Environmental regulation in African shallow lakes and wetlands

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ABSTRACT

An illustrated account is given of environmental conditions and their controlling mechanisms in African shallow lakes and associated wetlands. The subject is introduced by a relatively well-studied case-example, from the productive Lake George in Uganda; here interactions between physical, chemical and biotic factor-systems are emphasized. There is particular interest in wind-generated patterns of horizontal distribution in a basin of near-uniform morphometry, in hydrological buffering against any development of a flooding-drying cycle, and in the pervasive influence of diel cycles in a seasonally equable environment.

Individual components of the physical and chemical factor-systems are then treated on a comparative, pan-African basis. Seasonal cycles of water temperature are related to the systematic variation of solar radiation input with latitude, with some important modifications associated with factors that control other components of the energy budget. The influence of altitude upon water temperature is quantified. Persistent temperature/density stratification is generally ill-developed in these shallow waters, but can be governed by a seasonal wind régime (e.g. harmattan) and displaced by a predominant solute/density stratification in saline waters. The range of total solute concentration is very wide, according to available inputs and opportunities for evaporative concentration. With it are correlated, positively or negatively, the concentrations of many chemical components. Of the major nutrient elements, Si is typically present — by world standards — in considerable concentration but is liable to depletion by diatom growth; forms of N (NH_4-N, NO_3-N) are typically in low concentration, with some influence from (temperature-sensitive) denitrification; and P is often in considerable concentration, especially in many — but not all — soda lakes. A guide is given, with examples, to the quantities incorporated in the biomass of algal or macrophyte communities. Further examples illustrate factors controlling the varying concentrations of dissolved gases (especially O_2, CO_2 : biogenic processes), of heavy metals (especially Fe, Mn, Cu) and also of man-made eutrophication of some shallow waters. Examples of chemical budgets are also given, especially the more complete ones for lakes Chad and Naivasha with variable chemical incorporation into the sediments. Qualitative and quantitative aspects of sediment generation are briefly reviewed.

Three types of cyclic environmental change in time are described, that involve concurrent changes in many variables. The diel (24 h) cycle is impressed by the daily short-wave radiation but often modified by wind-stress; it involves heat accumulation, temperature rise, density stratification with its constraints on vertical distributions, and aspects of photobiology that include O_2/CO_2 exchange. The annual (12 mo.) cycle can have radically different forms depending on whether it is or is not accompanied by extensive volume change of a flooding-drying cycle. The latter is well-developed in many African river floodplains. In many shallow lakes subject to irregular rainfall (e.g. Chad, Chilwa) there tends to be annual carry-over and cycles of longer period. The contraction phase is one of terrestrial recovery followed by aquatic stress that may include biological effects of higher salinity. Reflooding during the

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expansion phase can induce a flush of nutrient release as well as a longer-term salinity change and aquatic recolonization.

KEY WORDS : Tropical — Swamps — Radiation — Temperature — Stratification — Salinity — Nutrients — Sediments — Budgets — Cycles.

RÉSUMÉ

LE RÔLE DES CONDITIONS DE MILIEU DANS LES ZONES HUMIDES ET LES LACS PEU PROFONDS D'AFRIQUE

Les conditions de milieu et leur influence dans les lacs peu profonds d'Afrique et les marais associés sont décrites. L'exemple du lac George, en Ouganda, est d'abord donné en introduction, en soulignant les interactions entre les composantes physiques, chimiques et biologiques. Dans ce lac, sont particulièrement soulignées les distributions horizontales générées par le vent dans un bassin quasi-circulaire, la stabilité du niveau de l'eau et l'influence des cycles nycthéméraux dans un climat dépourvu de variations saisonnières sensibles.

Les différentes combinaisons de facteurs physiques et chimiques sont ensuite abordées sur une base comparative pan-africaine. Les cycles saisonniers de la température de l'eau sont mis en relation avec les variations de l'énergie solaire incidente, et les influences sensibles des autres composants du bilan énergétique. L'effet de l'altitude est quantifié. Une stratification de température/densité est en général peu développée dans les milieux peu profonds, mais peut être régulée par la saisonalité des vents (par exemple l'harmattan) ou déplacée par une prédominance des effets de la salinité dans certains milieux. Les gammes des concentrations de solutés est très large, et fonction des apports et des conditions d'évaporation. Beaucoup de concentrations des divers éléments dissous sont corrélées, positivement ou négativement, à la charge dissoute totale. Parmi les éléments nutritifs, le Si est en général présent en très fortes concentrations, relativement aux moyennes mondiales, mais est aussi susceptible de fortes baisses liées à la croissance des diatomées. Les formes de l'azote (NH_4-N et NO_3-N) sont, de façon caractéristique, en faible concentration, avec une influence de la dénitrification liée aux températures élevées. Le phosphore est souvent en forte concentration, particulièrement dans beaucoup de lacs sodés. Un diagramme est proposé, avec des exemples, des quantités incorporées dans la bomasse micro- ou macrophytique. D'autres exemples illustrent les facteurs qui contrôlent les concentrations des gaz dissous (particulièrement O_2 et CO_2 liés aux processus biologiques), des métaux lourds (Fe, Mn, Cu) et aussi de l'eutrophisation d'origine anthropique. Des bilans bio-géochimiques sont également présentés, notamment pour les lacs les mieux étudiés comme le Tchad ou le L. Naivasha où les sédiments jouent un rôle important. La néogénèse des sédiments, sous ses aspects qualitatif et quantitatif, est rapidement passée en revue.

Trois types d'évolution cyclique de l'environnement sont décrits. Le cycle nycthéméral (24 h) dépendant des radiations de courte longueur d'onde est souvent modulé par les effets du vent; il inclut l'accumulation de chaleur, l'augmentation de température, la stratification thermique avec ses effets sur les répartitions verticales, et des effets de photobiologie incluant les échanges O_2/CO_2. Le cycle annuel (12 mois) peut être très différent selon qu'il est associé, ou non, à une forte variation de volume liée au cycle hydrologique de crue-décrue. Ce dernier aspect est surtout sensible dans les plaines d'inondation. Dans beaucoup de lacs peu profonds soumis à un régime pluviométrique instable (L. Tchad, L. Chilwa), des effets de rémanence se font sentir avec des cycles de période plus longue. La phase de récession est une phase de recolonisation terrestre suivie d'une perturbation aquatique, et peut faire intervenir des effets biologiques liés à une augmentation de salinité. La remise en eau peut induire une remise en solution d'éléments nutritifs ainsi qu'une modification durable de la salinité.

MOTS CLÉS : Environnement tropical — Marais — Lacs — Afrique — Conditions de milieu — Physico-chimie.

1. INTRODUCTION

In the shallow inland water-bodies of Africa, as in freshwaters elsewhere, environmental conditions are determined by an interacting array of external and internal influences. In these physical and chemical, abiotic and biotic, processes participate (Fig. 1). Their operation encounters recurrent constraints from the conditions of shallow basin morphometry, involving limited storage capacity. Further restrictions are set by the prevailing tropical and subtropical climates.

Although individual factors are numerous, they are ultimately traceable to input-output relationships of energy (e.g. radiant or sensible forms) and of materials (e.g. water, solutes, particulates, gases),

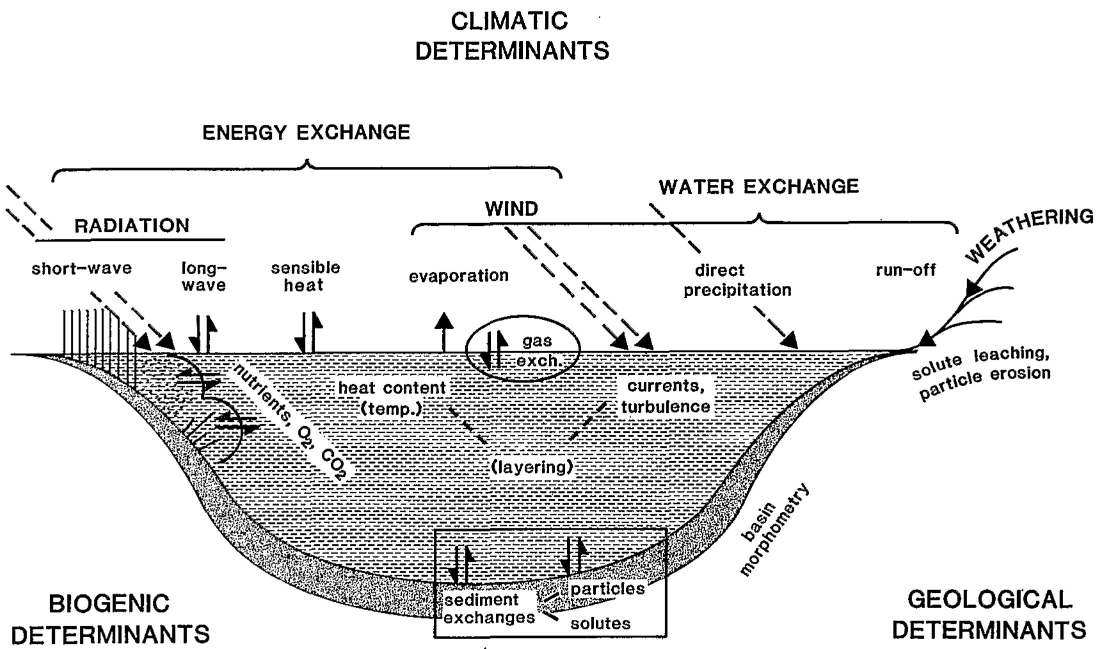

FIG. 1. — Diagrammatic representation of components involved in the control of environments by climatic-atmospheric, geological and biogenic determinants.
Schéma des composants du système aquatique influencés par les facteurs climatique-atmosphérique, géologique et biologique.

and to their internal transformations and storage. All contribute to the variability in time and space reviewed in this account, yet such variability is often dominated by a relatively small number of components. Their influence may derive from their magnitude, their variability, or their involvement of a qualitatively critical constituent. Examples include the component of short-wave solar radiation in the energy balance and hence temperature regime; of the geological availability of leachable substrata for solute inputs and hence ionic composition; of the incidence and magnitude of rainfall and hence inflow terms in the hydrological cycle; of extreme values of the surface outflow term, as when large in relation to storage volume (low retention time) or small in relation to inflow (salinization); of the frequency of wind stress in excess of values required for vertical mixing in open water; and of biological reactions upon the water-mass and sediments in situations of high areal density of biomass.

This review is primarily concerned with natural water-bodies of mean depth < 5 m. A single case-study is first used to illustrate important factors and their interaction. A comparative survey is then made of the variation of individual environmental factors in shallow waters over Africa as a whole. Chemical budgets are illustrated by the two more complete examples from African shallow lakes, and modes of net transfer of material to sediments are outlined. Attention is finally given to some major systems of change in time, which involve many concurrent variations and are of especial importance for shallow water-bodies. Biological implications are noted briefly; they are examined more fully by DUMONT (in press).

Although there is no previous integrated and specific treatment of the present topic, much relevant information can be found in the pan-African surveys of TALLING and TALLING (1965), GRIFFITHS (1972), BEADLE (1981), SYMOENS *et al.* (1981), LIVINGSTONE and MELACK (1984), and DENNY (1985a). Some important water-bodies ('case studies') are described in recent monographs or symposia, notably Lake George (GREENWOOD and LUND, 1973), the Nile system (RZÓSKA, 1976), Lake Chilwa (KALK *et al.*, 1979), Lake Sibaya (ALLANSON, 1979), and Lake Chad (CARMOUZE, DURAND and LÉVÊQUE, 1983). Fig. 2 shows the location of these and other waters to which frequent mention is made in the text.

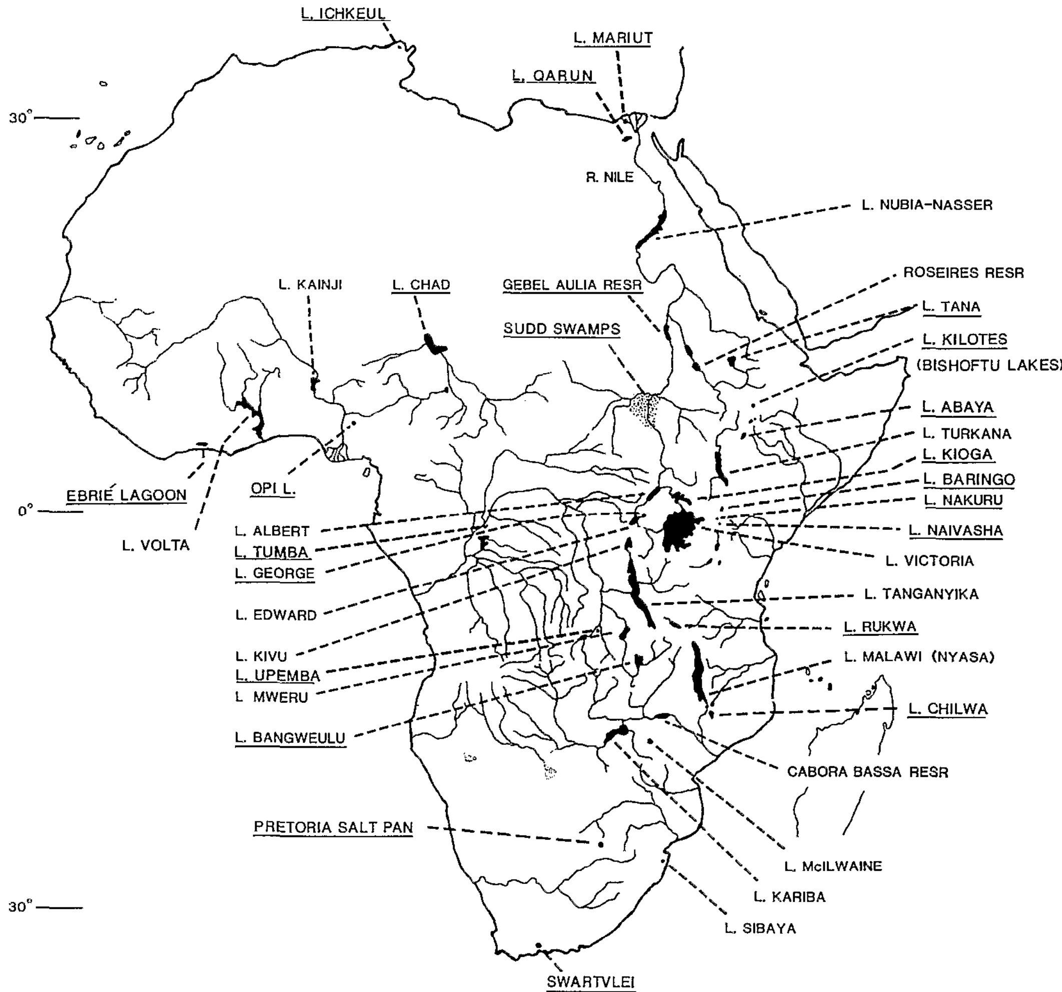

FIG. 2. — Distribution of important water-bodies in Africa. Names of shallow lakes and wetlands mentioned frequently in the text are underlined. From TALLING (1990).

Les plans d'eau importants d'Afrique. Les noms des milieux peu profonds cités souvent dans le texte sont soulignés. D'après TALLING *1990.*

2. CASE STUDY · LAKE GEORGE

Lake George (Fig. 3) is a shallow water-body of considerable size (area 250 km², mean depth 2.4 m) but simple morphometry, situated on the equator in West Uganda on the floor of the Western Rift Valley. The following information is largely derived from the intensive studies of an IBP Team during 1967-1972, for which the symposium volume organized by GREENWOOD and LUND (1973) and the reviews of GREENWOOD (1976) and BURGIS (1978 — with detailed bibliography) — provide convenient and integrated summaries. The lake contrasts with other case-studies, as of L. Chad, L. Chilwa, and the Pongolo floodplain, in the reduced variability of temporal change, excepting that of the diel cycle. Such stability has several modes of origin, from relatively invariant inputs and from local buffering mechanisms.

The seasonal climate at L. George is such that systematic variations of the short-wave solar radiation input are small. According to VINER and SMITH (1973), 10-day means have an annual variation between 1720 and 2210 J (411 and 529 cal) cm^{-2} day^{-1}. The estimated mean rate of evaporation, 5 mm day^{-1}, is equivalent to a loss of 1446 J (346 cal) cm^{-2} day^{-1} and involves little seasonal variation (Fig. 4a). The corresponding variations in other major compo-

FIG. 3. — Map of Lake George, Uganda, with adjacent water-bodies and relief. From VINER and SMITH (1973).
Le lac George, Ouganda, avec les lacs et marécages associés, et le relief. D'après VINER et SMITH, 1973.

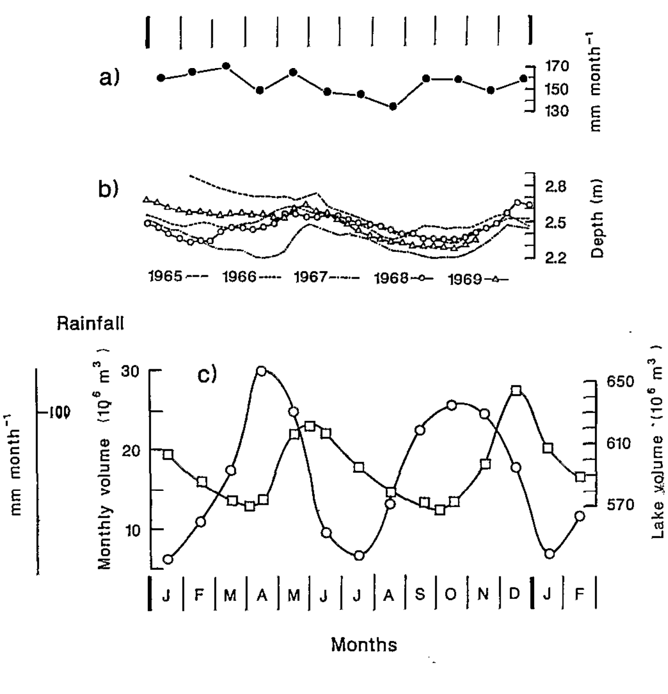

FIG. 4. — Lake George: monthly changes of characteristics associated with the water-balance, including (a) evaporation (b) lake level (c) direct rainfall onto the lake (o) and lake volume (□), showing out-of-phase relation. Adapted from VINER and SMITH (1973).
Le lac George : variations mensuelles de variables associées au bilan hydrique : a) évaporation, b) niveau du lac et c) déphasage entre la pluie directe sur le lac (○) et le volume lacustre (□). D'après VINER et SMITH, 1973.

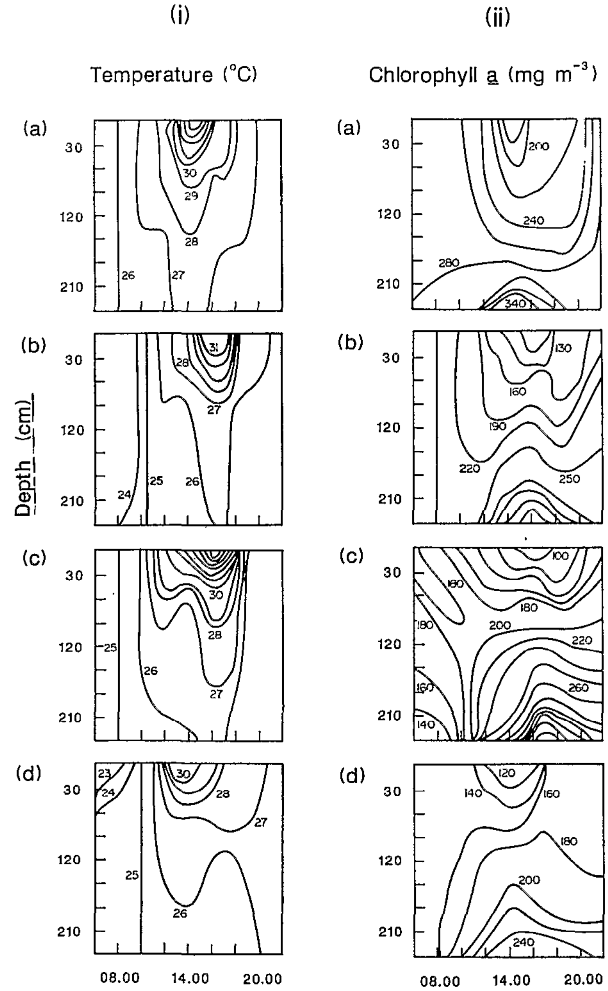

FIG. 5. — Lake George : examples of daily (diel) cycles in the depth-time distribution and layering of (i) temperature (isotherms in °C) and (ii) chlorophyll *a* content of phytoplankton (isopleths in mg $m^{-3} = \mu g\ l^{-1}$). Dates : (a) 18 May 1967, (b) 5 July 1967, (c) 26 March 1968, (d) 5 February 1968. Adapted from GANF (1974b).

Le lac George : exemple de cycles journaliers de répartition de la température (isothermes en °C) et en concentration de la chlorophylle (isoplètes en mg m^{-3}). Dates: a) 18 mai 1967, b) 5 juillet 1967, c) 26 mars 1968, d) 5 février 1968. D'après GANF, 1974b.

nents of energy balance (net back-radiation, sensible heat transfer) are not known, but are also likely to be small, as the lake bottom temperature varies only between 23 and 25 °C.

In the upper half of the water-column, however, the diurnal change in solar radiation flux leads to net energy storage of about 2.6 kJ (620 cal) cm^{-2} within an absorptive shallow layer and hence elevated temperatures there. The latter not uncommonly reach afternoon maxima of > 30 °C. Thus a pattern of temperature and density stratification, with barriers to vertical exchange, is set up with a diel frequency (Fig. 5). The resulting subdivision of the water-mass makes a corresponding impress on other entities in dynamic flux, including the concentrations of oxygen (Fig. 6b) and carbon dioxide with pH (Fig. 6c) influenced by photosynthesis with respiration and surface exchange, and the biomass concentrations of positively or negatively buoyant phytoplankton (Fig. 5). The daily stratification is ended by increased vertical mixing due mainly to a combination of reduced radiation input, increased wind strength late

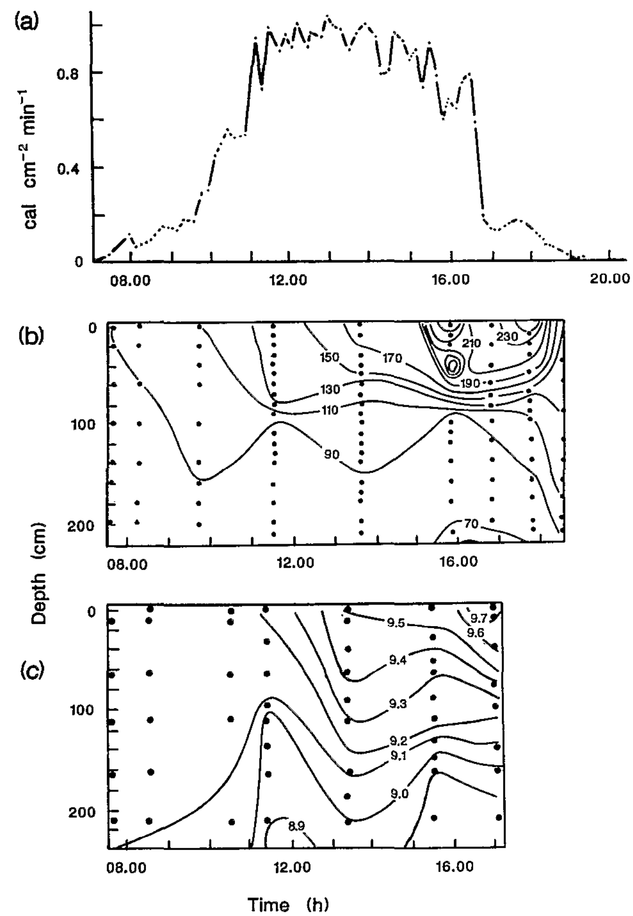

FIG. 6. — Lake George : diel variation during 26 March 1968 in (a) incident solar radiation and, as depth-time diagrams, (b) percentage oxygen saturation and (c) pH. Adapted from GANF and HORNE (1975). For temperature see Fig. 5c.

Le lac George : variations journalières le 26 mars 1968 de a) rayonnement solaire incident et b) répartition espace-temps du pourcentage de saturation en oxygène et c) du pH. D'après GANF et HORNE, 1975. Pour la température, voir la figure 5c.

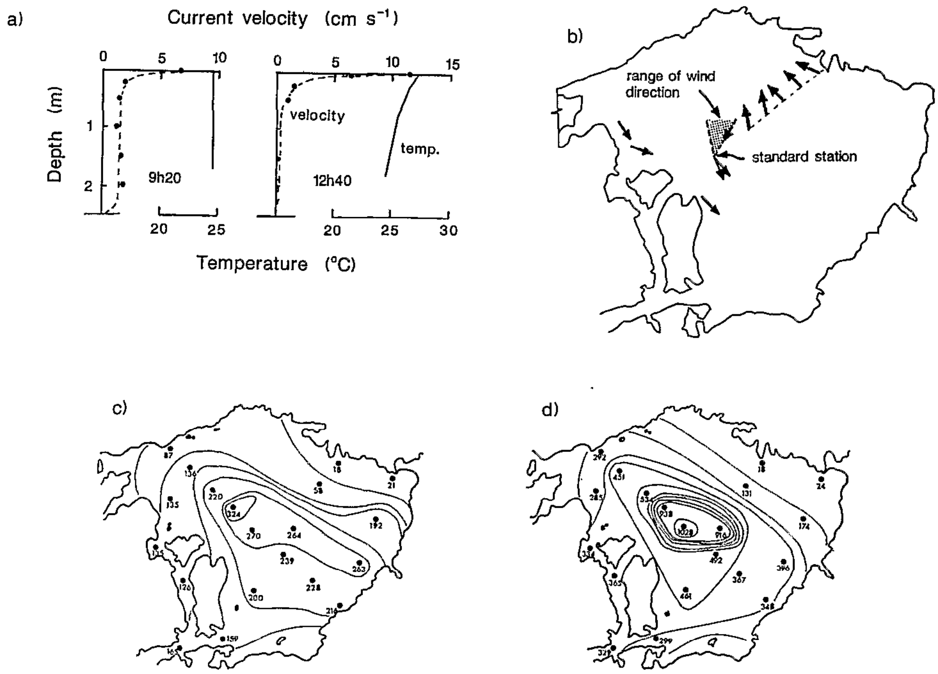

Fig. 7. — Lake George : examples of (a) depth-distribution of current velocity and temperature, and (b) the horizontal distribution of current direction, on days when light winds were blowing, with possible consequences in concentric distribution patterns of (c) phytoplankton density as mg chlorophyll *a* m^{-3} (= μ 9 l^{-1}) and (d) density of zooplankton Crustacea as μg dry mass l^{-1}. Adapted from Viner and Smith (1973) and Burgis *et al.* (1973).

Le lac George : exemples a) de répartition verticale de la vitesse du courant, b) de répartition horizontale des directions du courant par vent léger avec c) leur conséquences possibles sur la distribution concentrique de la chlorophylle (mg.m⁻³) et de la densité de crustacés du zooplancton (mg.m⁻³ de poids sec). D'après Viner et Smith, 1973 et Burgis et al., *1973.*

in the day, and transfer of sensible heat to a cooler nocturnal atmosphere with mean night minimum 16.5 °C.

Although the wind regime has a diel component of variability (Viner and Smith, 1973 Fig. 7) there is not a pronounced seasonality as the surrounding region largely escapes the July impact of the S.E. Trades influential elsewhere in East and Central Africa. Inputs of wind energy tend, as noted above, to counter by vertical turbulence the stratifying influence of near-surface accumulations of heat. They also evoke horizontal transfers of water, which were studied by Smith (*in* Viner and Smith, 1973) who introduced current measurements by aluminium drogues suspended at various depths. These demonstrated a rapid decline in the uppermost 10 cm of current velocity set up by light winds (Fig. 7a). Implications for disturbance of bottom sediments were also explored theoretically ; a critical water velocity for disturbance of about 25-30 cm s^{-1} was estimated to correspond to an observed long-term sediment disturbance depth of 25 cm (frequent disturbance to only c. 5 cm, on chemical grounds — Ganf and Viner, 1973, and Fig. 11). Relationships were deduced between wind-speed of 1 h, length of its over-lake travel or ' fetch ', and theoretical water velocities (U_{D2} cm S^{-1} at the sediment-water interface near 2.5 m depth (Table I). From the incidence of wind speeds above 12.5 m s^{-1}, about 0.2 % of the time, Smith estimated that significant areas of the lake bed are likely to be disturbed about once every three weeks. Another important finding was a wind-

Table I

Wind velocity	Beaufort wind scale 5 (≈ 9.5 m s^{-1})	6 (≈12.5 m s^{-1})	7 (≈ 15 m s^{-1})	8 (≈ 19 m s^{-1})
fetch (km)	U_D	U_D	U_D	U_D
2.5	9.8	16.8	26.1	36.9
5.0	12.9	22.3	34.8	50.4
7.5	14.1	24.5	39.1	57.2
10.0	14.3	25.6	37.5	61.9

generation of rotatory water movements over the lake, anti-clockwise under northerly winds (Fig. 7b) and probably clockwise under southerly winds. Such water rotation has consequences for the often concentric distribution of phytoplankton and zooplankton densities (Fig. 7c,d) (GANF, 1974a). GANF (1974b) also used the physical data to examine stability relationships in a stratified water column, employing as criterion estimates of the Richardson number, in relation to vertical movements of phytoplankton.

The hydrological balance is such that pronounced seasonal changes in water level do not occur, the typical annual variation of level being not more than $\pm$ 0.2 m (Fig. 4c). However there is a small bimodal variation (peaks about June and December) which can be related, with lag, to a corresponding variation in rainfall (peaks about April and October). Such bimodality of rainfall, characteristic of much of East Africa, causes water input to be extended seasonally. Extension also results locally by the supply of water from generally higher and prolonged rainfall on the adjacent Ruwenzori Mountains. Finally, a peculiar outflow channel (Kazinga Channel : see Fig. 3) of very slight gradient but considerable volume, and the downstream Lake Edward, act hydrostatically as further local buffers to level fluctuation. The following estimates of the main quantities in the annual hydrological budget were made by VINER and SMITH (1973) :

inflow	(R_i)	1948 ($\times$ 10^6 m^3)
direct rainfall on lake	(P)	205
evaporation from lake	(E)	456
surface outflow (by difference)	(R_o)	1697
underground drainage (assumed)	(G_o)	0

As the mean lake volume is 600 $\times$ 10^6 m^3, the mean retention time (as volume/outflow) is approximately 4.3 months but would vary seasonally by an order of magnitude. During the drier seasons evaporation is calculated (as c. 1.25 $\times$ 10^6 m^3 day^{-1}) to be larger than outflow (as c. 0.8 $\times$ 10^6 m^3 day^{-1}) as a source of water loss.

The last type of difference, when more pronounced in other African lakes, can induce appreciable seasonal or long-term increase in the total ionic concentration or salinity (also indicated by electrical conductivity). Such fluctuation is small in L. George (VINER, 1969; see Fig. 8), where the ionic concentration is close to the averaged characteristics of the inflows. Drainage to the latter does not extend from the very distinctive geological sources of Na^+, K^+, and Mg^{2+} in the Virunga volcanic field, which increase both the total salinity and the proportions of these ions in many rivers and other lakes of the

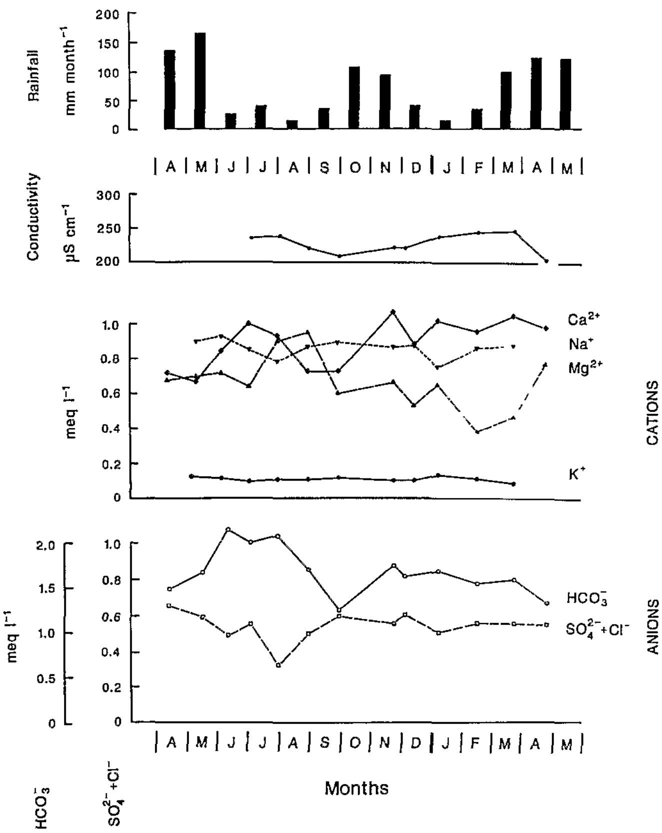

FIG. 8. — Lake George : seasonal changes in lake water of conductivity and the concentrations of major ions, in relation to mean monthly rainfall, 1967-8. Adapted from VINER (1969). *Le lac George : changements saisonniers de la conductivité et des concentrations en ions majeurs en fonction de la pluviométrie mensuelle en 1967-68. D'après VINER, 1969.*

Western Rift Valley (TALLING and TALLING, 1965). Instead, the ions Ca^{2+} and HCO_3^- predominate in both inflows and lake (Fig. 8), and the latter is of relatively low salinity and conductivity (at 20 °C, circa 220 $\pm$ 20 $\mu S\ cm^{-1}$).

Some properties or constituents of the lake water are likely to control, or be controlled by, the dense phytoplanktonic biomass present. The latter, plus a considerable background concentration of filter-passing organic material (10-15 mg C and 0.5-0.8 mg N l^{-1} : GANF and VINER, 1973), produce a high and spectrally selective attenuation of light (Fig. 9). Phytoplankton accounts for most of the total content of nitrogen and especially of phosphorus (Fig. 10), with forms of inorganic nitrogen (NH_4-N, NO_3-N) and soluble reactive phosphate (PO_4-P) existing in very low residual quantities that are presumably in active turnover (VINER, 1973, 1977c ; GANF and VINER, 1973). To these fluxes, bacteria and also zooplankton contribute strongly (GANF and BLAŽKA, 1974); estimates of NH_4-N excretion by fish are an order of magnitude lower (GANF and VINER, 1973). Input fluxes of N and P to the lake include considerable atmospheric components, based on solutes in rainwater (VINER and SMITH, 1973; GANF and VINER, 1973; see Table III) and N_2-fixation by blue-green algae (HORNE and VINER, 1971; GANF and HORNE, 1975; Section 4.4). The concentration of another plant nutrient, silicon, is so high (c. 9 mg l^{-1}) as to be little affected by the Si-consuming diatom populations present. In the upper illuminated layer, photosynthetic activity induces a diurnal increase (to super-saturation) of oxygen and decline of total carbon dioxide, the latter being linked to an increase

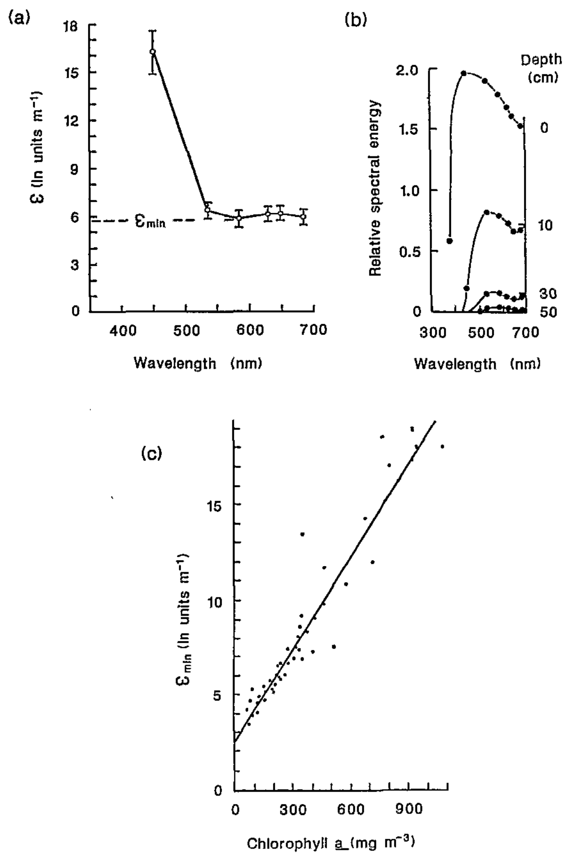

FIG. 9. — Lake George: some characteristics of underwater light attenuation, including (a) spectral variation of the vertical attenuation coefficient ε, (b) relative energy distribution at various depths, (c) relationship between chlorophyll *a* concentration and the minimum value, over the spectrum, of the vertical attenuation coefficient ε_{min}. Adapted from GANF (1974c).

Le lac George : caractéristiques optiques de l'eau a) spectre du coefficient ε d'atténuation verticale de la lumière, b) répartition spectrale de l'énergie à différentes profondeurs et, c) relation entre la concentration en chlorophylle a et ε_{min} le coefficient d'atténuation verticale minimal sur le spectre. D'après GANF 1974c.

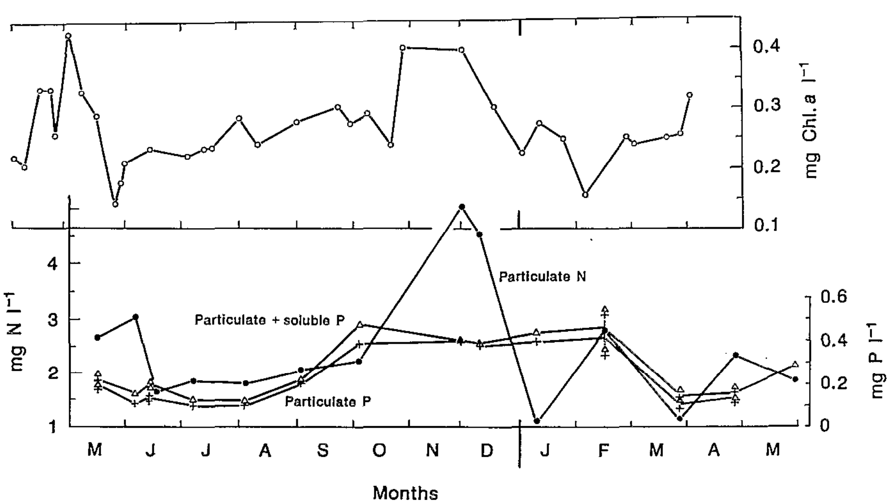

FIG. 10. — Lake George: changes in concentrations (mg l^{-1}) of chlorophyll *a*, particulate N, particulate P and total (particulate+soluble) P during 1967-8. From VINER (1977c).

Le lac George : variations de la concentration en chlorophylle (mg.l^{-1}), de l'azote particulaire, du phosphore particulaire et total (particulaire+dissous) en 1967-68. D'après VINER, 1977c.

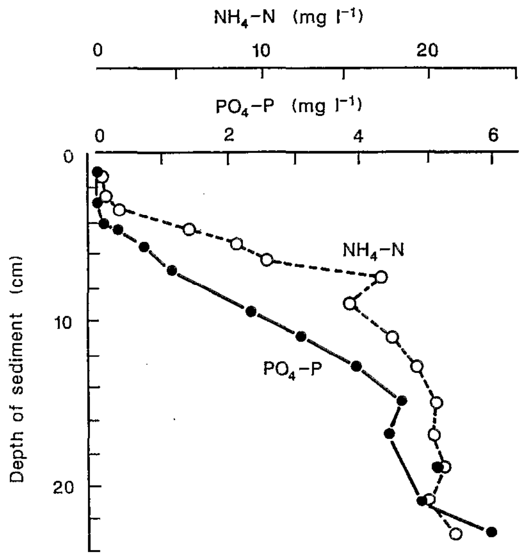

FIG. 11. — Lake George : depth-distribution in offshore sediment columns of soluble, H_2O-washable, PO_4-P and NH_4-N, showing reduction in the upper zone (ca. 0-5 cm) affected by frequent turbulence. Adapted from GANF and VINER (1973).
Le lac George : répartition verticale dans les sédiments du P-PO_4 et N-NH_4 soluble, extrait par l'eau. Les faibles teneurs dans les 5 premiers centimètres correspondent à l'épaisseur soumise à la turbulence. D'après GANF et VINER, 1973.

of pH which can exceed 10. There is evidence for increased nucleation of solid carbonate (presumably largely $CaCO_3$) in such alkaline water (TALLING, unpublished), where the solubility product of $CaCO_3$ is often exceeded (GOLTERMAN and KOUWE, 1980, Fig. 4.5). A further combination with phosphate to form hydroxy-apatite is also possible (VINER, 1975e).

These and reverse changes at depth, where respiration predominates (GANF, 1974d), are controlled in space and time by the intermittent daily temperature-density stratification and wind-induced turbulence. Disturbance of bottom sediments by the latter can be recognised in their chemical profiles, e.g. of NH_4-N and PO_4-P content (Fig. 11); conversely, an upper layer may be recruited from recently sedimented phytoplankton. These are examples of a wider range of sediment-water interactions. Some sediments, brought in by inflow streams, contribute to a limited development of swamps off the northern shoreline. Elsewhere the shorelines are marked by an abrupt fall in the soft substratum, and a shelving littoral zone is not developed.

A 24-h or diel cycle of change (see Fig. 6) is predominant for many features mentioned above (temperature, O_2, pH, phytoplankton layering) and also for various types of biological activity shown in Fig. 39. Although changes over the longer time-scales (< 24 h) are generally small and indicate a considerable — and, for shallow lakes, exceptional — stability under an equable climate, there is evidence that this condition is delicately poised and so easily disturbed during and after episodes of unusually prolonged and enhanced stratification which occasionally develop during calm weather. It is likely that the consequences for some gases, especially deoxygenation, lead to biological disturbances that include sporadic fish-kills (GANF and VINER, 1973).

3. REGULATION OF THE PHYSICAL ENVIRONMENT

The physical environment is dominated by inputs of energy (e.g. from solar radiation, wind) and their transformations within the water-mass.

3.1. Solar radiation input

The distribution of solar radiation over the landmass of Africa is determined partly by directional or 'geometrical' factors of beam-incidence related to latitude and season, and partly to more locally variable modifications due to atmospheric turbidity. These factor-groups can be summarised, for a given 24 h period, by fractional transmission values of ε_g and ε_a respectively. Their mutual product with the solar constant (1.36 kJ m^{-2} s^{-1} or 1.95 cal cm^{-2} min^{-1}) determines the daily radiation flux on a horizontal

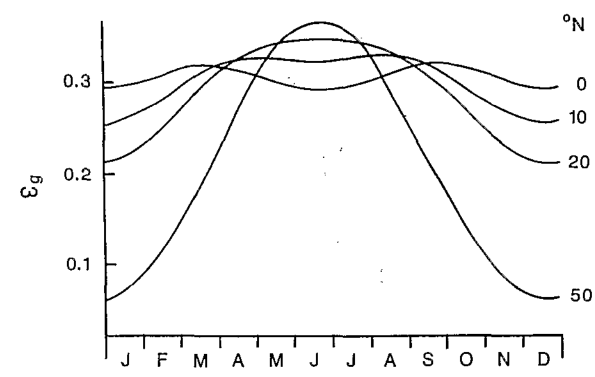

FIG. 12. — Seasonal variation, at four latitudes North, of the geometrical or directional factor ε_g governing the daily flux of short-wave solar radiation on a horizontal surface. From MONTEITH (1972).
Variations saisonnières, pour 4 latitudes de l'hémisphère nord, du coefficient géométrique ε_g déterminant le flux solaire (ondes courtes) sur un plan horizontal. D'après MONTEITH, 1972.

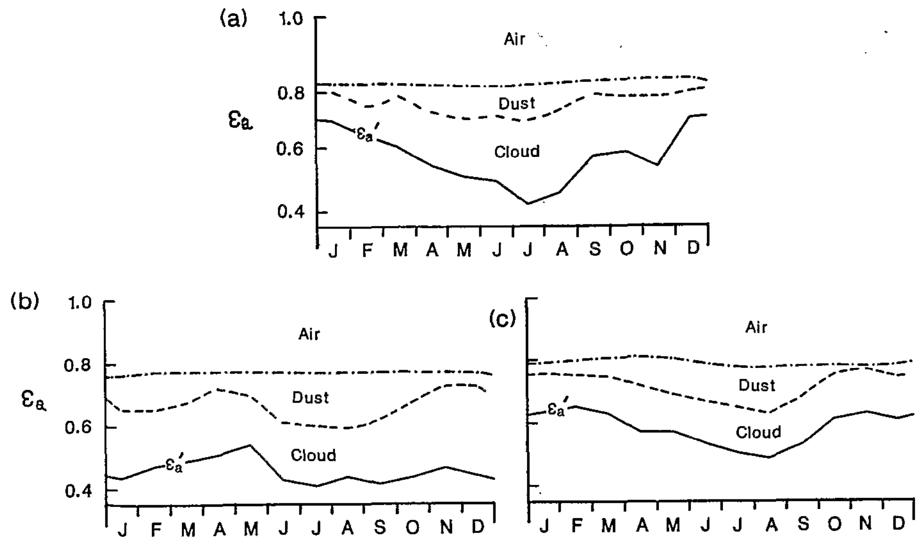

FIG. 13. — Annual variation in atmospheric transmission factors ε_a for solar radiation, including the overall actual transmission factor ε_a (-), that applicable to a cloudless dust-free atmosphere (-.-), and that obtained from mean monthly radiation maxima and applicable to a near-cloudless but dust-containing atmosphere (---); (a) Sumaru, Nigeria (b) Kinshasa, Zaïre (c) Muguga, Kenya. Adapted from MONTEITH (1972).

Variation annuelle du coefficient de transmission atmosphérique εa. En trait continu, coefficient global réel; en trait mixte pour une atmosphère sans nuages et sans poussière; en tireté, pour la radiation maximale moyenne mensuelle, sans nuage mais avec poussière. a) : Sumaru (Nigeria), b) : Kinshasa (Zaïre) et c) : Muguga (Kenya). D'après MONTEITH, 1972.

surface (Q_x). Thus if $\varepsilon_g = 0.3$ and $\varepsilon_a = 0.5$, the daily flux

$Q_r = 1.36 \times 10^{-3} \times 0.3 \times 0.5 \times 3600 \times 24 = 17.6$ MJ m^{-2} $day^{-1} = 1.76$ kJ cm^{-2} day^{-1} (422 cal cm^{-2} day^{-1}). The two fractional transmission values are illustrated by MONTEITH (1972) in diagrams shown here as Figs 12 and 13. The first shows the dependence of the 'geometrical factor' upon latitude and season, with similar values (circa 0.3) over low latitudes and many seasons and a marked winter reduction at higher latitudes. Comparison was made of calculated daily fluxes at the top of the atmosphere with those measured at three African sites, deriving an atmospheric transmission factor to which calculated contributions by air, fine dust particles (aerosol) and cloud were distinguished (Fig. 13). The last two contributions are often of similar magnitude, expressive of the prevalence of smoke and soil-derived dust during dry seasons.

The following discussion deals chiefly with day-integrated measures of short-wave radiation on a horizontal surface (Q_r), expressed in MJ m^{-2} (or kJ cm^{-2}) day^{-1} or cal cm^{-2} day^{-1} (1 cal cm^{-2} = 41.8 kJ m^{-2}).

Diurnal variability is fundamentally controlled by day-length and maximum (solar-noon) solar elevation. The variation of these is minimal at the equator, and values of both can be found from meteorological tables, such as the Smithsonian Meteorological Tables (1951). The same Tables provide values of Q_r as a function of latitude and month, both uncorrected for atmospheric absorption and corrected for various values of atmospheric transmission per unit air mass. A value of 0.8 for the last factor was used by WOOD *et al.* (1976) to estimate potential clear-sky radiation income for the Bishoftu lakes (Ethiopia) and compare with observed values which were markedly lower during the rainy season.

Published measurements of Q_r at sites in Africa are not numerous and still fewer relate to freshwater sites. Some examples of its seasonal variability are shown in Figs. 14 and 17, with minima attributable to the latitude-dependent geometrical factor or to pronounced seasonal cloud cover. These patterns are further discussed by TALLING (1990) in relation to temperature cycles. More geographically comprehensive but idealized contour-maps of Q_r have been constructed from calculated and measured values. The sets (Fig. 15) illustrated here, from BLACK (1954) and THOMPSON (1965), show latitudinal swings of maxima and minima with season together with local modifications. For the last cloud cover is important; an example-distribution, in May, is seen from space in Fig. 16.

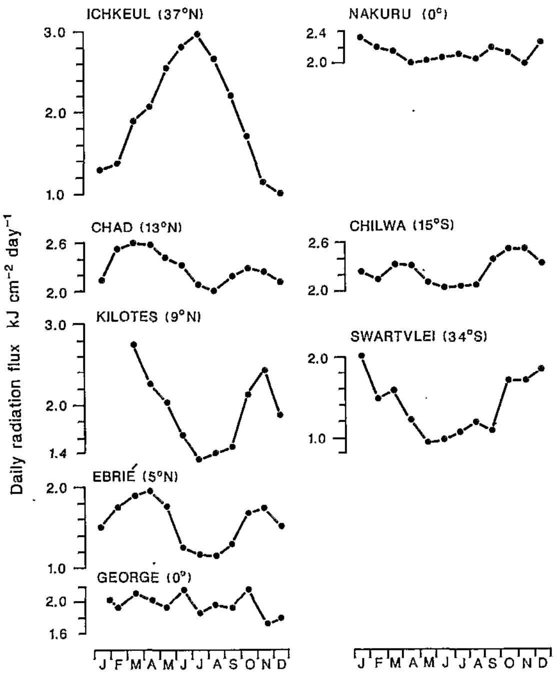

FIG. 14. — Annual changes of incident solar radiation (horizontal surface) for eight shallow African lakes; (a) L. Ichkeul (from LEMOALLE, pers. comm.), (b) L. Chad (from CARMOUZE *et al.*, 1983), (c) L. Kilotes (from WOOD *et al.*, 1976), (d) the Ebrié lagoon (from PAGÈS *et al.*, 1981), (e) L. George (from VINER and SMITH, 1973), (f) Nakuru (from VARESCHI, 1982), (g) L. Chilwa (from KALK *et al.*, 1979), (h) Swartvlei (from HOWARD-WILLIAMS and ALLANSON, 1981).

Variations annuelles de l'énergie solaire incidente (sur un plan horizontal) pour 8 lacs peu profonds; a) L. Ichkeul (J. LEMOALLE, comm. pers.), b) L. Tchad (CARMOUZE et al., *1983), c) L. Kilotes (WOOD* et al., *1976), d) Lagune Ebrié (PAGÈS* et al., *1981), e) L. George (VINER et SMITH, 1973), f) L. Nakuru (VARESCHI, 1982), g) L. Chilwa (KALK* et al., *1979) et h) Swartvlei (HOWARD-WILLIAMS et ALLANSON, 1981).*

3.2. Temperature

As in other continents, the seasonal progression of water surface temperature at higher latitudes broadly follows that of solar radiation input, usually with some lag indicative of the energy-accumulative character of water temperature (Fig. 17). This pattern is expressed in a series of seasonal curves from north to south (Fig. 18). Although most of the lakes involved are 'deep' (exceptions : L. Chad, L. Bangweulu) the gross features of seasonal pattern would also apply to shallow lakes. More examples for the latter are given in Fig. 19. Among these, pronounced temperature minima arise during the months June-August for different reasons in the Ebrié lagoon at 5° N (cloudy-rainy season) and Lac Ihotry at 21°05′ S (winter season with trade winds). At lakes George (0°) and Ihema (1°50′ S) the seasonal differences do not exceed 2 °C, whereas at Swartvlei (34°03′ S) (Fig. 17), and L. Ichkeul (37° 10′ N) there is a pronounced winter minimum related to the latitudinal-geometrical factor of solar radiation.

The fall in surface temperature with altitude is most easily depicted for equatorial water-bodies in which seasonal variation is small. It is illustrated in

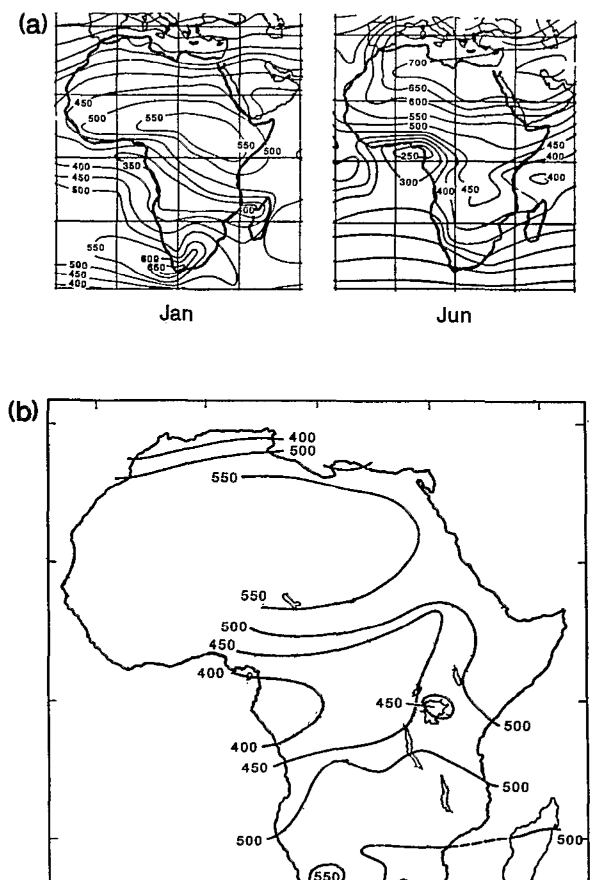

FIG. 15. — The distribution over Africa of incident solar radiation on a horizontal surface, expressed (a) as calculated mean daily values (cal cm^{-2} day^{-1}) in January and June, adapted from BLACK (1956), (b) as mean values (kcal cm^{-2} yr^{-1}), adapted from THOMPSON (1965).

Répartition de l'énergie solaire incidente en Afrique a) moyennes mensuelles calculées en janvier et juin (d'après BLACK, 1956) et b) moyennes annuelles (kcal. cm^{-2}.an^{-1}) d'après THOMPSON, 1965.

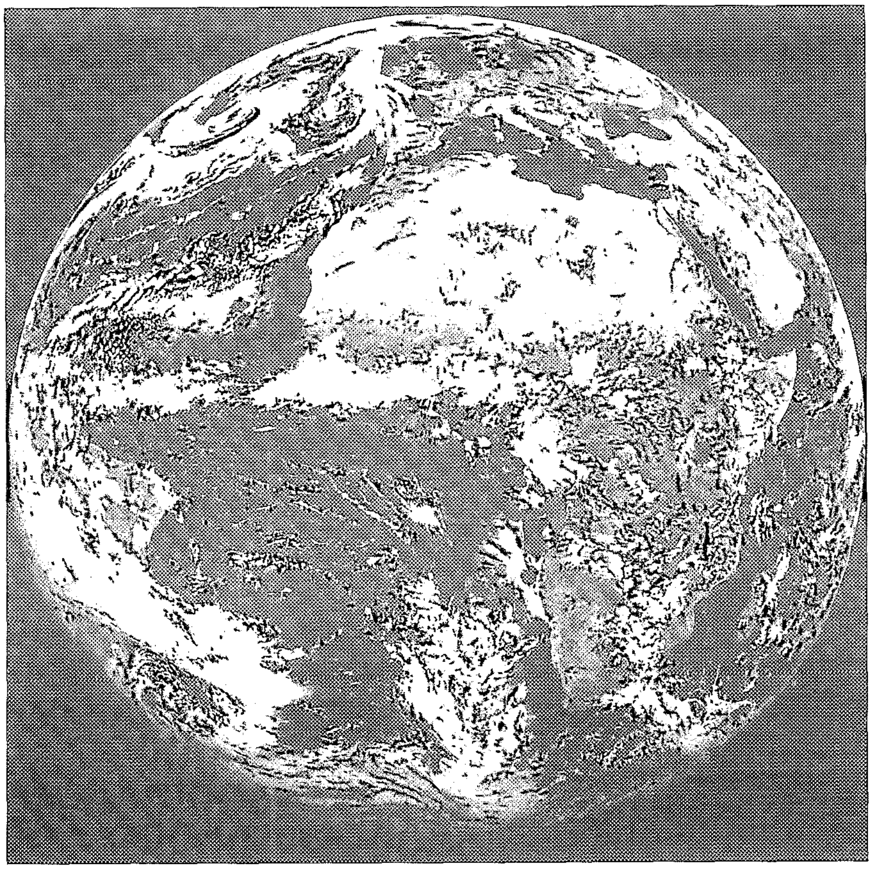

FIG. 16. — Distribution of cloud over the African continent at 11.55 GMT on 31 May 1978, as recorded from the European Space Agency's geostationary weather satellite Meteosat 1. Photo by courtesy of the Meteorological Office, U.K.
La couverture nuageuse sur l'Afrique le 31 mai 1978 à 11 h 55 GMT, vue par le satellite géostationnaire de l'Agence Spatiale Européenne, Meteosat 1. Image aimablement communiquée par l'Office de Météorologie du Royaume Uni.

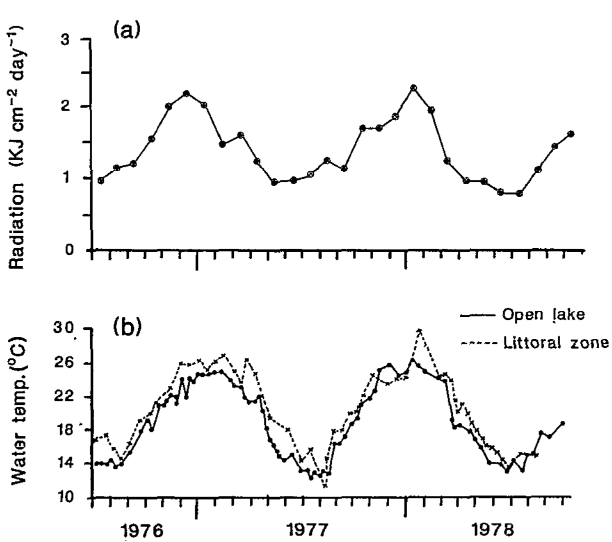

FIG. 17. — (a) Annual variation of daily solar radiation (as monthly mean values) at Swartvlei, S. Africa, and its relation to (b) the temperature of surface water measured in the open lake and the littoral macrophyte-rich zone. From HOWARD-WILLIAMS and ALLANSON (1981a).
Moyennes mensuelles de l'énergie solaire incidente journalière à Swartvlei, Afrique du Sud, et température de surface dans les eaux libres et dans la zone littorale à macrophytes. D'après HOWARD-WILLIAMS et ALLANSON, 1981a.

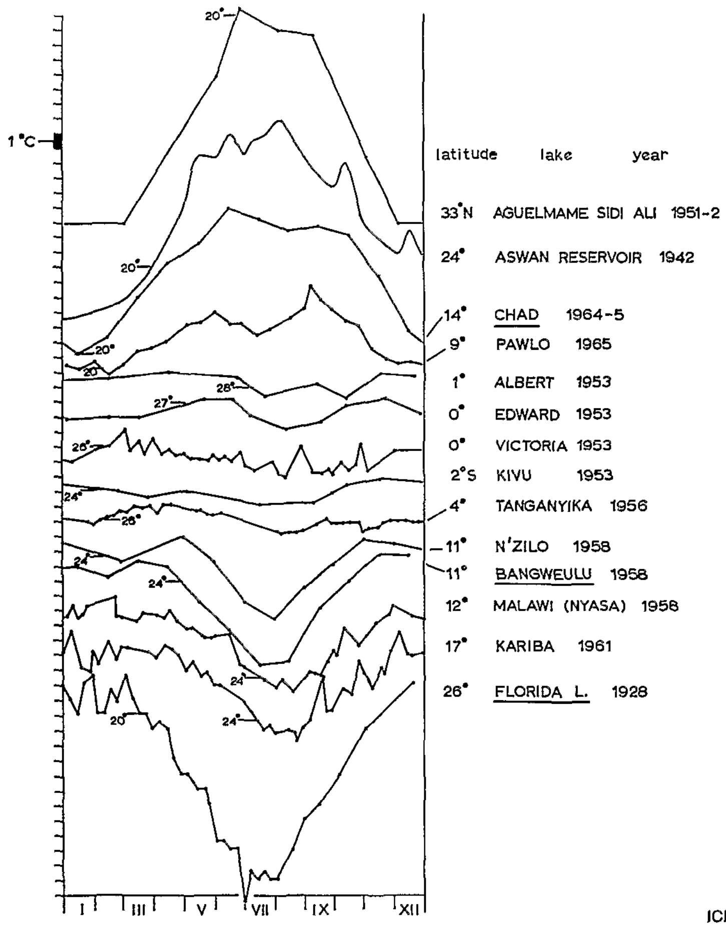

FIG. 18. — Annual variation of surface temperature in a series of 14 African lakes (shallow underlined), arranged by latitude. Successive curves are displaced downwards, and the common temperature scale (left) refers to differences only. Absolute values can be located using the single temperature marked on each curve. From TALLING (1969).

Variations annuelles des températures de surface dans 14 lacs africains (le nom des lacs peu profonds est souligné). Les différentes courbes sont déplacées successivement vers le bas, l'échelle de gauche n'indiquant que l'amplitude des variations. Les valeurs obsolues peuvent être déduites de la température de référence indiquée sur chaque courbe. D'après TALLING, 1969.

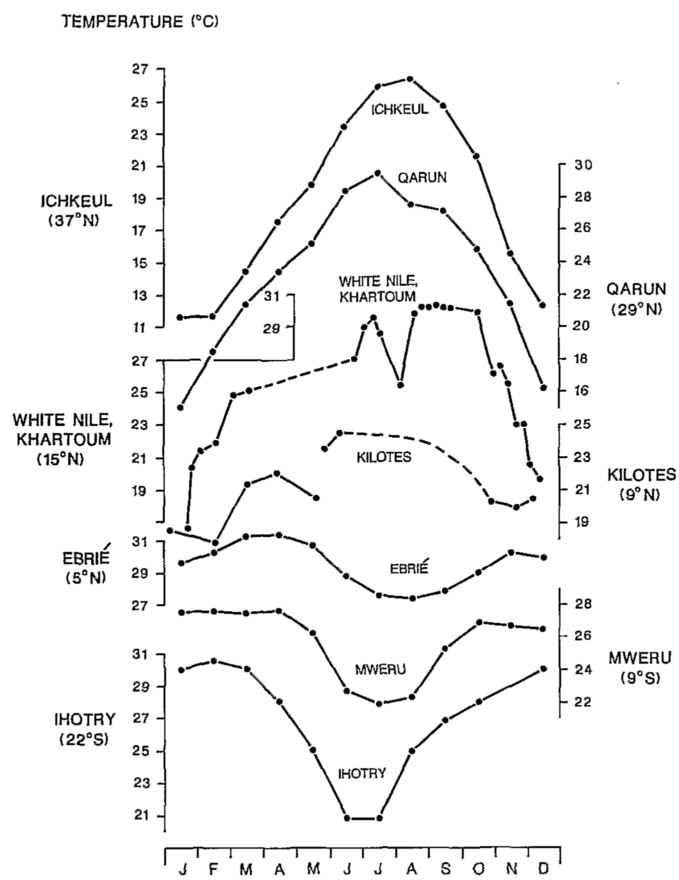

FIG. 19. — Annual variation of surface temperature in seven shallow African waters. Data from LEMOALLE (pers. comm.), GORGY (1959), TALLING (unpubl.), WOOD *et al.* (1976), DURAND and CHANTRAINE (1982), DE KIMPE (1964), and MOREAU (1982).

Variations annuelles des températures de surface dans sept lacs peu profonds d'Afrique et Madagascar. Données de LEMOALLE (comm. pers.), GORGY (1959), TALLING (non publié), WOOD et al. (1976), DURAND et CHANTRAINE (1982), DE KIMPE (1964) et MOREAU (1982).

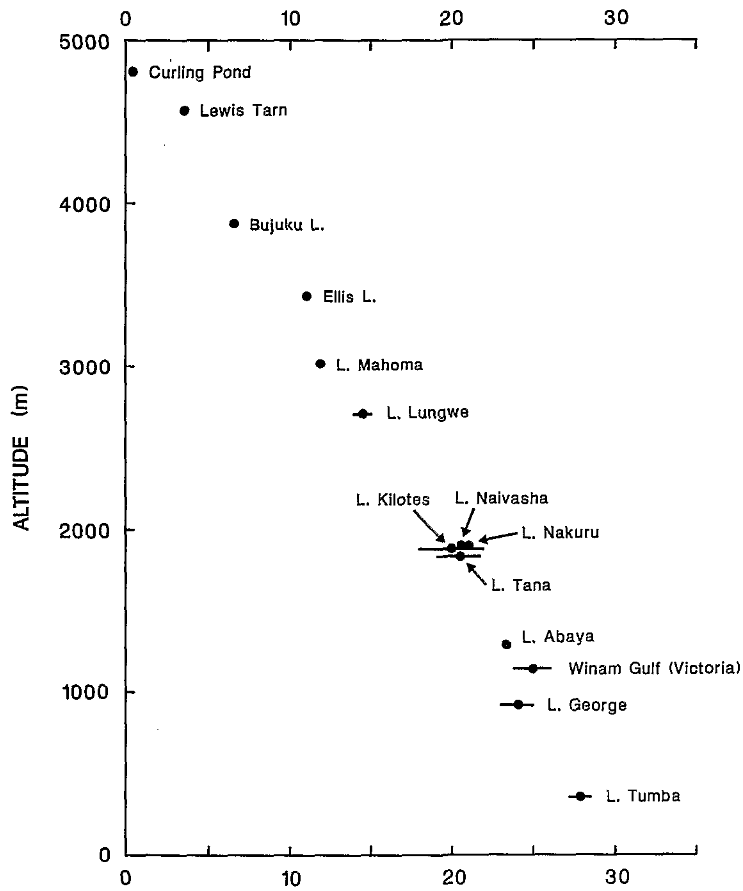

FIG. 20. — Decrease with altitude of near-bottom temperatures measured in various tropical African water-bodies. Bars indicate seasonal ranges. Values from LÖFFLER (1964, 1968), DUBOIS (1955), WOOD *et al.* (1976), GAUDET (1979), VARESCHI (1982), MORANDINI (1940), TALLING (unpubl.), VINER and SMITH (1973), and DUBOIS (1959). From TALLING (1990).

Décroissance de la température près du fond en fonction de l'altitude des plans d'eau africains. Les traits horizontaux indiquent l'amplitude saisonnière de variation. D'après les données de LÖFFLER (1964, 1968), DUBOIS (1955), WOOD et al. *(1976), GAUDET (1979), VARESCHI (1982), MORANDINI (1940), TALLING (non publié), VINER et SMITH (1973), et DUBOIS (1959). D'après TALLING (1990).*

Fig. 20, and by LÖFFLER (1968) and GASSE *et al.* (1983). There are few high-altitude waters on which seasonal measurements of temperature are adequate, but the observations of MORANDINI (1940) on L. Tana (1820 m), of DUBOIS (1955) on L. Lungwe (2710 m), and the much more detailed studies on the Bishoftu crater lakes (1870-2000 m) of WOOD *et al.* (1976), can be mentioned.

Shallow lakes are thermally distinctive by the usual lack of any persistent temperature stratification, because mixing by wind-induced turbulence and convection frequently affects the entire water-column. However, diel cycles of stratification are typically well developed (see Sections 2, 6.1). As energy transfer is predominantly across the water surface, a shallow water-column of limited heat-capacity per unit area tends to accentuate both diel and seasonal maxima and minima of temperature. The low capacity factor is accentuated when much daytime energy consumption is confined to a near-surface layer by high turbidity. This situation favours the diurnal development of very strong but superficial temperature gradients, as recorded by WOOD *et al.* (1976) in phytoplankton-rich lakes of Ethiopia. The diel differences of temperature in surface water of L. Chad, relative to the seasonal differences, are shown in Fig. 21. In shallow African lakes, as elsewhere, horizontal differences of temperature and its stratification can develop in several ways. Thus a cooler or warmer inflow may locally

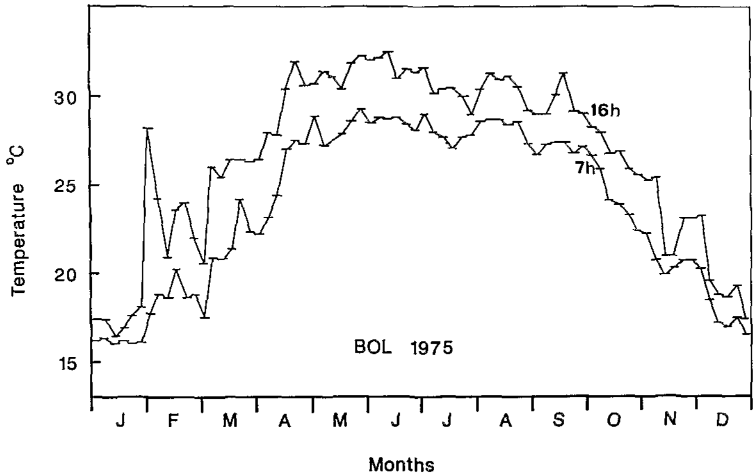

FIG. 21. — Annual variation in L. Chad at Bol of surface temperature measured near the daily minima (7 h) and maxima (16 h), and expressed as mean values over 5 consecutive days. Adapted from CARMOUZE, CHANTRAINE & LEMOALLE (1983).
Températures de surface du L. Tchad à Bol, près du minimum (7 h) et maximum (16) journaliers. Moyennes sur 5 jours consécutifs. D'après CARMOUZE, CHANTRAINE et LEMOALLE, 1983.

impress its effect; shallow marginal areas can often grow warmer by day (Fig. 17b) and cooler by night, with profile-bound density currents possible from the latter (TALLING, 1963, 1969); the thermocline (even a diel one) may be tilted down-wind, as measured in L. Kilotes (WOOD *et al.*, 1976); and vegetation cover, as floating mats or weed-beds, may lead to local temperature increase by energy interception and limitation of water transfer. The last situation is analysed in detail by ROOM and KERR (1983) for the floating weed *Salvinia molesta*.

Where a lower more saline layer exists in a very shallow fresh water, the temperature of that layer may be considerably elevated by solar heating. Examples are given by BEADLE (1943) from Algeria, MELACK and KILHAM (1972) from Uganda (L. Mahega), and by ASHTON and SCHOEMAN (1983, 1988) for the Pretoria Salt Pan where an additional warm middle layer develops daily (Fig. 22). Instances of salinity stratification without such temperature increase are not uncommon in coastal lakes with some input of sea water (e.g. Swartvlei : ROBARTS and ALLANSON, 1977; ALLANSON and HOWARD-WILLIAMS, 1984).

3.3. Turbidity and light attenuation

Light attenuation under water is governed mainly by particulate material and by more dispersed 'colour' ('gelbstoff' or 'gilvin'). The latter is strongly developed in most swamp waters and in not a few shallow lakes, including Chilwa (Moss and Moss, 1969), Kilotes (TALLING *et al.*, 1973), Chad (LEMOALLE, 1979), Tana (TALLING, unpubl.), Abaya (WOOD *et al.*, 1978), and Swartvlei (ALLANSON and HOWARD-WILLIAMS, 1984). However, high or variable turbidity, associated with particulate content, is the most dominating influence in most shallow African waters. It may arise from a heavy development of plankton, usually predominantly phytoplankton, or from the suspension of sediment and plant detritus. The commonest measure of turbidity, or its inverse of *transparency*, is the depth of visibility of a white disc (Secchi disc), but gravimetric measurements of suspended solids are sometimes available. For phytoplankton-dominated waters, estimations of chlorophyll *a* concentrations are also appropriate. In L. Chad it has been possible to obtain large-scale synoptic information from remote (satellite) sensing, cross-referenced and interpreted in terms of Secchi disc transparency (LEMOALLE, 1979).

Generation of turbidity by the wind-disturbance of bottom sediments is widespread in waters less than circa 5 m deep, and is accentuated when the wind-fetch is long (cf. L. George, Table I). Episodes of high turbidity then follow strong winds. Episodes can also result from land run-off in rainy seasons, when silt-rich flood-water of high turbidity moves down a drainage system and may be injected into reservoirs (e.g. ENTZ, 1978), lagoons or pans (e.g. ROGERS and BREEN, 1980; AKHURST and BREEN, 1988). Detailed studies exist for the White and Blue Niles (TALLING and RZÓSKA, 1967), where (as often

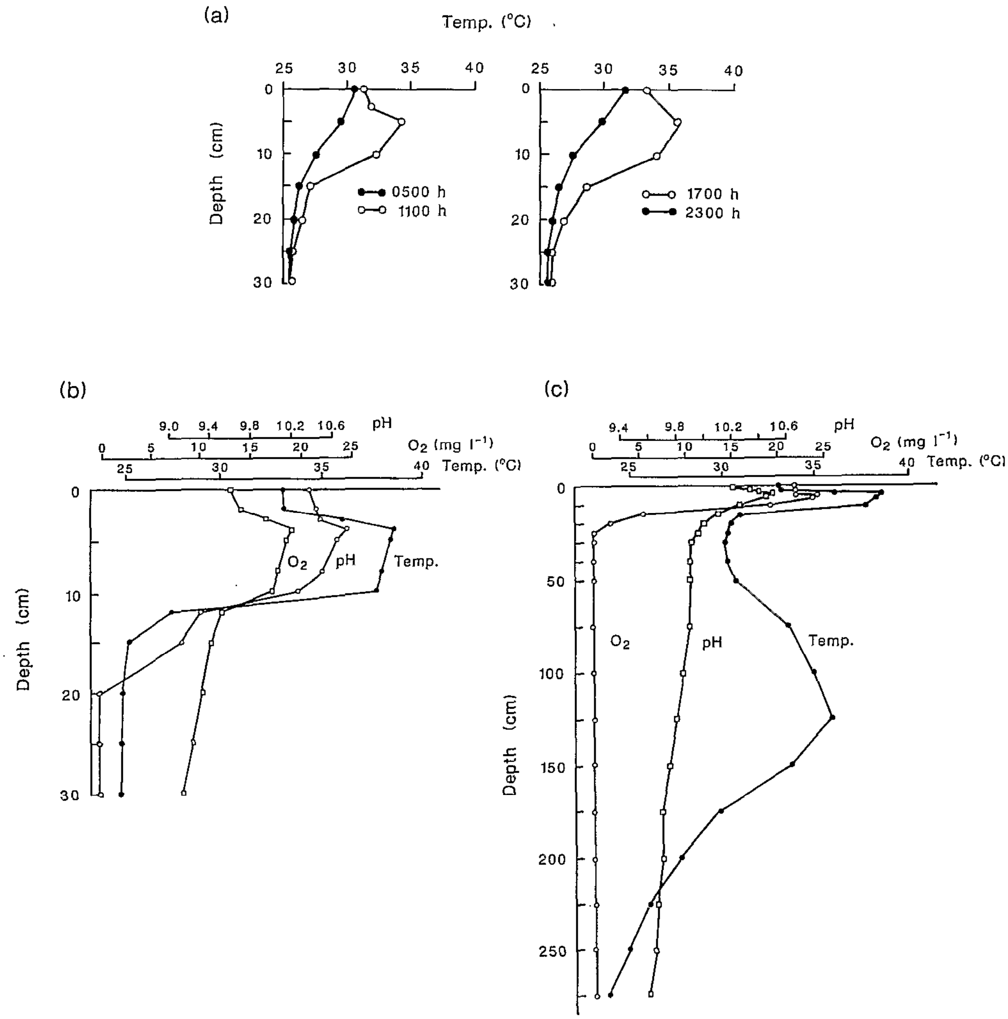

FIG. 22. — Stratification in the Pretoria Salt Pan on 29 December 1979 : (a) daily change in temperature at a shallow station, and (b, c) typical depth profiles of temperature, pH, and dissolved oxygen at a shallow and a deep station. Adapted from ASHTON and SCHOEMAN (1983).

Stratification dans le Pretoria Salt Pan, le 29 décembre 1979 : (a) variation journalière dans une station peu profonde, et (b et c), profils typiques de température, pH et oxygène dissous dans une station profonde et une station peu profonde. D'après ASHTON *et* SCHOEMAN, *1983.*

elsewhere) the turbidity of shallow impoundments and lagoons is determined by two opposing influences — the sedimentation of larger silt particles and the production of denser phytoplankton. In Lake Chad, the reduction of turbulence associated with the enhanced growth of macrophytes at low water levels led in some areas to greater sedimentation and higher transparency (LEMOALLE, 1979; CARMOUZE *et al.*, 1983). However the low-level phase could also be accompanied by low transparency (circa 0.1 m) from algal growth and resuspension of clay sediments (CARMOUZE *et al.*, 1983). There is also evidence elsewhere (MCLACHLAN and MCLACHLAN, 1976; AKHURST and BREEN, 1988) that clay precipitation can be accelerated at higher levels of salinity and conductivity.

Where phytoplankton is an important cause of turbidity, its persistence in time will be governed by biological cycles or other fluctuations. Even in waters with a persistently dense phytoplankton, such as L. George, the variability may be sufficient to allow a relationship between biomass concentration and light attenuation (or transparency) to be established (Fig. 9c : GANF, 1974c). Many soda lakes are turbid with phytoplankton but at least some have a considerable background attenuation (e.g. L. Kilotes : TALLING *et al.*, 1973 ; L. Nakuru : VARESCHI, 1982), often from soluble or dispersed organic material. The same is true for some relatively dilute shallow lakes (e.g. L. Abaya = Margherita, L. Chamo, L. Baringo) rich in both blue-green algae and total iron (TALLING and TALLING, 1965; WOOD and TALLING, 1988).

Quantitative relationships between light attenuation, Secchi disc transparency, and concentrations of absorbing components (e.g. chlorophyll *a*, silt) have been explored in several shallow waters — notably L. George (Fig. 9c : GANF, 1974c), L. Chad (LEMOALLE, 1979, 1983b), L. McIlwaine (ROBARTS, 1979) and the Ebrié lagoon (DUFOUR, 1982c). Spectral components of differing attenuation have been distinguished in these and other (chiefly East African — TALLING, 1957a, 1965) lake and river waters, which demonstrate the 'red shift' in maximum transmission — i.e. its displacement towards longer wavelengths — characteristic of most turbid waters. For one water, L. George, an experimental approach using high resolution spectroradiometry has been made (TALLING, 1970) and estimated spectral distributions of underwater radiation (Fig. 9b) have been published (GANF, 1974c ; GANF and HORNE, 1975). In one turbid South African impoundment such spectral distributions, shifting with depth, have been measured directly by submersible spectroradiometer (WALMSLEY *et al.*, 1980).

A common but approximate guide to the depth-extension of appreciable photosynthetic activity is the euphotic zone limit (z_{eu}) set by the 1 % level of the surface-penetrating and photosynthetically active radiation (PAR). Examples for shallow waters are given by TALLING (1965), TALLING *et al.* (1973), GANF (1975), LEMOALLE (1973, 1983b), MELACK (1979a, b, 1981), ROBARTS (1979) and PAGÈS *et al.* (1979). When the euphotic depth (z_{eu}) is only a small fraction (> c. 0.2) of the mixed depth (z_{mix}) the phototrophic growth of phytoplankton is likely to be impeded even under tropical conditions of high insolation. GANF and VINER (1973) consider this limitation with reference to depth-relations found in L. George (z_{mix} = 2.4 m, $z_{eu} \simeq$ 0.75 m) and the ecological stability of its phytoplankton. From this and other examples it would appear that shallow lakes can be optically quite deep, with implication for light-limitation of the net production and growth rates of phytoplankton and submersed aquatic macrophytes. Thus a near-absence of the latter from lakes George and Chilwa has been attributed to high light attenuation associated with dense phytoplankton and fine suspended sediment respectively. An observed decline of macrophytes in Swartvlei may also be due to increased light attenuation, associated with run-off from a deteriorating catchment (TAYLOR, 1982; ALLANSON and HOWARD-WILLIAMS, 1984).

3.4. Water movement

Water movements originate in relation to gravity-flow (streams, rivers) or to wind-stress on a water surface. They are obviously important for horizontal transport, for vertical turbulence, and for interactions at the water-air and water-sediment surfaces. Most observations are indirect and qualitative, as from the distribution (and deposition) of suspended objects, of temperature or chemical composition, or of correlated wind-stress. Specific examples include : the nocturnal destruction of thermal stratification in L. George (GANF, 1974b ; see Figs. 5,6); the complex horizontal distribution of Na^+ concentration and conductivity in L. Chad indicative of a predominantly northwards water transfer from the southern inflow (CARMOUZE, 1972, 1976; CARMOUZE and LEMOALLE, 1983; see Fig. 23); and the local reduction of horizontal flow during the phase of macrophyte abundance in L. Chad (CARMOUZE *et al.*, 1983). Swamp vegetation is a widespread impeding factor for water movement, operating partly through shelter of the water surface from wind. Its influence on water movement at L. Chilwa is described by HOWARD-WILLIAMS and LENTON (1975).

Direct measurements in shallow standing waters of the velocity of movement, its spatial pattern, and its relation to wind stress, are few. One notable study on L. George has been described in the case-study (Section 2). Simple drogues were also used by DENNY (1978) on the Nyumba ya Mungu reservoir, Tanzania. By measurements from a hydrologist's multi-vane current meter, RZÓSKA (1974, Fig. 2) described the horizontal gradients in flow velocity between mid-river and adjacent swamps of the Upper White Nile, and also (RZÓSKA, 1976) the reduction of velocity downstream along the axis of a Nile reservoir in relation to plankton development. Low velocities of water movement have also been measured in East African lakes by a hot-wire current meter (MCINTYRE, 1981), especially for the meromictic though shallow L. Sonachi (MCINTYRE and MELACK, 1982), and by Ekman and Åanderåå current meters in the Ebrié lagoon (GALLARDO, 1978).

Circulation gyres, of the type illustrated for lakes George (Fig. 7) and Chad (Fig. 23), are especially likely to develop in shallow lakes under wind stress. This is because a wind-driven transport of surface

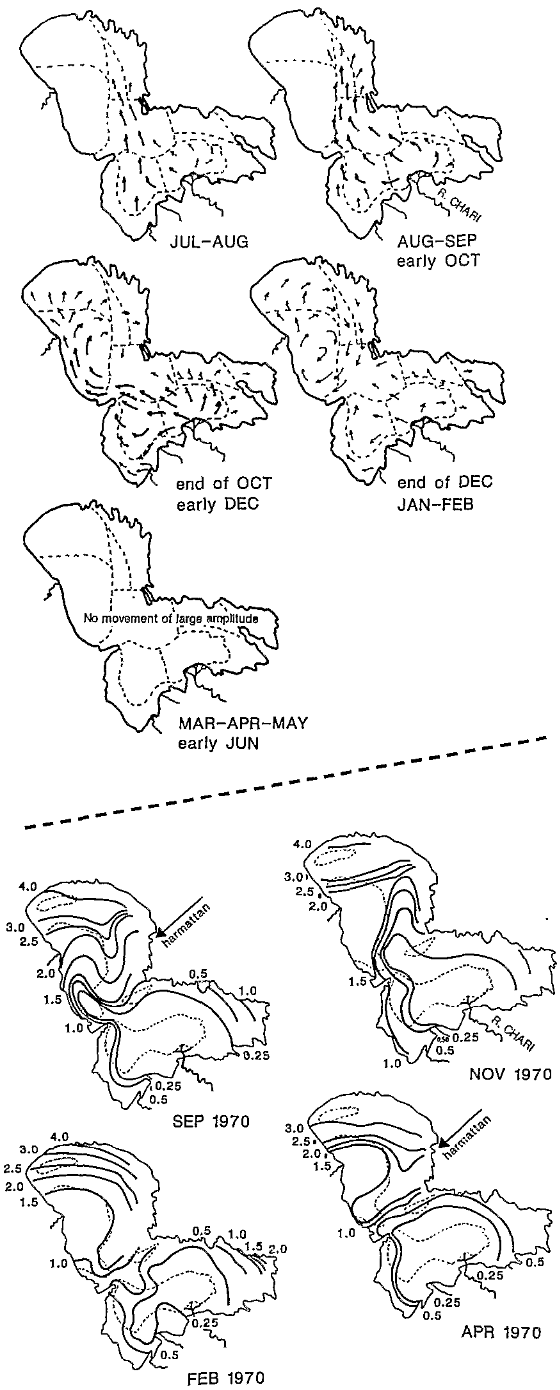

FIG. 23. — Lake Chad : (above) seasonal changes of circulation patterns in the water-mass; (below) distribution of Na^+ concentrations (in meq l^{-1}) in 1970. Adapted from CARMOUZE and LEMOALLE (1983) and CARMOUZE (1972).

Le lac Tchad. En haut, évolution saisonnière de la circulation générale; en bas, répartition de l'ion Na^+ (en méq. l^{-1}) durant l'année 1970. D'après CARMOUZE et LEMOALLE (1983) et CARMOUZE (1972).

TABLE II

				cal cm^{-2}		
Lake	Date	Q_r	Q_s	Q_b	Q_e	Q_c
Tana	a) 24h, 2-5 March 1937	-	+	-	293	-
	b) night 12h only	0	-258	16	147	95
Qarun	24h, July 1950	612	+	233	517	-188
Kilotes	24h, 1 Jan. 1966	548	294 (calc.) 90 (obs.)	33	221	+
Chad	a) 24h, 15 Dec. 1970	545	0	216	114	-11
	b) day 12h only	545	585	108	57	-10
	c) night 12h only	0	-585	108	57	-1

+ assumed negligible.

water is compensated by a return flow not at depth, as in deeper lakes, but in horizontally adjacent areas.

3.5. **Energy budgets**

Modes of energy transfer to and from a water-body include short-wave (solar) radiation input (Q_r) corrected for a mean surface loss by reflection plus scattering of c. 10 % (Q_r'); long-wave («thermal») radiation both incoming and outgoing, often combined as net back-radiation (Q_b); sensible heat transfer of variable direction down thermal gradients between water and atmosphere (Q_c); and the latent heat of evaporation loss (Q_e). For waters in low latitudes, attempts to partition them with energy storage (Q_s) within an energy budget

$$Q_r' = Q_s + Q_b + Q_e + Q_c$$

are few and, in Africa, rudimentary; see however studies of GORGY (1959) on L. Qarun, WOOD *et al.* (1976) on the Ethiopian Bishoftu lakes, EGGERS and TETZLAFF (1978) on L. Chad and TALLING (1990) on the Jebel Auliya (Nile) reservoir; of NEUMANN on L. Kinneret in Israel (SERRUYA, 1978), and of CARMOUZE and AQUISE (1983) and TAYLOR and AQUISE (1984) on L. Titicaca in the Andes. Some rough estimates for four shallow African lakes (Tana MORANDINI, 1940; Qarun GORGY, 1959; Kilotes WOOD *et al.* 1976; Chad *Eggers* and *Tetzlaff*, 1978) are given in Table II. In a hot dry African climate as is found in the Sahel and Sahara, an evaporation rate of 9 mm day^{-1} can be reached; this implies an energy transfer of about 622 cal (2.6 kJ) cm^{-2} day^{-1}, a similar order of magnitude to that transferred in solar radiation (as also at L. George, Section 2; L. Qarun, Table II). Evaporative cooling is therefore of quantitative importance, especially in shallow waters. Its energy-relations are considered in detail by GORGY (1959) for L. Qarun, Egypt. Here its severe reduction in winter (GORGY, 1959; MESHAL and MARCOS, 1981) will limit the cooling then observed in the lake water. In the Bishoftu lakes of Ethiopia, including the shallow

L. Kilotes, evaporative loss was probably mainly responsible for the non-coincidence between periods of cooling and minimal insolation (WOOD *et al.*, 1976). Here concomitant seasonal measurements on four adjacent lakes of varying depth showed that near-surface temperature in the shallowest lake (Kilotes, $z_{max} = 6.5$ m) was generally lower by several degrees than that in the deeper lakes; enhanced heat loss per unit volume by back-radiation, and by evaporation at a more exposed site, may be suspected. Seasonal energy storage as heat per unit area (the so-called 'annual heat budget') of a shallow water-mass tends to be restricted for purely morphometric reasons, as to the value of 1.3×10^3 cal cm^{-2} for L. Kilotes. Heat storage in sediments has apparently not been evaluated, and although relatively larger in shallow than deep lakes is likely to be a small component of the daily and annual energy budgets. On the diurnal time scale water-column storage can be of similar magnitude to the daily input of short-wave radiation, often circa 400 cal cm^{-2} (= 2 °C rise over 0-2 m, or 1 °C rise over 0-4 m). This is approaching the magnitude of the seasonal heat storage cited above, instead of being about 1 order of magnitude lower as in many deep tropical African lakes (TALLING, 1990) and nearly 2 orders of magnitude lower as is commonplace in deep temperate lakes.

4. REGULATION OF THE CHEMICAL ENVIRONMENT

4.1. Chemical sources

Inland water-bodies receive material inputs (other than water) in three main ways — from their inflows and seepage, from atmospheric precipitation both wet and dry, and from gaseous exchange with the atmosphere. The last involves no distinctively African features, although specific forms of swamp vegetation (e.g. floating swamp) create particular barriers to vertical exchange.

The significance of the second pathway, atmospheric precipitation, is little known in the African context. Near the sea coast a considerable contribution of 'cyclic' sea salt, via sea-spray, can be anticipated but quantitative assessments appear to be lacking. Even well inland, as in East Africa and Ethiopia, the contribution is appreciable and for various ions can be gauged from the Cl^- content (GAUDET and MELACK, 1981; WOOD and TALLING, 1988). Very varied results have been reported from the chemical analysis of rainwater (VISSER, 1961; TALLING and TALLING, 1965; LEMOALLE, 1973b; HEMENS *et al.*, 1977; RODHE *et al.*, 1981; LEMASSON and PAGÈS, 1982), both as regards major ions and such plant nutrients as forms of N and P. This varia-

TABLE III

Constituent		L. Naivasha (1)	N'Djamena Chad (2)	L. George (3)	East Africa (4)	L. Ebrié (5)
NO_3-N+ NH_4-N	(g m^{-2} yr^{-1})	-	0.47	1.11	-	1.05
NO_3-N	(µg l^{-1})	-	181	<20 - 890	-	274
	(g m^{-2} yr^{-1})	-	0.12	-	-	0.59
NH_4-N	(µg l^{-1})	-	535	130 - 4100	-	216
	(g m^{-2} yr^{-1})	-	0.35	-	-	0.46
Total N	(µg l^{-1})	-	-	-	-	1440
	(g m^{-2} yr^{-1})	-	-	-	-	3.08
PO_4-P	(µg l^{-1})	-	37	4 - 1700	-	111 (c.10-800)
	(g m^{-2} yr^{-1})	-	0.024	0.48	-	0.23
pH		c. 5.7	-	-	6.4	-
Ca^{2+}	(mg l^{-1})	0.19	-	-	0.39	-
Mg^{2+}	(mg l^{-1})	0.23	-	-	0.08	-
Na^+	(mg l^{-1})	0.54	-	-	0.63	-
K^+	(mg l^{-1})	0.31	-	-	0.30	-
Cl^-	(mg l^{-1})	0.41	-	-	0.60	-
SO_4^{2-}	(mg l^{-1})	0.72	-	-	0.75	-
Conductivity, k_{25}	(µS cm^{-1})	-	-	-	10.0	-

(1) GAUDET and MELACK 1981, (2) LEMOALLE 1973, VINER and SMITH 1973, GANF and VINER 1973, (4) RODHE *et al.* 1981, (5) LEMASSON and PAGÈS 1982.

bility may include secondary changes during collection and storage, technical error, and a changing contribution from atmospheric dust. Some analyses are given (as means or medians) in Table III.

The contribution from inflows depends, quantitatively and qualitatively, upon the general hydrology and the geochemical character of the catchment, plus its biological development as by cultivation, fringing swamp, floodplain, and human settlement. In a few instances attempts have been made (GAUDET and MELACK, 1981; WOOD and TALLING, 1988) to distinguish the surface-denudative component from atmospheric input, the latter obtained from data on precipitation and estimates of its evaporative concentration. Thus GAUDET and MELACK (1981) estimated the Malewa R. input to L. Naivasha to carry a total solute load of 91 kg ha^{-1} day^{-1}, of which in 1973-4 only 21 % was derived by surface chemical denudation.

Effects of human settlement, influencing organic balance, dissolved oxygen, plant nutrients, and phytoplankton production, are well illustrated in regions of the elongate Ebrié lagoon subject to urban pollution from Abidjan (DUFOUR, 1982b; DUFOUR and DURAND, 1982). Another coastal water in which the chemical and biological consequences of heavy pollution have been studied is Lake Mariut and the adjoining Hydrodrome, that receive sewage from Alexandria (ELSTER and VOLLENWEIDER, 1961; BANOUB and WAHBY, 1961; ALEEM and SAMAAN, 1969; SAAD, 1973, 1980; WAHBY *et al.*, 1978; WAHBY and ABDEL-MONEIM, 1979; SAMAAN and ABDALLAH, 1981). More generally in the Delta Lakes of Egypt, chemical conditions change with the relative influence of marine ingress and of drainage water from agricultural areas, the latter nutrient-rich and increased in the post-High Dam era. Examples include L. Edfu (SAAD, 1976, 1978; BANOUB, 1979, 1983) and L. Manzalah (EL-HEHYAWI, 1977; SHAHEEN & YOSEF, 1978). For the former, estimates of net annual consumption of N, P, and Si in the lake have been made (BANOUB, 1983).

In regions of high rainfall and runoff, such as the Zaïre basin, the effects of dilution and past leaching tend to produce dilute inflow waters. The same consequence may result by drainage from ancient and long-weathered land surfaces, widespread throughout Africa; the upper Zambezi catchment is an example from a region of lower and strongly seasonal rainfall. In general, freshwaters of low ionic content (conductivity < 70 µS cm^{-1}) are much more common in West than East Africa (VISSER, 1974; VISSER and VILLENEUVE, 1975; JOHN, 1986). The geological influence is obviously enhanced in areas dominated by hard rocks such as granite, as in the upper drainage of the Niger and the Senegal River (GROVE, 1972). Well-leached sandy or lateritic soils can also bear very dilute water-bodies; SYMOENS (1968) and HARE and CARTER (1984) give examples of conductivity < 15 µS cm^{-1}. Conversely, soft rocks and formations rich in soluble salt deposits can lead to more saline inflows of distinctive ionic composition. Examples include areas of limestone (e.g. the Blue Nile gorge), of fossil evaporites of marine origin (e.g. the Afar (Danakil) depression), and the K^+ — and Mg^{2+} — rich rocks of the Virunga volcanic region. Nevertheless, most strongly saline waters are of more secondary origin and owe their development to their situation in basins of closed drainage and a predominance of evaporation in the hydrological budget.

Some peculiarly biological pathways of chemical input and output deserve mention.

Mobile animals can transfer material horizontally and vertically, as by the spatial separation of grazing and excretion by hippopotami (VINER, 1975a; KILHAM, 1982), elephants and ungulates (S.M. McLACHLAN, 1970, 1971), and by the mass emergences of chironomids and chaoborids or 'lake-flies' (examples in RZÓSKA, 1976).

Nutrient uptake by rooted swamp vegetation, subject to growth and decay, can transfer solutes from the substratum to surface water. Although an active transfer through the living plants has been postulated, there is no substantive evidence for this (Denny, 1985b), but a 'nutrient pump' movement sediment → macrophyte → water is completed by senescence and decay of vegetation. For one element, carbon, the sequence is atmosphere → emergent macrophyte → water, with net CO_2 transfer. The stock per unit area (Table IV), subject to growth and decay, of such elements as K, Si, N and C can be high in reedswamps (e.g. of *Phragmites australis* in L. Chad : CARMOUZE *et al.*, 1978; CARMOUZE, 1983). Comparative examples for various dense stands of reedswamp, floating and submerged macrophytes, and a dense phytoplankton can be found in Fig. 46. For some macrophytes the time-course of release by decay has been followed (e.g. *Cynodon dactylon* : FURNESS and BREEN, 1982; *Potamogeton crispus* : ROGERS and BREEN, 1982; *Potamogeton pectinatus* : HOWARD-WILLIAMS and DAVIES, 1979; *Typha domingensis* : HOWARD-WILLIAMS and HOWARD-WILLIAMS, 1978; HOWARD-WILLIAMS, 1979; and *Cyperus papyrus* : GAUDET, 1977).

Interactions between swamp and open water also include the *horizontal translocation* of chemical components. Horizontal gradients for many constituents have often been demonstrated in transects, as by BEADLE (1932), CARTER (1955), TALLING (1957, and in RZÓSKA 1974), HOWARD-WILLIAMS (1972),

TABLE IV

Plant	Place	Biomass density (g dry wt m^{-2})	Relative content (% dry weight)					Stand-stock ($g\,m^{-2}$)				
			N	P	K	Na	SiO_2	N	P	K	Na	SiO_2
Cyperus papyrus(1) (y = young shoots o = old shoots)	L. George	5020	y 1.76 o 1.06	0.105 0.106	3.88 1.54	0.39 0.43	- -	61.6	5.43	103.2	20.9	-
Phragmites australis(2)	L. Chad											
(a) subaerial		3100	-	-	2.05	0.025	3.0	-	-	63.5	0.77	93
(b) underground		4340	-	-	0.34	0.04	19.1	-	-	14.8	1.74	829
(c) total		7440	-	-	1.05	0.03	12.4	-	-	78.3	2.51	922
Typha domingensis(3)	L. Chilwa	2537	0.55	0.083	0.55	1.19	-	22.7	2.1	13.9	30.3	-
Potamogeton pectinatus (4) (dominant)	Swartvlei	1027	1.2	0.12	-	-	-	13	1.3	-	-	-
Potamogeton crispus(5) (seasonal max.)	Tete Pan (Pongolo R.)	41	2.9	0.6	1.8	2.0	-	1.2	0.3	0.8	0.8	-

(1) GAUDET 1977, (2) CARMOUZE *et al* 1978, (3) HOWARD-WILLIAMS and LENTON 1975, (4) HOWARD-WILLIAMS 1977, (5) ROGERS and BREEN 1980.

HOWARD-WILLIAMS and LENTON (1975), and GAUDET (1976). Swamp-water concentrations are typically higher (e.g. for total ionic content and conductivity, HCO_3^- -alkalinity, CO_2, NH_4-N, PO_4-P, total Fe and Mn), with the obvious and notable exception of O_2. Corresponding chemical influence on through-flowing river systems has been studied for the Sudd swamps of the White Nile (TALLING, 1957a ; BISHAI, 1962) and for the Malewa River inflow to L. Naivasha (GAUDET, 1978, 1979). For other shallow lakes the work of Howard-Williams and co-workers on the L. Chilwa-swamp system, summarized by HOWARD-WILLIAMS (1979), is particularly notable. HOWARD-WILLIAMS and LENTON (1975) gave examples of horizontal chemical exchange induced by wind stress and by stream inflow; they also drew attention to the probable effects of swamp anoxia on sediment → water transfer of solutes and organic inputs to the open water. Littoral solute contributions are generally likely to be favoured from sheltered depositional as opposed to exposed erosional shores, as the former favour both swamp development and accumulation of fine sediment.

As swamp vegetation can incorporate relatively large stocks per unit area of the elements C, N, P, K and Si, a major secondary supply by re-cycling — as opposed to a primary or 'new' input — is set up. Generalized aspects of input-output, storage, and loading relationships for N and P in swamp systems are reviewed by HOWARD-WILLIAMS (1985).

Besides setting up chemical storage and secondary inputs, biological accumulation often determines chemical concentrations by inducing complementary nutrient depletions in the water-mass. Examples are given later in relation to the elements C, N, P, and Si. Biological storage *post mortem* occurs extensively in the *sediments* of shallow lakes and swamps (see 5.3). The role of sediments as secondary chemical sources would be expected to be stronger in shallow water-bodies, but high biological productivity in the water-mass may accentuate a 'short-circuit' recycling there (e.g. L. George : GANF and VINER, 1973 ; VINER, 1977a,b,c).

4.2. **Total solutes**

Shallow waters (Table V) encompass virtually all of the very wide range of ionic content or salinity established by a general chemical survey of African lakes (TALLING and TALLING, 1965 ; Fig. 25). They range from very dilute water-bodies on hard mountain rocks (e.g. tarns of Mt Kenya : LÖFFLER, 1964) to evaporation pans where the saturation limit depends mainly upon the predominant anions. Thus, using the convenient index of electrical conductivity measured at 20 °C (k_{20}), or 25 °C (k_{25}, $\simeq k_{20} \times 1.12$), carbonate-bicarbonate dominated waters (e.g. L. Magadi) attain conductivity values (k_{20}) of about 1×10^5 $\mu S\,cm^{-1}$, and chloride waters (e.g. L. Afrera) even higher. Almost all saline lakes are shallow (MELACK, 1983); in Africa L. Shala (Ethiopia) is the most outstanding exception.

There is an obvious connection between high salinities in inland waters and the hydrological water balance when outflow both surface (R_o) and underground (G_o) is small and evaporation (E) relatively high. Evaporative concentration of salts supplied

TABLE V

Lake	Country	date	k_{20} (µS cm^{-1})	Σ cations	Σ anions	Na^+	K^+	Ca^{2+}	Mg^{2+} (meq l^{-1})	alk	Cl^-	SO^{2-}_4	tot.P	PO_4-P (µg l^{-1})	Si (mg l^{-1})	tot.Fe (µg l^{-1})	pH	Reference
Nabugabo	Uganda	Jun 67	25	0.198	0.199	0.090	0.028	0.060	0.020	0.140	0.040	0.019	-	-	-	-	7.0-8.2	Beadle. 1981
Tumba	Zaire	55	24-32	-	-	-	-	0.03	0.02	0	-	-	-	-	-	-	4.5-5.0	Dubois. 1959
Bangweulu	Zambia	60	-	0.285	0.293	0.113	0.033	0.075	0.066	0.260	0.08	0.02	-	-	-	-	-	Talling & Talling. 1965
Opi A	Nigeria	Jan-Feb 80	-	0.315	-	0.113	0.049	0.100	0.053	-	-	-	-	-	-	-	-	Hare & Carter. 1984
		May 80	15.3	-	-	-	-	-	-	0.1	-	-	-	15	-	100	6.5	
Mweru	Zambia-Zaire	Jul 61	76	1.03	1.05	0.20	0.032	0.375	0.418	0.83	0.141	<0.1	-	-	4.9	-	-	Talling & Talling. 1965
Tana	Ethiopa	Mar 64	137	1.68	1.62	0.24	0.040	0.945	0.45	1.52	0.044	0.052	-	30	6.8	-	8.4	Wood & Talling. 1988
Ras Amer	Sudan	Jan 56	178	-	-	-	-	1.20	-	0.81	-	-	-	200	11	-	9.1	Talling. unpubl.
George	Uganda	Jun 61	201	2.37	2.39	0.59	0.11	1.01	0.66	1.91	0.25	0.23	412	<18	8.5	250	9.6	Talling & Talling. 1965
Kabara	Mali	Feb 76	(19[illegible]	2.63	2.55	0.40	0.37	1.30	0.56	1.70	0.48	0.37	-	-	-	-	-	Dumont *et al*.. 1981
Mulehe	Uganda	Jun 61	260	2.94	3.09	0.470	0.246	1.085	1.131	2.18	0.34	0.65	272	220	15.9	48	8.0	Talling & Talling. 1965
Naivasha	Kenya	Jun 61	330	3.92	3.97	1.96	0.58	0.76	0.63	3.31	0.41	0.25	122	-	15.2	500	-	Talling & Talling. 1965
Zwei	Ethiopa	Mar 64	322	3.72	3.80	2.11	0.30	0.70	0.615	3.34	0.24	0.22	-	-	21.1	-	8.0	Wood & Talling. 1988
Baringo	Kenya	Dec 79	530	6.3	6.11	4.85	0.33	0.70	0.35	4.93	0.82	0.36	70	-	14.0	5410	-	Talling & Rigg. unpubl.
Chad. N	Chad-Nigeria	Jul 76	(565)	6.66	-	1.87	0.76	2.22	1.81	6.27	-	-	-	-	11.8	-	8.7	Carmouze *et al*.. 1983
Chad. SE		Aug 76	(45)	0.55	-	0.12	0.07	0.20	0.16	0.46	-	-	-	-	4.5	-	7.7	Carmouze *et al*.. 1983
Mohasi	Uganda	May 52	-	7.47	7.19	3.791	0.235	1.390	2.05	3.10	4.06	0.022	-	-	4.1	-	-	Damas. 1954
Kitangiri	Tanzania	Jul 61	785	8.60	9.15	6.74	0.123	1.205	0.55	6.65	1.80	0.10-0.71	1020	-	16.1	-	-	Talling & Talling. 1965
Abaya	Ethiopa	Feb 64	623	9.1	9.1	7.70	0.41	0.76	0.22	7.41	1.10	0.60	128	-	18.7	-	-	Wood & Talling. 1988
Tete pan	S. Africa	Mar 76	(187)	3.18	-	1.70	0.03	0.30	1.15	-	-	-	-	4	-	-	-	Rogers & Breen. 1980
		Oct 76	(720)	11.04	-	6.70	0.05	1.26	3.03	-	-	-	-	34	-	-	-	
Hippo Pool	Uganda	Nov 69	978	8.58	8.25	0.65	2.61	2.60	2.72	5.27	2.82	0.15	-	1120	-	-	6.4	Kilham. 1982
Chamo	Ethiopa	Jul 66	-	10.8	11.7	9.1	0.36	0.70	0.64	9.4	1.66	0.62	-	14	18	-	8.9	Wood & Talling. 1988
Chilwa	Malawi	Jan 70	1000	12.85	-	11.3	0.35	0.60	0.60	6.7	7.89	-	-	5100	-	-	8.5	McLachlan. 1979
		Dec 70	2500	35.85	-	33.9	0.59	0.66	0.70	19.0	14.51	-	-	5200	-	-	8.8	
Sonachi	Kenya	Dec 79	4770	58.6	59.9	53.4	4.41	0.33	0.44	52.6	4.41	2.91	450	-	32	530	-	Talling & Rigg. unpubl.
Mariut. Sta.1	Egypt	66	-	59.1	59.3	45.03	1.45	2.80	9.83	5.23	45.15	8.88	-	-	-	-	-	El-Wakeel *et al*.. 1970a.b
Rukwa N	Tanzania	61	5120	51.7	67.7	49.6	2.17	<0.05	<0.08	53.3	10.79	3.44	4500	-	54	-	-	Talling & Talling. 1965
Kilotes	Ethiopa	Apr 63	-	75.7	77.4	70.5	4.5	0.7	<0.6	63.4	13.6	0.4	-	5500	15.0	-	9.6	Wood & Talling. 1988
Nakuru	Kenya	Dec 79	10500	139.0	139.0	136.0	29.6	0.05	0.01	107.0	25.3	6.7	650	-	66	620	-	Talling & Rigg. unpubl.
Elmenteita	Kenya	Jul 69	11700	172	182	165	7.3	<0.1	<0.1	107.0	55.5	2.8	-	9200	83	-	9.4	Hecky & Kilham. 1973
Abiata	Ethiopa	Mar 64	15800	228.5	240.5	222	6.5	<0.1	<0.1	166.5	51.5	22.5	-	50	60	-	10.3	Wood & Talling. 1988
Eyasi	Tanzania	Aug 69	23500	301	324	300	0.24	0.15	0.16	116.4	186.5	17.3	-	86000	8.4	9.5	9.5	Hecky & Kilham. 1973
Qarun	Egypt	Jun 78	-	616	532	493	6.1	23.7	93.3	3.6	181	347	191	-	-	-	-	Talling & Rigg. unpubl.
Bogoria (Hannington)	Kenya	Jan 70	57400	1245	1205	1235	9.9	<0.05	0.18	965	180	4.5	-	-	122	-	10.6	Hecky & Kilham. 1973
Pretoria Salt Pan	S. Africa	78-80	(52000)	1264	1249	1260	3.3	<0.05	<0.1	400	845	5.0	9000	7000	120	-	10.4	Ashton & Schoeman. 1983
Metahara	Ethiopa	May 61	72500	784	831	774	10.4	<0.15	<0.6	580	154.6	97.5	11000	-	-	500	9.9	Wood & Talling. 1988
Manyara	Kenya	Jun 61	94000	937	1097	935	2.4	<0.5	<2.5	806	244	47.5	65000	-	8.9	-	-	Talling & Talling. 1965
Magadi	Kenya	Feb 61	160000	1666	1867	1652	13.7	<0.5	<2.5	1180	637	50	11000	-	117	-	-	Talling & Talling. 1965
Mahega	Uganda	May 71	(111300)	2879	2870	2565	302	0.76	11.0	150	1450	1270	-	9600	13	-	10.1	Melack & Kilham. 1972
Gaar (Wadi Natrun)	Egypt	Aug 76	-	-	5620	5959	34.8	-	-	220	4900	500	-	4120	-	-	10.9	Imhoff *et al*.. 1979

( ) conductivity corrected from 18 or 25 °C.

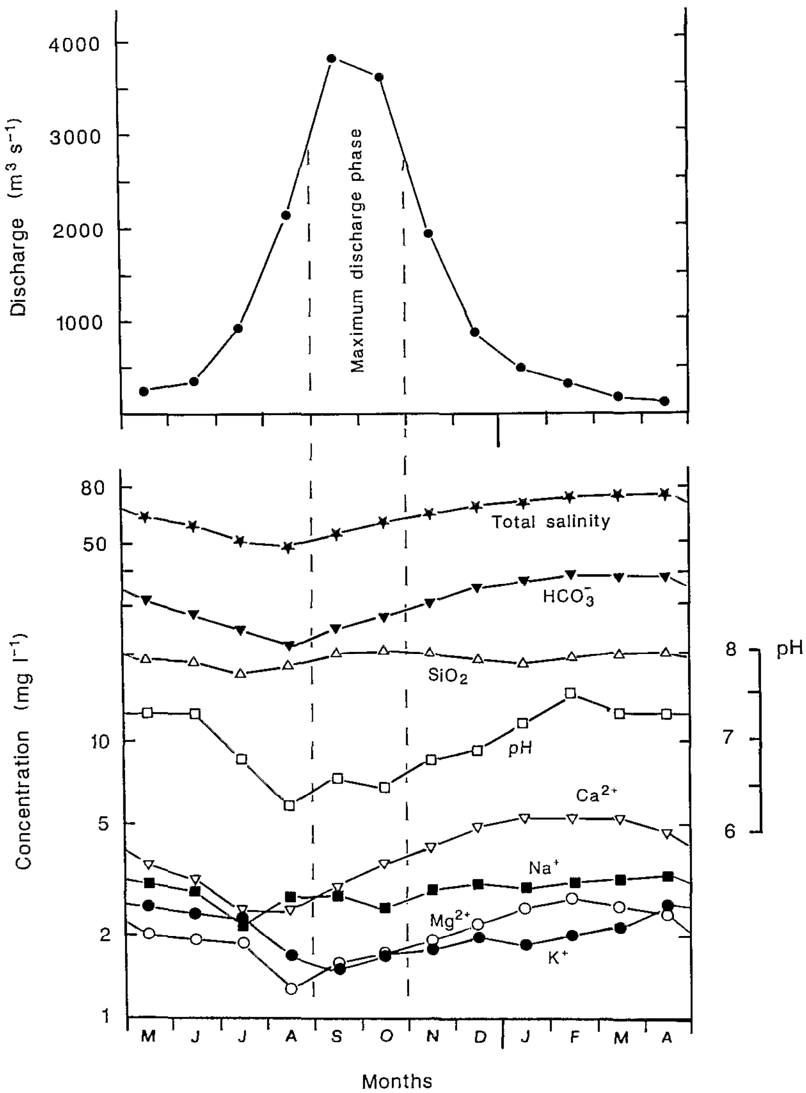

FIG. 24. — Monthly changes in (above) the discharge of the main inflow to L. Chad and their relation to (below) chemical concentrations in the upper lake basin. From GAC (1980).

Variations mensuelles des apports principaux au lac Tchad par le Chari (en haut) et leur relation avec les caractéristiques chimiques de l'eau dans le bassin versant.

mainly in surface run-off (R_i) then occurs. This situation is widespread in endorheic lakes of closed basins ($R_o = 0$), in which salinity varies in time with varying rainfall and hence R_i. Such variation also occurs during the brief existence of temporary rain pools and their often remarkable fauna (e.g. RZÓSKA, 1957). Estimates of evaporative concentration factors can sometimes be obtained with respect to time or hydrological interface (e.g. inflow/lake) from ratios of Cl^- concentration, where local sources are slight (e.g. Ethiopian waters : WOOD and TALLING, 1988).

The hydrological relationship has been directly illustrated, from many-year records, for lakes Chilwa (KALK *et al.*, 1979), Nakuru (VARESCHI, 1982), and Chad (GAC, 1980; CARMOUZE *et al.*, 1983). In the last lake, salinity (and so conductivity) increases northwards away from the main inflow, whose seasonal discharge contributes to the spatial and temporal patterns (Figs. 23, 24). Here, and in L. Naivasha, an underground efflux (G_o) limits the expected increase in salinity, augmented by chemical incorporation into the sediments (see 4.7). The salt balance may be

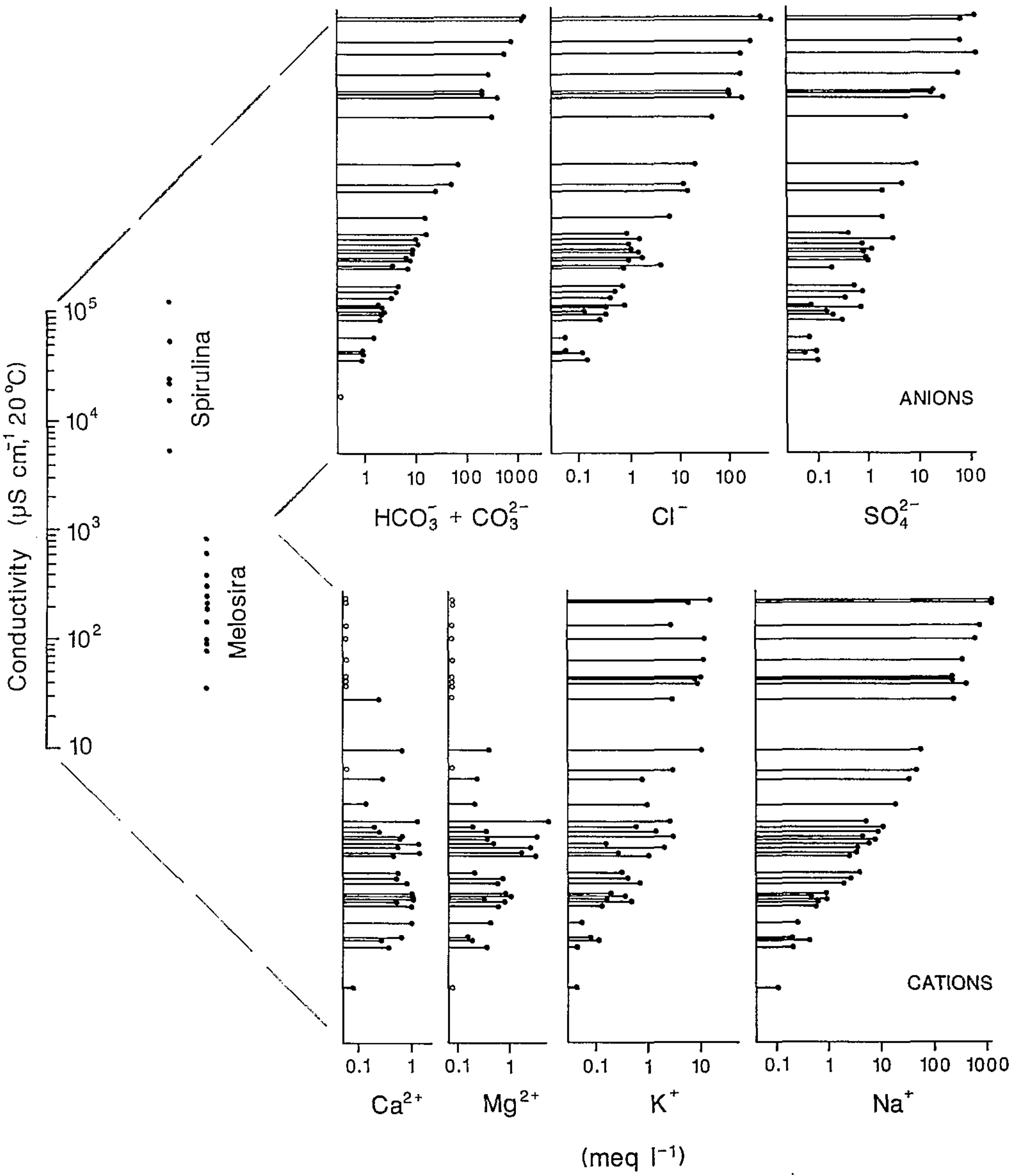

FIG. 25. — Concentrations of (a) major anions and (b) major cations in relation to conductivity in a series of East and Central African lake waters. Distributions of two groups of phytoplankters, *Melosira (Aulacoseira)* spp. and *Spirulina fusiformis ('platensis')*, are also shown. From FRYER and TALLING (1986).

Concentrations en ions majeurs, anions et cations, en fonction de la conductivité dans une série de lacs d'Afrique Centrale et de l'Est. La distribution de deux groupes de phytoplancton, Melosira (Aulacoseira) *spp. et* Spirulina fusiformis (platensis), *est aussi figurée. D'après* FRYER *et* TALLING, *1986.*

complicated by underground reserves of saline water supplying the surface evaporating basin as discussed by GUEST and STEVENS (1951), BAKER (1958), and WOOD and TALLING (1988) for some East Rift soda lakes, by HEEG *et al.* (1978) and HEEG and BREEN (1982) for the Pongolo pans, and represented (Maglione, 1976) in the temporary waters of Kanem (Chad). It is noteworthy that the special case of a largely atmospheric control of the water budget in large lakes, with direct precipitation (P) $\simeq$ evaporation (E) > inflow (R_i), is compatible with not inconsiderable solute concentration as evidenced by lakes Victoria, Tana and Malawi.

Another special case is constituted by shallow coastal waters (e.g. lagoons) with a limited and sometimes intermittent connection to the sea, from which saline water enters. Thus the horizontal distribution of salinity is often uneven. Studied examples include some Delta lakes of Egypt (Section 4.1); Lake Ichkeul, Tunisia (LEMOALLE, 1983a); the elongate Ebrié lagoon (Ivory Coast : DUFOUR, 1982a ; DURAND and CHANTRAINE, 1982); Lake St Lucia (South Africa); and Swartvlei (South Africa) in which the denser saline inputs can stabilize a deep-water layer (ROBARTS and ALLANSON, 1977). With another type of lagoon cut off from a relatively dilute lake, salinity may develop internally from evaporative concentration. An example off L. Tanganyika is described by CALJON (1987).

Solid salt deposits (see Section 5.2) are a conspicuous feature of the margins of many shallow saline lakes. Some periodic removal by wind may occur. The relatively insoluble carbonates are particularly common, notably trona ($Na_2CO_3.NaHCO_3.2H_2O$) and less frequently a tufa of calcium and magnesium carbonates (e.g. Gac, 1980). Sodium chloride occurs occasionally (e.g. L. Katwe in W. Uganda).

4.3. Major ions and pH

Almost all the ionic content is contributed by four major cations (Ca^{2+}, Mg^{2+}, Na^+, K^+) and three major anions or anion-pairs ($HCO_3^- + CO_3^{2-}$, Cl^-, SO_4^{2-}). Variation of their concentration is shown in Table V and further illustrated for many East and Central African lakes, shallow and deep, in Fig. 25; these are largely bicarbonate-carbonate dominated waters. A wide range of water-types is represented in the chemical surveys of LIVINGSTONE (1963), SYMOENS (1968), KILHAM (1971), HECKY and KILHAM (1973), VISSER (1974), VISSER and VILLENEUVE (1975), VINER (1975a), GASSE *et al.* (1983), and WOOD and TALLING (1988), as well as in detailed descriptions of individual lake basins as by VINER (1969) for L. George, CHANTRAINE (1978), GAC (1980) and CARMOUZE (1983) for L. Chad, and GAUDET and MELACK (1981) for L. Naivasha.

Chloride-dominated waters are most strongly represented in coastal or near-coastal situations with present or past ingress of sea-water. They include many lagoons of north and west Africa (e.g. Ebrié lagoon : DUFOUR, 1982a); L. Asal (GASSE *et al.*, 1983, WOOD and TALLING, 1988) and L. Afrera (= L. Giulietti) (MARTINI, 1969; GONFIANTINI *et al.*, 1973) near Djibouti; Swartvlei (ROBARTS and ALLANSON, 1977), L. Sibaya (ALLANSON, 1979) and some other coastal lakes (ALLANSON and VAN WYK, 1969) in South Africa ; and L. Qarun in Egypt (MESHAL and MORCOS, 1980) — the last with many marine organisms (e.g. plankton : El MAGHRABY and DOWIDAR, 1969). There are also some more inland sites with local sources of chloride as with L. Katwe in Uganda (TALLING and TALLING, 1965; ARAD and MORTON, 1969) and L. Mohasi in Ruanda (DAMAS, 1954), L. Ihotry in Madagascar (MOREAU, 1982), and various Saharan salt lakes (e.g. Dawada, Kufra).

In the commonest, bicarbonate-carbonate, type of African inland water, increase in salinity (and conductivity) is associated (Fig. 25) with a steady rise in the concentrations of Na^+, rather less regular rise (affected by local sources) in those of K^+, and the final loss by precipitation of Ca^{2+} and Mg^{2+}. Thus the ratio of monovalent to divalent cations increases, and in saline waters Na^+ is predominant. This trend has been further analysed by TALLING and TALLING (1965) and WOOD and TALLING (1988) from comparisons of many African lake waters, and by GAC (1980) from both observations and experiments involving the concentration with time of water from L. Chad and its main inflow (Fig. 26). In the survey Table V all lakes of high salinity (cationic or anionic content > 100 meq l^{-1}) have Na^+ as the dominant cation, but if with low alkalinity (e.g. L. Ihotry) the concentrations of Ca^{2+} and Mg^{2+} can be considerable — as in seawater. A contrasting situation of very low Mg^{2+} concentration (< 0.02 meq l^{-1}) was encountered by Löffler (1964) in high altitude lakes on the East African mountains Ruwenzori and Mt. Kenya. Although many biological consequences of the overall salinity series are well documented, the influence of individual ions and ion ratios is more controversial (BEADLE, 1981). Thus WOOD and TALLING (1988) tentatively related a strong representation of some phytoflagellates with lower monovalent to divalent cation ratios.

Given a predominance of bicarbonate+carbonate (= alkalinity), the more saline waters are also intensely alkaline in reaction, a feature accentuated by the photosynthetic removal of CO_2 by their frequently dense phytoplankton. In this respect it is interesting to compare the productive East African lakes Nakuru and George. If air-equilibrium prevailed with respect to CO_2, their expected pH would be about 9.9 and 8.2 respectively (TALLING and TALLING, 1965, Fig. 3); in reality that of L. Nakuru lies between 10 and 11 (TUITE, 1981 ; VARESCHI, 1982), and that of the less buffered, low alkalinity waters of L. George is typically between 9 and 10. Thus carbon deficits, relative to air-equilibrium conditions, are set up in productive waters. Much lower values of pH are usual in saline, chloride-dominated waters

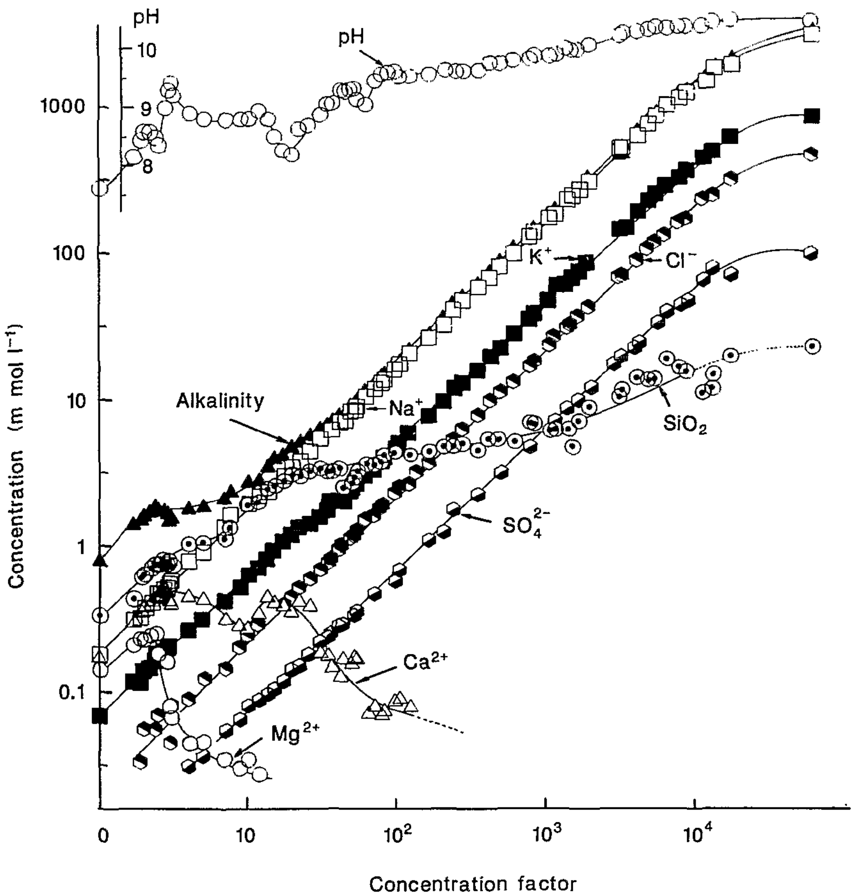

FIG. 26. — Evaporation experiment with water from the inflow Chari River to L. Chad, showing differential changes with time of chemical concentrations in relation to the overall volumetric concentration factor. From GAC (1980).
Évaporation expérimentale de l'eau du Chari qui parvient au lac Tchad. Certains ions suivent une évolution différente lorsque le facteur de concentration évaporitique augmente. D'après GAC, 1980.

of relatively low alkalinity, such as those influenced by sea water. As alkalinity (and HCO_3^- concentration) fall towards zero, typically in waters of very low ionic content, pH approaches c. 5. Still lower values of pH are associated with free acidity, although the latter is only rarely analysed directly — as for the water of L. Tumba on the Zaïre river system with pH 4.5-4.9, free acidity 0.1-0.7 meq l^{-1}, conductivity (18 °C) 24-32 µS cm^{-1} (DUBOIS, 1959).

At very high (> 10) or very low (< 4) values of pH the ions OH^- and H^+ respectively exceed c. 0.1 mmol l^{-1} and then can influence conductivity appreciably, although their proportion of the total ionic content is usually small. BERG (1961) gives examples from acidic waters of the Congo (Zaïre) basin; there, at pH 3.5, a conductivity value of c. 130 µS cm^{-1} would be expected. Below pH 4.2 waters were inhibitory to the invasive water hyacinth, *Eichhornia crassipes*.

In some East African waters, usually of high alkalinity, the fluoride ion exceeds 10 mg l^{-1} (sometimes > 1 g l^{-1}). It may then have adverse effects on certain freshwater organisms (KILHAM and HECKY, 1973) and on human utilization for drinking water.

4.4. **Plant nutrients**

Aspects of the distribution, and especially the exchanges, of nutrients in African freshwaters have been reviewed by THORNTON (1986) and (for phosphorus) MELACK and MAC INTYRE (in press). Most major ions are also plant nutrients, but are usually presumed to be present in excess of growth-limiting

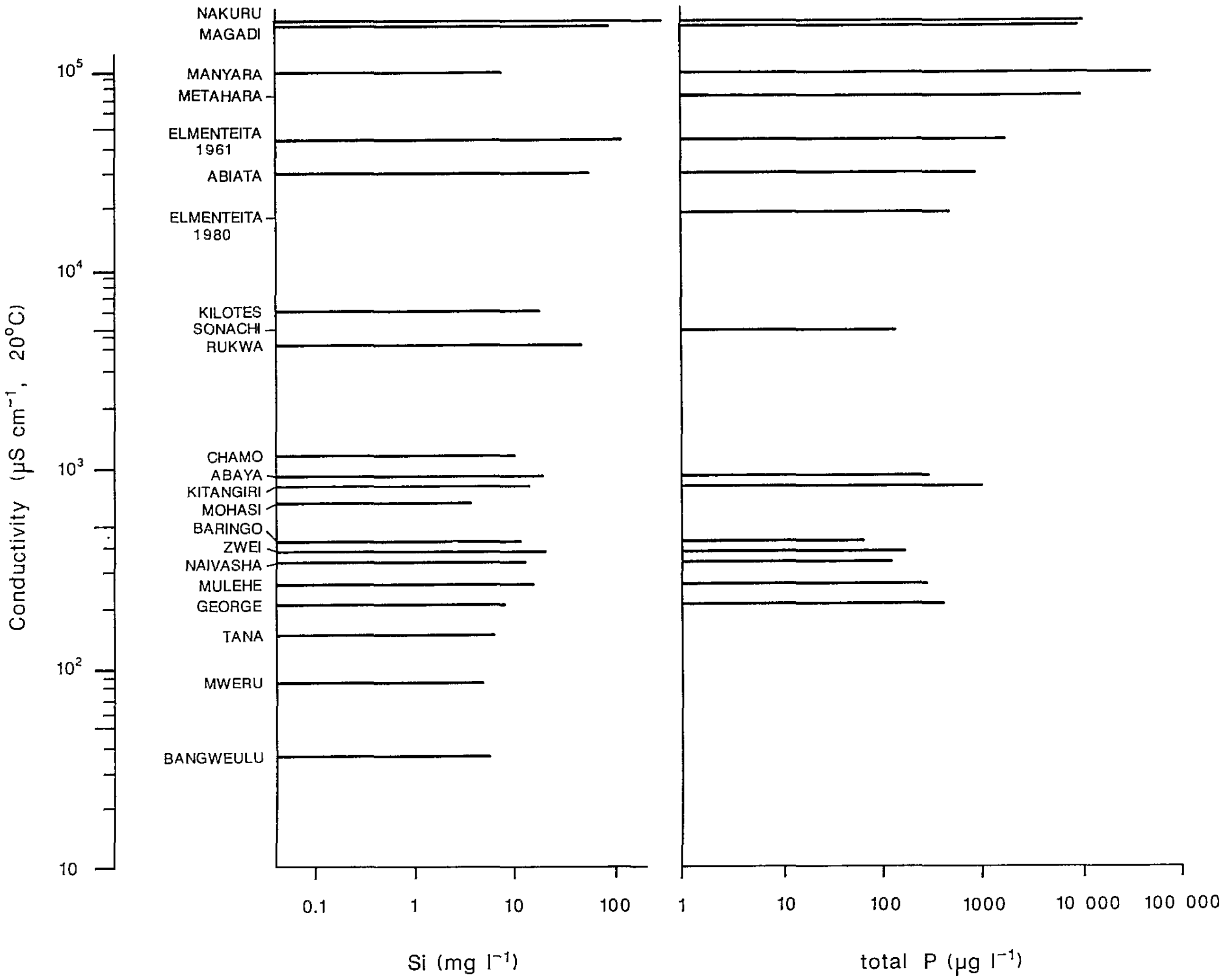

FIG. 27. — Concentrations of soluble reactive silicon and total phosphorus in relation to conductivity in a series of shallow East and Central African lake waters. Adapted from TALLING and TALLING (1965), KALFF (1983), and WOOD and TALLING (1988).
Concentration du silicium soluble réactif et du phosphore total en fonction de la conductivité dans une série de lacs peu profonds d'Afrique Centrale et de l'Est. D'après TALLING et TALLING (1965), KALFF (1983) et WOOD et TALLING (1988).

concentrations — a view challenged by BEAUCHAMP (1953) for sulphate and possibly questionable for the lower concentrations of potassium encountered in some African waters. Here we are concerned with forms of the elements N, P, and Si. When variability in their concentrations is viewed against total ionic concentration or conductivity (Table V and Fig. 27) there is little regularity — although saline carbonate lakes typically have high concentrations of Si and total P. Besides their biological significance in the bulk-water phase, their presence and uptake from sediments is important for many rooted macrophytes (see Denny, 1985a). Carbon is another plant nutrient, derived from free CO_2 (section 4.5) or $HCO_3^- + CO_3^{2-}$ (section 4.3); it can also provide a comparative measure of biomass and organic detritus, as in studies of Lake George (BURGIS *et al.*, 1973) and the shallow Wuras Dam (GROBBELAAR, 1985; GROBBELAAR and TOERIEN, 1985).

Silicon, present in solution as silicic acid ($Si(OH)_4$) or silicate, is of significance for the growth of diatoms. In most African shallow waters its concentration is greatly in excess of those levels (< circa 0.3 mg or 10 µmol Si l^{-1}) at which a possibility of growth

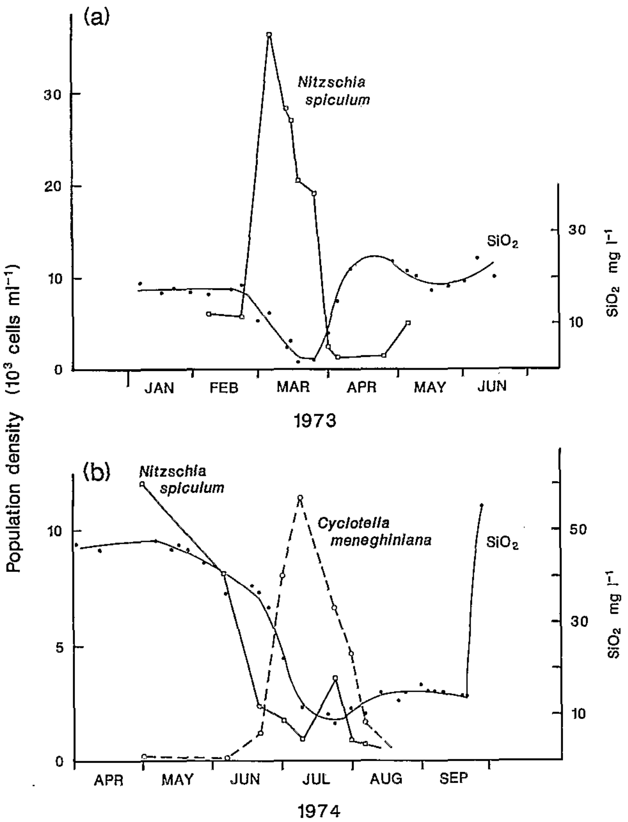

FIG. 28. — Large depletions of soluble reactive Si (expressed as SiO_2) during two episodes of diatom growth at the station Bol on L. Chad in (a) 1973 (b) 1974. From LEMOALLE (1978).
Fortes variations de la silice réactive (exprimée en Si O_2) au cours de deux épisodes de développement important des diatomées dans le lac Tchad à Bol en 1973(a) et 1974(b). D'après LEMOALLE, 1978.

rate-limitation might be suspected. For water of the Ebrié lagoon (Ivory Coast), application of a biological assay procedure gave no indication of a limiting role in phytoplankton production (DUFOUR and SLEPOUKHA, 1981). The suggestion of KILHAM (1971) of a qualitative influence of higher concentrations on diatom floras was not clearly supported by the survey of GASSE *et al.* (1983). In many shallow lakes (and rivers) concentrations of 5-20 mg l^{-1} are found, which are high by world standards and probably influenced by tropical weathering. Examples include L. George (TALLING and TALLING, 1965; VINER, 1969), L. Naivasha (TALLING and TALLING, 1965; GAUDET and MELACK, 1981), L. Chad (LEMOALLE, 1978; GAC, 1980; CARMOUZE, 1983), and L. Tana, L. Abaya, L. Chamo, and L. Baringo (TALLING and TALLING, 1965; WOOD and TALLING, 1988). There are few series of seasonal analyses in relation to the abundance of diatom populations, but in L. Chad (LEMOALLE, 1978 — see Fig. 28) and in shallow inshore waters of L. Victoria (TALLING, 1966) some periodic depletion can occur. However in these lakes, as in the Ebrié lagoon, availability of Si is generally unlikely to limit the growth of diatom populations. Soda lakes of high alkalinity (e.g. Nakuru, Elmenteita, Magadi, Kilotes, Abiata) are invariably of very high Si content (TALLING and TALLING, 1965; WOOD and TALLING, 1988); its abiogenic transformation from solute to solid (sedimentary) phases has been studied for L. Magadi (EUGSTER, 1967; EUGSTER and JONES, 1968), as well as for the relatively low alkalinity waters of L. Chad (CARMOUZE, 1983).

PHOSPHORUS

Of the several measures of phosphorus concentration, that of total phosphorus (obtained by digestion) is probably the most informative for comparative purposes. In silt-rich water, however, it can merely indicate the abundance of a variable particulate

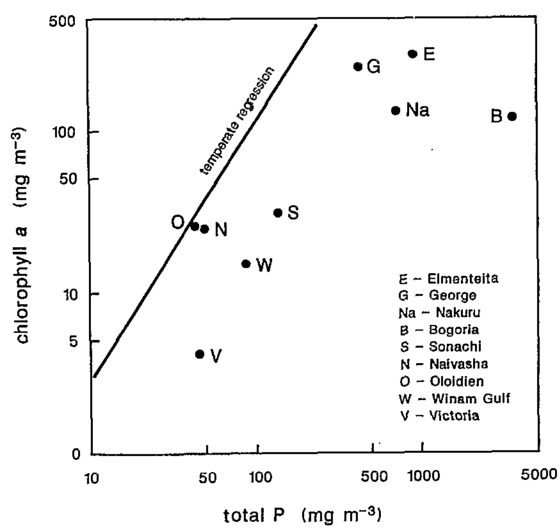

FIG. 29. — Phytoplankton abundance, as indicated by mean values of chlorophyll *a* concentration, in relation to the associated concentrations of total phosphorus in various African lake waters. The inserted line is a regression from DILLON and RIGLER (1974), relating the winter-spring concentrations of total P with the mean summer concentrations of chlorophyll *a* in various temperate lakes. Adapted from KALFF (1983), with correction for L. Victoria.
Abondance du phytoplancton (exprimée par la concentration moyenne en chlorophylle a) en fonction du phosphore total dans divers lacs d'Afrique. La droite correspond à la relation de DILLON et RIGLER (1974) reliant P total en hiver-printemps et la chlorophylle moyenne d'été dans différents lacs de zone tempérée. Modifié de KALFF, 1983 avec une correction pour le lac Victoria.

phase. Unfortunately it is available in few chemical surveys of African waters (e.g. TALLING and TALLING, 1965; see Table V and Fig. 27), and most analyses are of soluble reactive phosphate. Still fewer analyses refer to particulate phosphorus; here detailed studies on shallow lakes include VINER (1977) for L. George (Fig. 10), GAUDET (1976, 1979) and KALFF (1983) for L. Naivasha, HOWARD-WILLIAMS (1977) and HOWARD-WILLIAMS and ALLANSON (1981) for Swartvlei (Figs. 30, 31), and DUFOUR (1984) for the Ebrié lagoon.

Analyses of total phosphorus show that — presumably for geological reasons — the content in many shallow African waters is considerable (> 30 µg l^{-1}) by world standards. Comparative examples are given in Fig. 29 and Table V, and in a recent review by MELACK & MACINTYRE (in press). There is a tendency, as elsewhere, for higher concentrations per unit volume to be present in shallow than in deep lakes, and also in more saline than in dilute waters. However analyses for the last class — which include the important L. Bangweulu and most West African waters — seem especially deficient. Phosphate may share a phase of progressive concentration, during hydrological contraction, with total ionic concentration (e.g. in L. Chilwa : MCLACHLAN *et al.*, 1972). The many shallow lakes which bear dense and long-lasting phytoplankton are inevitably high in total phosphorus as the converse of dense phytoplankton but low total phosphorus is excluded. In such waters most phosphorus can be incorporated as particulate phosphorus in the algal populations (Fig. 10), with only a small fraction of soluble reactive phosphorus (e.g. < 2 µg l^{-1} in L. George : GANF & VINER, 1973; VINER, 1977c). Turnover of the latter fraction can then be expected to be rapid, as demonstrated experimentally with PO_4-P uptake for L. George (VINER, 1973, 1977c) and with ^{32}P by PETERS and MCINTYRE (1976) for L. Elmenteita and by KALFF (1983) for lakes Oloidien and Sonachi. In the last lake there is evidence of P- limitation from the response of phytoplankton to added phosphate, but not ammonium, and from low ratios of sestonic P/C and P/N (MELACK *et al.*, 1982). In other shallow lakes (e.g. Nakuru) with a greater excess of soluble reactive phosphate, the experimental turnover of radio-phosphorus was slower. The situation in L. Naivasha, studied by KALFF (1983), appeared intermediate and included marked seasonal variation. The partitioning of radio-phosphorus has also been followed in 3.5 m — deep isolation columns within the Midmar reservoir, Natal (TWINCH and BREEN, 1984). Water from this lake, and its columns, has been used for systematic enrichment and assay experiments (TWINCH and BREEN, 1981, 1982). Algal responses varied with season or prior enrichment, but positive response to P enrichment was frequent even when the total phosphorus already exceeded 30 µg l^{-1}. In lakes with dense weed-beds of submerged macrophytes, the latter may dominate P-uptake and recycling. This occurred during the seasonal growth and decline of *Potamogeton pectinatus* (+associated *Cladophora*) in Swartvlei (HOWARD-WILLIAMS, 1981; HOWARD-WILLIAMS and ALLANSON, 1981b; see Fig. 30). In this lake the P- fractions are also stron-

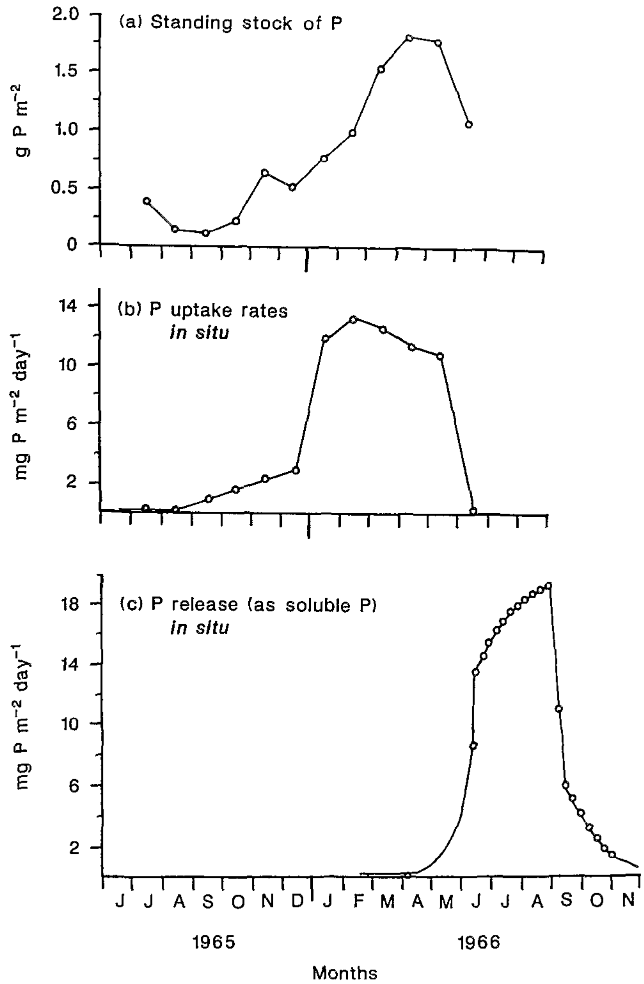

FIG. 30. — Seasonal changes of P quantities in Swartvlei, showing time-relationships of (a) the maximum in standing stock of plant biomass with (b) estimated rates of uptake and (c) release as soluble P. Redrawn from HOWARD-WILLIAMS and ALLANSON (1981b).

Évolution saisonnière de diverses formes du phosphore, qui montre les évolutions successives a) du maximum du stock dans la biomasse primaire, b) des estimations des vitesses d'assimilation et c) de la remise en solution du phosphore. Modifié d'après HOWARD-WILLIAMS et ALLANSON, 1981b.

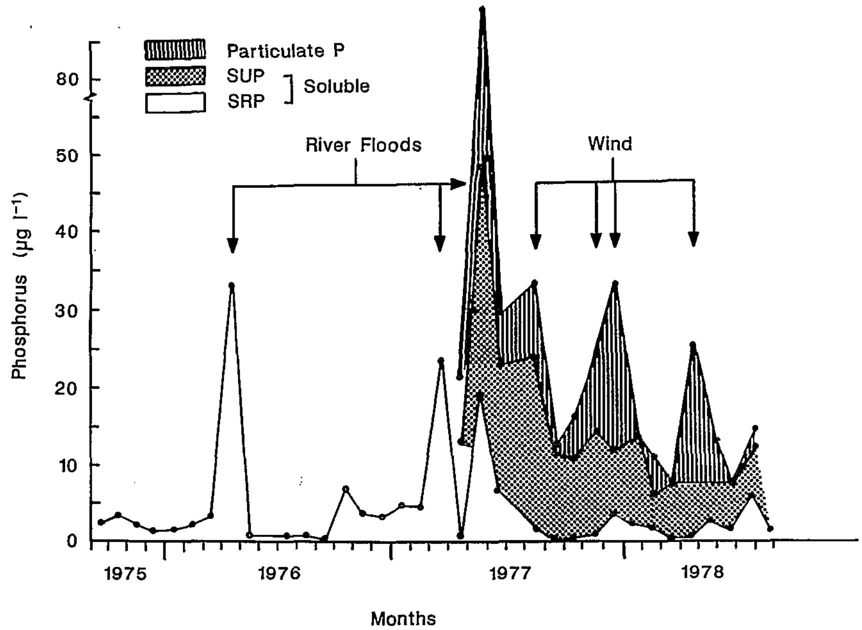

FIG. 31. — Monthly variation in Swartvlei, over 3 years, of the concentrations of total P and its component fractions of soluble reactive P (SRP), soluble unreactive P (SUP), and particulate P, showing the relationship of maxima to episodes of river floods and wind disturbance. Redrawn from HOWARD-WILLIAMS and ALLANSON (1981).

Concentrations mensuelles de diverses formes du phosphore dans le Swartvlei au cours de 3 années successives, avec les influences des crues des rivières et des turbulences dues au vent. SRP = phosphore réactif dissous, SUR = phosphore non réactif dissous, Particulata P = phosphore particulaire. La somme constitue le P total. Redessiné d'après HOWARD-WILLIAMS et ALLANSON, 1981.

gly influenced by inflowing floodwater and by wind-disturbance of sediments (Fig. 31).

In shallow lakes the biological importance of sediment-water exchange of phosphate (and ammonium) is enhanced by the large ratio of sediment area to water volume, the short-lived (usual diel) character of thermal barriers, and possibly by wind-disturbance of sediments. Detailed studies of such exchange have been made for L. George by VINER (1975d,e, 1977a,b) and for the Ebrié lagoon by LEMASSON *et al.* (1982); VINER believed that in the very productive L. George most recycling of N and P occurred in the water-column rather than the sediments. For L. Kioga a modelling approach to sediment-water exchange has been used (KAMP-NIELSEN *et al.*, 1980). Suspended sediment with adsorbed phosphate is abundant in many shallow waters, and no doubt plays a role as a nutrient reserve. In swamps with rooted macrophytes the nutrient-P pathway from sediments to water via plant uptake and decay may be quantitatively important (DENNY 1985a).

Although the phosphorus content of plant biomass is variable, some indication of the quantities (µg l^{-1}) likely to be incorporated in phytoplankton crops of various densities can be obtained from Fig. 32. Detailed seasonal and experimental observations have been made on L. George (VINER, 1973, 1977c) and in the Ebrié lagoon (DUFOUR, CREMOUX & SLEPOUKHA, 1981; DUFOUR, LEMASSON & CREMOUX, 1981) where the mean internal cellular subsistence quota for P was estimated as a ratio 0.0055 : 1 by atoms to sestonic C (i.e. C/P quotient of 182).

Nitrogen. The following forms or fractions of combined nitrogen can be distinguished : nitrate-N, ammonium-N, nitrite-N, hydroxylamine-N, dissolved organic N, particulate N, and total N. Most analytical information for African shallow waters refers to the first two of these. Nitrite-N is generally negligible quantitatively, although it is an important intermediate and has been used experimentally by VINER (1973, 1977c) to trace N-uptake by phytoplankton in L. George. Its seasonal and spatial distribution in L. Edku, Egypt, has been followed by SAAD (1978). Hydroxylamine-N has been specifically studied only in some Ethiopian lakes, where it was probably a significant N component (BAXTER *et al.*, 1973; PITWELL, 1975; WOOD *et al.*, 1984). For sur-

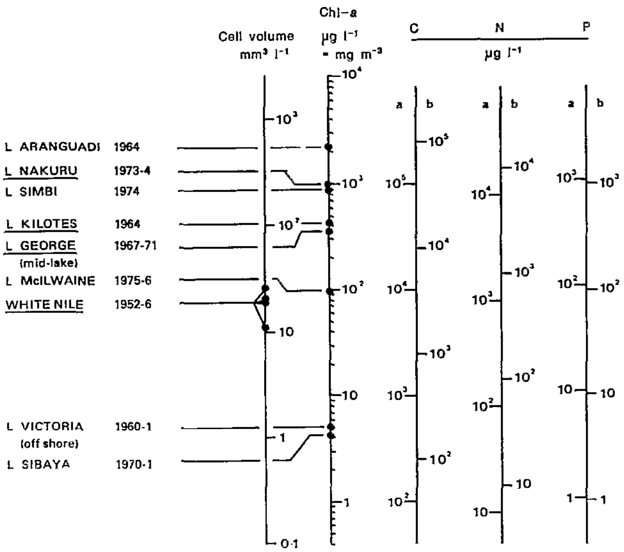

FIG. 32. — Approximate interrelations, read horizontally across vertical logarithmic scales over 4 orders of magnitude, of concentrations of two indices of phytoplankton biomass (cell volume, chlorophyll *a*) observed in 9 African waters (shallow underlined), and estimates of associated quantities of cellular C, N, and P. The interrelations are based on a chl-*a* content per unit cell volume of 4 µg mm^{-3}, a C/chl-*a* mass ratio of 40, and C/N and C/P ratios that are (a) the mean values for L. George recorded by VINER (1977), (b) the generalized Redfield values. Adapted from TALLING (1981).

Interrelations, en échelle logarithmiques sur 4 ordres de grandeur, de diverses caractéristiques phytoplanctoniques : volume algal, concentration en chlorophylle a, et estimation des quantités correspondantes de C, N et P. Les correspondances sont calculées sur la base de Chla/volume cellulaire de 4 µg. mm^{-3}, C/chla en masse de 40, C/N et C/P d'après a) VINER (1977) pour le lac George et b) le rapport de Redfield. D'après TALLING, 1981.

face waters generally, nitrate-N or dissolved organic N are usually predominant in the total N. In Africa dissolved organic N is the more likely, although there are only few supporting analyses of it or of total N (e.g. DUBOIS, 1959; VINER, 1977c; GAUDET, 1979; ASHTON, 1981; DUFOUR, CREMOUX and SLEPOUKHA, 1981; KALFF, 1983).

The concentrations and dynamics of particulate N are perhaps best known from studies of swamp regions dominated by macrophytes as at L. Chilwa (HOWARD-WILLIAMS and HOWARD-WILLIAMS, 1978; MCLACHLAN, 1979), the littoral of L. Kariba (S. M. MCLACHLAN, 1970), L. Naivasha (GAUDET, 1979; GAUDET and MUTHURI, 1981a, b), Swartvlei (HOWARD-WILLIAMS, 1977), and L. Victoria (GAUDET, 1976). In such vegetation stands the amounts of plant-N present per unit area (Fig. 46) are much higher than those in most phytoplankton communities, for which the probable magnitude of concentrations per unit volume can be located from Fig. 32. Particulate N concentrations and dynamics have been studied directly by VINER (1973, 1977c) for the dense phytoplankton of L. George, where in 1967-8 concentrations varied between 1 and 5 mg N l^{-1} (Fig. 10), and by DUFOUR, LEMASSON and CREMOUX (1981) for the less productive Ebrié lagoon where they ranged generally between 150 and 400 µg N l^{-1} but rose to 700 µg l^{-1} in eutrophic areas.

Such high concentrations are rarely reached for inorganic nitrogen in the surface region of any productive shallow water. In L. George, for example, concentrations of NH_4-N are typically < 10 µg l^{-1} with NO_3-N and NO_2-N usually undetectable (GANF and VINER, 1973; VINER, 1977c). For N therefore, as for P, turnover by the metabolically active phytoplankton must be rapid and rates of regeneration crucial. Profiles of NH_4-N accumulation in the bottom sediments (GANF and VINER, 1973; see Fig. 11) indicated periodic disturbance and release to the overlying water, but VINER (1975c, 1977b) believed that the sediment contribution to overall N-cycling was small.

The lack of prolonged thermal (density) stratification in the open water of most shallow lakes generally eliminates accumulation of NH_4-N in deeper water, although VINER found that some small increase occurs on a diel time-scale even in the shallow L. George. In sheltered, often anoxic swamp water, rich in (and often overlain by) vegetation in various stages of decay, the situation is quite otherwise. Transects of various African swamps have shown considerable (often > 1 mg N l^{-1}) accumulations of NH_4-N away from the open margin (CARTER, 1955; HOWARD-WILLIAMS, 1972; GAUDET, 1976, 1979; review in HOWARD-WILLIAMS and GAUDET, 1985), and release to the open water may significantly influence the latter (e.g. L. Chilwa : HOWARD-WILLIAMS, 1972; HOWARD-WILLIAMS and LENTON, 1975; HOWARD-WILLIAMS and HOWARD-WILLIAMS, 1978). An accumulation of NH_4-N (> 1 mg l^{-1}) is also known in anoxic water below a salinity-density barrier of the shallow Ebrié lagoon (DUFOUR, 1984).

In shallow temperate waters it is common to find a seasonal (usually winter-spring) phase of higher nitrate concentration. This is generally lacking in shallow African waters, excepting some at higher latitudes (e.g. L. Mariut, Egypt; ALEEM and SAMAAN, 1969; the Midmar reservoir, Natal : TWINCH and BREEN, 1981), unless subject to seasonal flood-water rich in nitrate. The Blue Nile flood (TALLING and RZÓSKA, 1967) provides one example; another is the elevation of nitrate concentrations in an estuarine region of the Ebrié lagoon early in the rainy season (DUFOUR and DURAND, 1982). A temporary flush of nitrate on reflooding of dry lake sediment (see Section 6.3) is probably widespread, as is a flush of nitrate in savanna soils and their run-off after the beginning of a rainy season (see, e.g., VINER, 1975a).

Fixation of gaseous nitrogen (N_2) by certain bacteria and cyanophytes is undoubtedly widespread in African waters, but has been studied quantitatively in very few, including L. George (HORNE and VINER, 1971, and Fig. 39; GANF and HORNE, 1975) and Rietvlei (ASHTON, 1979, 1981), where fixation by cyanophytes was estimated to be an appreciable contribution to the N- economy of the lakes. There are reports of N-fixation by microbes associated with various floating African macrophytes (e.g. *Salvinia molesta, Eichhornia crassipes, Cyperus papyrus*), but its quantitative significance is generally uncertain. The subject is reviewed in DENNY (1985a).

The converse process of denitrification, mediated by bacteria and liberating N_2, has rarely received specific study in African fresh waters. Promoted by higher temperature, it is possibly crucial in maintaining the generally low levels of nitrate, and hence the inorganic N/P ratio of interest in relation to the control of plant growth (e.g. TALLING, 1966; KALFF, 1983). Direct measurements of the denitrification of added nitrate have been made by VINER (1982) for sediments from L. Naivasha and nearby waters.

4.5. Dissolved gases

The gaseous content of shallow waters is, to a great extent, influenced by the exchange pathway across the water/air interface. If such exchange were the dominant influence on gaseous concentrations, the latter would be set by the partial pressures of atmospheric gases, their intrinsic solubilities in water, and the modifying influences of temperature and salinity. In reality, large modifications can be introduced by barriers to vertical exchange and by biological activities. The latter include the metabolic exchanges of O_2 and CO_2 in photosynthesis and respiration, and — in O_2 depleted zones — the bacterial production of H_2S and CH_4 as reduced end-products.

Dense and illuminated populations of submerged aquatic plants, planktonic or macrophytic, generate concentrations of oxygen in excess of air-equilibrium values. The accompanying consumption of CO_2 is rarely measured directly (as for L. George — GANF and MILBURN, 1971) but is reflected in increase of pH (e.g. Figs 6c, 22). As daylight is discontinuous, diel oscillations are set up in the concentrations of O_2 and total CO_2 (comprising free CO_2, HCO_3^-, and CO_3^{2-}) which are inversely related, and in pH which varies inversely with the total CO_2 content. In highly buffered waters, such as L. Nakuru (VARESCHI, 1982), the diel pH changes are insignificant. The diel cycle usually includes nocturnal O_2 levels below air-saturation, whereas the pH and CO_2 levels in such productive waters are typically indicative of maintained CO_2- deficiency relative to the air-equilibrium state. This difference in behaviour of the two gases is influenced by the relatively low partial pressure of CO_2 in the atmosphere and the equilibria uniquely relating this gas to ionic reserves (HCO_3^-, CO_3^{2-}). The shallow African waters in which such diel fluctuations have been studied include a lagoon and reservoir on the White Nile (TALLING, 1957b), bays of L. Victoria (WORTHINGTON, 1930; TALLING, 1957b), L. George in Uganda (GANF, 1974b, GANF and HORNE, 1975 : Fig. 6), L. Nakuru in Kenya (MELACK and KILHAM, 1974), L. Kilotes in Ethiopia (TALLING *et al.*, 1973), the Ebrié lagoon (VARLET, 1978), and the Pretoria Salt Pan (ASHTON and SCHOEMAN, 1983 : Fig. 22). In all these waters the diel gaseous changes were primarily due to dense phytoplankton.

Barriers to vertical exchange can develop from temperature-density and salinity-density stratification, or from layers of macrophytes, especially when these form floating mats (e.g. MUSIL *et al.*, 1976). Although temperature-density stratification is short-lived (often diurnal) in most shallow waters, when combined with intense biological activity it can result in steep vertical gradients of oxygen, carbon dioxide, and pH. Examples are provided by the diel studies cited above, here illustrated in Figs. 6, 22 38. It is uncommon, although known (TALLING *et al.*, 1973; ASHTON and SCHOEMAN, 1983; Fig. 38), for complete anoxia to develop or persist in water below the diurnal density barrier. Production of CH_4 and H_2S has apparently not been recorded in this context. They are known to accumulate below a salinity-density barrier in coastal lakes or lagoons to which seawater has entered, as in parts of the Ebrié lagoon and in Swartvlei.

The situation is quite otherwise for swamp conditions, characterised by a large input of decomposable organic material and the common development of floating plant mats, such as the rhizome-layer of *Cyperus papyrus*. Anoxia is widespread in the water beneath such mats, except very close to outer exposed margins or when streams renew the water rapidly (e.g. at L. Naivasha : GAUDET, 1978, 1979). An onshore wind has been shown to drive oxygenated lake water deep inside fringing swamps of *Typha domingensis* at L. Chilwa (HOWARD-WILLIAMS and LENTON, 1975). Illustrative sections through papyrus swamps bordering rivers or lakes have been made by various workers (e.g. BEADLE, 1932a; CARTER,

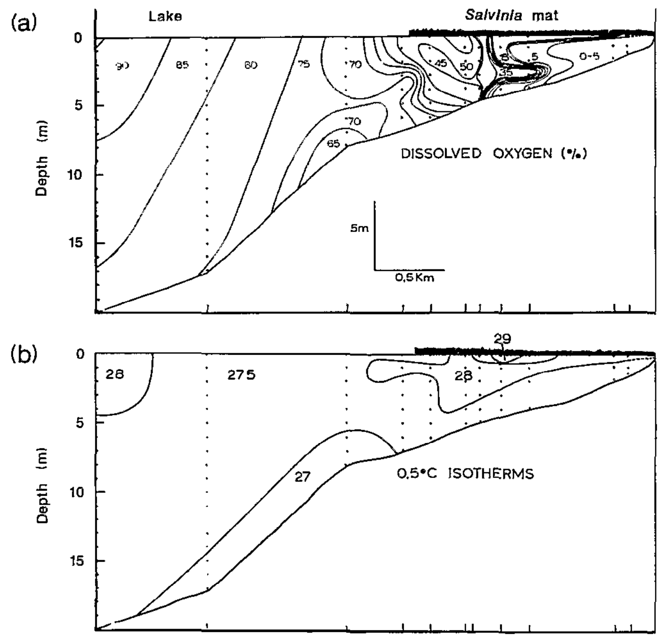

FIG. 33. — Transect at L. Kariba from deeper lake to shallow estuary of the inflowing Mwenda River, showing (a) the vertical distribution of dissolved oxygen in relation to (b) temperature stratification and the extent of a surface mat of *Salvinia molesta*. The intrusion of more oxygenated lake water underneath the mat is probably due to compensation currents resulting from a wind-induced movement of surface water away from the mat. From BOWMAKER (1976).

Section dans le lac Kariba des zones profondes vers l'estuaire peu profond de la rivière Mwenda. Répartition de l'oxygène (a) en relation avec celle de la température (b) et l'extention d'un tapis de Salvinia molesta. *L'intrusion d'eau lacustre mieux oxygénée sous le tapis de* Salvinia *résulte probablement de courants de retour compensant un courant de surface s'éloignant des rives sous l'action du vent. D'après BOWMAKER, 1976.*

1955; TALLING in RZÓSKA, 1974; GAUDET, 1979). Considerable accumulations of dissolved CO_2 can occur under the mats, and in some cases CH_4 also. There is, however, little evidence for prolonged accumulations of H_2S, although the removal of sulphate undoubtedly occurs (e.g. in the Sudd swamps: TALLING, 1957a). For further information on these and other chemical aspects of swamp environments in Africa, the reader is referred to GAUDET (1976, 1979), BEADLE (1981), THOMPSON and HAMILTON (1983), HOWARD-WILLIAMS and GAUDET (1985), and DENNY (1985a).

More diffuse free-floating mats of plant aggregates, widespread in both shallow and deeper waters of Africa, include the species *Pistia stratiotes*, *Eichhornia crassipes*, and *Salvinia molesta*. *Eichhornia* and *Salvinia* mats in particular can lead to reduced concentrations of oxygen in the water below. Excellent seasonal examples, for *Salvinia*, are provided by the studies of BOWMAKER (1976) on the estuary of a river-inflow to L. Kariba (Fig. 33). Experimental studies of ASHTON (1977) showed how floating mats of *Azolla filiculoides* could alter the characteristics (e.g. pH) of water underneath. Conversely, in dense weed-beds of submersed aquatics, local conditions of high O_2 content and pH often develop during daytime (e.g. MUSIL *et al.*, 1976).

4.6. Metals and organic complexes

Local geochemical and man-made sources determine appreciable inputs of heavy metals to some shallow African lakes, such as of Cu to L. George (BUGENYI, 1979, 1982) and possibly several Kenyan waters (KOEMAN *et al.*, 1972; WANDIGA, 1981). Their significance lies in possible biological toxicity, also conditioned and lessened by complexing behaviour. Thus, for L. Nakuru, KALLQUIST and MEADOWS (1978) showed clear toxic effects of experimentally added Cu on rotifers and the blue-green *Spirulina fusiformis* (formerly identified as *S. platensis*) in quantities > 100 µg l^{-1}, much in excess of the pre-existing amounts.

Contents of the two most abundant metals in shallow water-bodies, Fe and Mn, usually depend strongly on other internal factors — their susceptibility to mobilization on chemical reduction and to stabilization as coloured organic complexes in dispersed and colloidal phases. In L. Chad there is a significant flux of Fe from water column to sediments (LEMOALLE, 1973a, 1979; CARMOUZE, 1983). In productive waters it is common for sediments to be highly reducing and for the content of 'dissolved' (or colloidal) organic matter to be high. During a wide survey of African lake waters (TALLING and TALLING, 1965), the higher concentrations of total Fe (> 500 µg l^{-1}) and total Mn (> 100 µg l^{-1}) were generally found in shallow productive lakes. Concentrations of total Fe reached 5 000 µg l^{-1} or more even in well-oxygenated surface waters of the Eastern Rift lakes Baringo, Zwei, Abaya, and Langano, where a reddish-brown coloration could be seen *in situ*.

A relatively high content of 'dissolved' organic matter in a fresh water is usually associated with yellow coloration, humic and fulvic acid fractions, and high spectrophotometric absorbance in the blue and ultra-violet regions. Such water can be contributed from swamps to adjacent river or lake systems, as seen in examples on the Upper White Nile (TALLING, 1957a) and at L. Chilwa (MOSS and MOSS, 1969). It is especially prevalent in water-bodies of

TABLE VI

	Water volume (10^9 m^3)	Na^+	K^+	Ca^{2+}	Mg^{2+}	HCO_3^-	$Si(OH)_4$
A. Hydrology							
(i) lake volume	72 (range 42.5-91)						
(ii) component flux, yr^{-1}							
river discharge	41.5 (range 20.1-57.2)						
rainfall	6.3 (range 2.7-8.7)						
lake evaporation	44						
seepage - out	3.8						
B. Mean quantity of solutes in lake							
South Basin : concentration (mM)		0.355	0.110	2.205	0.15	1.15	0.595
stock (10^9 Mol)		8.95	2.82	5.22	3.86	29.2	15.0
North Basin : concentration (mM)		2.05	0.605	0.85	0.70	5.65	0.88
stock (10^9 Mol)		96.2	28.3	39.8	32.8	263.0	41.1
Total lake stock (10^9 Mol)		105.2	31.1	45.0	36.6	292.2	56.1
C. Solute fluxes (10^9Mol)							
South Basin							
inputs : river discharge		5.60	2.05	4.35	3.30	22.4	16.1
outputs : seepage out		0.46	0.14	0.27	0.20*	1.50	0.77
sedimentations		0*	0.15	0.99	0.60	3.23	3.30
North Basin							
input : river discharge (via South Basin)		5.14	1.76	3.09	2.50	17.6	9.03
outputs : seepage - out		5.15	1.51	2.13	1.75	14.05	2.19
sedimentations		0*	0.25	0.96	0.75	3.60	6.83

* assumed

low ionic content, as in the Zaïre basin (BERG, 1961). Besides an ecological role in metal-binding (e.g. with Fe in L. Tumba, Zaïre : DUBOIS, 1959), and possibly in Ca-organic complexes, dissolved organic material is an important determinant of light attenuance and hence photosynthetic activity in many waters. Lake Kilotes, Ethiopia, is one example (TALLING *et al.*, 1973); Swartvlei, South Africa, is another (ALLANSON and HOWARD-WILLIAMS, 1984).

4.7. Chemical budgets

A variety of chemical interrelationships in African water-bodies have been discussed under the heading of 'chemical budgets' or 'nutrient budgets' (e.g. VINER *et al.*, 1981). Examples include an assessed component of a total flux (e.g. % N fixation in N income : HORNE and VINER, 1971), the relationship between input load and final concentration (THORNTON and WALMSLEY, 1982), the partitioning of 'export' of nutrient elements (C, N, P) between outflow and sediments (VINER, 1977c), the comparison of phytoplankton incorporation and nutrient-solute depletion (PROWSE and TALLING, 1958; DUFOUR, CREMOUX and SLEPOUKHA, 1981), and the use of concentration data to calculate changes per unit area. As THORNTON (1986) has pointed out, there is very limited information available for African waters on the dynamics of nutrient transfer between compartments. This is especially true of internal nutrient loading and recycling. A true budget involves the quantitative comparison and equating of inputs and outputs plus storage for a system. As applied to a range of inorganic chemical components, such is apparently available only for lakes Chad and Naivasha among African shallow lakes, although the relatively deep L. Turkana has received parallel treatment (YURETICH and CERLING, 1983). Partial information on the nitrogen and phosphorus budgets of Lake George is summarized by LIVINGSTONE and MELACK (1984). A detailed but 1-component budget exists for chloride in a shallow lake of Senegal, lac de Guiers, subject to marine incursions (COGELS and GAC, 1982; 1983). Likewise, a nitrogen budget for the Rietvlei Dam, S. Africa (ASHTON, 1981) deserves mention, with increments in outflow above inflow influenced by N-fixation; also

TABLE VII

	Water volume, 10^6 m^3											
	1973	1974	1975	Na^+	K^+	Ca^{2+}	Mg^{2+}	HCO_3^-	SO_4^{2}	Cl^-	F^-	SiO_2
A. Hydrology												
(i) lake volume (Dec'74)		680										
(ii) component flux, yr-1												
surface runoff	0.6	0.7	0.4									
river discharge	90.8	204.0	260.5									
rainfall	106.1	114.2	77.1									
seepage - in	37.0	42.3	50.8									
total input	234.5	361.2	388.8									
evapotranspiration	14.3	13.2	13.3									
Lake evaporation	309.5	276.0	278.2									
seepage - out	17.6	36.6	78.3									
irrigation off-take	7.0	14.0	15.0									
total output	348.4	339.8	384.8									
change in storage	-113.9	+21.4	+4.0									
B. Mean concentrations of solutes :							mg l^{-1}					
rain water				0.54	0.31	0.19	0.23	1.2	0.72	0.41	-	-
Malewa River				9.0	4.3	8.0	3.0	70	6.2	4.3	0.4	17.2
Gilgil River				16.1	7.4	4.4	2.2	75	9.6	3.9	0.8	18.2
seepage -in				44	31	23	10.2	227	11	28	1.7	47
seepage - out				40	22	22	6.7	203	3	13	1.3	16
main lake				40	20	21	6.4	192	6.2	14	1.5	34
C. Relative solute flux, as % total input or total output:							%					
Inputs : rainfall				0.5	0.9	0.3	0.5	0	1.2	1.4	-	-
river discharge				11	7	12	21	25	11	10	5	14
seepage - in				17	30	13	26	24	7	24	8	12
sediment exchange				72	61	79	52	51	81	73	86	74
outputs : seepage - out				15	11	8	11	16	2	10	9	3
sediment exchange				85	89	92	89	84	98	90	91	97

another for the Hartbeespoort Dam (ASHTON, 1985).

A mean annual solute budget for L. Chad (1954-1972) is described by CARMOUZE (1983); it is summarized, with related hydrological quantities, in Table VI. Chloride and sulphate are not included. Although the estimated inputs and outputs balance, this is generally not an independent check on the budget validity as some components are estimated by difference. Sedimentation fluxes are calculated from ionic ratios and the assumption that the sedimentation of Na is negligible. Considerable between-year variation exists behind many of the mean values cited (e.g. of solute concentrations).

The budget indicates how a lake of relatively low salinity can exist without surface outlet in a tropical region with high open-water evaporation. Although solute concentration in the river input (predominantly the Chari R.) is low, this would not prevent a progressive rise of salinity in the absence of losses other than evaporation. The other important net losses are by seepage and sedimentation. The first is unselective with respect to solute-components, but occurs chiefly from the deeper northern basin whose input is already with ionic content increased and qualitatively modified from that of the main southern inflow river. Sedimentation is partly by biological agents, with $CaCO_3$ deposition by molluscs, Si and K incorporation by macrophytes (CARMOUZE *et al.*, 1978), and Si incorporation by diatoms (LEMOALLE, 1978; CARMOUZE, 1983) all quantitatively important. For example, LÉVÊQUE (1972) has estimated that annual production by a rich molluscan benthos of 1970 would remove 7×10^5 t of Ca, equal to four times the annual river input or half the dissolved stock in the lake. Dissolution and recycling of Ca are therefore important. Non-biological transfer to sediments occurs on a large scale by transformations of sediment minerals (= neoformation of clay smectites, 'reverse weathering') favoured by an alkaline medium rich in soluble silicate. The latter is consumed, together with quantities of Ca^{2+} and Mg^{2+}, and some HCO_3^- tranformed to CO_2. Finally, some precipitation of calcite, $CaCO_3$, occurs especially in the northern basin.

A solute budget for another lake without surface outflow, L. Naivasha, has been estimated by GAUDET and MELACK (1981). It is summarized, with related hydrological quantities, in Table VII. Here also some components (water seepage-out, sediment exchange of solutes) were estimated by difference; all major ions, plus F^-, were included. The relatively low salinity of the lake is ascribed to the major dilute inputs of river water and direct rainfall, an appreciable unselective loss by seepage (+irrigation off-take), and a selective net accumulation of solutes in sediments. Estimated by difference, in which constituent-errors may be compounded, the absolute magnitude of the last and especially its resolution into (? overestimated) input and output components must be uncertain. There is good evidence for uptake and sedimentation of the silicon stock by diatoms, but appreciable effects from sedimentary neoformation ('reverse weathering') were considered unlikely. The study was further notable for a direct use of seepage meters, and a Cl^--based assessment of the proportion of cyclic sea-salt in the river solute input, and hence by difference the proportion ($\sim$ 30%) attributable to chemical denudation.

5. GENERATION OF SEDIMENTS

Interactions between water-mass and sediments, exemplified in the discussion of chemical budgets, are likely to be of particular importance in shallow water-bodies. Sediments can act as both source and sink of solutes and particulates, in bulk accretion as morphometric determinants, in permeability as hydrologic agents, and in interface properties and texture as biological determinants. Their generation — illustrated schematically in Fig. 34 — can be traced to three types of processes.

5.1. Allochthonous transfer of particles

Such transfer from outside the water-body is predominantly as suspended sediment in communicating river-systems. WALLEN (1984) has reviewed estimates of annual yield per unit area of catchment and its variation over Africa. A wide range of about 1-4000 t km^{-2} yr^{-1} is likely, with only limited areas of $>$ 100 t km^{-2} yr^{-1}. There is also a small component of aerial dust that includes pollen grains as potential indicators of biological history. Sediment types can also be specific to distant origins, as in those contributed from the Ethiopian highlands to sediments along the Blue Nile and Main Nile below (McDOUGAL *et al.*, 1975; RZÓSKA, 1976). This system also illustrates how heavy loads are carried during a short seasonal period of flood-water and, in deposition, have provided the framework for the shallow Delta lakes and the recent massive sediment accumulations in the reservoirs of southern Lake Nubia (ENTZ, 1976, 1978) and Sennar. The quantities of allochthonous sediment deposited per unit area in a lake typically decrease horizontally from the point of entry, conspicuously in examples of some fringing swamps (as at L. George : Case example), deltas (as of the Omo River in L. Turkana and of the Semliki River in L. Albert), and between successive basins as in L. Chad.

5.2. Chemical precipitation

Abiogenic chemical precipitation may or may not be related to an evaporative concentration of saline waters. This process can go to completion in evaporites around the receding margins of shallow lakes, leaving conspicuous white deposits as of trona (Na_2CO_3. $NaHCO_3$. $2H_2O$) or — less commonly —

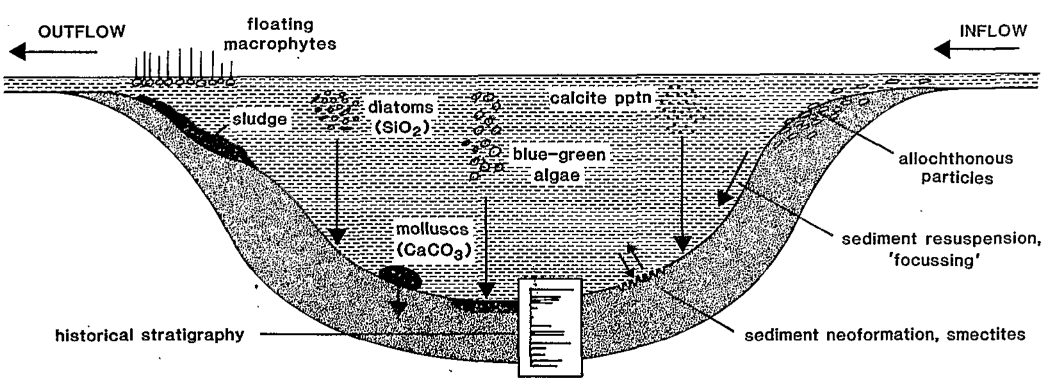

FIG. 34. — Diagrammatic representation of components of sediment generation.
Schéma des divers processus contribuant à la sédimentation.

halite (NaCl). Gaylussite has also been detected in trona deposits of Kanem (MAGLIONE, 1968). In the case of Lake Magadi, Kenya, almost all the lake basin is occupied by thick deposits of trona which are exploited commercially; the chemical origin of the preceding brines and the derivation of solid deposits are traced by EUGSTER (1970), JONES *et al.* (1977) and MONNIN and SCHOTT (1984). In Lake Chad, the marginal salt deposits formed during recession constituted a salt loss which had an appreciable buffering effect on the salinity of the residual lake water (CARMOUZE, 1983).

At a much earlier stage in such evaporative concentration of a water with HCO_3^-/CO_3^{2-} predominant among anions, the divalent cations Ca^{2+} and Mg^{2+} are likely to be depleted by precipitation as carbonates. This can be inferred from correlations between ionic composition and salinity (Fig. 25), demonstrated in model experiments (GAC, 1980; see Fig. 26), or traced from the identification of the carbonates in recently deposited lake sediments. Thus, in L. Chad, there is normally no appreciable sedimentation of $CaCO_3$ in the less saline southern basin, but in the saline northern basin the sediments contain c. 5-10 % of calcite (CARMOUZE, 1983). In this lake CARMOUZE (1976) believed that precipitation began when the product of the activities of free Ca^{2+} and free CO_3^{2-}, $\{Ca^{2+}\}.\ \{CO_3^{2-}\}$, exceeded 18 times the solubility product of calcite. Elsewhere, independently of salinization, the photosynthetic elevation of pH can cause a periodic precipitation of $CaCO_3$, as on the leaves or stems of aquatic macrophytes.

One form of abiogenic sedimentary accretion is represented by the neoformation of smectites with chemical transfer from solutes. Such 'reverse weathering' is probably widespread in alkaline, silicate-rich waters. It is a significant component of the chemical budget of L. Chad (see Section 4.7).

5.3. Biological deposition

The biologically derived components of lake sediments often predominate in the more dilute waters distant from inflows (e.g. offshore L. Victoria). Both organic matter and inorganic skeletal constituents can be involved. Important among the latter are the calcareous shells of molluscs and the siliceous frustules of diatoms. In some waters the faecal pellets of micro-crustacea are a significant fraction (e.g. L. Tanganyika : HABERYAN, 1985).

The chemical budget of L. Chad (Section 4.7) has already illustrated a large annual incorporation of $CaCO_3$ by an abundant molluscan fauna on the sediments. It also indicated dissolution and re-cycling of this component from sediment to water column. Such quantitative estimates do not seem to exist for other African lakes with a rich molluscan zoobenthos, which include the deep L. Albert and the shallow L. Tana. However identifiable remains of molluscan shells are widespread in African lake sediments and some (e.g. in the Kaiso beds of L. Albert-L. Edward) are important indicators.

The bio-sedimentation of silica as diatom frustules has also few quantitative chemical estimates. Nevertheless massive or prolonged fluxes are indicated by extensive deposits of diatomite related to various shallow lakes, past or present, in Africa, and most lake sediments have detectable — if less massive — diatom remains. Diatom records from past sediments have been used widely in Africa to reconstruct lake history, as for the shallow waters of the Faiyum Lake (ALEEM, 1959), L. Naivasha (RICHARDSON and RICHARDSON, 1971), L. George (HAWORTH, 1977), Pilkington Bay of L. Victoria (KENDALL, 1969), L. Chad (SERVANT-VILDARY, 1978; SERVANT and SERVANT, 1983), L. Manyara (HOLDSHIP, 1976; RICHARDSON *et al.*, 1978), and lakes Abhe, Asal, Afrera, and Gamari in the Afar-Danakil region (GASSE, 1974a-b, 1975, 1977; GASSE and DELIBRIAS, 1976).

Organic deposition invariably accompanies bio-sedimentation. Thus VINER (1977c) estimated a current deposition rate of 15-20 g organic matter m^{-2} yr^{-1} in the productive Lake George. The relative content of organic matter in the final sediment varies widely (McLACHLAN, 1974), being low in allochthonous silt deposits and high in peats. Related to the latter, but distinctive in location, is the deposit of 'sludge' which develops below floating mats of papyrus (GAUDET, 1976). Recent algal sedimentation, as of blue-greens in L. George (GANF and VINER, 1973; GANF, 1974b), can generate very high organic contents in superficial sediments which are partly composed of living cells. Rapid decomposition can occur (VINER, 1975b) but is not inevitable even at high tropical temperatures, as illustrated by observations (BEAUCHAMP, 1958) and experiments (HESSE, 1958) on the highly organic near-surface sediments of shallow inshore bays of L. Victoria. The possibility that organic residues may be sources of petroleum from African lakes is currently under investigation.

6. TIME-RELATED SYSTEM CHANGES

Shallow waters are subject to cyclic patterns of change with time, on various time-scales, in which many factors vary concurrently. Three examples are described below, that vary in period from 24 h to

1 year or longer, and are set up by different evoking factors.

6.1. **Diel (24 h) cycle**

This type of cycle has been introduced by the case-example of L. George (Section 2, Figs 5, 6). The dominant evoking factor is the diel flux of short-wave solar-radiation. As described already (Section 3.1), its daily amplitude is potentially higher in the tropics than at higher latitudes, although subject to modification by atmospheric turbidity. In combination with other less variable components of energy balance (including long-wave back-radiation, favoured by clear night skies), it induces with some lag a corresponding cycle of energy storage, viz. temperature. Examples for two shallow water-bodies (Lake Chad, Jebel Auliya reservoir) are described by TALLING (1990), with resolution of component flux densities. There may be indirect effects upon wind-regime, although the coupling is very variable. Thus there is a diel component of on- and off-shore breezes in the shallow marginal areas of L. Victoria (Fish, 1957; Evans, 1961), and in other examples wind stress was greatest at night (Jebel Auliya reservoir : TALLING, 1957b), morning (L. Chad : CARMOUZE *et al.*, 1983), or late in the afternoon (L. George : VINER and SMITH, 1973).

The diel temperature cycle is susceptible to day-to-day and seasonal changes of weather, as illustrated in Fig. 35 for a Kanem soda lake and reservoir at Nairobi (latitude 1°20′ S), and by HARE and CARTER (1984, Fig. 6) for a small lake in Nigeria (latitude 6°45′ N). Interactions between the temperature cycle, wind regime, and water depth further determine whether a diel pattern of density stratification will develop. Areas of plant cover which obstruct water movement also tend to promote stratification. It may be absent in very shallow waters (e.g. a Nile lagoon : TALLING, 1957b) or with persistent wind stress or low insolation. Variations with weather have been described by TALLING (1957b) on a day-to-day basis for a bay of L. Victoria and on a seasonal basis for the Jebel Auliya reservoir. In the latter, more pronounced diel stratification during a phase of high water temperature (~ 30 °C) is probably influenced by the then greater rate of change of density with temperature. The same non-linear relationship between density and temperature will tend to generally accentuate diel cycles of stratification in warm tropical waters. In waters deeper than a few metres, it is not uncommon for a superficial stratum with a pronounced diel stratification to overlie deeper water with more persistent stratification. L. Sonachi, a crater lake in Kenya (MELACK, 1981) (Fig. 36), L. Aranguadi, one in Ethiopia (TALLING *et al.*, 1973), and the Pretoria Salt Pan (ASHTON and SCHOEMAN, 1983, 1988) (Figs 22, 38), are well-studied examples. In all these, the diel stratification patterns are probably enhanced by wind-shelter from the crater rims — a feature quantified by MELACK (1978).

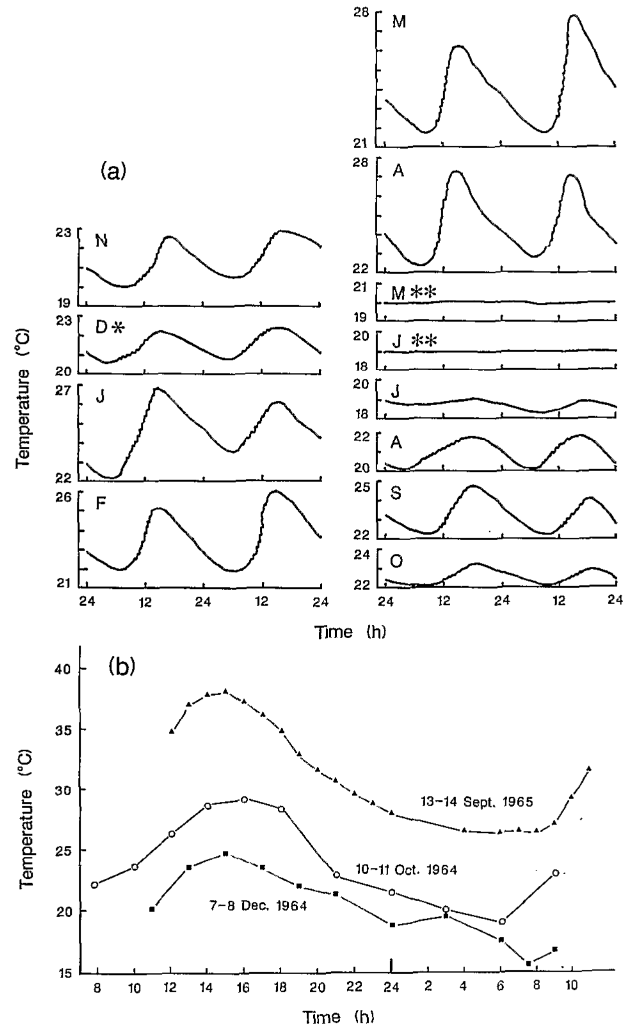

FIG. 35. — Seasonal shifts in diel temperature cycles measured (a) by continuous recording at 0.6 m depth in a reservoir (Wellcome Dam) near Nairobi, in or near the last two days of the months indicated during 1971-2 (* = short rains, ** = long rains) (b) by separate surface determinations during three months on a Kanem lake in Chad (mare de Latir). Adapted from YOUNG (1975) and ILTIS (1969).

Évolution des cycles diurnes de la température de l'eau au cours de l'année a) pour les différents mois de novembre 1971 à novembre 1972 dans un lac de barrage, Wellcome Dam près de Nairobi, à 0,6 m sous la surface; enregistrement continu b) pour 3 mois différents dans la mare de Latir, dans le Kanem au Tchad. D'après YOUNG (1975) et ILTIS (1969).

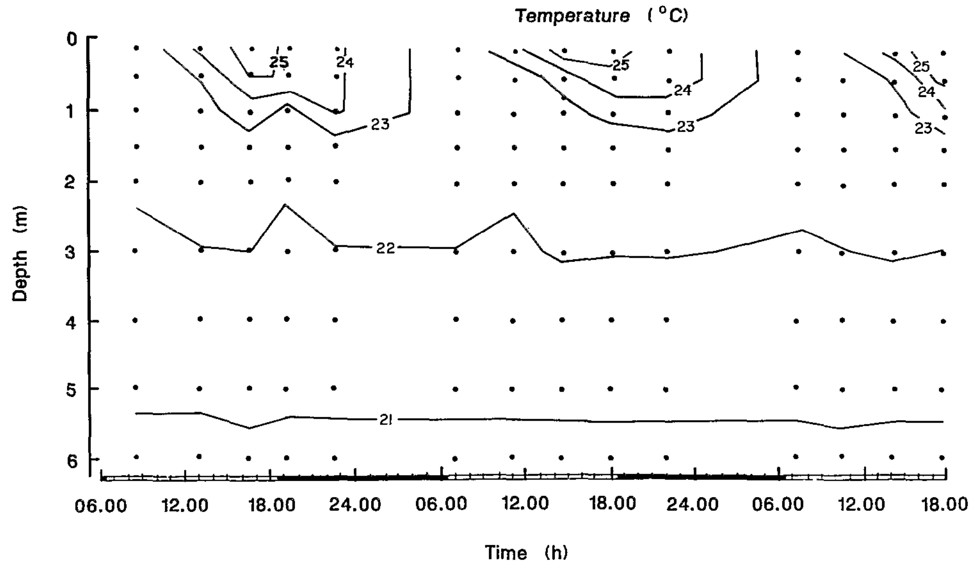

FIG. 36. — Lake Sonachi, Kenya : the depth-time distribution of temperature during 5-7 March 1973, showing the regular generation of diel stratification cycles. From MELACK (1981).
Le lac Sonachi, Kenya : diagramme profondeur — temps des températures du 5 au 7 mars 1973, montrant l'établissement régulier des stratifications journalières. D'après MELACK, 1973.

WEIR (1969) has described how a daily stratification, with surface temperatures > 35 °C, can develop in very shallow pans unless disturbed by visiting herds of ungulates (Fig. 37).

Once established, a diel density stratification is likely to constrain the distribution patterns of other constituents that are in rapid change. Examples include dissolved oxygen (Figs. 6, 38), carbon dioxide, and pH in productive waters (Sections 2, 4.3); and the population density of positively or negatively buoyant, or migratory, plankters (Section 2, Fig. 5c). Diel cycles of environmental origin

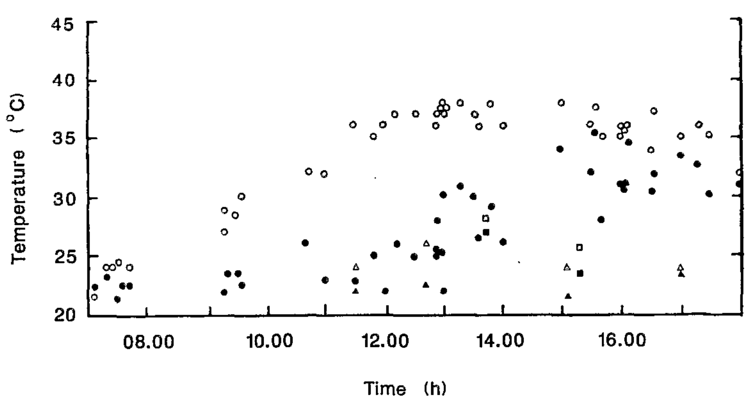

FIG. 37. — Temperature values measured at various times during January in pools of the Wankie National Park, Zimbabwe, showing diurnal divergence between surface water (O) and bottom mud (●) in one pool during warm cloudless days, of corresponding values on overcast rainy days (△, ▲) and of corresponding values on warm cloudless days in a pool stirred by herds of visiting ungulates (□, ■). From WEIR (1969).
Températures mesurées à différents moments de la journée, dans différentes mares du Parc National Wankie, Zimbabwe; les mesures indiquent la divergence entre la surface (○), le sédiment superficiel (●) dans une mare pendant des jours ensoleillés, et pendant des jours pluvieux ou nuageux (△, ▲), et par jour clair et chaud mais avec perturbation par des troupeaux d'antilopes (□, ■). D'après WEIR, 1969.

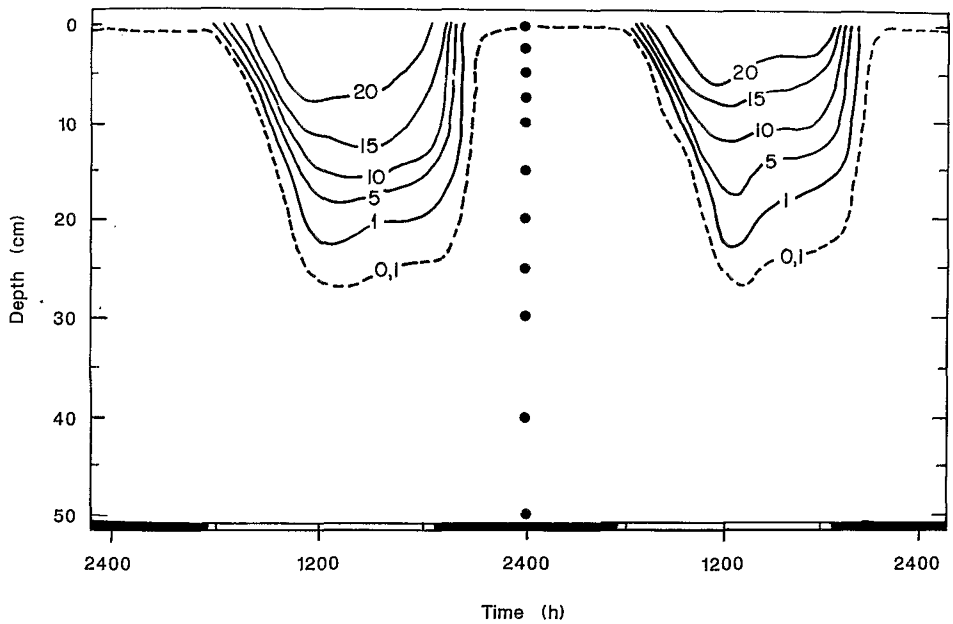

FIG. 38. — Pretoria Salt Pan : the depth-time distribution of dissolved oxygen indicated by isopleths in mg l^{-1} during 28-29 December 1979, based on hourly sampling at the depths indicated. From ASHTON and SCHOEMAN (1983).

Pretoria Salt Pan : diagramme profondeur — temps de l'oxygène dissous (en mg. l^{-1}) les 28-29 décembre 1979. Les mesures ont été faites chaque heure, aux profondeurs indiquées. D'après ASHTON et SCHOEMAN, 1983.

may also interact with biological ones that have a marked endogenous control. This is exemplified (Fig. 39) by the diel variability of ingestion, digestion and excretion by a copepod *(Thermocyclops hyalinus)* and two fishes *(Sarotherodon (Tilapia) niloticus, Haplochromis nigripinnis)* in L. George (MORIARTY *et al.*, 1973; GANF and BLAŽKA, 1974).

The destruction of diel stratified structure by vertical mixing may be induced by strong winds at any time, but most often occurs at night when the water column has a negative energy balance (cf. Table II, L. Tana). This nocturnal mixing pattern may be often reinforced by the diel wind regime in some waters (e.g. Jebel Auliya reservoir : TALLING, 1957b) but not in others (e.g. L. Chad : ROBINSON, 1968). Especially near dawn, surface heat loss may lead to an unstable inverse stratification with near-surface water cooled below that at depth (e.g. Fig. 5(i)d). The resulting convection may cause significant redistributions, as of dissolved oxygen, in waters of both lakes (L. Naivasha : BEADLE, 1932b; L. Nyumba ya Mungu : DENNY *et al.*, 1978) and swamps (BEADLE, 1932a).

In a small number of examples, diel cycles have been analysed in terms of the changing content of oxygen below unit area of surface in relation to primary production (TALLING, 1957b; TALLING *et al.*, 1973; MELACK and KILHAM, 1974; GANF, 1975).

6.2. **Seasonal cycle with small volume change**

Cycles of this kind are familiar and much-studied among lakes generally. For African shallow lakes and wetlands their frequency is reduced by the common intermittency of rainfall combined with basin topography and limited storage capacity. Known site-examples are associated with situations of seasonally extended water input and/or large size relative to the input-output fluxes. Thus Lake George (see *Case study*, Section 2) has a regime of extended and seasonally bimodal rainfall, permanent inflow streams from adjacent mountains, and a peculiar outflow-buffer channel. The last feature reappears in another form in many brackish coastal lagoons with some connection to the sea (e.g. Ebrié lagoon), through which outflow may reverse to inflow. A completely freshwater analogue would be a shallow and semi-enclosed gulf of a large lake, such as the Nyanza (Winam, Kavirondo) Gulf of L. Victoria. Small lakes in a more seasonal climate, such as the Bishoftu crater lakes of Ethiopia, may have

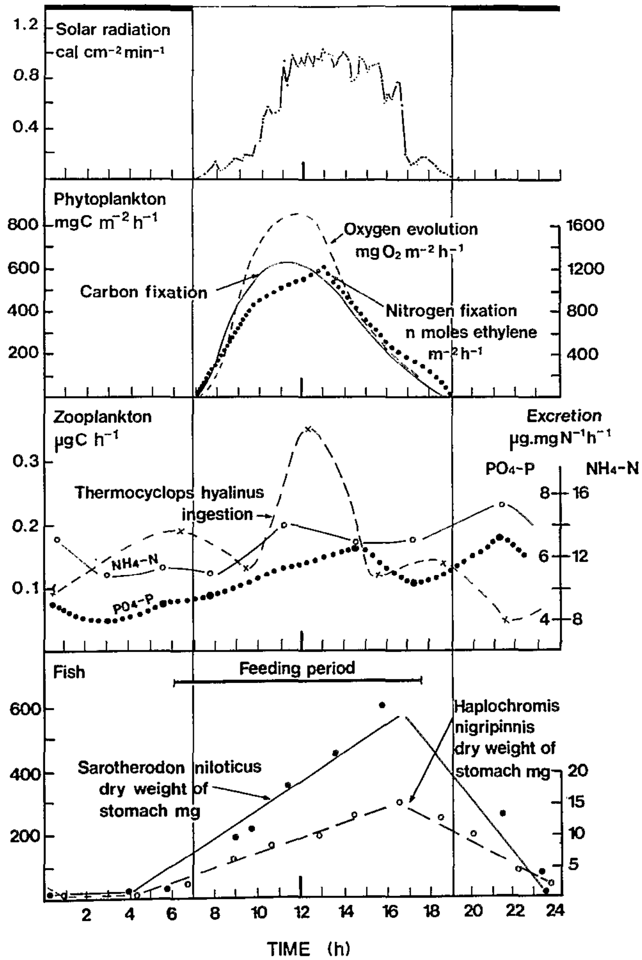

FIG. 39. — Comparative examples of diel cycles at L. George, including solar radiation, fixation of C and N with evolution of O_2 by phytoplankton, N and P excretion by zooplankton, and ingestion of food by a zooplankter (*Thermocyclops hyalinus*, as C per individual) and two species of fish (*Sarotherodon niloticus, Haplochromis nigripinnis*, as stomach weight). From BURGIS (1978).

Exemples de cycles nycthéméraux au lac George : rayonnement incident, assimilation de C et N_2 et production de O_2 par le phytoplancton, excrétion de N et P par le zooplancton, ingestion de nourriture par le microcrustacé Thermocyclops hyalinus, *exprimée en C par individu) et par deux espèces de poisson (*Sarotherodon niloticus, Haplochromis nigripinnis, *exprimé en poids d'estomac). D'après BURGIS, 1978.*

maintained seepage-input from a relatively stable water-table. Large shallow lakes of long retention and fairly stable level include L. Tana and L. Abaya (= Margherita) in Ethiopia, L. Bangweulu and L. Mweru (DE KIMPE, 1964) in Zambia-Zaire, and L. Baringo in Kenya.

In the deeper African lakes, numerous conditions in the water-mass are normally associated in an annual periodicity that is linked to a seasonal stratification cycle, itself conditioned by varying energy exchanges including the wind regime. Such cycles are widespread even near the equator (TALLING, 1969). The common denominator of seasonal persistent stratification is characteristically lacking from shallow lakes. Its place does not seem to be taken by any other general 'master-system' of seasonal variability; perhaps as a consequence, in a hydrologically stable equatorial lake like L. George, there is a lack of pronounced seasonal changes in the physical and chemical environment. However, in extra-tropical Africa the increased amplitude of seasonal radiation and temperature changes possibly dominate, or — especially in water-bodies of small retention time — the varying quantity and quality (solutes, silt content) of inflows. In contrast to L. George, there are few extended seasonal studies of

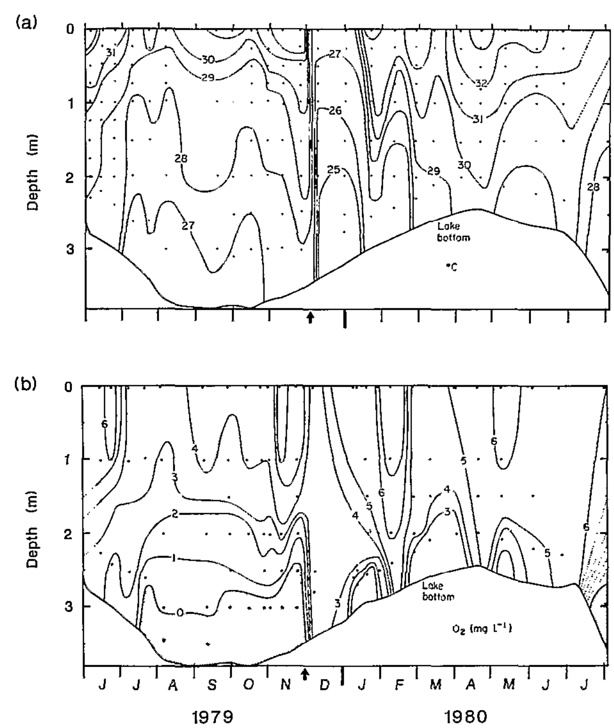

FIG. 40. — Opi Lake, Nigeria : depth-time distribution over 13 months of (a) temperature and (b) dissolved oxygen, showing changes of temperature stratification and associated oxygen depletion in deeper water. From HARE and CARTER (1984).

Lac Opi, Nigeria : diagrammes profondeur-temps durant 13 mois de la température (a) et de l'oxygène dissous (b) montrant la stratification thermique et l'évolution associée de l'oxygène dans l'hypolimnion. D'après HARE et CARTER, 1984.

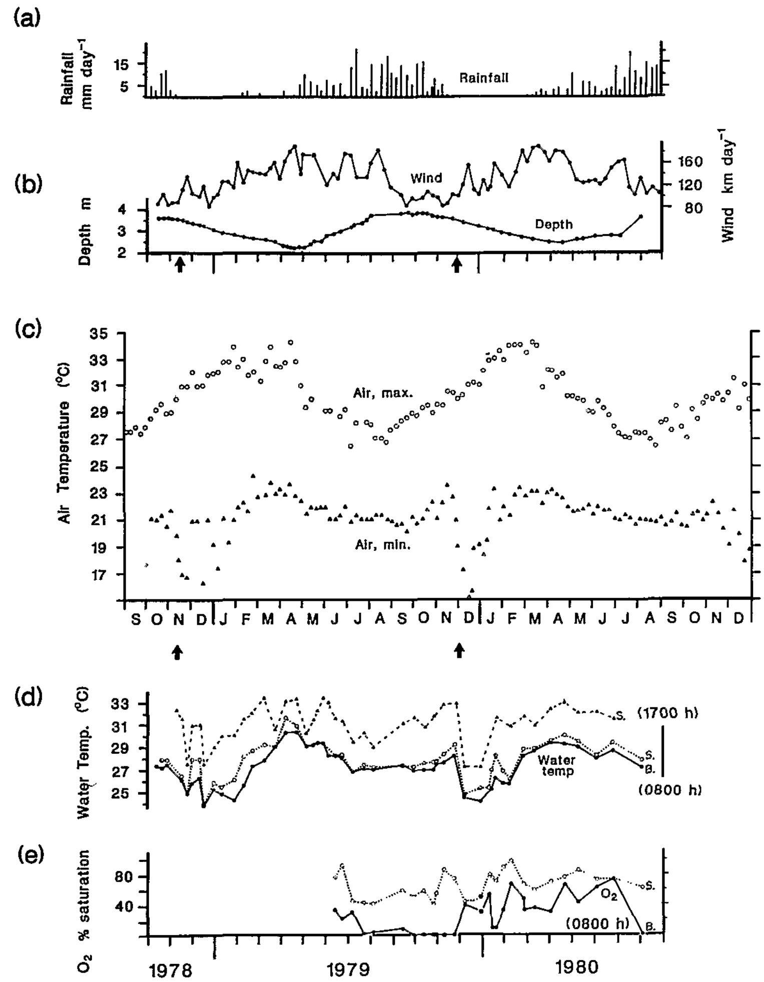

FIG. 41. — Opi Lake, Nigeria : seasonal variation, over 2 years, of (a) rainfall (b) daily wind run and water depth (c) air temperature (d) water temperature measured at the surface (S) and bottom (B) at 08.00 and 17.00 h (e) oxygen content in surface (S) and bottom (B) water. Arrows indicate onset of the harmattan wind regime. Adapted from HARE and CARTER (1984).

Lac Opi, Nigeria : évolution, au cours de deux années, de la pluviométrie (a), du vent total journalier et de la profondeur (b), des températures de l'air et de l'eau en surface (S) et au fond (B) à 8 h 00 et 17 h 00 (d) et, en bas, de l'oxygène en surface et au fond (e). Les flèches indiquant l'établissement de la période d'harmattan. Modifié de HARE et CARTER, 1984.

such water-bodies in Africa. That of HOWARD-WILLIAMS and ALLANSON (1981) on the coastal lake Swartvlei (S. Africa) is notable for the impact of a seasonal cycle of macrophyte *(Potamogeton pectimatus)* growth and decay on phosphate depletion and regeneration in the lake (Fig. 30). The important class of shallow coastal lakes is also exemplified by the Delta lakes of Egypt (see RZÓSKA, 1976) and of the Ebrié lagoon in West Africa (e.g. DURAND and CHANTRAINE, 1982; DUFOUR, 1982a), all of variable salinity. Observations of BOWMAKER (1962) on a lagoon at L. Bangweulu also deserve mention; here too variable hydrological inputs dominate seasonal change.

Aspects of meteorological control, and some unusual factor-combinations, are illustrated in the seasonal cycle of Opi Lake A (HARE and CARTER, 1984), a very small (area 1.4-2.0 ha) and shallow (max. depth 2.4-3.95 m) lake in the Nigerian savanna at latitude 6° 45′ N. Here the seasonal range of temperature is little greater than the typical diel range (3-4 °C) in surface water. In spite of this diel variability and the shallow depth, vertical mixing is apparently incomplete in the rainy season and anoxia then develops in near-bottom water (Fig. 40). Overall, seasonal change is mainly evoked not by change in solar radiation but by the alternation of humid maritime and dry continental (Saharan) air masses, the latter marked by the northerly Harmattan wind regime. Onset of the Harmattan in Nov.-Dec. (Fig. 41) induces a steep fall of water temperature, and enhanced mixing which ends anoxia, in part by the increase in evaporative heat loss. Thus the lake water cools at a period of high solar insolation and daily-maximum air temperature, but lowered daily-minimum air temperature. The alternation of wet and dry seasons is associated with a 2 ½-fold range of water volume, a discontinuous surface outflow and marked changes in depth and area.

6.3. **Flooding-drying cycle**

In a shallow basin of gently shelving morphometry, large changes of water volume due to hydrological factors lead to corresponding large horizontal excursions of water level as well as changes in mean depth. Such excursions may take numerous forms.

A water-body of simple outline may undergo predominantly radial extensions and contractions, whether it is a rain-pool fed by intermittent precipitation or a deeper river-fed lake such as L. Nakuru. L. Chilwa is a more complex case, with markedly asymmetric (N-S) distribution of river inflow and shallows plus swamp which led to a ' freshwater ring ' of water during refilling after drought (HOWARD-WILLIAMS and LENTON, 1975; MCLACHLAN, 1979). Still more complex is L. Chad, with two main basins, the deeper at greater distance from the main inflow. This fact, and the development at low level of aquatic vegetation as obstacle to flow between basins, led to isolation of the deeper northern basin during the low levels of 1973 and final drying out in a period (1975-6) when water was being replenished in the more accessible basin (CARMOUZE, DURAND and LÉVÊQUE, 1983; see Fig. 42). In a third region, of a north-east dune-archipelago, isolated depression pools developed and dried out during low lake level. Yet another, more linear pattern is represented by river floodplains (WELCOMME, 1979), annually covered by overspill of water from the river channel. Such water can replenish previously isolated or dried-out lagoons or pans, as on the ' internal delta ' of the Middle Niger (BLANC *et al.*, 1955) and the Pongolo floodplain in northern Natal (HEEG and BREEN, 1982; see Fig. 44) or augment others in permanent connection to the river (e.g. Shambe lagoon, Sudd swamps, Sudan : RZÓSKA, 1974). Such floodplains merge with the littoral regions of elongate reservoirs or ' river-lakes ' subject to seasonal drawdown.

The flooding-drying cycle, as expressed by water level change with time, has a common asymmetry. Water influx with rising level is typically more abrupt than the later subsidence conditioned by evaporation and reduced run-off. An example from the floodplain of the Senegal River is illustrated by THOMPSON (1985, Fig. 3.3). The periodicity may be seasonal-annual, long-term and inter-annual, or a combination of both as illustrated in the records from lakes Chad and Chilwa (Figs. 42, 43). These lakes also demonstrate that the seasonal amplitude of environmental conditions tends to be greater when the seasonal cycle occurs at a low-level and low-capacity stage of a long-term oscillation (L. Chad : CARMOUZE *et al.*, 1983; L. Chilwa : KALK *et al.*, 1979) or after a particularly dry summer (South African highveld pan : ROGERS *et al.*, 1989).

Water characteristics which tend to be especially

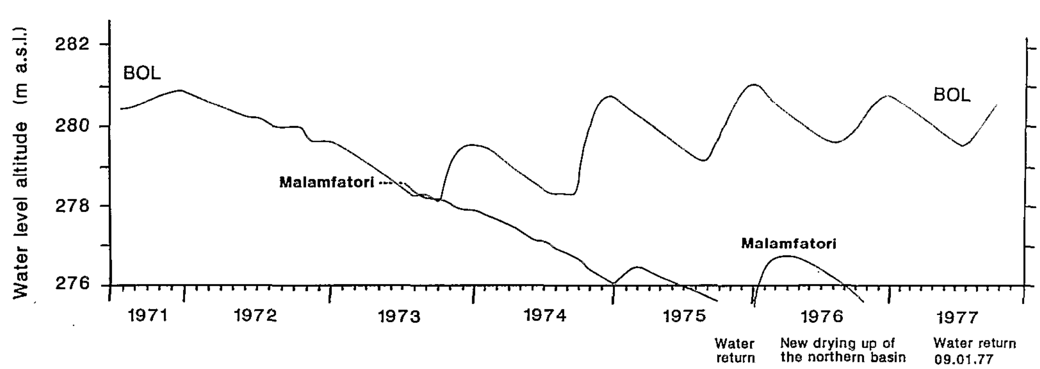

FIG. 42. — Time-variation in water levels of L. Chad during a drought phase, 1971-7, showing divergence between those in the southeastern archipelago at Bol and the northern basin at Malamfatori. Redrawn from CARMOUZE and LEMOALLE (1983).
Évolution du niveau du lac Tchad au cours de l'installation d'une période de sécheresse en 1971-77. Divers bassins s'individualisent : l'archipel du sud-est à Bol, et la cuvette nord du lac, suivie à Malamfatori. Redessiné d'après CARMOUZE et LEMOALLE, 1983.

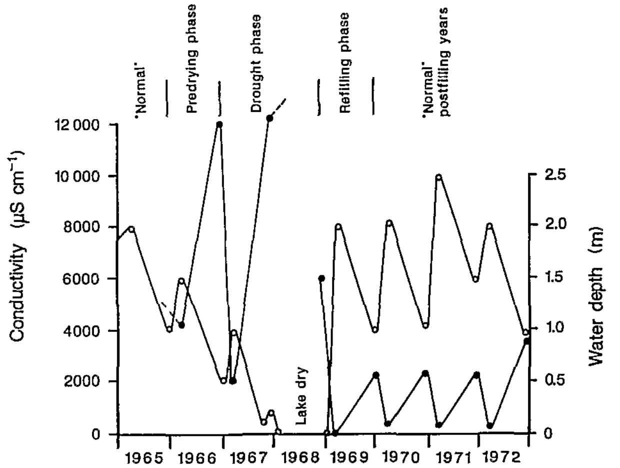

FIG. 43. — Lake Chilwa : the relationship between changes in seasonal maxima and minima of water-depth at one station before, during, and after a drought phase (o) and those of ionic concentration reflected by conductivity (at 20 °C) (●). From McLACHLAN (1979).

Lac Chilwa : relation entre maximums et minimums de profondeur (s) et (s) de conductivité (à 20 °C) avant, pendant et après une phase de sécheresse. D'après McLACHLAN, 1979.

influenced by the lower-level stages of a flooding-drying cycle include temperature, turbidity, water circulation, salinity, and dissolved oxygen content. Thus, in lake Chilwa, the last phase of open water before desiccation was marked by elevated daytime temperature, high turbidity due to dense algal growth, reduced horizontal circulation of water, raised salinity and phosphate concentration, and oxygen depletion at a short distance below the surface. Most of these conditions occurred in the low level 1973 stage of L. Chad, although here macrophyte growth rather than algal growth often predominated. For 1972, BENECH *et al.* (1976) describe how a tornado at Bol disturbed sediment and displaced water-masses; concentrations of oxygen fell below 5 % saturation, and a heavy fish-kill resulted.

A cycle of ionic content normally accompanies a flooding-drying cycle. This is illustrated Fig. 43 for a station in L. Chilwa, where water level and conductivity are inversely related (McLACHLAN *et al.*, 1972; McLACHLAN, 1979). Parallel data exist for L. Nakuru (VARESCHI, 1982), L. Chad (CARMOUZE, CHANTRAINE and LEMOALLE, 1983), and the Pongolo pans (HEEG and BREEN, 1982; see Fig. 44). Never-

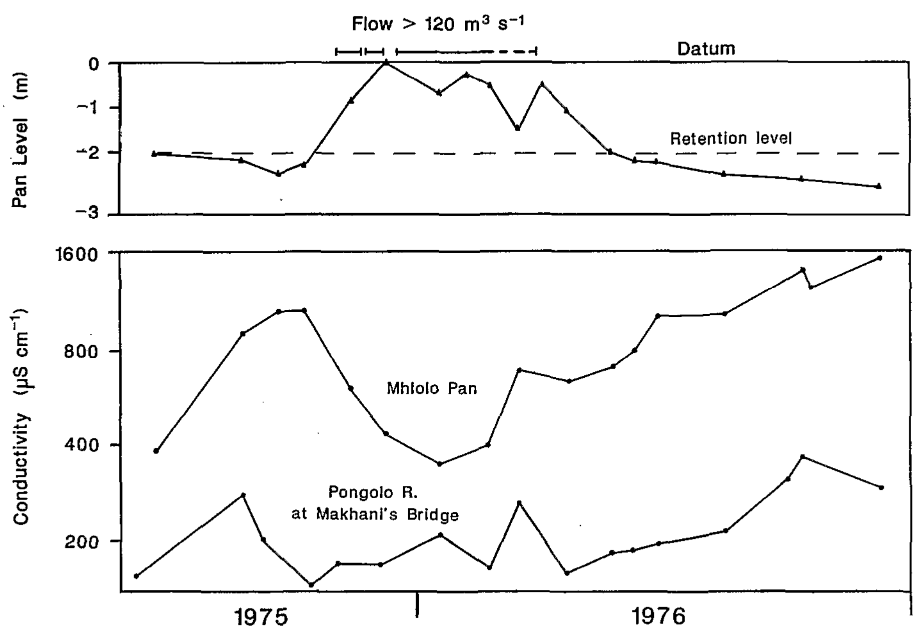

FIG. 44. — Mhlolo Pan, Pongolo floodplain : conductivity changes, indicative of concentration and flushing, in relation to pan water-level and river flow and conductivity. Adapted from HEEG and BREEN (1982).

Mhlolo Pan, dans la plaine d'inondation du Pongolo : les variations de conductivité indiquent les périodes de dilution et de concentration, en relation avec le niveau du lac, la conductivité et le débit du fleuve. D'après HEEG et BREEN, 1982.

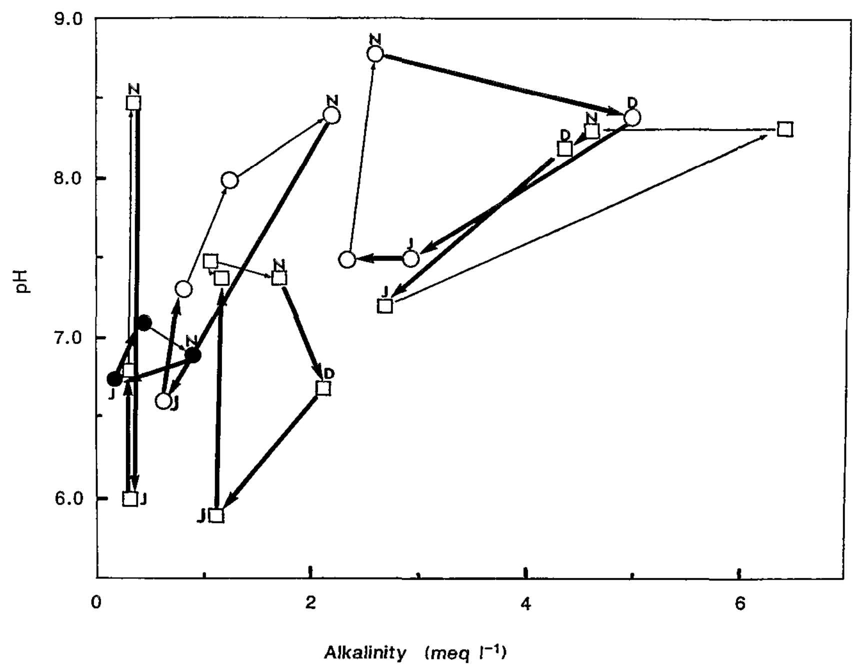

FIG. 45. — Seasonal succession (arrowed) of combinations of pH and alkalinity in 6 shallow pools (pans) of the Wankie National Park, Zimbabwe. Measurements made in the wet season from November (N), December (D), January (J) to April are connected by thick arrows, and those from April, September, to November by thin arrows. Adapted from WEIR (1968).
Évolution, au cours des saisons, de la relation alcalinité — pH dans 6 mares peu profondes (pans) du Parc National Wankie au Zimbabwe. Les mesures en saison des pluies de novembre, décembre et janvier à avril sont reliées par des flèches épaisses; les mesures d'avril, septembre à novembre sont reliées par des flèches fines. Adapté de WEIR, 1968.

theless there are both spatial and ion-specific complications. In L. Chilwa the renewal of river and swamp inflow may generate a ring of fresher water that is at first distinct from more central remnant saline water. In the low-level L. Chad of 1973-5, particularly high salinity developed in the isolated northern basin, from which later influx of low-salinity water from the main southern inflow, the Chari River, was obstructed by exposed sediment and macrophyte barriers. At another extreme of size, the salinity, alkalinity and conductivity of rainpools tend to increase during prolonged isolation and contraction (RZÓSKA, 1961, 1984), as do those of pans studied in the Pongolo floodplain (HEEG and BREEN, 1982) and in Zimbabwe (WEIR, 1968; see Fig. 45). The latter show an element of 'chemical hysteresis' in the cycle, with pH values usually relatively depressed during the expansion and re-dilution phase, presumably by CO_2 accumulation after decomposition.

However, the sensitivity of salinity to lake volume may be offset or 'buffered' by several factors, including direct on-lake rainfall, the separation of marginal salt deposits outside the main water mass and their aerial deflation by wind, their re-contact to the water-mass at times of advancing level, and geochemical sedimentary transformations or 'reverse weathering'. These processes are documented for L. Chad in CARMOUZE, DURAND and LÉVÊQUE (1983).

The seasonal or longer-term salinity cycle can involve disproportionate changes in some constituents; some may be represented in the sedimentary history (e.g. carbonate-rich horizons). One mechanism is the precipitation of divalent cations, Ca^{2+} and Mg^{2+}, from water of increasing alkalinity and pH, a process demonstrated from systematic observation and experiment on L. Chad (CHANTRAINE, 1978; GAC, 1980; CARMOUZE, 1983; see Fig. 26) and L. Guiers (COGELS and GAC, 1983). Another is the uptake and subsequent release of nutrient elements (N, P, K) during associated growth cycles of plants, especially macrophytes, as in L. Chilwa (HOWARD-WILLIAMS and LENTON, 1975) and the Pongolo floodplain (HEEG and BREEN, 1982; ROGERS and BREEN, 1982). The areal stocks of these nutrients in dense

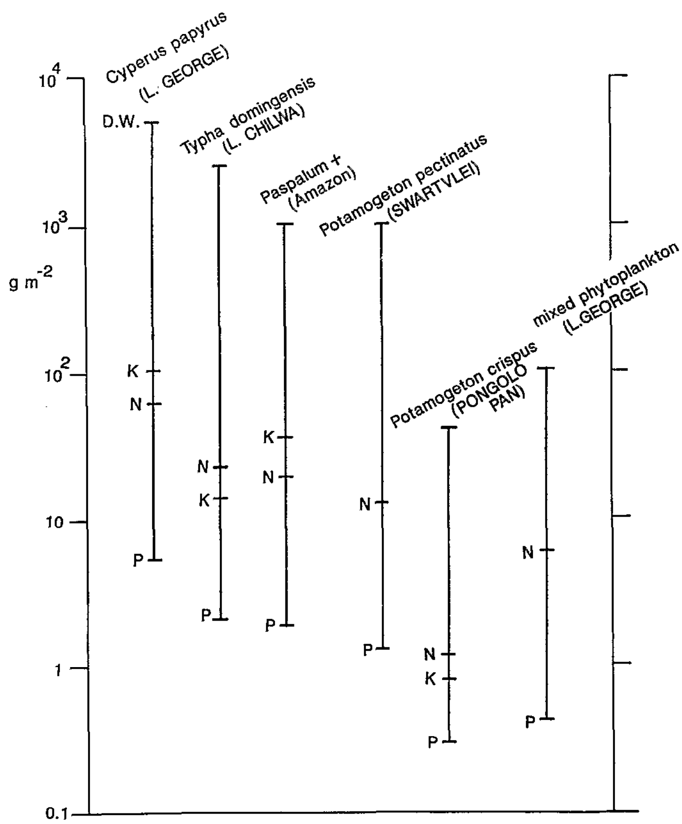

FIG. 46. — Stocks per unit area of the elements K, N and P in dense stands of reedswamp, submerged macrophytes and phytoplankton of varied dry weight (D. W.). Based, respectively, on data in GAUDET (1977), HOWARD-WILLIAMS and LENTON (1975), HOWARD-WILLIAMS and JUNK (1977), HOWARD-WILLIAMS (1977), ROGERS and BREEN (1980), and VINER (1977c) with BURGIS *et al.* (1973). Values from L. Chilwa, Swartvlei and the Pongolo Pan are at or near seasonal maxima.

Stocks de K, N et P et de poids sec par unité de surface dans des peuplements denses de roseaux, de macrophytes immergés ou de phytoplancton. Les données utilisées sont, respectivement, de GAUDET (1977), HOWARD-WILLIAMS et LENTON (1975), HOWARD-WILLIAMS et JUNK (1977), HOWARD-WILLIAMS (1977), ROGERS et BREEN (1980), et VINER (1977c) avec BURGIS et al. *(1973). Les valeurs pour les lacs Chilwa, Swartvlei et Pongolo Pan sont proches ou égales au maximum saisonnier.*

macrophyte stands are high and typically exceed those in most phytoplankton communities; comparative examples appear in Fig. 46. A nitrate-flush can follow the re-wetting of soil and sediment, as noted for a *Typha* swamp at L. Chilwa (HOWARD-WILLIAMS, 1972, 1979), and re-flooding can induce nutrient release from grasses and the dung of large herbivores (S. M. MCLACHLAN, 1971). During such initial re-flooding, the mass-release of available solutes to a limited volume of water often produces a transient peak of total ionic concentration, as at L. Chilwa (MCLACHLAN, 1979) and elsewhere (MCLACHLAN, 1974).

Biologically, the expansion phase of the cycle can be viewed as aquatic recovery followed by terrestrial stress (e.g. on the grass *Cynodon dactylon* : FURNESS and BREEN, 1982, 1986), and the contraction phase as terrestrial recovery followed by aquatic stress. The components of aquatic stress may include supra-optimal salinity (e.g. for the macrophyte *Potamogeton crispus* in the Pongolo pans : HEEG and BREEN, 1982; mortality of a cichlid fish in L. Chilwa : MORGAN, 1972, 1979) and adversely limiting light attenuation (e.g. for algae in L. Chilwa : MOSS and MOSS, 1969) as well as the ultimate deficiency of water itself.

7. SYNOPSIS : DISTINCTIVE ENVIRONMENTAL CONTROLS IN SHALLOW AFRICAN WATER-BODIES

Drawing on the previous extended account, it may be useful to single out distinctive features of environmental control in shallow African water-bodies.

i. Storage capacity in the water-column per unit area is limited. In consequence an area-related input or loss may more readily induce large relative changes of concentration. Examples are changes of heat content (temperature) in relation to solar input or evaporation loss; of oxygen content, including complete anoxia, in relation to photosynthetic gain or respiratory consumption; and of water content.

ii. The shallow water-column is relatively susceptible to wind-induced turbulence and convective mixing. It therefore usually lacks any persistent temperature-density stratification, except in some extreme cases of salinity-layering. However, a diel temperature-density stratification normally develops in relation to the diurnal input of short-wave solar radiation. It is often associated with other interacting diel cycles (e.g. of O_2, CO_2, phytoplankton redistribution).

iii. Interactions involving underwater sediments are often enhanced. Thus superficial sediments are often disturbed and resuspended by wind-induced currents; they may be sufficiently well-illuminated as to support benthic growth of algae and macrophytes. Their ratio to the water-mass, physico-chemical reactivity, and hydrodynamic accessibility may lead them to dominate chemical recycling — unless a dense and buoyant plankton transfers the preponderance of such processing to the water-column. The form of the water-basin is relatively sensitive to sediment generation and accumulation.

iv. Shallow water-bodies provide the conditions under which most saline lakes have developed. These include a favourable ratio of cumulative evaporation to lake volume and the possible location in a spring-fed supply of recycled saline reserves. Where such reserves are absent, and seepage-out and possibly 'reverse weathering' of sediments appreciable, a shallow water of only moderate salinity is compatible with the absence of surface outflow (lakes Chad, Naivasha).

v. The development is favoured of high areal stocks of biomass (and incorporated nutrient elements) in swamp macrophytes and of higher biomass concentrations per unit volume in phytoplankton. The former plants are environmentally important for local spatial gradients, shelter, niche-diversification, and nutrient pathways — including net upward transfer as a 'nutrient pump'. The latter often produce, by photosynthetic activity, large diel fluctuations in concentrations and layering of O_2 and CO_2, with elevated pH. However such activity is countered, as regards areal productivity, by increased light attenuation due to phytoplankton and background pigments. Thus many productive shallow lakes are optically deep.

vi. There is increased liability in African climates, with periodic rainfall and high insolation, to large horizontal excursions of water level in a flooding-drying cycle. These have numerous correlates in a time-sequence of physical, chemical, and biological conditions.

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