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The contribution of aerosol- and water-borne nutrients to the functioning of the Okavango Delta ecosystem, Botswana

M. Garstang[1], W.N. Ellery[2], T.S. McCarthy[3]*, M.C. Scholes[4], R.J. Scholes[5], R.J. Swap[1] and P.D. Tyson[1]

[1]Climatology Research Group, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa; [2]Department of Geographic and Environmental Sciences, University of Natal, Durban 4041; [3]Department of Geology, University of the Witwatersrand; [4]Department of Botany, University of the Witwatersrand; [5]Division of Water, Environment and Forest Technology, CSIR, P.O. Box 395, Pretoria 0001.

The role of water- and airborne sediments and nutrients is examined in the nearly closed system of the Okavango Delta. The total annual sediment load carried by the Okavango River into the delta is estimated at 620 000 tonnes. Annual deposition on the delta from the atmosphere under anticyclonic conditions only is estimated at 250 000 tonnes. Nutrient supply to the delta system from these two sources is estimated for the papyrus-dominated habitats of the permanent swamps. Maximum and minimum waterborne and aerosol contributions are determined for potassium, phosphorus and nitrogen species. On an annual basis, atmospheric inputs range from 6–60% of the total. The existence of large reservoirs of nutrients in the peat cannot account for the observed variability in papyrus productivity on the channel fringes and in the backswamp areas, due to low rates of mineralisation (8.1 and 0.12 kg $ha^{-1}yr^{-1}$ *for nitrogen and phosphorus, respectively). Enhanced productivity exists on channel fringes due to flowing water; more even distribution of nitrogen and phosphorus over the delta comes from the atmosphere. Aerosol inputs of 3.9 and 0.13 kg* $ha^{-1}yr^{-1}$ *for nitrogen and phosphorus, respectively, are compared with corresponding aquatic supplies of 108 and 2.25 kg* $ha^{-1}yr^{-1}$*. The effect of these contributions on papyrus productivity is discussed. The results obtained for the Okavango Delta suggest that atmospheric supply of nutrients may be equally important in more complex southern African ecosystems.*

The Okavango Delta is a hyperoligotrophic ecosystem.[1] The low nitrogen status is indicated by the presence of a diverse insectivorous flora, including *Utricularia* spp. and *Drosera madacascarensis*, as well as the wide occurrence of nitrogen-fixing blue-green algae. The reasons for the low nutrient concentrations are: the delta is situated on a substratum of eolian sand of very low inherent nutrient status; and most of the catchment of the Okavango River, which supplies water to the delta, similarly lies on Kalahari sand, although it is situated in a relatively high rainfall area at present (*c.* 1000 mm per annum). The general absence of chemical weathering in the catchment results in a very low dissolved solid load in the water of the Okavango River (*c.* 30 ppm),[2] most of which consists of silica and calcium and magnesium bicarbonates. Nutrient species occur at extremely low concentrations: nitrogen (as nitrate and ammonia) is typically 0.08 ppm, phosphorus 0.04 ppm and potassium 2.9 ppm.[1]

Analysis of satellite imagery suggests a general decline in biological productivity away from the distributary channels as well as an overall decline in productivity downstream.[3] This has been assumed to reflect the abstraction of the limited supply of nutrients in the source water close to points of supply. Satellite imagery, however, also shows large areas of the delta in which growth is anomalously prolific.[3] These anomalous areas may reflect either unusual hydrological conditions or the addition of nutrients to the system from the atmosphere.

Deposition of airborne material has been shown to be an important source of nutrients in ecosystems showing tight nutrient cycling, such as the Amazon rainforest,[4] and in certain nutrient limited systems (e.g. the Sargasso Sea in the North Atlantic Ocean). Tyson *et al.*[5] have recently found that large quantities of material circulate in anticyclonic systems over southern Africa, and have estimated that 11.5 million tonnes of material is transported annually across the Okavango region. Moreover, Swap[6] has demonstrated significant fallout of this material over northern Namibia, downwind of the Okavango Delta.

In the light of these observations, we have investigated the importance of airborne particulates as a source of nutrients in the Okavango Delta, and as a contributor to net aggradation in the region.

Hydrology of the Okavango Delta

The Okavango Delta is situated in a semi-arid region (rainfall *c.* 500 mm per annum), in which potential evaporation exceeds rainfall by a factor of three.[7] The water of the delta is supplied by the Okavango River, which rises in subtropical central Angola. The rainy season in the catchment occurs between January and March, and peak discharge at the head of the delta occurs in April. This flood wave passes down the delta very slowly, taking four to five months to traverse the 250 km from apex to toe. While base flow in the Okavango River sustains some 3 000 to 4 000 km^2 of permanent swamp, the annual flood seasonally inundates a further 4 000 to 8 000 km^2. The average depth of flooding is less than 1 m. Only 1.5% of the inflow leaves the delta as outflow. Maximum aerial extent of flooding occurs during the winter season (July to August), when aerosol loading over the southern continent is at its maximum.[8]

Atmospheric transports

At the time of the annual flooding, much of southern Africa south of 15°S, particularly regions to the west and south of the Okavango, have been without any significant rain for four months. In the late winter season, ground cover is approaching its annual minimum and fires in the region are nearing the annual maximum in frequency of occurrence.[9–11] Subcontinental-scale anticyclones occur over northern South Africa and Botswana with a frequency of 4 out of every 5 days in winter, dominating the weather of the region at this time of year.[12] Subsiding air within these high-pressure systems results in clear skies, low humidities and pervasive, absolutely stable layers at altitudes of around 3 km (~700 hPa level in the atmosphere) and 5 km (~500 hPa).[13] Such conditions combine to produce a maximum in aerosol loadings in the atmosphere below these stable

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*Corresponding author: Department of Geology, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa (e-mail: 065mct@cosmos.wits.ac.za).

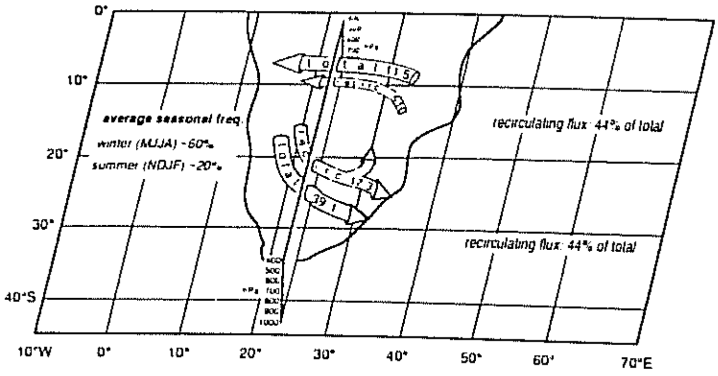

Fig. 1. Total and recirculating transport fluxes (in Mt yr^{-1}) associated with continental anticyclonic circulation systems. Fluxes are given for the vicinity of the central meridian over South Africa within the frequently occurring haze layer capped by the ~500 hPa, absolutely stable discontinuity (after Tyson *et al.*[5]). Percentage recirculation fluxes on the equatorward and poleward flanks of the recirculation vortex are indicated.

discontinuities.[5,14]

Tyson *et al.*[5] show that a significant fraction of the total annual transport of airborne material through a meridional plane between the surface and 500 hPa at the latitude and longitude of the Okavango is embedded in the large-scale anticyclonic circulations. Figure 1 shows that the average seasonal frequencies of anticyclonic circulations is 60% in the winter months (May–August, MJJA) and 20% of all days in the summer months (November–February, NDJF). On an annual basis these anticyclonic circulations transport a total of 11.5 Mt across the meridional plane in the vicinity of the Okavango. Of the 11.5 Mt yr^{-1}, 5.1 Mt yr^{-1} (44%) of the material is embedded in return flow recirculating over the subcontinent. The aerosols contained in these anticyclonic circulations originate at some considerable distance from the Okavango and cross the delta approximately normal to the north-west, south-east axis of the delta.

The following annual estimates of deposition of airborne material into the Okavango Delta are made for these persistent and clearly defined anticyclonic flow regimes. Such estimates based only upon the contribution by the atmosphere under anticyclonic conditions will of necessity underestimate the total annual contribution by the atmosphere. The complexities of the other atmospheric flow regimes, although subject to similar estimates, are less well defined for the Okavango Delta.[12]

The total annual mass of 11.5 Mt of aerosols transported by the atmosphere under anticyclonic conditions as estimated by Tyson *et al.*[5] passes through a vertical plane at the longitude of the Okavango Delta. This vertical plane, centred on the delta, and extending 1000 km north and south and 3.5 km above the surface of the delta, is illustrated in Fig. 2. The total area of the plume of aerosols on the meridional plane is 8.4×10^9 m^2. The average daily mass transport through this plane, normalised to an area of 1 ha (10^4 m^2) in the vertical plane is 38.0 kg ha^{-1} day^{-1}. Averaged over 1 m^2, this amount of 38.0 kg ha^{-1} day^{-1} translates to 3.8 g m^{-2} day^{-1}, a value which can be compared to aerosol concentrations of 50 µg m^{-3} observed in arid continental dust plumes.[4,15,16] If an average 24-h wind speed of 1 m s^{-1} is assumed, then at a concentration of 50 µg m^{-3}, 4.3 g passes through 1 m^2 in one day, a value comparable to the above estimate of 3.8 g m^{-2} day^{-1}.

Annual deposition on a horizontal vegetated surface typical of the Okavango Delta can be estimated from the horizontal transport of an aerosol load of 38 kg per day through a vertical plane of 100 m × 100 m (10^4 m^2). Such a one-hectare plane is illustrated schematically in Fig. 2.

Passive and active deposition on the horizontal surfaces of the delta occurs due to fallout and dry and wet deposition. Vegetation of all sizes will act as a filter to the aerosols advected across the delta.

In the presence of freewater surfaces and new biomass production, evaporation and evapotranspiration will be at a maximum. Specific humidity in the first two metres above the water surface is expected to reach 15 g kg^{-1}. Night time conditions typical of anticyclonic circulations with clear skies and low humidities in the middle and upper atmosphere will promote rapid surface cooling. Air temperatures at night are expected to drop well below the dew point, especially on the fine vegetation elements of the swamp grasses and palms.[17] Heavy dew formation would be a nightly occurrence and would serve to remove dry deposition from the vegetation and effectively capture airborne particles by a wet deposition process.

Swap[6] determined depositional rates for Etosha National Park, Namibia (19°S, 16°E), from aerosol mass loss over a distance of 6° of longitude (~600 km) using concentrations of aerosols measured in filters exposed at 10 m. For a 45-day period during the spring of 1992, the average rate of deposition was 0.25 kg ha^{-1} day^{-1}. This value represents 0.7% of the total horizontal mass transport of 38 kg ha^{-1} day^{-1} through a square 100 m × 100 m in the lowest atmosphere.

Scavenging of cloud or fog water droplets by collectors mounted vertically (normal to the wind) has been compared to

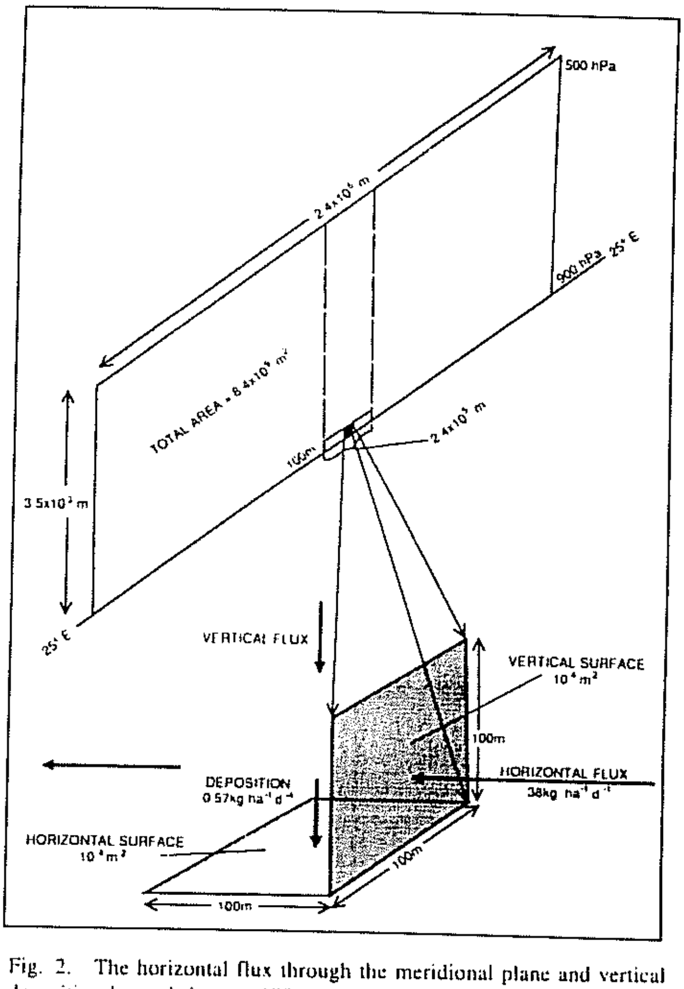

Fig. 2. The horizontal flux through the meridional plane and vertical deposition beneath it on a 100-m × 100-m surface over the Okavango Delta.

rainfall measured on a horizontal surface.[18] Such scavenging frequently exceeds the rainfall by 100%. Vegetation canopy roughness also increases moisture capture and dry deposition, resulting in nutrient-enriched throughfall. Georgii *et al.*[19] reported rainfall to throughfall in the ratio of 1:5 with total amounts of aerosol deposited below the canopy of a spruce and beech forest in the Solling mountains to a range between 5 and 88 kg ha^{-1} yr^{-1} for six different elements. Consideration of the differences between conditions which yield the measured rate of deposition of aerosols at Etosha and those prevailing in the Okavango Delta suggest that a very conservative rate of deposition for the delta would be about twice the above value of 0.7%, or 1.5% of the total load, equal to 0.57 kg ha^{-1} day^{-1}.

Removal of 1.5% per day of the aerosol load in the lower 100 m of the atmosphere by the vegetation of the delta could be easily sustained by:

a) downward transport in the aerosol layer which extends vertically in the atmosphere to the persistent stable layer near 6 km above sea level (500 hPa);
b) net horizontal transport into the delta from sources upwind; and
c) production in the delta reducing the loss from the atmosphere. Nutrient exchanges can occur, however, under conditions of zero mass flux (for instance when delta fires supply surface material to the atmosphere).

Aerosol and water contributions to nutrient stocks

The total annual waterborne load of sediment deposited in the delta is estimated at 620 000 tonnes per year, consisting of 420 000 tonnes of dissolved material and 200 000 tonnes of particulates.[20] Deposition from the atmosphere under anticyclonic conditions alone at a rate of 0.57 kg ha^{-1} day^{-1} over an area of 12 000 km^2 represents 250 000 tonnes per year. The atmosphere therefore contributes about 30% of the total material deposited annually in the delta and about 55% of the particulate sediment.

The maximum and minimum rates of annual atmospheric contribution to nutrient stocks can now be determined using the above rate of total aerosol fraction deposited (0.57 kg ha^{-1} day^{-1}) and observations of the percentage contribution of three trace species to the aerosol load.[6] Table 1 gives the maximum and minimum rates of atmospheric deposition for K^+, NO_3^-, NH_4^+ and PO_4^{3-}.

The annual flow of water into the Okavango Delta is estimated at 9 km^3. The maximum total area covered by this inflow is estimated at 12 000 km^2. Cronberg *et al.*[1] provide estimates of maximum and minimum concentrations of the main chemical constituents introduced by river inflow into the delta. These are used to obtain comparative estimates of the maximum (Table 2) and minimum (Table 3) input of three nutrient species into the delta system by surface water and by the atmosphere.

Table 1. Maximum and minimum daily rates of atmospheric deposition based upon a deposition rate of 0.57 kg ha^{-1} day^{-1} and the observed maximum and minimum fractions obtained by Swap.[6]

	Average % of total load		Total atmospheric deposition (g ha^{-1} day^{-1})	
Species	Max.	Min.	Max.	Min.
K^+	1.1	0.02	6.3	0.1
NO_3^-	3.8	0.04	21.7	0.2
NH_4^+	1.3	0.1	7.4	0.6
PO_4^{3-}	0.2	0.01	1.1	0.06

Table 2. Comparison between the maximum total annual contributions of K^+, NO_3^-, NH_4^+ and PO_4^{3-} by river water and by the atmosphere. The volume of water inflow over one year is taken to be 9 km^3 and the total area of the delta affected to be 12 000 km^2 for both the water and the air.

			Total amount contributed	
Species	Max. concentration in river water (mg l^{-1})	Max. deposition rate from atmosphere (g ha^{-1} day^{-1})	By water (g yr^{-1} × 10^9)	By air (g yr^{-1} × 10^9) (%)
K^+	4.83	6.3	43.47	2.76 (6)
NO_3^-	0.79	21.7	7.11	9.50 (57)
NH_4^+	0.42	7.4	3.78	3.24 (46)
PO_4^{3-}	0.21	1.1	1.89	0.48 (20)

When maximum deposition occurs in both fluid systems (Table 2), the atmospheric contributions of all three nutrient species are considerable. Only potassium falls below a 10% supply by the atmosphere. Contribution from the air approaches or exceeds 50% for nitrate and ammonium and is 20% for phosphate.

Table 3. Comparison between the minimum total annual contributions of K^+, NO_3^-, NH_4^+ and PO_4^{3-} by river water and by the atmosphere. The volume of water inflow over one year is taken to be 9 km^3 and the total area of the delta affected to be 12 000 km^2 for both the water and the air.

			Total amount contributed	
Species	Min. concentration in river water (mg l^{-1})	Min. deposition rate from atmosphere (g ha^{-1} day^{-1})	By water (g yr^{-1} × 10^9)	By air (g yr^{-1} × 10^9) (%)
K^+	1.01	0.10	9.09	0.04 (0.4)
NO_3^-	0.0	0.20	0.00	0.09 (100)
NH_4^+	0.0	0.60	0.00	0.03 (100)
PO_4^{3-}	0.02	0.06	0.18	0.03 (14)

When minimum deposition rates are considered for each system (Table 3), the atmosphere supplies all of the nitrate and ammonium. In each case, however, (maximum and minimum) input from the atmosphere has been considered only for anticyclonic conditions. While these make up more than 40% of all days in the year and carry the highest aerosol loadings, contributions to the delta from the atmosphere under other than anticyclonic conditions can only increase the above estimates.

Nutrient dynamics

Nutrient budgets need to be considered in terms of nutrient stocks and turnover. Estimates of inputs alone as made above do not provide a complete picture of the importance of those contributions as they need to be seen in the context of nutrient cycling between the various reservoirs. Within the Okavango ecosystem a number of sub-habitats can be distinguished, for instance, island forest fringes and papyrus beds, each of which is characterised by its own nutrient pools and fluxes. Data to quantify these pools and fluxes are limited, with suitable information existing for only papyrus-dominated habitats of the permanent swamps. These data will be used to illustrate the complexity of assessing aerosol and water contributions to nutrient dynamics. This discussion will concentrate on N and P, as the above calculations suggest that the contribution of aerosols to the K budget is small.

Reservoirs

Plant N and P stocks

The biomass of *Papyrus* varies widely, depending on the location in the swamps. Backswamp and distal areas have biomasses of *c.* 3.5×10^3 kg ha^{-1} (dry mass), whilst productive areas adjacent to aggrading channels have an estimated biomass of 3.5×10^4 kg ha^{-1}. These estimates are for both above and below water portions. Nitrogen concentration in living papyrus is 0.68%, dropping to 0.35% in senesced tissue, whereas phosphorus constitutes 0.025% in the living plant and 0.007% in the senesced material.[21] These values clearly show the importance of internal translocation of nitrogen and phosphorus in papyrus, with 50% of the nitrogen and 72% of the phosphorus being transferred during senescence. The proportion of senesced material in the papyrus swamp is low (10%). The nitrogen in the standing stock therefore ranges from 24 to 2.4×10^2 kg N ha^{-1} and phosphorus from 0.9–9.0 kg P ha^{-1}.

Peat N and P stocks

Papyrus is rooted in peat, which consists of partly decomposed rhizomes and roots, with varying amounts of charcoal from surface fires and organic and inorganic detrital material. The relative proportions of organic and inorganic components vary and the ash content ranges from 6–75% by mass. Phosphorus occurs in both organic and inorganic fractions and these should be treated separately. The concentrations of phosphorus in these two components is shown in Fig. 3. The inverse correlation between ash and P arises from the mixing of an inorganic component which has a phosphorus content of 0.035% and an organic component containing 0.052%. The concentration of phosphorus in the peat is significantly higher than that in living and especially in senesced plant material, reflecting a lower C:P ratio in peat possibly due to carbon oxidation. There is a maximum of 2.6×10^2 kg P ha^{-1} to a depth of 0.5 m, which is the rooting depth. It is important to note that even with its significantly higher concentration in the peat, the phosphorus is tightly bound and not readily available to the system.

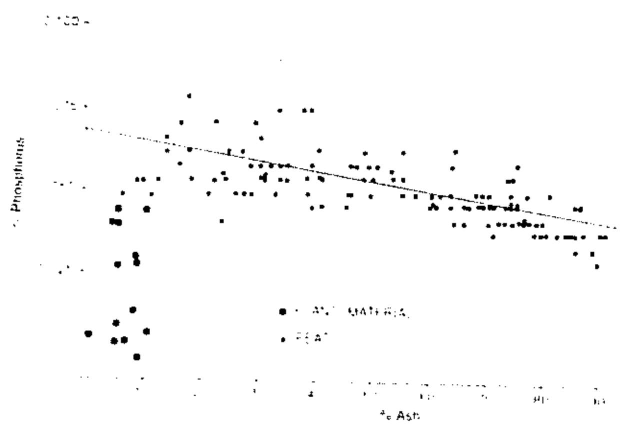

Fig. 3. Plot of total phosphorus in ash against ash content for peat of the permanent swamps of the Okavango (after McCarthy, unpublished).

There is also an inverse correlation between nitrogen concentration and ash content of peat. If the ash component is corrected for, the average nitrogen concentration of the peat is 3.4%. This is significantly higher than the nitrogen content in plant material of approximately 0.9%. The amount of nitrogen in the peat is therefore considerably higher than in the living biomass. There is a maximum of 1.73×10^4 kg N ha^{-1} to a depth of 0.5 m.

Turnover

Plant productivity and uptake rates. Papyrus biomass values are given above. It is estimated that the papyrus turns over annually with there being five living culms present on each rhizome at any one time. From these estimates the productivity of papyrus in the permanent swamps ranges from 3.5×10^3 kg ha^{-1} yr^{-1} in the backwaters to 3.5×10^4 kg ha^{-1} yr^{-1} on the channel fringes.[3] There is between 50–75% internal translocation of nitrogen and phosphorus within the papyrus before the plant material is shed and becomes litter. Multiplying the production of the papyrus by the nitrogen and phosphorus content of the senesced material leads to estimates of 12–120 kg N ha^{-1} yr^{-1} and 0.25–2.5 kg P ha^{-1} yr^{-1}, which the plants need to acquire to sustain the observed productivity. These uptake rates are at least two orders of magnitude smaller than the total amount of nitrogen and phosphorus in the top 50 cm of peat.

Mineralisation of nitrogen and phosphorus from peat. Nitrogen and phosphorus in the peat are associated with both organic and inorganic forms. Microbial attack on the organic carbon skeletons frees the nitrogen and phosphorus, making them available for plant uptake. If the C:N ratio of the substrate is greater than 16, the freed ammonium is likely to be taken up immediately by the microbes involved in the decomposition process. Thus the decaying material will release no nitrogen for plant uptake and in many cases may reduce the available nitrogen. The C:N ratio of the peat is 14.2 and close to the threshold of immobilisation.[22] Phosphorus mineralisation rates are expected to be an order of magnitude smaller than nitrogen mineralisation rates.[23] No *in situ* estimates of peat decomposition are available but can be calculated (see Figs 4 and 5).

Aerosol and water inputs. The maximum and minimum aerosol and water inputs for potassium, phosphorus and nitrogen species are shown in Tables 2 and 3. On an annual basis the atmospheric contributions ranges from 6–60% depending on species, with nitrogen being predominantly supplied from atmospheric sources and phosphorus from river water. The total aerosol inputs are 3.9 kg N ha^{-1} yr^{-1} and 0.13 kg P ha^{-1} yr^{-1}. Measurements of nutrient contributions to papyrus are not available but can be estimated (see Figs 4 and 5).

Other inputs. Nitrogen-fixing organisms, particularly blue-green algae, are common in backswamp areas but their contribution to the nitrogen budget is unknown. Phosphorus accumulates on islands and is exported to wetland habitats. Many of the plants which characterise islands are typical of nutrient-rich soils (e.g. *Cynodon dactylon*) and have high forage quality. Hippopotamuses are known to favour such grasses, and export these nutrients in faecal material to aquatic habitats.

The abundance of organic nitrogen in Okavango water considerably exceeds nitrogen as nitrate and ammonia[1] and is potentially available to plants following mineralisation.

Possible losses. Fire, denitrification and volatilisation probably account for the majority of losses from the system. The proportion of the nitrogen in plant tissue and litter which is lost to the atmosphere during combustion depends on the fire temperature. Loss of nitrogen is virtually complete above 600°C, which

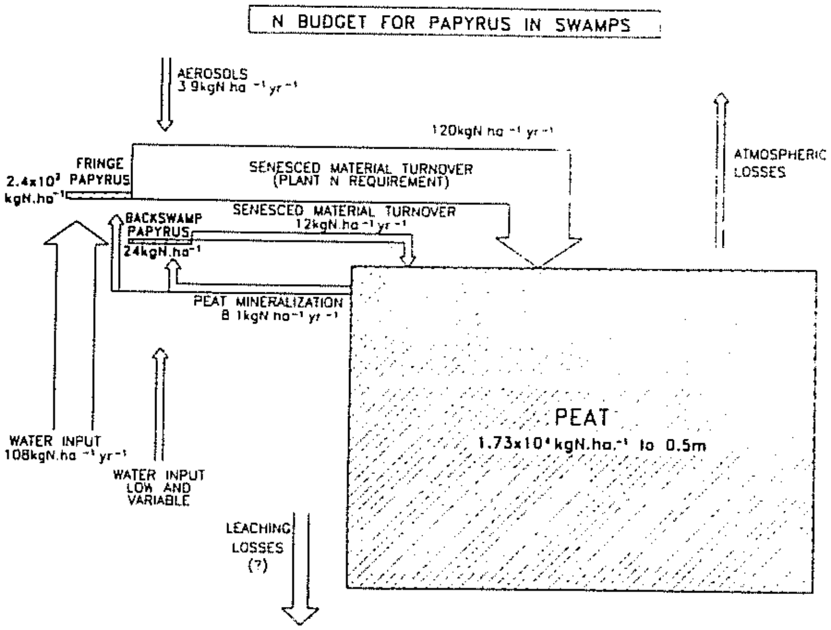

Fig. 4. The nitrogen cycle of the papyrus ecosystem of the Okavango Delta. The size of the boxes is approximately proportional to the pool size in midsummer. Arrows represent annual flux.

could occur during periodic burning of the senesced papyrus culms and litter.[23] Export of phosphorus during burning occurs only at extremely high temperatures, so losses via this route are expected to be small.[23]

Denitrification losses via the conversion of NO_3^- to gaseous nitrogen or volatile oxides of nitrogen mostly occur in anaerobic conditions. Conditions in the peat favour denitrification but no estimates are available.

Volatilisation is the process whereby ammonium-N is lost to the atmosphere. This route is active at pHs above 7.5 and these conditions could exist in the swamps and island centres. In addition, volatilisation from animal dung would add to losses. Again no estimates of the effects of these processes are available.

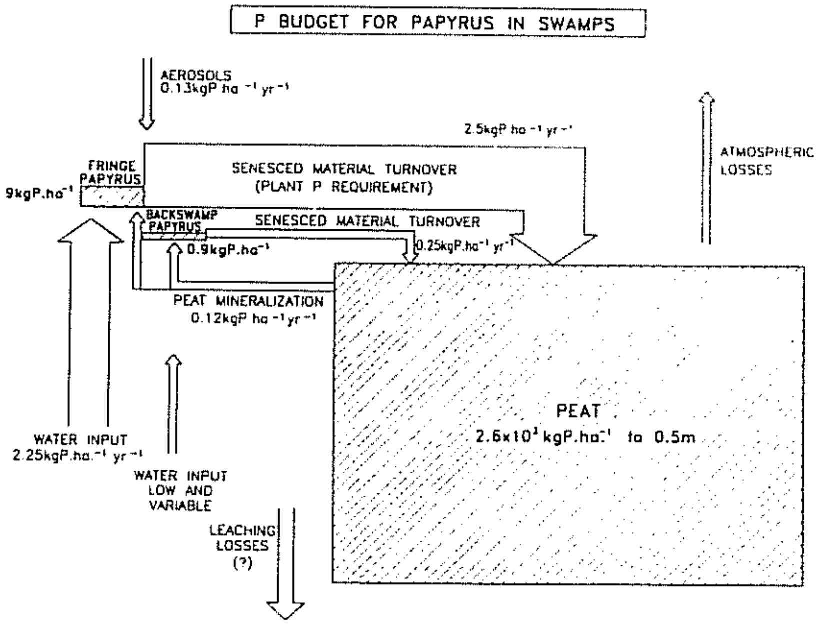

Fig. 5. The phosphorus cycle of the papyrus ecosystem of the Okavango Delta. The size of the boxes is approximately proportional to the pool size in midsummer. Arrows represent annual flux.

Discussion

In the channel fringe papyrus biomass and productivity is high and falls with increasing distance from the channel. A similar decline in productivity occurs with increasing distance from the delta apex. Papyrus is rooted in similar substrate throughout the swamp, and the total nutrient stocks associated with the substrate are similar in the high and low productivity areas. These reservoirs are large in relation to calculated uptake rates by papyrus, indicating that the bioavailability of the nitrogen and phosphorus in peat must be low.

If it is assumed that the backswamp receives no nutrients from the water, then the 12 kg N ha^{-1} and 0.25 kg P ha^{-1} required to generate the observed productivity must be supplied by the 3.9 kg N ha^{-1} and 0.13 kg P ha^{-1} in the aerosols and peat mineralisation, which supplies the difference of 8.1 kg N ha^{-1} and 0.12 kg P ha^{-1}. These are minimum mineralisation estimates as they are based on the assumption that all the aerosol nitrogen and phosphorus inputs are available to the vegetation. Peat acts as an accumulator of N and P, effectively removing P from the vegetative system. The C:N and C:P ratios of peat are significantly lower than in living biomass. In the case of P, accumulation is probably in the form of insoluble apatite whereas N is probably retained by microorganisms.

Gradients in productivity along channels are related to water flow. Biological productivity is high in the channel reaches with a high rate of leakage through the margin.[3] It may be inferred that nutrient withdrawal from the water in the channel margins results in waters in the backswamp and distal areas of the swamps being impoverished in nutrients. The nutrient supply to the fringe community by the water can be estimated if it is assumed that the peat mineralisation rate is the same in channel fringes and backswamp areas. The plant nutrient requirement of 120 kg N ha^{-1} yr^{-1} and 2.5 kg P ha^{-1} yr^{-1} must be met from the atmosphere, peat mineralisation and water. By difference, the water inputs are 108 kg N ha^{-1} and 2.25 kg P ha^{-1}. Again these are minimum estimates.

These nutrient relationships are shown diagrammatically in Figs 4 and 5. The wetland habitats are probably a sink for nitrogen and phosphorus and contain large reserves which are not available to the wetland communities. This is a consequence of the aggradational nature of the system. Losses of phosphorus from the system are negligible, whereas nitrogen may be exported to the atmosphere during peat burning and biogenic emissions. In the channel fringe, water supplies 90% of the nitrogen and phosphorus needs of the plants. In contrast, in the low productivity areas aerosol supplies 30% of the nitrogen and 52% of the phosphorus requirements. However, other sources of nitrogen are available which have not been considered, especially blue-green algae and other nutrient importers such as hippopotamuses and birds. These would reduce estimated aerosol contributions.

The analysis of the nitrogen and phosphorus dynamics in the papyrus community, as shown in Figs 4 and 5, has highlighted the complexities of nutrient supply and availability. In spite of the existence of large reservoirs of nutrients in the peat, mineralisation rates are low and cannot account for the observed variability in productivity. Periods of wetting and drying would lead to enhanced nitrogen mineralisation but will have less effect on phosphorus; in the permanent swamps of the upper fan from which most of the data have been collected, however, drying of the peat is a very uncommon occurrence. Enhanced productivity on the channel fringes is therefore determined by nutrients supplied by the flowing water. Atmospheric inputs across the delta are more uniform than contributions from water, resulting in a more even distribution of nitrogen and phosphorus in the channel fringes and distal areas. In backswamp and distal areas it is likely that atmospheric sources play the major role in supplying nutrient requirements. Nitrogen and phosphorus have been highlighted in this discussion as they are considered to be the primary determinants of plant productivity. Given the nature of the catchment and the substrate, it is possible that essential trace elements, for example molybdenum, could also limit plant productivity.

Papyrus has been emphasised in the above discussion because of the availability of data. Other habitats are even more important as they occupy the largest area of the delta. *Miscanthus junceus* (a grass)-dominated subhabitats, which are found in large areas of the permanent swamps, are expected to have similar nutrient budgets to those described for papyrus. No information exists on the nutrient status of the seasonal swamps which form a large proportion of the wetland. The water which reaches these areas has been processed in the permanent swamp and has low nutrient status. Atmospheric contributions to the seasonal floodplains are therefore likely to play an important role in the overall nutrient budget of the ecosystem.

It has been shown that phosphorus tends to become progressively concentrated in the surface soils of the deltaic islands.[24] This has been interpreted as a consequence of nutrient importation by birds, mammals and insects. However, because islands support large trees, in an environment which is dominated by grasses and sedges, they are likely to trap relatively large quantities of airborne particulates. It is therefore possible that a significant proportion of the soil phosphorus originates from aerosols.

Although the concentration of K in Okavango River water is low, calculations suggest that inflowing water is the dominant source of potassium in the ecosystem. It should be noted that although K is being continuously supplied by inflow, it is also being continuously removed from the soluble pool in the groundwater by the formation of potassium feldspar.[25] The introduction of potassium via aerosols may therefore be more important than the results of the calculations in Table 2 suggest.

Conclusions

Analysis of relative sources of water-borne and aerosol nutrients to the Okavango Delta suggests that the role of aerosols may be significant. However, the delta is effectively the terminus of its drainage system and hence is a net sink for all inputs except water and possibly nitrogen. The contribution of aerosols to overall productivity therefore must be seen in the context of accumulation and recycling of nutrients within the ecosystem.

A detailed analysis of the nutrient budgets of one community, namely papyrus, for which appropriate data are available, has indicated that while large reservoirs of nutrients, especially N and P, are present, mineralisation rates are very low, and the contained N and P are largely unavailable. Quantitative estimates of mineralisation rates and papyrus nutrient requirements indicate that in the channel fringe areas water is the dominant source of nutrients but that in backswamps aerosols may provide as much as 50% of the phosphorus. In addition, the channel fringes occupy less than 10% of the permanent swamp making the aerosol contributions to the majority of the permanent swamp communities critical. Water entering the seasonal swamps has been processed in the permanent swamp and is therefore likely to be nutrient deficient; hence aerosols may be very important suppliers of nutrient to the plant communities. It therefore appears that nutrients transported by the atmosphere, and especially phosphorus in the form of phosphates, probably contribute significantly to the productivity of the swamp ecosystem.

This study has shown that more than half of the particulate sediment entering the delta is derived from aerosols borne by the atmosphere under anticyclonic conditions. Inclusion of transports due to all atmospheric conditions can only increase the estimates of the contribution of the atmosphere to the total sediment and nutrient load. Moreover, no contribution by the atmosphere to either the sediment or nutrient loading of the catchment area of the delta has been considered. While the Okavango Delta can be treated as a nearly closed system, more open ecosystems extending across the entire subcontinent are certainly subject to atmospheric transports. The role of the atmosphere in these more complex ecosystems is likely to be as important as in the more restricted conditions of the delta.

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1. Cronberg G., Gieske A., Martins E., Prince Nengu J. and Stenstrom I-M. (1995). Hydrobiological studies of the Okavango Delta and the Kwando/Linyanti/Chobe River, Botswana. I. Surface water quality analysis. *Botswana Notes Rec.* **27**, 151–226.
2. Hutchins D.G., Hutton L.G., Hutton S.M., Jones C.R. and Loenhart E.P. (1976). A summary of the geology, seismicity, geomorphology and hydrogeology of the Okavango Delta. *Botswana Geol. Survey, Bull.* 7, pp. 27.
3. McCarthy T.S., Franey N.J., Ellery W.N. and Ellery K. (1993). The use of SPOT imagery in the study of environmental processes of the Okavango Delta, Botswana. *S. Afr. J. Sci.* **89**, 432–436.
4. Swap R., Garstang M., Greco S., Talbot R. and Kallberg P. (1992). Saharan dust in the Amazon basin. *Tellus* **44**(b), 133–149.
5. Tyson P.D., Garstang M. and Swap R. (1996). Large-scale recirculation of air over southern Africa. *J. appl. Met.* **35**, 2218–2236.
6. Swap R.J. (1996). *Transport and impact of southern African aerosols.* PhD dissertation, University of Virginia, Charlottesville.
7. Wilson B.H. and Dincer T. (1976). An introduction to the hydrology and hydrography of the Okavango Delta. In *Symposium of the Okavango Delta*, Botswana Society, pp. 33–48. Gaborone.
8. Piketh S.J., Annegarn H.J and Kneen M.A. (1996). Regional scale impacts of biomass burning over southern Africa. In *Biomass Burning and Global Change*, ed. J. Levine, pp. 320–326. MIT Press, Cambridge, Mass.
9. Cahoon D.R.J., Stocks B.J., Levine J.S., Cofer W.R., O'Neil K.P. (1992). Seasonal distribution of African savanna fires. *Nature* **359**, 812–815.
10. Justice C.O., Kendall J.D., Dowty P.R. and Scholes R.J. (1996). Satellite remote sensing of fires during the SAFARI campaign using NOAA advanced very high resolution radiometer data. *J. geophys. Res.* **101**, D19, 23851–23864.
11. Kendal J.D., Justice C.O., Dowty P.R., Elvidge C.D. and Goldammer J.G. (1997). Remote sensing of fires in southern Africa during the SAFARI 1992 campaign. In *Fire in Southern African Savannas: Ecological and Atmospheric Perspectives*, eds B. van Wilgen, M.O. Andraea, J. Goldammer and J.A. Lindesay, pp. 89–133. Witwatersrand

University Press, Johannesburg.

12. Tyson P.D., Garstang M., Swap R., Kallberg P. and Edwards M. (1996). An air transport climatology for subtropical southern Africa. *Int. J. Clim.* **16**, 265–291.
13. Cosijn C. and Tyson P.D. (1996). Stable discontinuities in the atmosphere over South Africa. *S. Afr. J. Sci.* **92**, 381–386.
14. Garstang M., Tyson P.D., Swap R., Edwards M., Kallberg P. and Lindesay J.A. (1996). Horizontal and vertical transport of air over southern Africa. *J. geophys. Res.* **101**, D19, 23,721–723,736.
15. Talbot R.W., Harriss R.C., Browell E.V., Gregory G.L., Sebacher D.I. and Beck S.M. (1986). Distribution and geochemistry of aerosols in the tropical North Atlantic troposphere: relation to Saharan dust. *J. geophys. Res.* **91**, 5153–5182.
16. Swap R., Ulanksi S., Cobbett M. and Garstang M. (1996). Temporal and spatial characteristics of Saharan dust outbreaks. *J. geophys. Res.* **101**, D2, 4205–4220.
17. Larom D., Garstang M., Lindeque M., Raspet R., Zunckel M., Hong Y., O'Beirne S. and Sokolic F. (1997). Meteorology and elephant infrasound at Etosha National Park, Namibia. *J. Acco. Soc. Am.* **101**, 1710–1717.
18. Nel C. and Olivier J. (1997). Meteorological features of orographic clouds along the eastern escarpment of South Africa. Preprint of paper presented at the *American Meteorological Society Fifth International Conference on Southern Hemisphere Meteorology and Oceanography,* Pretoria, 7–11 April 1997, pp. 334–335.
19. Georgii H.W., Perseke C. and Rohbok E. (1986). Investigation of the wet and dry deposition of acidic and heavy metal components. In *Chemistry of Multiphase Atmospheric Systems*, ed. W. Jaeschke. NATO ASI Series, vol. G6, pp. 227–248. Springer-Verlag, Berlin.
20. McCarthy T.S. and Metcalfe J. (1990). Chemical sedimentation in the Okavango Delta, Botswana. *Chem. Geol.* **89**, 157–178.
21. McCarthy T.S., McIver J.R., Cairncross B., Ellery W.N. and Ellery K. (1989). The inorganic chemistry of peat from the Maunachira channel-swamp system, Okavango Delta, Botswana. *Geochem. Cosmochim. Acta* **53**, 1077–1089.
22. Myers R.J.K., Palm C.A., Cuevas E., Gunatilleke I.U.N. and Brossard M. (1994). The synchronisation of nutrient mineralisation and plant nutrient demand. In *The Biological Management of Tropical Soil Fertility,* eds P.L. Woomer and M.J. Swift, pp. 81–116. John Wiley, Chichester.
23. Scholes R.J. and Walker B.H. (1993). *An African Savanna: Synthesis of the Nylsvley Study,* pp. 81–110. Cambridge University Press, London.
24. McCarthy T.S., Ellery W.N. and Dangerfield J.M. (in press). The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. *Earth Surface Processes Land Forms.*
25. McCarthy T.S., McIver J.R. and Verhagen B.Th. (1991). Ground water evolution, chemical sedimentation and carbonate brine formation on an island in the Okavango Delta swamp, Botswana. *Appl. Geochem.* **6**, 577–596.

Additional human fossils from the Middle Stone Age of Die Kelders Cave 1, South Africa: 1995 excavation

Frederick E. Grine

Departments of Anthropology and Anatomical Sciences, State University of New York, Stony Brook, NY 11794-4364, USA (e-mail: fgrine@mail.som.sunysb.edu).

Die Kelders Cave 1 (DK1) preserves Middle Stone Age (MSA) horizons, the uppermost of which date to between 60 and 80 kyr ago. Excavation of these layers in 1995 yielded 12 human specimens, comprising 10 isolated teeth, a mandibular fragment, and a partial manual middle phalanx. This sample brings the inventory of human remains from the DK1 MSA to 27. Most of the 1995 specimens represent juvenile individuals: four are deciduous teeth, three of the permanent crowns exhibit little or no wear, and the mandible contains an unerupted permanent incisor. The preponderance of immature individuals in this sample is consistent with those excavated earlier. Some of the DK1 crowns tend to be larger than most recent African homologues, and comparable to the teeth of penecontemporaneous populations from Eurasia, which might be expected for teeth of such antiquity. Other of the DK1 crowns, however, are smaller than the majority that have been sampled for the Late Pleistocene archaic inhabitants of Eurasia. The majority of morphological variants displayed by the DK1 crowns characterise the teeth of recent sub-Saharan Africans, and in some instances the resemblances between the DK1 and recent African teeth are in traits that differentiate sub-Saharan Africans from other geographic populations. The similarities between the teeth of the MSA inhabitants of DK1 and recent Africans, however, do not necessarily signify modernity of the former, because these crown variants may also have characterised earlier populations from which the MSA peoples were derived. Currently available dental samples are inadequate to determine crown variant frequencies in earlier African (MSA or ESA) populations.

The Die Kelders site complex (34°32′S, 19°02′E) comprises a pair of contiguous caves, Die Kelders 1 (DK1) and Die Kelders 2 (DK2), that are situated at sea level on the southern coast of the Western Cape Province. The site is located about 1 km from the town of De Kelders, which is 120 km southeast of Cape Town. Excavations in DK1 by F.R. Schweitzer from 1969 to 1973 revealed Later Stone Age middens separated by largely sterile sands from a thick series of Middle Stone Age (MSA) layers below.[1] His work resulted in the recognition of 17 superimposed lithological units.[2–4] Of these, layers 4 through 15 were seen to represent alternating MSA occupation and non-occupation horizons. The occupation (even numbered) horizons were rich in archaeological debris, and were typically highly compacted and heavily organic. The non-occupation layers were rich only in microfauna, and contained less organic material.[2–4] Sedimentological and faunal evidence placed the MSA sequence in a cold interval, perhaps equivalent to oxygen-isotope stage 4, between approximately 74 and 59 kyr.[5]

Schweitzer's work resulted in the recovery of numerous MSA lithic artifacts and animal bones, and 13 human teeth. The stone tools, faunal remains and nine of the human teeth recovered by him were described by Grine *et al.*[5] The four other human fossils were described in Avery *et al.*[6] Analysis of the artifacts yielded a tentative suggestion that the Howiesons Poort might be represented in layer 12 because of the high proportion (61%) of silcrete pieces, although it was acknowledged that the backed and truncated artifacts that are characteristic of this MSA variant in other South African sites were absent from the DK1 assemblage.[5]

Two eight-week excavation seasons in 1992 and 1993