Water quantity and quality as factors driving the Serengeti Ecosystem, Tanzania

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Water quantity and quality as the factors driving the Serengeti ecosystem, Tanzania

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Abstract

Thirty nine years of rainfall data from 232 sites, 5 years of river discharge data from 3 rivers, 4 years of animal migration data and 4 years of water quality data at 60 sites were explored to quantify the role of water in the Serengeti ecosystem. Seasonal variations in rainfall are largely predictable; interannual fluctuations are huge and not predictable solely from the Southern Oscillation Index. The wildebeest and zebras start their annual migration at the end of the wet season well before surface water runs out, however these waters are very saline (salinity ≈ 5–17 psu). The timing of the migration appears predictable from a salinity model. Salinity is also important for the vegetation because high salinity coincides with the transition between wooded savanna and grassland. This transition has moved markedly southward in the last 30 years, this change may be due to decadal changes in annual rainfall. Most rivers are commonly ponded, with ponds having a flushing rate of 1 month in the wet season and zero flushing in the dry season. These ponds form the only source of water for wildlife for several months a year. The water quality varies spatially and temporally. pH values vary between 5.9 and 10 and are correlated with salinity. Surface waters are heavily eutrophicated from animal dung. As a result, the dissolved oxygen concentration near the surface fluctuates widely between 1 and 200% of saturation. Direct solar heating is restricted to the top few cm because of low visibility. A strong thermal stratification in temperature (2 °C/m) results and inhibits aeration. Bottom waters can be anoxic and are aerated only when hippopotamus stir the water. Poor water quality may affect wildlife health and production.

Introduction

The Serengeti National Park (Fig. 1), Tanzania, is drained by the Mbalageti, Grumeti and Mara rivers, all flowing westward to lake Victoria. The Mara River drains a large area in Kenya, 10 300 km^2, and flows through the park draining only the far north region of the Serengeti at 1300–1500 m elevation. The Grumeti River drains much of the central and northern hills with a catchment area of 1100 km^2, much of it in the park and most is wooded savanna. The Mbalageti River drains 2680 km^2 of the southern open, tree-less grasslands and hills, nearly all in the park. Most of the grasslands are at an elevation of 1600–1660 m.

The park is famous for its spectacular annual, mass migration of wildebeest and zebras. These herds in turn support one of the largest lion populations on earth. This ecology has been analyzed using biomass models involving grass, ungulates and carnivores (McNaughton, 1979, 1985, 1988, 1990; Ruess & McNaughton, 1987, 1988; McNaughton et al., 1988; Ruess, 1988; Ruess & Halter, 1990; Ruess & Seagle, 1994; Sinclair & Arcese, 1995). Some attention has been paid to the selection of grazing sites by moving herds as a function of the minerals (Jager, 1982; McNaughton, 1988, 1990; Tracy & McNaughton, 1995). These models attempt to estimate biomass transfer from grass to ungulates to carnivores. They assume spatial homogeneity. These models do not consider water. They do not consider unused forage, do not explain why the animals migrate and do not explain why the timing of the migrations varies from year to year by up to 4 months.

Presumably, however, the hydrology is important because in the dry season the southern grasslands are arid; no feed or water is available at that time for the huge migrating herds; these herds migrate back there only in the wet season. The hydrology of the park however has received little attention. Hydrological data were obtained, for instance rainfall data were collected daily by park staff for the last 38 years but these data remained largely unexplored. River discharge data were collected for 5 years and not used. Vegetation changes over decadal time scales were reported by casual observers but not documented. Gereta & Wolanski (1998) reported preliminary water quality data for two sampling trips in 1996. These studies have since continued over 4 years. In this study we merge all the hydrological and water quality data and from an analysis of the data we propose that water is the dominant force driving the Serengeti ecosystem, in particular that water quality and quantity drive the migration and control the vegetation.

Methods

Monthly rainfall data from 1960 to 1999 were available from 232 stations spread in the Serengeti ecosystem. Not all stations were available at any one time. These data were visualised using IBM Data Explorer (King et al., 1996).

Daily river discharge data in 1970–1974 are available (SMEC, 1977; Brown et al., 1981) for the Mbalageti and Grumeti rivers at the point where they leave the park and for the Mara River in Kenya near the point where it enters the park.

We measured the pH, salinity (S), dissolved oxygen concentration (DO) and temperature near the surface (nominal depth = 20 cm) of most rivers and water bodies in the park from April 1996 to April 1999 at 49 stations at about three monthly interval. Sites 1–18 were along the Seronera River (Fig. 1; site 1 = downstream in the wooded savanna; site 18 = upstream in the grassland). At some sites we also sampled the vertical distribution of these parameters using a 400 cc Niskin bottle. Salinity was measured using a TPS LC84 salinity-conductivity-temperature meter and a refractometer. The units for salinity are psu (practical salinity units); at our study sites these are practically equivalent to parts per thousands (ppt). pH was measured using a Hanna model 9024 pH meter. Dissolved oxygen was measured using a temperature-compensated microcomputer model HI9024. Visibility was also estimated by dipping a rod in water.

Undisturbed water samples were collected for suspended matter using a microscope slide with a well and a cover slip following the technique of Wolanski & Gibbs (1995), and the material was photographed using a macro-lens camera and an inverted microscope with magnification ranging from 40 × to 400 ×.

Results

Monthly mean rainfall varied seasonally (Fig. 2), with maximum rainfall in April and a minimum in June–July. The inter-annual variability of rainfall, shown as error bars in Figure 2, was considerable. The seasonal cycle however remained the same in a ‘dry year’ and in a ‘wet year’. The annual rainfall fluctuated widely inter-annually with no clear cycle. The annual rainfall did not correlate significantly ($r^2 < 0.5$) with the Southern Oscillation Index (Fig. 3), only the major El-Nino events were clearly reflected in increased rainfall.

Monthly rainfall also varied spatially (Fig. 4). While the seasonal fluctuations were fairly predictable, there were also major spatial variations. These views for 1979 illustrate that the migration of wildebeest and zebras is driven by water. The animals moved to the southern grasslands after they had been wetted. From July to October there was no rain in the grasslands which became arid, the animals migrated to the far north where light rain still occurred, and to the northwest where the Grumeti River still retained water in scattered river ponds. In December the rain started again in the southern grasslands and the animals started migrating back there. The animals started to migrate out of the southern grasslands although there was still abundant forage and water available, and the timing of the migration varied by up to three months from year to year, suggesting that a clue other than a biological clock or the availability of water triggered the northward migration. Because of orographic effects, the highest rainfall occured in the Ngorongoro mountains located southeast of the southern grasslands and in the northern mountains. A rain shadow downwind of Ngorongoro mountains led to the southern grasslands being the driest part of the ecosystem. An

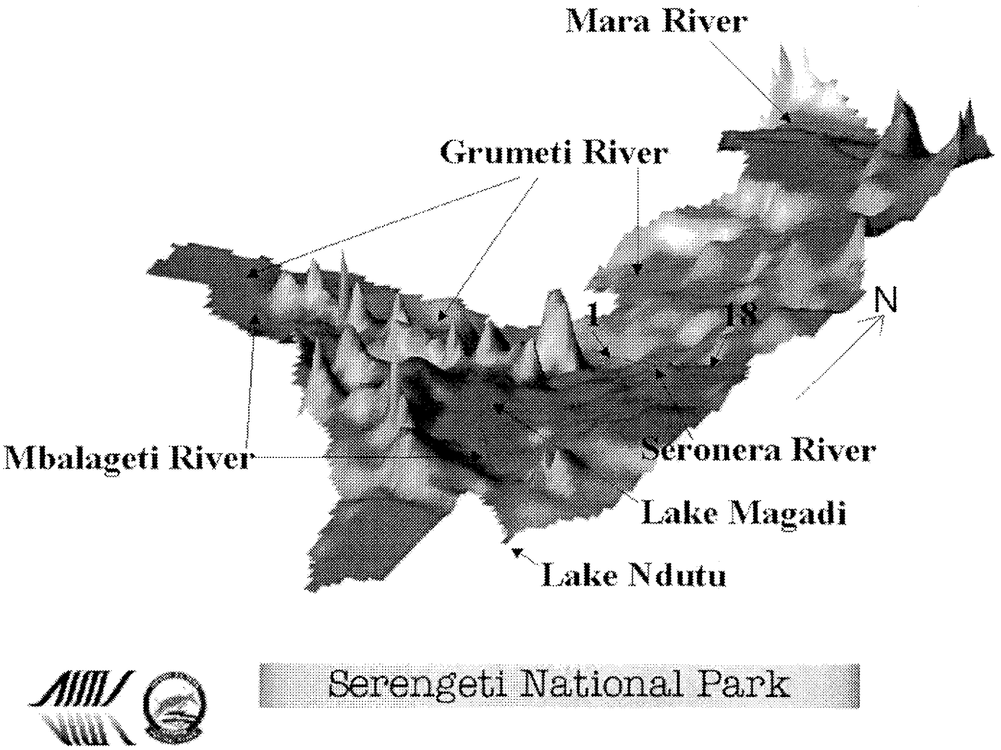


Figure 1. 3-D visualisation of the topography of the Serengeti National Park. The elevation varies from a minimum of about 1140 m in the western corridor to a maximum of about 2000 m in the northeast, hilly corner of the Grumeti River catchment. The northern area is wooded savanna. The southern area encompassing Lakes Ndutu and Magadi and the upper Seronera River is open grasslands, and the transition between these two habitats occurs mid-way along the Seronera River. Orographic effects generated by the topography are apparently responsible for this vegetation gradient. Water quality was measured at 49 sites, 18 of them were located along the Seronera River between site 1 (downstream, in the wooded savanna) and site 18 (upstream, in the open grasslands).

examination of the computer-animated monthly rainfall maps shows that in the wet season the rainfall intruded into the Serengeti as two fronts from both southeast and the north. However, there is considerable inter-annual variability; generally but not always the rainfall from the southeast dominates the pattern in a 'wet' year (i.e. one of the four years out of 39 years of data with the largest annual rainfall; e.g. 1989 and 1998) and from the north in a dry year (i.e. one of the four years on record with the smallest annual rainfall, e.g. 1969 and 1993). This results in considerable inter-annual variability (Fig. 5). As a result in 1969 and 1993, two of the driest years on record, minimal rainfall fell over the southern grasslands which in those years were inhospitable to the migrating herds (M. Borner, pers. comm.). By contrast, in 1972, 1989 and 1998, among the wettest years on record, rainfall was abundant everywhere in the southern grasslands, which received the migrating herds (M. Borner, pers. comm.).

The three rivers crossing the Serengeti experience widely different flow regimes. Maximum recorded flow was about 40 m^3 s^{-1} for the Mbalageti River, 200 m^3 s^{-1} for the Grumeti River and 1000 m^3 s^{-1} for the Mara River. The Seronera River is a small tributary of the Grumeti River and is not gauged. After the rains, the river discharge decreases exponentially to base flow maintained by groundwater seepage, this decrease took a few months for the Mara River, a few weeks for the Grumeti River and a few days for the Mbalageti River. As a result the flow is episodic and transient throughout the year in the Mbalageti and Grumeti rivers (Brown et al., 1981). The rest of the time, most of the year, these rivers do not flow and are just a series of stagnant pools tens to hundreds of meters long. These pools are shallow; rarely is depth >1 m and then only usually where hippos dig out the pool. These pools are essentially stagnant, with zero flushing in the dry season. These pools are the only source of drinking water for wildlife.

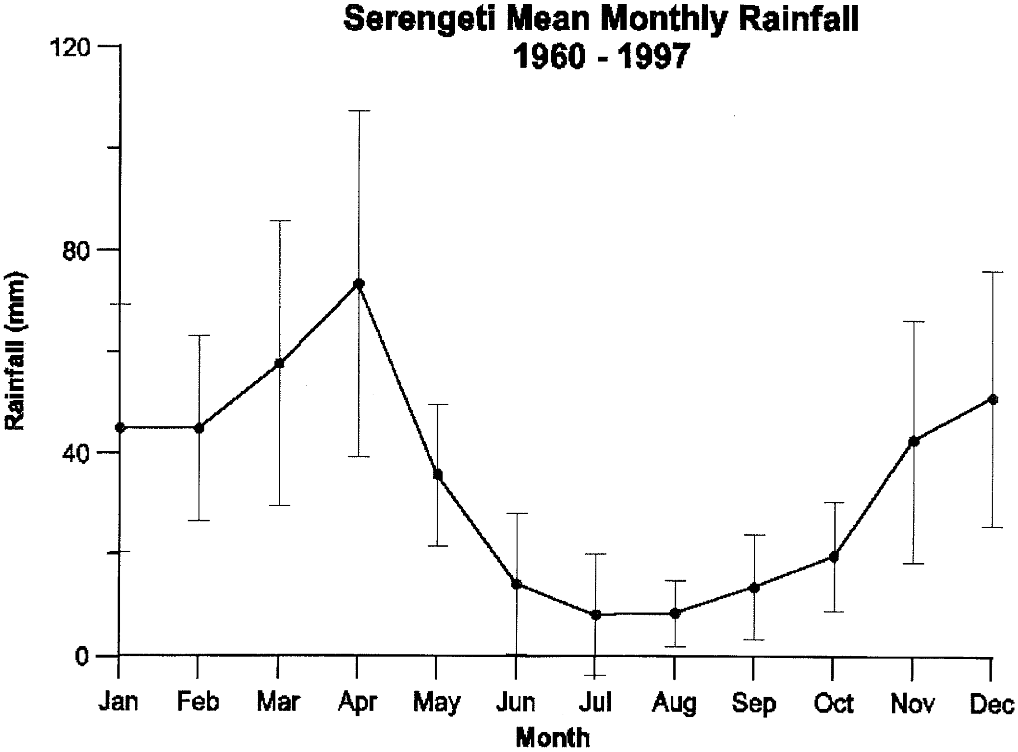


Figure 2. Monthly mean rainfall over the Serengeti ecosystem and standard deviations of the monthly rainfall, plotted as error bars, from 232 stations between 1960 to 1997.

The salinity of surface waters varies spatially, higher salinity occurring in the grasslands to the south and lower salinity in the wooded savanna to the north (Fig. 6). The seasonal cycle of salinity was pronounced in the southern grasslands (Fig. 6) and apparently controlled by the rainfall. Indeed, during the dry season of 1996 evaporation dried out the water holes of the southern grassland, leaving the salt behind. When the water returned with the seasonal rains in March 1997, the salt was dissolved again. As a result of a dilution, smaller rainfall in 1997 resulted in higher salinity than in 1996. The transition from low to high salinity in the Seronera River (Figs 6 and 7, particularly the November 1996 distribution) corresponds also to the transition between wooded grasslands to the north and the open grasslands to the south.

This spatial gradient in salinity was apparent in all surface waters. At the peak of the wet season, April 1996, salinity was commonly 5–15 psu in the southern grassland, 0.5–20 in the Seronera River and 1.8–5.8 in the Mbalageti River. It peaked at 0.5 in the Grumeti River and <0.1 in the Mara River (Fig. 6). For the Seronera River which was the most intensively sampled (18 sites) a strong correlation (r^2 =0.7) existed between salinity and alkalinity for salinity >5) (Fig. 8); for salinity <5 psu there was considerable unexplained variability in pH.

Table 1. Salinity (psu) in alkaline lakes in the southern grasslands in April (during the wet season) from 1996 to 2001. Rainfall in the wet season was about 300 mm in 1996, 220 mm in 1997, 830 mm in 1998, 460 mm in 1999 and 169 mm in 2000.

	Year					
	1996	1997	1998	1999	2000	2001
Lake Nudtu	21	24	13	26	NA	NA
Lake Magadi	22	28	10	17	100	13

The alkaline lakes Ndutu and Magadi are the most saline. The higher was rainfall, the smaller was salinity in the wet season (Table 1). At the peak of the 1996 season, the salinity was >20 psu. During the 1997 wet season, where rainfall was less than in 1997, the salinity was also higher. The salinity was only about 10–12 psu during the 1998 wet season, which had rainfall much higher than in 1996. The inverse relationship

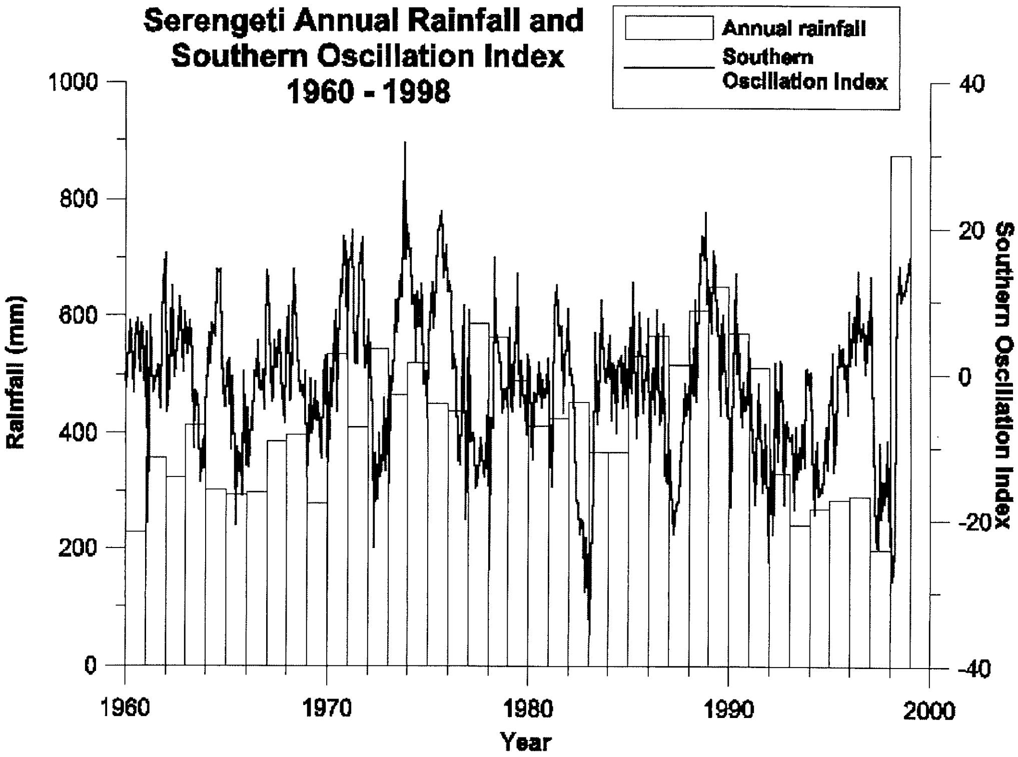


Figure 3. Time series plot of the monthly Southern Oscillation Index from 1960 to 1998 and the annual rainfall (mm/yr) over the Serengeti ecosystem. Annual rainfall from 1960 to 1997 is the arithmetic mean from all stations (typically 20).

between salinity and rainfall suggests there is a pool of salt seasonally diluted in the wet season.

The spatial gradients of salinity are readily apparent in the Seronera River (Fig. 7). The salinity varied seasonally between 0.4–1.12 at site 1 (downstream, in the wooded savanna) to 12.6–22 at site 18 (upstream, in the grasslands).

The stagnant water ponds are heavily used by wildlife. Animal dung generates alga blooms in surface waters in most ponds (Fig. 9a). The wildlife tramples the bottom mud, further increasing turbidity so that commonly visibility is <3 cm; about 40% of the ponds have visibility <1 cm. Hence except for the top few cm the waters are in complete darkness. The suspended material generating this turbidity is made of macro-aggregates (Fig. 9b), typically 500–5000 μm in diameter, comprising organic matter and small mud flocs (<100 μm in diameter). The high turbidity generates a strong vertical stratification in temperature (2 °C/m; Fig. 10a). This stable stratification inhibits vertical mixing and aeration of the sub-surface water (Fischer et al., 1979). During our sampling over a diurnal cycle, aeration occurred only when hippos stirred the water and near the bottom when warmer water was occasionally present – this would introduce convective overturning in the bottom 1/3 of the water column. We speculate that this phenomenon was due to heating from decaying animal dung and other organic matter. These processes result in large vertical gradients of dissolved oxygen concentration (Fig. 10b). This concentration also fluctuated at diurnal frequency, 1.1–8 ppm (15–111% saturation) at the surface and 0–4.5 ppm (0–15% saturation) near the bottom (Fig. 10b). The bottom waters were anaerobic about 10% of the time.

Discussion

Rainfall

Rainfall over the Serengeti has large but predictable seasonal fluctuations and a large, unpredictable inter-annual variability. Only during a strong ENSO event is the annual rainfall correlated with the SOI. Other teleconnections are known to also influence the sub-Saharan climate anomalies. These include

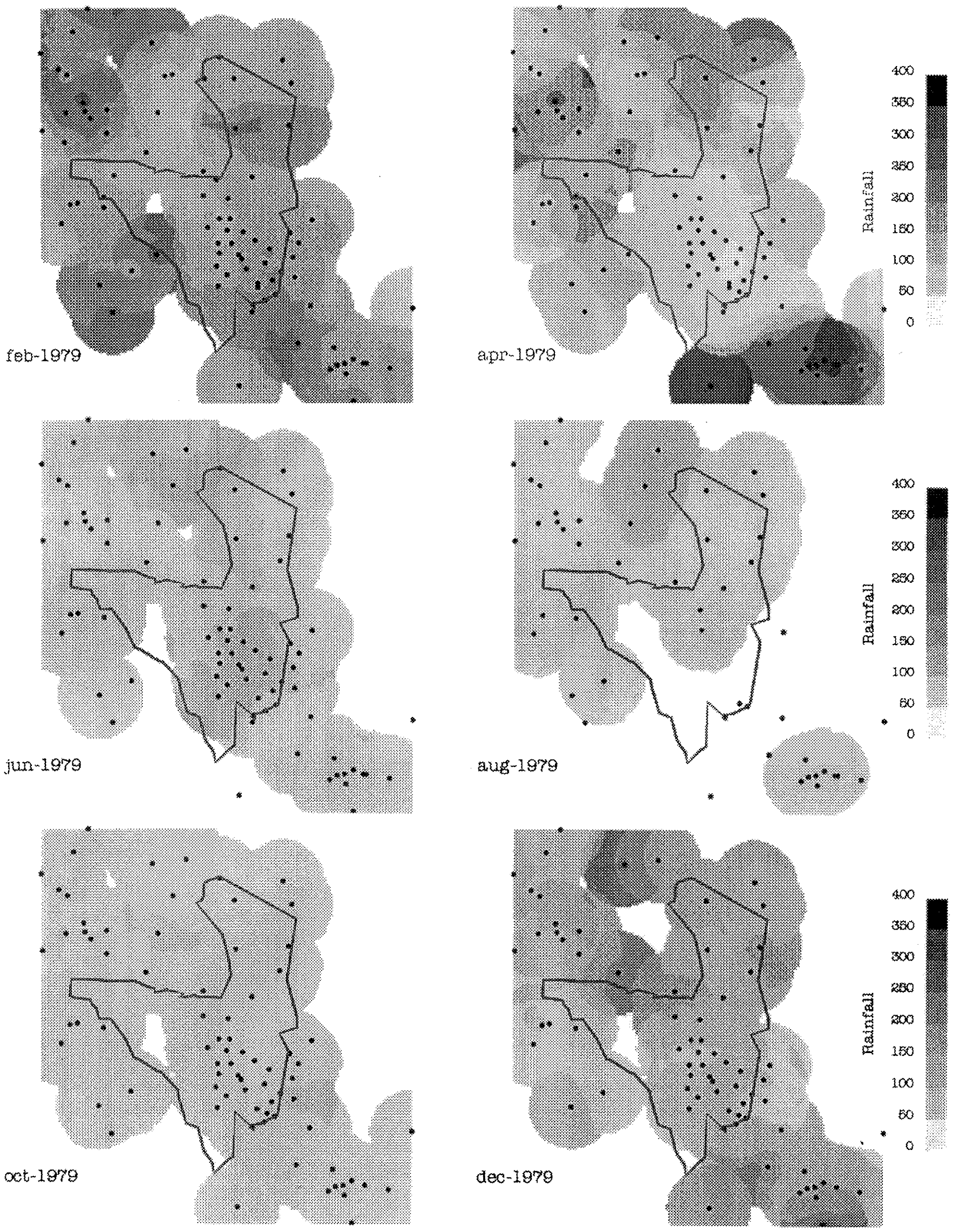


Figure 4. Spatial distribution of the monthly rainfall (0.1 mm) over the Serengeti ecosystem. Note the large spatial differences. Orographic effects (see the topography in Fig. 1) explains the rainfall being largest in the mountains in the north and being smallest in the southern grasslands because this area is located in the rain shadow of the Ngorongoro mountains to the southeast.

QBO signals and the interaction between the global ENSO signal with the tropical Atlantic and Indian Ocean coupled processes, including tropical monsoon convection, with resulting time lags typically 12–18 months (McIntyre, 1993; Jury et al., 1994; Sasi, 1994; Tourre & White, 1995; Semassi et al., 1998). ENSO-based predictability of rainfall is high only for Southern Africa (Jury, 1996).

Mean annual rainfall was about 50% higher in the mid-1970's and late-1980's than in early-1960's (Fig. 3). There has been a concurrent southward displacement of the limit between the wooded savanna and the open grasslands in the Seronera River catch-

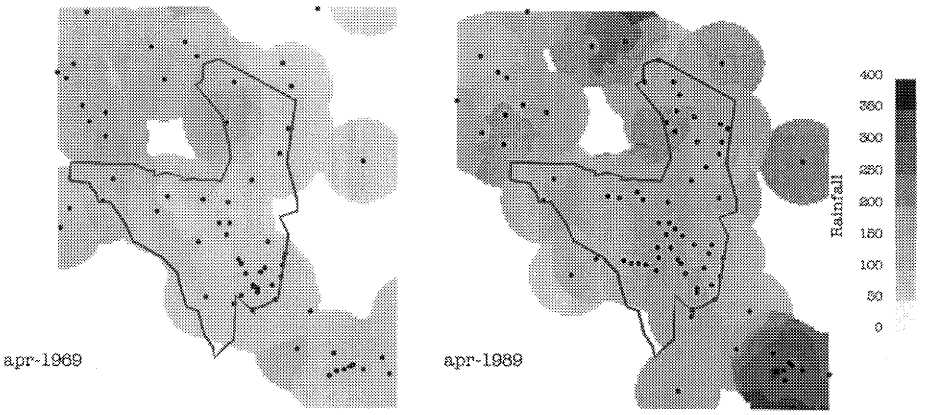


Figure 5. Spatial distribution of the monthly rainfall (0.1 mm) in April, the wettest month, in 1969 (one of the driest years on record) and 1989 (one of the wettest years on record). Note the major interannual differences in rainfall intensity and spatial distribution.

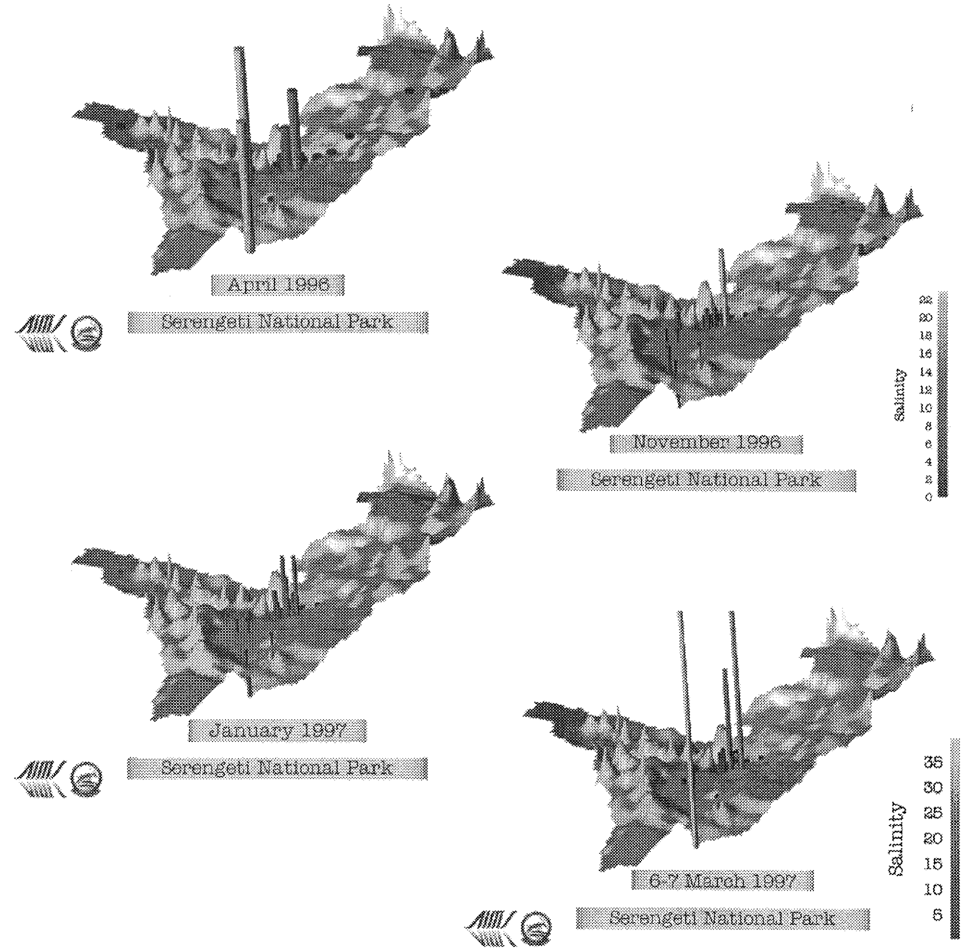


Figure 6. Spatial distribution of the salinity (psu) of surface waters at four months in 1996 and 1997. Note the large seasonal variations of salinity. Many water bodies dry out at the end of the dry season especially in the southern grasslands, these dry water holes are shown as black pins. Salinity is high as soon as water inundates the water holes in the wet season. Salinity increases after rainfall as evaporation results in concentrating the salt. For the wet season, note the higher salinity in 1997 than in 1996; 1996 was a wetter year than 1997. These data are consistent with the hypothesis of a fixed amount of salt being diluted by rainwater.

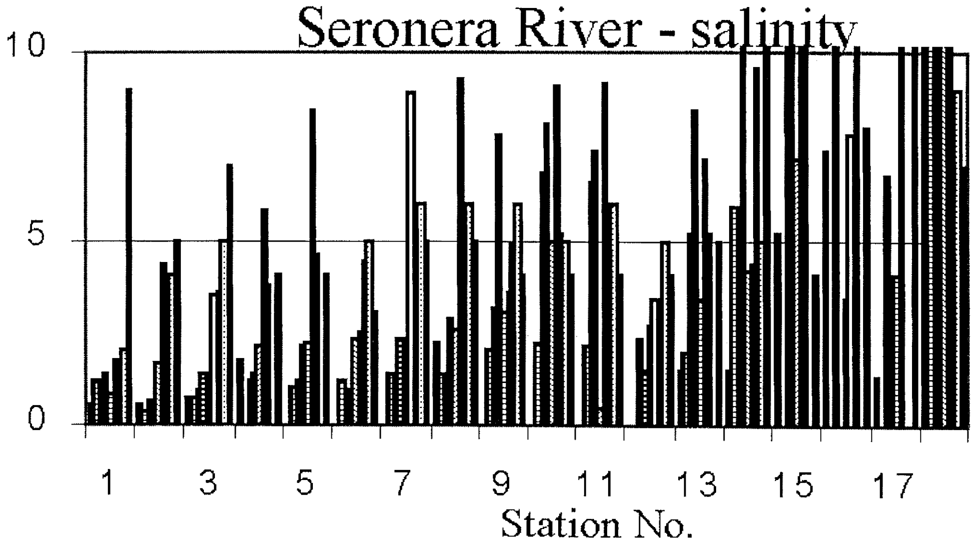


Figure 7. Along-river variation of salinity for the Seronera River in 1996-1998. Site 1 is located downstream in the wooded savanna, site 18 upstream in the open grasslands (see Fig. 1 for a location map). Note the up-river gradient of salinity and the interannual variability.

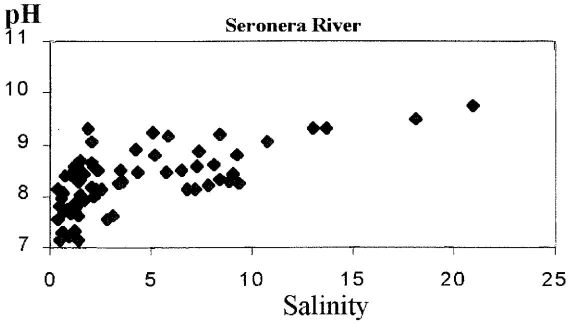


Figure 8. Relation between water salinity (psu) and pH for the Seronera River in 1996 and 1997.

ment (Fig. 11). Rainfall variations at decadal time scales may thus explain the changes in vegetation, though other factors could also be important. These include the policy of discouraging man-made fires and the killing by poachers of 70% the elephants in the 1980's. As an example of the role of elephants, in Congo's Virunga National Park the killing of elephants led to in 20 years to transforming open grasslands into densely wooded savanna though wild fires continued (Verschuren, 1993).

Salinity

Salinity of surface waters of the grasslands at the end of the wet season in a 'normal' year (e.g. 1996 and 1997) is high, commonly >5 in the headwaters of the Mbalageti River, 10–15 in the headwaters of the Seronera River and >20 in the alkaline lakes. When salinity >4 no grass grows along the banks of the rivers and lakes. The salinity decreases rapidly with distance downstream, being typically <1 in the lower reaches of these two rivers (Fig. 6). In both rivers at a salinity of about 2, the vegetation changes from grasslands upstream to wooded savanna downstream. Coincidentally, this limit is also that for the maximum salinity of water that can be used to irrigate rice. Thus, we suggest that salinity at decadal time scales may determine the discontinuity between grasslands and wooded savanna.

Salinity varies inter-annually as a function of rainfall, for instance during the 1998 'wet' year, salinity was about half that in other, normal years (Table 1). This suggests the mass of salt was diluted by about twice as much water in 1998 (an exceptionally wet year) than in 1996–1997 (normal years). An intermediate salinity occurred in 1999. An examination of Table 1 suggests there exists an inverse relationship between wet season salinity and rainfall.

It appears that excessive salinity may be the trigger that starts the annual mass migration of wildebeest and zebras near the end of the wet season away from the southern grasslands. The timing of these migrations varies annually by as much as four months, the onset of the migration is thus not driven by a biological clock. We observed that in 1996 and 1997 the migrations started when there was still plenty of edible forage and surface water in the grasslands where the

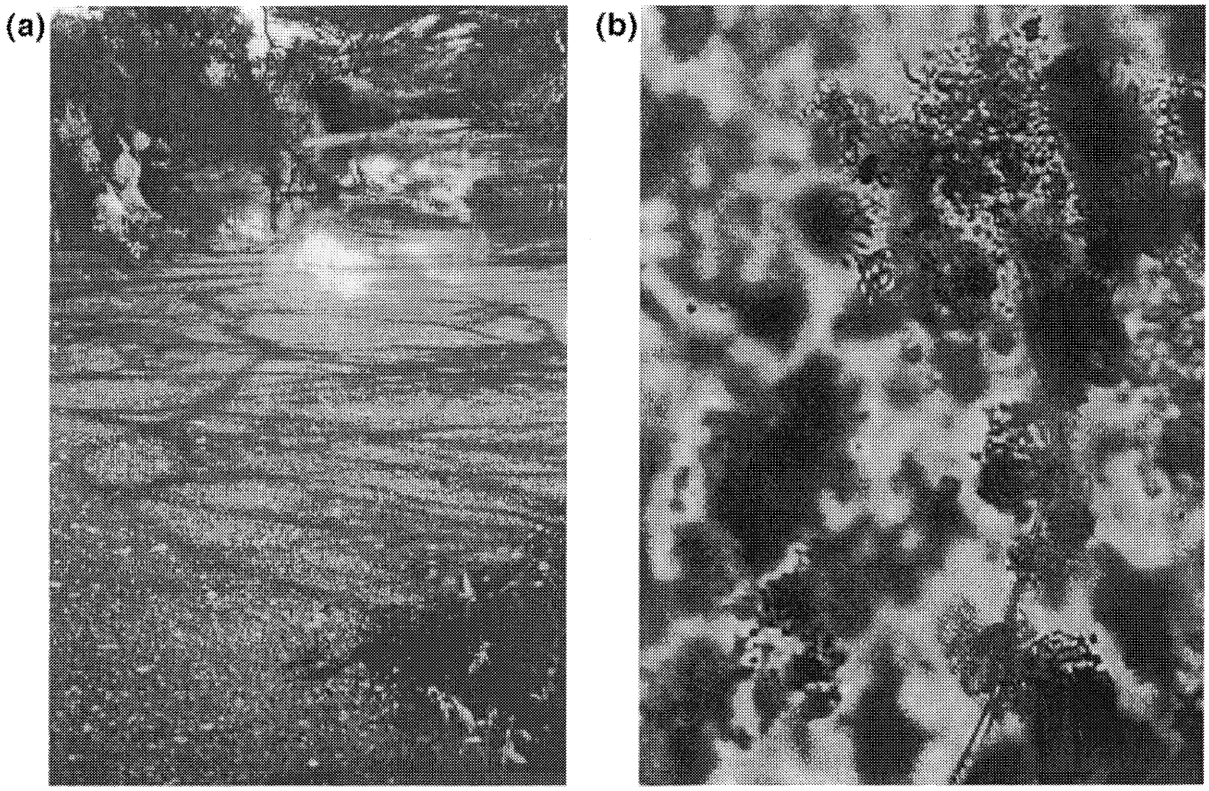


Figure 9. (a) Photograph of the thick alga mat on the surface of a river pond in the Seronera River in the dry season. (b) Microphotograph spanning 500 μm of suspended matter 0.5 m below the surface in the same pond, showing micro-aggregates of decaying organic matter and mud.

herds were, apparently enough to sustain the herds for a while more. However at that time that water was excessively saline (Figs 6 and 7). Mammals cannot survive indefinitely drinking high salinity water.

No data are available on the length of time zebras and wildebeest can survive on such high salinity water. A salinity of 10 psu appears to be the upper limit for sheep for a few months (Child et al., 1981). In the arid Kalahari-Gemsbok National Park, South Africa, groundwater is pumped to ponds for wildlife. Where this water is hard and saline, the wildebeest migrate; where this water is sweet the wildebeest are stabilized (Child et al., 1981).

We propose below a model for timing the onset of the migration based on the hypothesis that the migration is triggered by excessive salinity. Salinity is rainfall-dependent. Because salinity varies spatially and a single value is necessary for a model, we use Lake Magadi as an overall indicator of salinity in the grassland, simply because it is located at the vegetation discontinuity between open grasslands to the south and wooded savanna to the north. This assumption does not imply this lake is a main source of drinking water. The Seronera and Mbalageti rivers and small ephemeral ponds scattered in the grasslands are the main source of drinking water. Their salinity is smaller than that of the lakes, but proportional (with a factor <1) to that of Lake Magadi. Lake Magadi salinity is thus a representative indicator. It has a natural spillway at its mouth; excess water readily spills out; what remains is trapped by the sill and stagnates; the lake then becomes an evaporation pond. In the model the origin of time (t=0) is April 15 (near the end of the wet season). At that time S_o is the salinity of Lake Magadi. Since salt is a conservative substance, the salinity S of Lake Magadi at time t (in days) is:

$$S = S_o h_o/(h_o - Et + R), \qquad (1)$$

where h_o is the mean water depth (m) of Lake Magadi at t=0, h the water depth at time t, E the evaporation rate (0.007 m/day) and R the rainfall (m) between t=0 and t. Because the model starts near the end of the wet season, $R\approx0$. h_o (= 0.8 m) is invariant from year to year because of the natural spillway at Lake Ndutu.

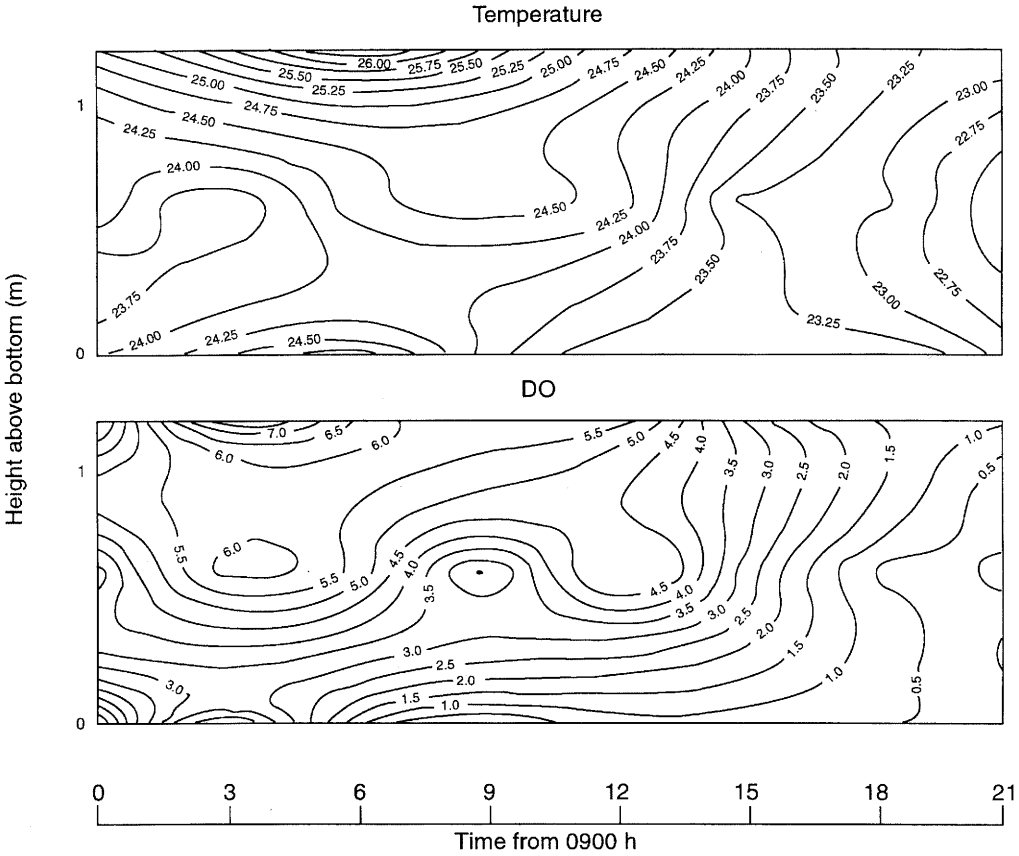


Figure 10. Time series of (a) the temperature (°C) and (b) the dissolved oxygen concentration (ppm) in a stagnant pool of the Seronera River, April 13–14, 1998. The lowest sampling point was about 0.3 m from the bottom and the upper point 0.3 m below the bottom. The pool was very turbid (visibility <2 cm). Though hippos occasionally stirred the water, anaerobic conditions occurred near the bottom.

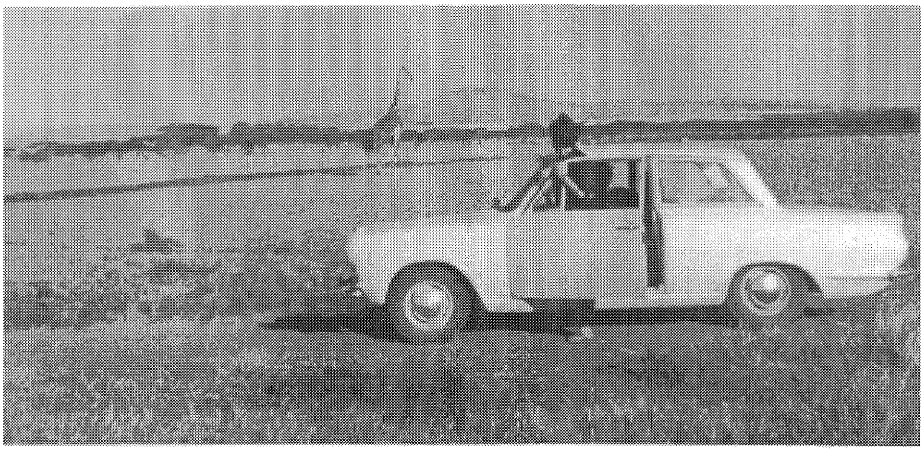
In this model, the migration starts when S exceeds a threshold value. In mid-April 1996 (Table 1), $S_0 = 22$. The migrating wildebeest left the open grasslands to enter the wooded savanna in mid-May 1996, i.e. t=30 days. From Equation (1) it results $S = 30$. The model is thus very simple: the northward migrating wildebeest herds leave the open grasslands and enter the wooded savanna when the salinity of Lake Magadi is 30 psu.

This simple model was tested for 1997, 1998 and 1999. In 1998, $S_0 = 10$ (Table 1) $S = 30$ is predicted to occur at t=85 days, hence on July 10. Field observations revealed the herds of wildebeest entered the wooded savanna in mid-July (with an error of only 4 days between observations and predictions). In 1998 and 1999 the migration was predicted from equation (1) to enter the wooded savanna in, respectively, early May and on June 23, and this prediction was in agreement with observations within an error of only 2 days between observations and predictions. In, 2000, $S_0 =$ 100; this predicted that the migration had already left the area, in agreement with the observations. In 2001, the model predicted that the migration would enter the woodland on June 13; this was observed to be completed by May 30, a two-week error suggesting that other factors are also important.

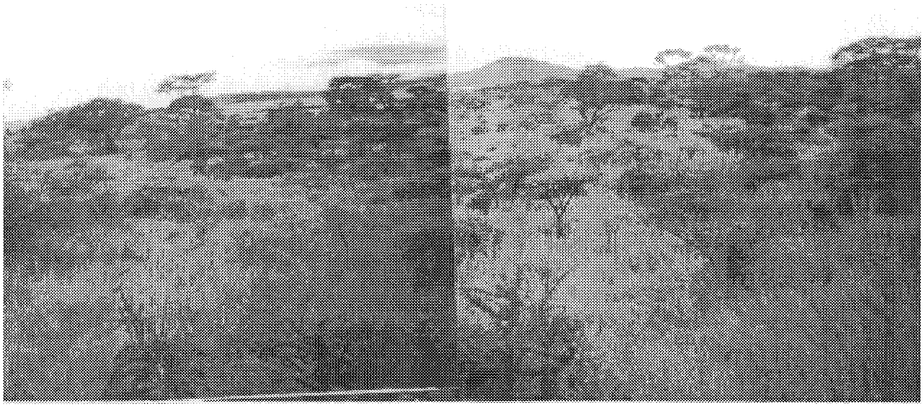
Water quality

The surface waters are used for drinking and are a scarce, heavily used resource. Most are grossly eutrophicated with anoxic conditions on the bottom. The effects of poor water quality on wildlife have not been studied and may be important if there is an analogy between cattle and wildlife husbandry. Indeed, the performance of cattle drinking from dugouts as opposed to troughs is severely diminished as a result of a harmful organisms, the palatability of water, and the release of methane, ammonium or hydrogen sulfide from the muck disturbed by the animals (Willms et

Lower Seronera River



August 1965



April 1998

Figure 11. These photographs of the same area in the Seronera River catchment about mid-way between stations 1 and 18 (Fig. 1) show the recent encroachment of wooded savanna over what was grasslands in the mid-1960's. Photographs by EW.

al., 1994, 1996). Similar effects could control wildlife in the Serengeti National Park and deserve detailed investigations.

Conclusions

We suggest that water is driving the Serengeti ecosystem. Firstly rainfall determines the salinity of the Mbalageti and Seronera Rivers, the two rivers that drain the grasslands; this in turns controls the discontinuity between open grasslands and wooden savanna. Secondly rainfall variation at decadal time scales are large (50% of the mean); they may shift southward or northward (i.e. downstream or upstream) the location of the salinity threshold determining this discontinuity. In turn this introduces changes at decadal time scales in vegetation. Thirdly excessive salinity, and not available forage and water, may be the trigger starting the annual migration of wildebeest and zebras at the end of the wet season. This migration is not driven by a biological clock because it can vary by up to 4 months from year to year. The timing of the migration is modeled on the basis of a threshold value for salinity, itself determined by rainfall and evaporation. The model was successful in predicting the timing of onset of the northward migration for 1996–2000.

Drinking water is a scarce resource for wildlife. It is over-used and results in poor water quality. The effects of poor water quality on wildlife population dynamics have not been studied and may be important if there is an analogy between wildlife and cattle husbandry. This is an important factor to consider when storing surface water to encourage resident wildlife for tourism.

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