bray & Kurtz, 1945).

Statistical analysis

Analysis of variance was performed using the SPSS 7·5 package. *Post hoc* analyses were performed using the Tukey test. In the analysis, group separation was based on habitat (floodplain, island or woodland), profile depth and the parameter studied, i.e. N, P or microbial population.

Results

Microbial populations

Table 1 shows probability levels for statistical significance for the different parameters. Significant variations due to vegetation zone, depth and month were observed. However, non-significant variations were obtained for nitrogen and the nitrogen × vegetation zone interaction. Microbial populations in the vegetation zones varied with both profile depth and month of the year. However, bacteria, fungi and actinomycetes showed different trends. Table 2 shows bacteria populations in the different vegetation zones at different depths during the dry period, before and during the flood. In all the samples from the different vegetation zones, bacteria populations were concentrated in the top 2 m of the soil profile with populations ranging from 10^7 to 10^8 CFU g^{-1} soil. Below 2 m, bacteria populations in all the vegetation zones decreased significantly to 10^5 CFU g^{-1} soil. With increases in profile depth, anaerobic bacteria populations

Table 1. *Probability levels for statistical significance for different parameters*

Variable	Probability
Vegetation zone	**
Depth	*
Months	**
Nitrogen	ns
Organic P	*
Inorganic P	*
N × Vegetation zone	ns
Organic P vegetation zone	**
Inorganic P × vegetation zone	*
Inorganic P × profile depth	*
Organic P × vegetation zone	*

*,**Statistical significance: at $p<0·05$ and $p<0·01$, respectively; ns = not significant.

Table 2. *Bacteria population in the different vegetation zones*

Profile depth (m)	Bacteria population in the different vegetation zones, profile depths and month								
	Flood plain			Island			Woodland		
	Feb	March	April	Feb	May	July	Feb	May	July
0·1	$2·5 \times 10^6$	$4·6 \times 10^8$	$3·6 \times 10^8$	$1·8 \times 10^7$	$3·8 \times 10^7$	$7·0 \times 10^8$	$1·2 \times 10^7$	$4·9 \times 10^6$	$2·5 \times 10^8$
0·5	$1·7 \times 10^8$	$4·5 \times 10^8$	$5·8 \times 10^8$	$2·3 \times 10^9$	$1·3 \times 10^9$	$5·4 \times 10^9$	$2·0 \times 10^8$	$4·8 \times 10^8$	$1·2 \times 10^8$
2·0	$1·1 \times 10^7$	$9·9 \times 10^7$	$7·5 \times 10^7$	$5·2 \times 10^7$	$3·7 \times 10^7$	$9·7 \times 10^8$	$1·1 \times 10^9$	$4·4 \times 10^7$	$4·6 \times 10^9$
3·0	$1·5 \times 10^6$	$1·4 \times 10^6$	$6·2 \times 10^6$	$1·1 \times 10^6$	$3·6 \times 10^6$	$9·5 \times 10^7$	$3·2 \times 10^7$	$3·9 \times 10^6$	Logged
4·0	$8·8 \times 10^6$	$1·1 \times 10^6$	$3·9 \times 10^6$	$1·4 \times 10^5$	$4·9 \times 10^5$	$8·8 \times 10^5$	$6·8 \times 10^7$	$4·2 \times 10^7$	Logged
5·0	$1·4 \times 10^6$	Logged	Logged	$1·1 \times 10^5$	$4·2 \times 10^7$	Logged	$1·1 \times 10^5$	$7·8 \times 10^6$	Logged

Logged = sample unavailable due to water logging.

increased. Anaerobic chamber counts in the top 0·5 m in all the profiles yielded populations of 10^1–10^2 CFU g^{-1} soil with highest populations in the woodlands. Below 2 m anaerobic chamber incubations revealed populations of 10^5–10^6 CFU g^{-1} soil. With the onset of floods, increases in bacteria population were only observed on the islands while no trends were observed in the woodland.

Actinomycetes populations in the top 0·1 m recorded were 10^6–10^7 CFU g^{-1} soil in all the vegetation zones. However, declines to 10^5 CFU g^{-1} soil were observed in all profiles with increase in depth. Very few or no actinomycetes were observed in all profiles at 2 m and below. Fungal populations in all the vegetation zones concentrated in the top 0·5 m as mycelium, yielding 10^3–10^4 CFU g^{-1} soil. Although samples from below 1 m depths yielded fungal populations on MEA, wet sieving and decanting of the soil suspensions and re-examination of the samples showed that these populations existed mostly as fungal spores. In general, fungi populations on islands were smaller than in soils of the other two locations.

Nitrogen and Phosphorus

Nitrogen analysis revealed very small or non-detectable amounts throughout the profiles in all vegetation zones. These insignificant amounts of nitrogen were observed only at 0·1 m in the floodplains and woodlands, with highest percentage nitrogen in the floodplain samples: 0·12% in February, 0·61% in March and 0·03% in May. In the woodland, concentrations were below 0·03%, while in island soils no nitrogen was detected at all.

Figures 2–4 show the levels of available P in the floodplain, woodland and island soils at different depths and months. Although P was analysed at all profile depths and months, only the data for the dry season (February) before the floods (March in the

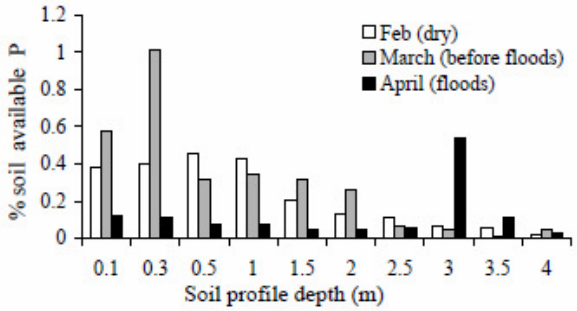

Figure 2. Influence of flooding on % available P in the floodplain.

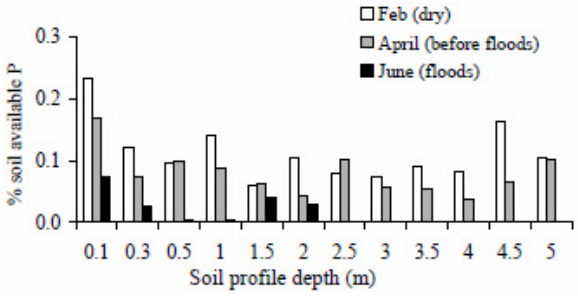

Figure 3. Influence of flooding on % available P in the woodland.

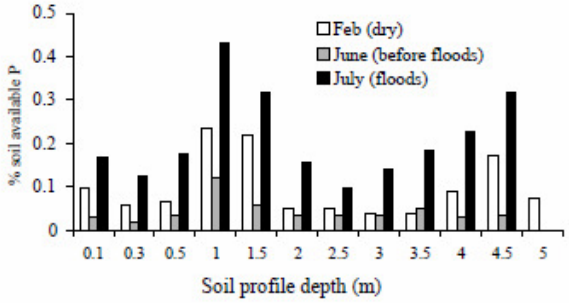

Figure 4. Influence of flooding on % available P in the island.

floodplain, June in the island and woodland) and the flood month (April in the floodplain, were taken). However, July data in the woodland and island was used as flood month data, because this is when the water table is less than 2 m (woodland sampling site) and 4 m (island sampling site) from the soil surface.

Analysis of available P in the soil profiles at different months within the three locations showed significantly higher values in the floodplains. However, there were no significant differences between the woodland and the island samples, although samples from the latter showed higher levels of available P. In island samples, flooding increased the amount of available P in the soil profile up to 4 m. However, this was not observed in the floodplain and woodland samples. Available P in the floodplain decreased with depth. The available P declined over the entire period, followed by significant increases in July/August sample on the island. The decline on the floodplain was most pronounced at 0·1 m, where concentrations dropped from 0·4% to 0·1% P in the 0·3 m.

Figures 5–7 show the organic P in the soils studied. These figures indicate that in the woodland and floodplain, the organic P is concentrated in the top 0·1 m. However, in the island there was no pattern on organic P concentration at the different soil depths.

Discussion

Microbial population studies in these soils concentrated in the top 0·5 m as reflected by the high fungi and actinomycete populations in the 0·1 and 0·5 m samples. This population was partly attributed to the aerobic nature of these organisms. The high population of these organisms could also be attributed to the increased substrate in the form of dead plant material on the soil surface and the top horizons. These high populations of fungi and actinomycetes are of significance in the decomposition of organic residues, especially in the woodland where organic debris in the form of dead tree leaves is concentrated at the top 0·5 m as also reflected by the high organic P content of the woodland soils (Fig. 6). Bacterial population (Table 1), on the contrary, showed no significant changes with profile depth, but instead were distributed throughout the profile. This lack of correlation with depth could be because both aerobic and anaerobic forms of soil bacteria exist (Gray & Parkinson, 1962), thus an even distribution throughout the profile is most likely to occur.

Throughout this study, low nitrogen levels were detected in the soils. The low nitrogen obtained was attributed to several factors, among which is leaching of nitrogen in the floodplain and island soils. Okavango soils are highly sandy (Staring, 1978). Consequently, the occurrence of seasonal floods in these sands could lead to

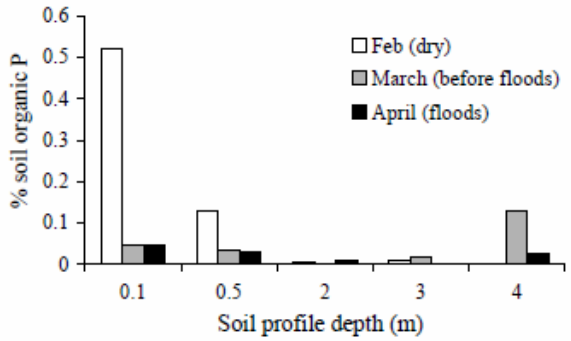

Figure 5. Levels of organic P in the floodplain.

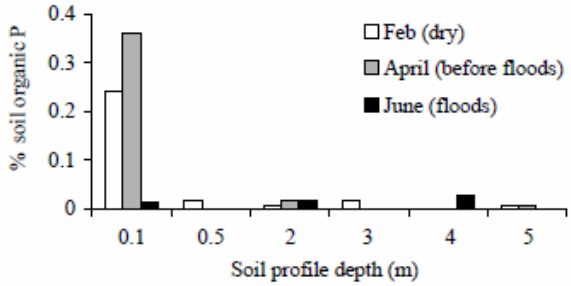

Figure 6. Levels of organic P in the woodland.

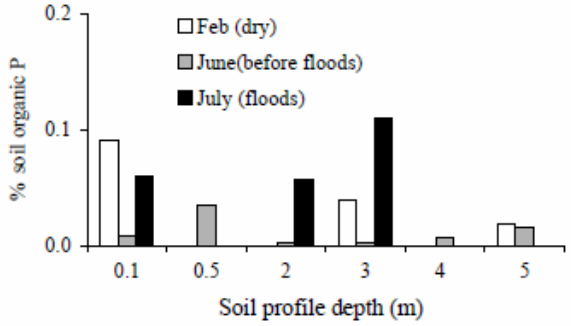

Figure 7. Levels of organic P in the Island.

nitrogen leaching, thus explaining the low levels of nitrogen observed in the floodplain and island soils. Nitrogen losses due to the percolation in sandy soils are quite common (Jones & Schwab, 1993). The low nitrogen values observed in the woodland and floodplains could also be attributed to denitrification losses. Losses of nitrate to gaseous nitrogen or volatile oxides of nitrogen mostly occur in anaerobic conditions such as flooded soils (Davidson & Leonardson, 1998, Baton *et al.*, 1999). The concentration of nitrogen in the top 0·1 m in the floodplain may arise from floodwater and plant debris decomposition as possible sources of nitrogen. The N detected during the dry months in the floodplain (0·12% in February, 0·61% in March and 0·03% in May) could be attributed to high plant mortality during dry months

resulting in increased organic material returns to the soil. The 0·1m depth is also characterized by high fungal and actinomycete populations, both of which have a high enzymatic activity required in the degradation of plant material. Although plants take up nitrogen mostly in the form of nitrates and also in the form of ammonium (Mengel & Kirkby, 1982; Wild, 1988), this study focused on total nitrogen because in most wetland soils, total soil nitrogen has been shown to be a better indicator for 'available' organic substances than the total organic carbon content (Yao *et al.*, 1999). The high fungal and actinomycete populations observed in the top 0·5 m also contribute to the N detected in this horizon. Upon death, these become mineralized and release nitrogen to the soil. Although bacteria may occur throughout the profile, their contribution to total nitrogen may be insignificant when compared to fungi and actinomycetes. Due to their fairly large size compared to bacteria, fungi may have a low population but contribute more to microbial biomass N and C than bacteria. Lack of fungi and actinomycete populations in the deeper horizons may also be the reason for the lack of significant nitrogen detection in lower horizons.

Floodplains and woodland have a dense vegetation population (Ellery & Ellery, 1997) and thus must utilize high amounts of nitrogen for both plant and microbial requirements. Possible sources of nitrogen in this system are the incoming floodwater which have a slightly higher nitrogen status than the soils (Cronberg *et al.*, 1995). Another possible source of nitrogen in this system may be the symbiotic and asymbiotic nitrogen fixing systems. Although no studies have been conducted, these waters have high populations of cyanobacteria, as seen by the typical green colour of algae infested water. These, together with the asymbiotic nitrogen fixing bacteria may help meet the nitrogen requirements of the vegetation in these soils.

Flooding significantly increased the levels of available P on the islands (Fig. 4). One likely explanation is that with the increased soil moisture, the redox potential of the soils decreases, reducing the cations which had bound P, resulting in the release of P (Brady, 1990), as the soils underneath the islands are characterized by relatively high values for aluminium and iron (McCarthy *et al.*, 1998). The released phosphorus may immediately be utilized by the woody vegetation in the riparian fringe and by grasses and sedges on the floodplain. Only in the island samples, due to lack of vegetation, the abrupt release may be noticeable.

The concentration of organic P in the top 0·1 m of the soil profile in the floodplain and woodland (Figs 5 & 6) was attributed mostly due to the contribution of dead plants and other organic residues at that depth. However, this high organic P content in the top 0·1 m does not occur in the island due to the lack of vegetation on these islands. These data are in agreement with the low fungal populations recorded on the island in comparison to the floodplain and woodland.

Summary

This study shows that soils of the seasonal swamps of the Okavango Delta are of low nitrogen and phosphorus status. It confirms observations, which described earlier that nitrogen is an important limiting nutrient of plant production in arid and semi-arid ecosystems (Scholes, 1990; Hooper & Johnson, 1999) as indicated by biotic and abiotic N pool sizes (Skujins, 1981). However, because this system sustains a dense vegetation cover, other sources of these elements in this system may exist. Although it has been suggested that besides the nutrients in the incoming floodwater (Cronberg *et al.*, 1992), dust deposits may play a role in nutrient supply (Garstang *et al.*, 1998), these sources may not be enough to meet the requirements. Thus, other possible sources of nitrogen such as nitrogen fixation and efficient nutrient cycling may play an important role in meeting the N requirements while mycorrhizae plant association

may also improve P availability to the plants as it has been shown that most of the Okavango Delta grasses form VA mycorrhizae associations (Coetzee, 2001).

The authors acknowledge the Harry Oppenheimer Okavango Research Centre (HOORC) and the Department of Biological Sciences for providing funding, assistance, support and access to the research site. Assistance from other members of the HOORC for transportation and sampling is greatly appreciated.

References

Baton, L., Maclay, C.D.A., Schipper, L.A. & Smith, C.T. (1999). Annual denitrification rates in agricultural and forest soils. A review. *Australian Journal of Soil Research*, **37**: 1073–1098.

Brady, N.Y. (1990). *The Nature and Properties of Soils* (10th Edn). New York: Macmillan Publishing Company. 621 pp.

Bray, R.H. & Kurtz, L.T. (1945). Determination of total, organic and available forms of phosphorus in soils. *Soil Science*, **59**: 39–45.

Cochran, W.G. (1950). Estimates of bacteria densities by means of the "most probable number". *Biometrics*, **6**: 105–106.

Coetzee, T. (2001). Effect of wet and dry cycles of the Okavango Delta on mycorrhizae–grass colonization. M.Sc. thesis, University of Botswana, Botswana, 87 pp.

Cronberg, G., Gieske, A., Martins, E., Prince-Nengu, J. & Stenstrom, I.M. (1995). Hydrobiological studies of the Okavango Delta and the Kwando/Linyanti/Chobe river, Botswana. I. Surface water quality analysis. *Botswana Notes Records*, 27: 151–226.

Currie, D.J. & Kalff, J. (1984). A comparison of fresh water algae and bacteria to acquire and retain phosphorus. *Limnology and Oceanogr*, **29**: 298–310.

Davidson, T.E. & Leonardson, L. (1998). Seasonal dynamics of denitrification activity in two water logged meadow. *Hydrobiologia*, **364**: 189–198.

Ellery, K. & Ellery, W. (1997). *Plants of the Okavango. A Field Guide*. Durban, R.S.A.: Tsaro Publishers. 225 pp.

Gachter, R., Meyer, J.S. & Mares, A. (1988). Contribution of bacteria to release phosphate in lake sediments. *Limnology and Oceanography*, **33**: 1542–1558.

Garstang, M., Ellery, W.N., McCarthy, T.S., Scholes, M.C., Scholes, R.J., Swap, R.J. & Tyson, P.D. (1998). The contribution of aerosol- and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana. *South African Journal of Science*, **94**: 223–229.

Gerhardt, P., Murray, R.G.E., Castilow, R.N., Nester, E.W., Wood, W.A., Kreig, N.R. & Phillips, B.G. (1981). *Manual of Methods for General Microbiology*. Washington, D.C., U.S.A.: *American Society of Microbiology*. 524 pp.

Gray, T.R.G. & Parkinson, D. (1962). *The Ecology of Soil Bacteria*, Liverpool: pp. 531–551. Liverpool University Press. 692 pp.

Hart, S.C., Stark, J.M., Davidson, E.A. & Firestone M.K. (1994). Nitrogen mineralization, immobilization and nitrification. In: Weaver, R.W., Angle, J.S. & Bottomley, P.J. (Eds), *Methods of Soil Analyses, Part 2, Microbiological and Biochemical Properties*, pp. 985–1018. Madison, WI: Soil Science Society of America. 1121 pp.

Heemstra, H.H. (1976). *Investigation of the Okavango as a Primary Water Resource for Botswana*, pp. 24–26. Gaborone, *BW: FAO with the Government of the Republic of Botswana, Technical Bulletin*. 50 pp.

Hooper, D.U. & Johnson, L. (1999). Nitrogen limitation in dry land ecosystems: responses to geographical and temporal variation in precipitation. *Biogeochemistry*, **46**: 247–293.

Jones, R.D. & Schwab, A.P. (1993). Nitrate leaching and nitrite occurrence in a fine textured soil. *Soil Science*, **155**: 272–282.

Kurst, E. & Williams, S.T. (1964). Selection of media for isolation of streptomycetes. *Nature*, **202**: 928–929.

Lawrence, J.R., & Germida, J.J. (1988). Most probable number procedure to enumerate sulfur oxidising , thiosulfate producing heterotrophs in soil. *Soil Biology & Biochemistry*, **20**: 577–578.

McCarthy, T.S., Ellery, W.N. & Dangerfield, J.M. (1998). The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes and Landforms*, **23**: 291–316.

Mengel, K. & Kirkby, E.A. (1982). *Principles of Plant Nutrition*. Switzerland: International Potash Institute of Bern. 864 pp.

Moistafa, M.Z. (1999). Analysis of phosphorus retention in freshwater surface treatment wetlands. *Hydrobiologia*, **392**: 41–53.

Murphy, J. & Riley, J.P. (1962). A modified simple solution method for determination of phosphate in natural waters. *Analytica Chimica Acta*, 27: 31–36.

Olsen, S.R. & Sommers, L.E. (1982). Phosphorus: In: Page, A.L., Miller, R.H. & Keeney, D.R. (Eds), *Methods of Soil Analyses, Part 2, Microbiological and Biochemical Properties*, pp. 411–413. Madison, WI: Soil Science Society of America, 1159 pp.

Richardson, A.E. (1994). Soil microorganisms and phosphorus availability. In: Pankhurst, E.E., Doube, B.M., Gupta, U.V. & Grace, P.R. (Eds), *Soil Biota*. East Melborne: CSIRO. 451 pp.

Scholes, R.J. (1990). The influence of soil fertility on ecology of southern African savannas. *Journal of Biogeochemistry*, **17**: 741–419.

Skujins, J. (1981). Nitrogen cycling in arid ecosystems. In: Clark, F.E. & Rosswall, T. (Eds), *Terrestrial Nitrogen Cycles, Ecological Bulletin*, Vol **33**: pp. 477–491.

Smith, J.L. (1994). Cycling of nitrogen through microbial activity. In: Hartfield, J.L. & Stewart, B.A. (Eds), *Soil Biology: Effects on Water Quality*, pp. 91–120. Boca Raton, FL: CRC Press, 169 pp.

Staring, G.J. (1978). *Soils of the Okavango Delta*. Gaborone, BW: UNESCO. 68 pp.

Wanatabe, F.S. & Olsen, S.R. (1965). Test of an ascorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. *Soil Science Society of America, Proceedings* **29**: 677–678.

Wild, A. (1988). *Russell's Soil Conditions and Plant Growth*, (11th Edn.) Great Britain. English Language Book Society/Longman. 991 pp.

Williams, S.T. & Wellington, E.M.H. (1982). Actinomycetes. In: Page, A.L., Miller, R.H. & Keeney, D.R. (Eds), *Methods of Soil Analyses, Part 2, Microbiological and Biochemical Properties*, pp. 972–987. Madison, WI: Soil Science Society of America. Wisconsin. 1159 pp.

Yao, H., Conrad, R., Wassmann, R. & Neue, H.U. (1999). Effect of soil characteristics on sequential reduction and methane production in 16 rice paddy soils from China, the Philippines and Italy. *Biogeochemistry*, 47: 269–295.