III. The balance of a lacustrine ecosystem during 'Normal Chad' and a period of drought

11. Phytoplankton production

Jacques Lemoalle

Two aspects of the photosynthetic activity (gross production) of the phytoplankton in Lake Chad were considered. Firstly an attempt was made to determine the photosynthesis-depth curve and the daily gross production. Secondly, an attempt was made to interpret variations which occurred with changing environmental conditions (Lemoalle 1973, 1979).

Changes in biomass and phytoplankton were thoroughly studied at Bol, a station in the Southeastern Archipelago. Environmental variations which were observed throughout the lake during the study period and which resulted from fluctuations in the water level all occurred at this station. The results of the study therefore permitted interpretation to be made of observed changes in different regions of the lake where measurements were made less frequently.

Although Landsat satellite data could be used under certain conditions to extrapolate the discrete *in situ* measurements to the entire water body, the production estimates for the different regions were necessarily approximate and valid only for certain periods. While the main drawbacks were the size, the heterogeneity and the variability of the lake, the considerable changes in environmental conditions during the period of study (1968–1976) required major consideration for understanding the interactions between the different parameters.

11.1 Methods

The principles of the methods are briefly mentioned here, the details and discussion having already been published (Lemoalle 1973, 1979).

The chlorophyll concentration, with no correction for the decomposition products, was estimated after grinding dried filters in 90% cold acetone. A coefficient of 11.9 (Talling and Driver 1963) was applied to the difference of the optical densities which were measured at 665 and 750 nm.

Phytoplankton activity was measured by the oxygen method with incubation in bottles either *in situ* or in an incubator in the laboratory.

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Photosynthetic activity (gross production) was designated by A(mg $O_2m^{-3}h^{-1}$). Generally, the hourly rate per unit area ΣA (mg $O_2m^{-2}\,h^{-1}$) was measured around midday. Successive incubations were used to evaluate the daily production.

The optimum activity which corresponds to the maximum value of A on the photosynthesis-depth curve was designated by A_{opt}. The irradiance in the incubator was determined experimentally so that the photosynthetic activity was equal to A_{opt} measured *in situ*.

11.2 Photosynthesis parameters

The phytoplankton was considered here as a photosynthetic system distributed in a body of water. We examined the shape of the photosynthesis-depth curves in relation to water transparency, phytoplankton concentration and temperature, as well as the relationships between instantaneous gross production and daily production. The experimental determination of these relationships was used to reveal the main factors involved in the photosynthetic activity of the phytoplankton and to provide a set of equations allowing production estimates to be made from the available field measurements.

11.2.1 *Shape of the photosynthesis-depth curves*

The photosynthesis-depth curves determined *in situ* around midday had a simple shape resulting from the environmental characteristics and from the experimental techniques. Due to the homogeneous vertical distribution of the phytoplankton, to the turbulence and the absence of stratification in the euphotic zone, a surface sample could be used for incubation in the whole profiles.

The results obtained at Bol in August 1972 and August 1975 are shown in Fig. 1 as an example of the curves obtained in water containing clay suspensions (1972) and water containing turbidity of organic origin (1975). The surface inhibition was considerable on all days with fine weather. A fairly violent tornado on the evening of 7 August, 1972 decreased the water transparency, SD, and induced the resuspension of deposited but viable phytoplankton. This phenomenon emphasizes the increasing importance of the bottom turbulence with decreasing depth (see Bénech et al. 1976).

Compared with Secchi disc transparency, SD, the optimum production occurred at a greater depth when turbidity was due to clay suspensions (1972) than when organic matter was the major cause of light absorption (1975). This difference was only partly due to the modification in the above-described relations (Chapter 3) between SD and K, the vertical light attenuation coefficient (mean over the 400–700 nm spectrum). The phytoplankton also

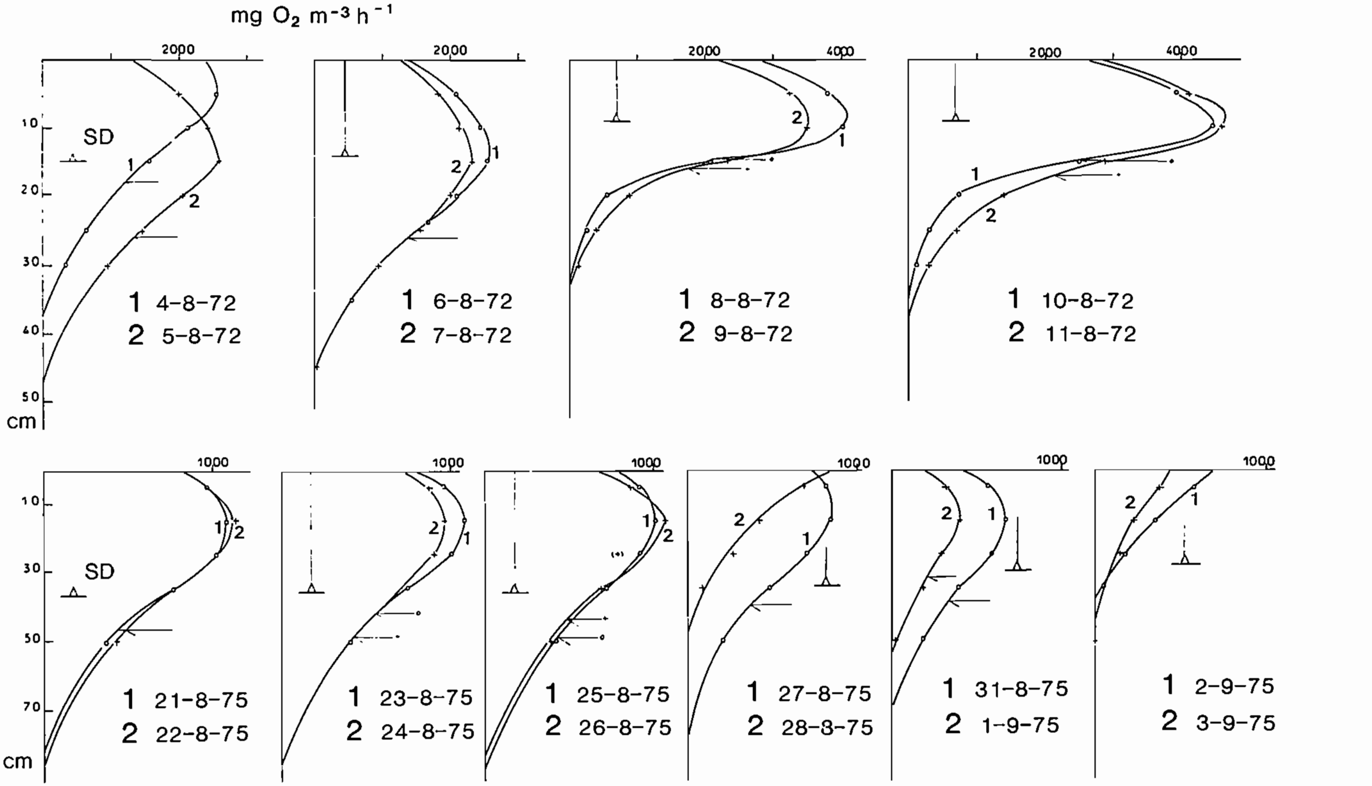

Fig. 1 Examples of photosynthesis-depth curves in Bol during August 1972 (water with suspended clay) and in August 1975 (water with organic matter). Water transparencies are indicated by the Secchi and Z_i by an arrow on each curve. Three hours incubation around midday.

responded differently to the light energy, probably because of the different spectral qualities of the types of water.

Given ΣA the integral of the mean hourly production in the water column ($mg\ O_2\ m^{-2}\ h^{-1}$), we can define the depth Z_i so that

$$A_{opt} . Z_i = \Sigma A$$

Z_i is a function of water transparency and of the response of phytoplankton to irradiance. In most cases, water transparency in Lake Chad was measured by the Secchi disc. Z_i was thus determined as a function of SD for the different types of water: with clay suspensions from 'Normal Chad' at Bol in 1968–70 (Fig. 2a) or in the whole southern basin in 1970–71 (Fig. 2b), and with organic turbidity (Fig. 2c) of phytoplankton-rich water (Fig. 2d).

The photosynthesis-depth curves obtained during fine weather have been used to compute the following relationships with the 95% confidence limits of Z_i for the range of water transparencies observed, expressed in meters:

—water with clay suspensions

$$Z_i = 2.07\ (SD) \pm 0.15 \qquad n = 142$$

— water with organic turbidity

$$Z_i = 1.20\ (SD) \pm 0.13 \qquad n = 28$$

— phytoplankton-rich water

$$Z_i = 1.55 (SD) \qquad \text{(fitted by eye)}$$

Using these equations the production per unit area, ΣA, can be estimated when A_{opt} and SD are known for a given type of water.

To compare the results obtained in Lake Chad with other primary production models, the experimental value of Z_i can be compared with $Z_{0.5}\ A_{opt}$, the depth at which the photosynthetic activity is equal to $0.5\ A_{opt}$. Practically, this depth was fairly well determined since it occurred in the part of the curve where the gradient dA/dz was steepest. It should also be mentioned that this last depth correspond to $Z_{0.5\ 1k}$ from Talling's model (1957). For the Lake Chad results, Z_i and $Z_{0.5\ A\ opt}$, have been estimated directly from the photosynthesis-depth curve. The mean value of the ratio of $Z_{0.5\ A\ opt}$ to Z_i for 170 profiles from different types of water was one (probability greater than 95%): $Z_i = Z_{0.5\ A\ opt}$.

Therefore, the characteristics of the photosynthesis-depth curves in Lake Chad fit Talling's model. The average irradiance I_K as defined by Talling averaged 8.8 $J\ cm^{-2}\ h^{-1}$ in water with clay suspensions and 15.9 in water with organic turbidity.

11.2.2 *Relationship between biomass (B) and optimal activity* (A_{opt})

The optimal activity A_{opt} was dependent upon numerous factors, the main one being the chlorophyll concentration B ($mg\ m^{-3}$). Its variations in time and

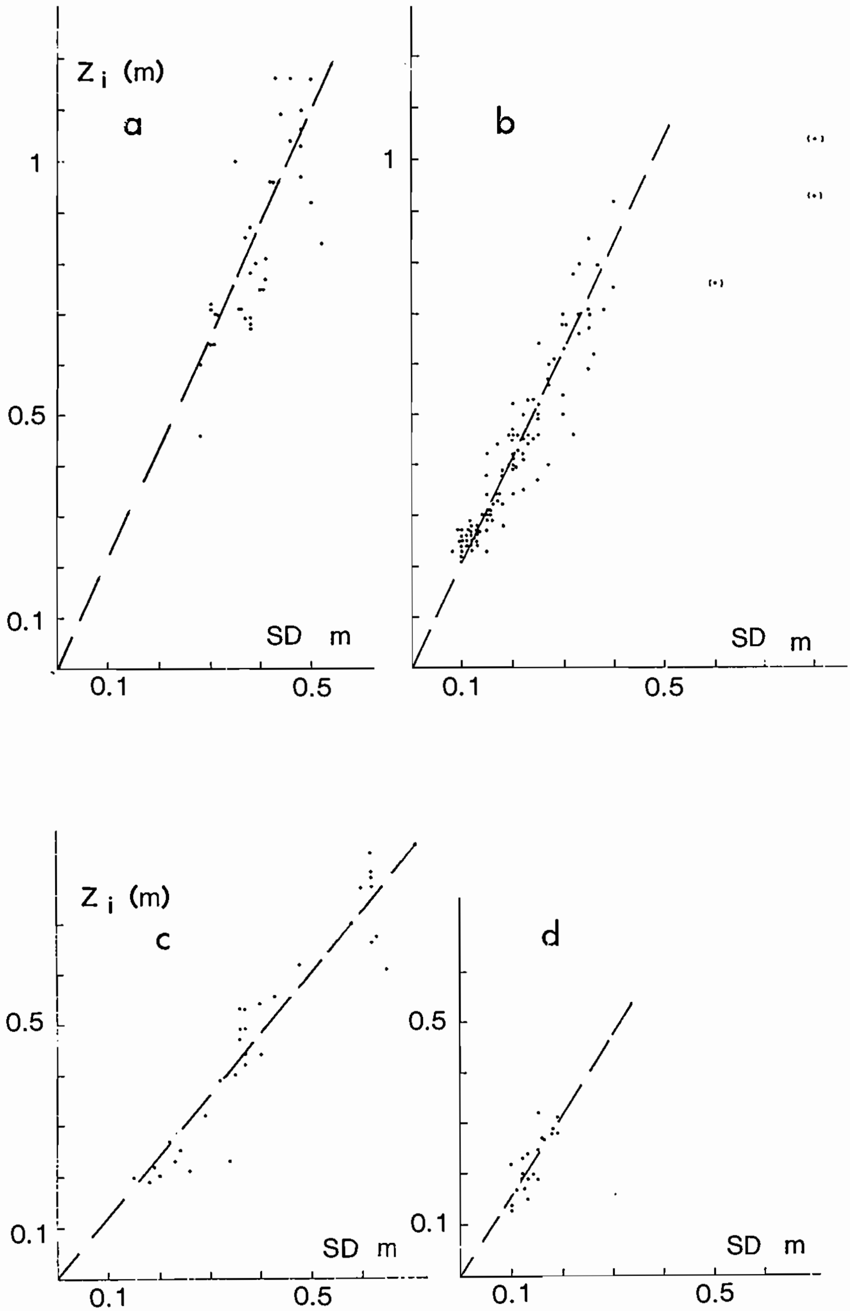

Fig. 2 Z_i as a function of SD, at Bol in 1968–70 (a); in the southern basin in 1970–71 (b), where the points (●) indicate waters with very few inorganic particles; during the period of 'Lesser Chad' with macrophytes at Bol in 1973–76 (c); and during the concentration phase (d).

space were particularly important in Chad, the representative values observed ranging from 4 to 3500 mg Chl a.m^{-3}.

The results obtained, either *in situ* or in the incubator led to the formulation of the regression equation:

$$\log A_{opt} = 1.22 + 1.044 \log B \qquad (1)$$

with a correlation coefficient $r = 0.97$ for $n = 298$ pairs of measurements. This equation represents the mean relation between the two parameters. The correlation coefficient indicates that 95% of the variance of A_{opt} resulted from variations in B. In the range $10 < B < 1000$ mg m^{-3}, the degree of uncertainty about the determination of log A_{opt} from an isolated measurement of B is ± 0.275 (probability 95%). The large variability of B thus concealed the effect of the other parameters which can influence optimal activity and especially the effect of temperature as will be seen later on.

Relation (1) indicates that the specific optimal activity, $\varphi_{opt} = A_{opt}/B$ increased with increasing B, the most frequent mean values ranging from

$$\varphi_{opt} = 18.4 \text{ for } B = 10 \text{ mg Chl } a.m^{-3}$$

and

$$\varphi_{opt} = 22.5 \text{ for } B = 1000 \text{ mg Chl } a.\ m^{-3}$$

These results are in agreement with the values 20 to 25 which are generally accepted for tropical lakes (Talling 1965b; Talling et al. 1973; Ganf 1975). Moreover, most of the high phytoplanktonic biomass in Lake Chad was observed during the hot season, and relation (1) can be affected by the effect of the temperature on φ_{opt}.

11.2.3 *The effect of temperature*

The effect of temperature on specific optimal activity φ_{opt} was evaluated by the value of the mean Q_{10} $\left(= \exp \frac{10}{\Delta T} \Delta (\log A)\right)$ over the range of temperature defined by the difference ΔT.

The mean value of φ_{opt} *in situ* was calculated at Bol (1968–1970) between 11.00 and 15.00 hours in two distinct temperature ranges, from 20 to 23°C and from 29 to 32°C.

Mean T: 20.4°C: mean $\varphi_{opt} = 20.4$ mg O_2 (mg Chl. $a)^{-1}.h^{-1}$

Mean T: 30.0°C: mean $\varphi_{opt} = 23.4$ mg O_2 (mg Chl. $a)^{-1}.h^{-1}$

If the laws of chemical kinetics are applied:

$Q_{10} = 1.15$ between 20 and 30°C

This low coefficient involved the *in situ* phytoplankton which can be generally considered as adapted to their environment.

The results of two surveys conducted in the southern basin in December 1970 and June 1971 gave significantly different specific optimal activity:

December 1970: mean $\varphi_{opt} = 18.82$ n = 30 $_m = 0.78$
June 1971: mean $\varphi_{opt} = 23.07$ n = 33 $\sigma_m = 0.78$

For mean temperatures of 20.0 and 30.5°C, the calculated coefficient was

$Q_{10} = 1.21$ between 20 and 30°C.

These results were applicable to the rather stable conditions in 'Normal Chad' and showed only the apparent value of Q_{10}, since changes in the environment other than the temperature could also occur in different seasons.

Other measurements of the temperature coefficients were made in an incubator, where bottles from the same sample were incubated at different temperatures. Unlike the previous measurements, the phytoplankton was then subjected to thermal shocks (reaching 10° within 15 minutes), while, the other environmental conditions remained similar.

It was then observed that φ_{opt} reached an optimum between 28 and 33°C, beyond which the activity then decreased quickly. Between 20 and 30°C, the different samples showed different behaviour regarding the Q_{10} as well as the value of φ_{opt}. While high values of Q_{10} occurred during the lake flood at Bol in October 1973 (from 2.8 to 4.7), all the other measurements had an average of 1.4.

The Q_{10} values observed in Chad were generally lower than most published values. The adaptation of the phytoplankton to the environment have resulted in the decrease of Q_{10}. Indeed, the mean temperature in the lake was close to the optimum temperature ranging between 28 and 32°C. Therefore, the curve $\log \varphi_{opt} = f(T)$ was close to its maximum and had a shallower slope than in the case of lower temperatures.

Furthermore, it was difficult to estimate the respective roles played by B and T in the variability of A_{opt}, since both variables were most often concomitant in their change ('Normal Chad'). When such was not the case (for instance during the 'Lesser Chad' at Bol), the use of the temperature in step-wise regressions did not improve the determination of A_{opt} and the residual variance must therefore be attributed to the variability of the other environmental conditions.

11.2.4 *Daily production*

In situ measurements of $\Sigma\Sigma A$, the daily gross production were made through successive incubations, the duration of which was dependent on phytoplankton concentration. The mean relation between $\Sigma\Sigma A$ and the mean hourly production around midday was determined with a probability of 95% for standard weather conditions (28 measurements).

$\Sigma\Sigma A/\Sigma A = 9.1 \pm 0.3$

Given the low variability of the day length at the latitude of Lake Chad, this ratio can be considered as constant throughout the year and compares with other determinations in tropical regions (Talling 1965; Ganf 1975).

11.2.5 *Model of photosynthetic activity*

Using the experimental relationships, production in various stations in the lake could be estimated from the measured variables (equations given in Table 1). In the case of statistical relations, two confidence limits (probability of 95%) were calculated: the confidence limit of the regression line (or of a mean value) determined from all the measurements, and the confidence limit of the determination of a single value of the function, the value of the variable being given. In this second case, we observed that the confidence limits did not vary significantly within the range studied.

11.3 Evaluation of production in different regions of the lake

It is difficult to generalise about the whole of the lake with the discrete measurements which were made. However, during each survey we tried to cover the entire range of variation in water transparency and chlorophyll. Therefore, the values given here may be considered as a range of estimations for photosynthetic activity of the phytoplankton in the main regions of the lake.

11.3.1 *Production at Bol and in the southern basin*

The seasonal variations in activity at Bol are given in Fig. 3 for three different years which can be considered as representative of the different periods of change in the lake in this region. The year 1969 represented the period of the low 'Normal Chad' (1968–72) with variations related to the seasonal fluctuations in water level, water transparency and temperature. The hourly production (measured *in situ*) ranged from 0.3 to 0.8 g O_2 m^{-2} h^{-1} with an annual average of 4.2 g O_2 m^{-2} day^{-1}.

The year 1973 was typical of the phytoplankton-rich water phase, along with a considerable and large flood in October. The available data indicate a maximum or 1.1 g O_2 m^{-2} h^{-1} during the warm season with biomass up to 600 mg Chl*a* m^{-3} and a minimum of 0.2 g O_2 m^{-2} h^{-1} after the flood. The annual average for daily activity, based on the curve of the monthly averages (Fig. 3) was 7.4 g O_2 m^{-2} day^{-1}.

Although higher values were observed in 1974 (up to 2 g $O_2.m^{-2}.h^{-1}$), the longest period of water circulation resulted in a similar mean activity during 1973 and 1974.

Table 1 Observed relationship between the production parameters.

Equation	Type of water	Statistical error		Range
		on the relationship	on a single measurement	
$\Sigma\Sigma A = 9.1\ \Sigma A_{midday}$	suspended clay standard day	± 0.3	± 1.6	$\Sigma A < 1000$ mg $O_2 m^{-2}\ h^{-1}$
$\Sigma A = A_{opt}\ Z_i$				
$Z_i = 2.07$ SD	suspended clay	± 0.013	± 0.15	$0.1 < SD < 1$ m
$Z_i = 1.55$ SD	concentration	—	—	$SD < 0.4$ m
$Z_i = 1.20$ SD	dissolved organic matter	± 0.02	± 0.13	$0.1 < SD < 1$ m
A, 3 hrs incubation		—	± 0.36	mg $O_2\ m^{-3}\ h^{-1}$
ΣA, 3 hrs incubation		—	$\pm 0.1 \Sigma A$	$200 < \Sigma A < 500$ mg $O_2 m^{-2}\ h^{-1}$
$\log A_{opt} = 1{,}22 + 1{,}044 \log B$	all	—	± 0.275	$10 < B < 1000$ (mgChl. *a*)m^{-1}
$Q_{10} = 1{,}2$	*in situ*			
$\varepsilon_{min} = \frac{1.95 + k_1}{SD}$	dissolved organic matter	$k_1 = \pm 0.11$	$k_1 = \pm 0.56$	$0.1 < SD < 1$ m
$\varepsilon_{min} = \frac{1.39 + k_2}{SD}$	suspended clay	$k_2 = \pm 0.11$	$k_2 = \pm 0.56$	$0.1 < SD < 1$ m
$E_K\ (= I_K) =$ 8.8	suspended clay			J.$cm^{-2}\ h^{-1}$
15.9	dissolved organic matter			

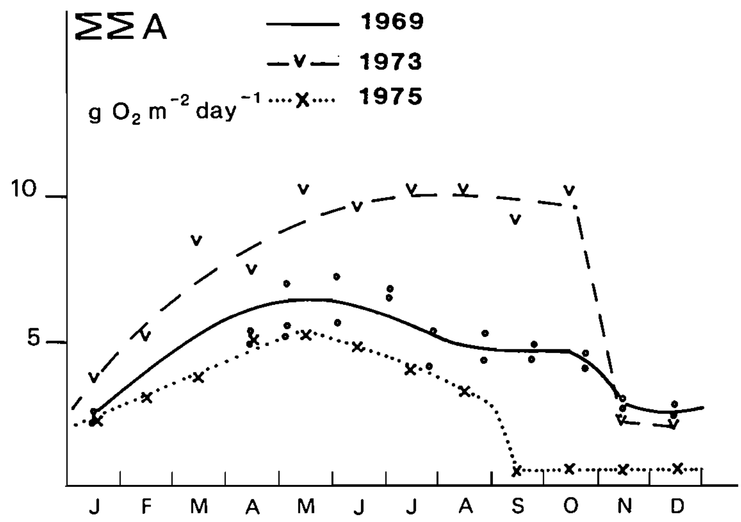

Fig. 3 Seasonal variations in the daily photosynthetic activity (gO_2m^{-2} day^{-1}) of the phytoplankton at Bol, during three years representative of the general changes in this region of the lake.

The return of the water to a 'normal' level was represented by the year 1975 with the action of the macrophytes being considerable when the water moved through the vegetation. Poor utilization of light (I_K higher) resulted in lower production (0.58 g O_2 m^2 h^{-1}) during the warm season. The annual mean production was 2.7 g O_2 m^{-2} day^{-1}.

The general change in B and ΣA over the period 1968–1976 is given in Fig. 4 (semi-logarithmic scale) and emphasizes the variability with time of production related to the environmental conditions.

The results obtained in 1970–71 have been used to estimate the phytoplankton production in the southern basin during the period of 'Normal Chad'. The results of June 1970 and June 1971 were pooled to emphasize the difference between the warm season (low water level) and the cold season (high level) which was influenced by the flood of the Shari. On the whole, 114 measurements (*in situ*) were used to divide the basin into 6 different regions (Fig. 5) (Table 2). This zonation which corresponded roughly to the large natural regions of the basin at that time was related to the zones of water transparency. The production appeared highest in the archipelago itself, and was clearly lower in zone under the influence of the Shari and in the Great Barrier both being transit zones of the flood waters.

During the period of 'Lesser Chad' with the growth of the macrophytes, the open water areas became very small in the archipelago where most of the primary production then resulted from the macrophytes and the epiphytes. The open water in the southern basin maintained a fairly constant area throughout the period 1974–76. The Landsat data were used to evaluate production in this region (Lemoalle 1978):

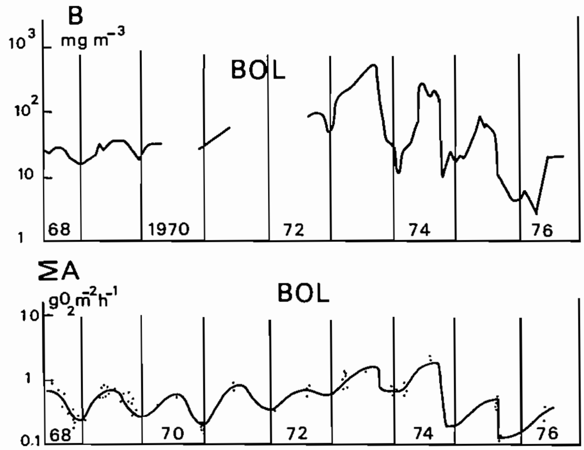

Fig. 4 The change with time of chlorophyll concentration B (mg m^{-3}) and of the production per unit area around midday (gO_2 m^{-2} h^{-1}) at Bol.

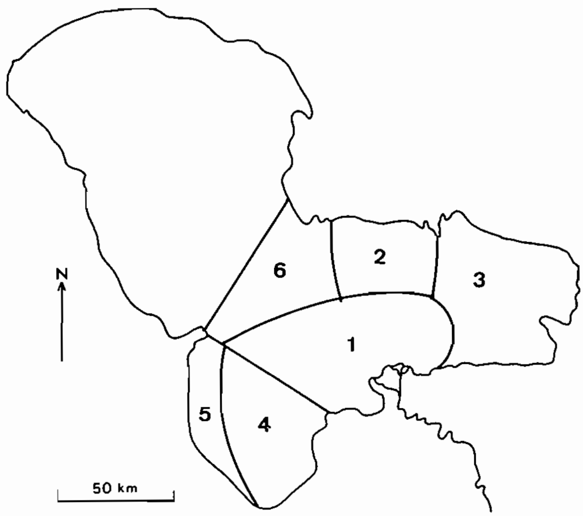

Fig. 5 Main zones of phytoplankton production in the southern basin during the period of 'Normal Chad' (1970–71).

open waters of the southern basin:
end of June 1975: 3.76 g $O_2.m^{-2}.d^{-1}$
October 8–10th 1975: 0.91 g $O_2.m^{-2}.d^{-1}$

As compared with the results of region 1 in 1970–71, these values show a considerable increase in the photosynthetic activity of the perideltaic region

Table 2 Transparency distribution (SD), optimum activity A_{opt} (mg O_2 m^{-3} h^{-1}) and daily production ΣΣA (g O_2 m^{-2} day^{-1}) in the southern basin during 1970–1971. See Fig. 5 for regions.

	June			December		
Region	SD (m)	A_{opt} mg $O_2.m^{-3}$ h^{-1}	ΣΣA g $O_2.m^{-2}.d^{-1}$	SD (m)	A_{opt} mg $O_2.m.^{-3}$ h^{-1}	ΣΣA g $O_2.m.^{-2}$ d^{-1}
1	0.20	500	2.3	0.25–0.40	150	0.9
2	0.25–0.30	1000	3.7	0.20	400	1.15
3	0.30–0.35	1200–1500	7.2	0.20	500	1.9
4	0.10–0.15	1200	3.1	0.25–0.40	150	0.9
5[a]	—	—	—	0.12	500	1.6
6	0.10	1000	1.9	0.15	300	0.9

[a]No representative data for June 1970 and June 1971.

after 1973, resulting from higher phytoplankton concentrations and slightly higher water transparencies. This difference can be attributed to the macrophytes, whose main effect was a decrease of the fetch and therefore of the turbulence.

11.3.2 *Production at Kindjéria and in the northern basin*

In order to estimate the production at Kindjéria from chlorophyll and transparency data, various values of the coefficient in the relationship $Z_i = k$ SD were used:

$k = 2.07$ before June 1974 (silty water)
$k = 1.55$ until drying up in October 1975 (phytoplankton-rich water)
$k = 1.20$ during 1976 (organic water)

The change in ΣA at Kindjéria is represented in Fig. 6 as well as the mean values of ΣA during the month of April, in a region of 20 km radius around the station of Kindjéria. These averages are rather close to the results obtained at Kindjéria; this station can be considered as representative of the surrounding region of 1256 km^2.

Given the large and rapid variations in the production at Kindjéria (Fig. 6) and the paucity of measurements, it is difficult to evaluate a mean annual production. Therefore, only the extreme values observed each year and the mean value of ΣA in April as determined on *n* stations with its standard deviation are given in Table 3.

Supposing that each station from the survey in April 1974 (Fig. 7) was representative of an identical water area, the mean value of the photosynthetic activity in the entire northern basin for 27 stations would have been ΣA = 1.49 g

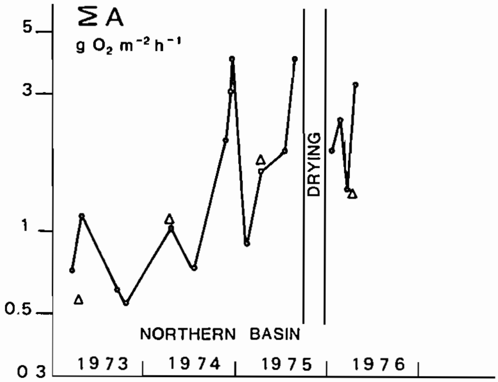

Fig. 6 Changes in hourly midday production in the northern basin at Kindjéria (O) and within a radius of 20 km around Kindjéria (△). Production was estimated from the values of chlorophyll and water transparency.

Table 3 Production in the northern basin, at Kindjéria.

Year	ΣΣA $g\ O_2.m^{-2}.day^{-1}$	ΣA $mg\ O_2.m^{-2}\ h^{-1}$	*n*	σ
1973	4.9–10	570	11	0.22
1974	6.7–36	1150	11	0.33
1975	9.1–36	1730	15	0.77
1976	12.7–30	1310	8	0.86

$O_2.m^{-2}.h^{-1}$ or 13.5 g $O_2.m^{-2}$ day^{-1} with an area of 6000 km^2, or a total daily production reaching 81 000 tons of oxygen. This result can be compared with the phytoplanktonic biomass which was estimated by Iltis (1977) to be between 167 000 tons and 200 000 tons fresh weight.

11.3.3 *Maximum production values in Lake Chad*

Figures of photosynthetic activity in very productive environments depend upon the method used: the highest values are given by the *in situ* oxygen balance, while the classical method, with incubation in bottles may give estimates that are half of the former in the same environment (Talling et al. 1973; Melack and Kilham 1974).

Four examples of high productions, are given in Table 4. Figure 8 shows daily changes in production measured by successive bottle incubations. The

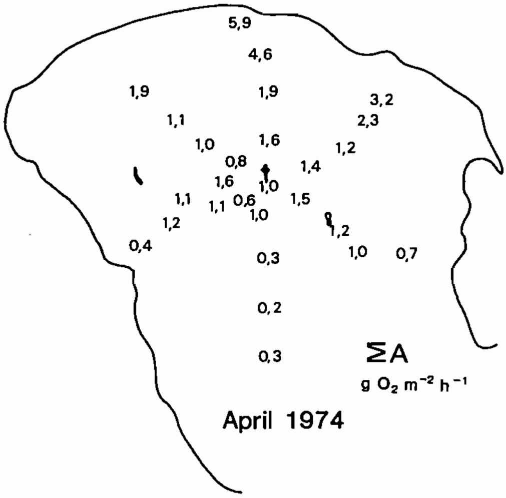

Fig. 7 Distribution of the hourly production around midday ($gO_2m^{-2}\ h^{-1}$) in the northern basin during April 1974.

Table 4 Examples of high photosynthetic activity.

Locality	Date	A_{opt} $g\ O_2\ m^{-3}.h^{-1}$	ΣA_{midday} $g\ O_2\ m^{-2}.h^{-1}$	$\Sigma\Sigma A$ $g\ O_2\ m^{-2}.d^{-1}$	SD m
Baga kiskra	7 March 1974	4.9	1.43	12.2	0.17
Baga kiskra	14 June 1974	10	1.87	16.8	0.12
N'Goudouboul	15 June 1974	28	3.48	31.0	0.10
Bol	28 June 1974	9.8	1.65	14.3	0.18

difference between the morning and afternoon rates was due mainly to the presence of clouds in the afternoon.

Talling et al. (1973) published a detailed analysis of the factors leading to high production in Lakes Kilotes and Aranguadi in Ethiopia. Due to the lack of data on irradiance and chlorophyll concentrations, the same was not possible here. However, it appeared that Lake Chad may approach the highest production values measured in the natural environment. Apart from the four examples mentioned, production higher than 9 $g\ O_2.m^{-2}.d^{-1}$ was measured in the archipelago around Bol as well as in the northern basin.

In these cases, environmental conditions were such that reduced water areas resulted, like isolated ponds, sheltered from the wind and with high water temperature and increased alkalinity caused by concentration of salts.

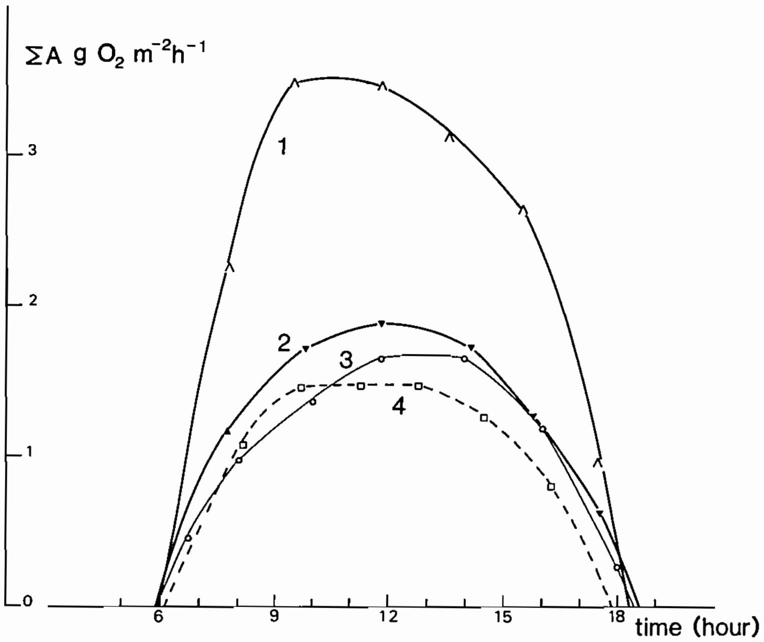

Fig. 8 Changes in ΣA throughout the day with very high production values in the northern basin and at Bol. *In situ* measurements. Each point indicates the mean time of each incubation period. 1 = N'Gouboudoul, June 15th; 2 = Baga Kiskra, June 14th; 3 = Bol, June 28th; 4 = Baga Kiskra, June 14th.

The absence of turbulence due to wind in a shallow environment limits the resuspension of the mineral particles of the sediments, whilst encouraging a vertical circulation at night which is sufficient for a redistribution of the nutritive elements. This situation also leads to the existence of a high value of p which is the percentage of the total light absorption which results from the phytoplankton absorbance.

Moreover, a high alkalinity means a large reserve of inorganic CO_2 and a considerable buffer capacity, both of which lead to high production. Most of the high photosynthetic activities in the tropical natural environment have been measured in rather alkaline waters:

— Lake Mariut, Egypt, 5–6 mé l^{-1} (Aleem and Samaan 1969);
— Lakes Kilotes and Aranguadi, 51–57 mé l^{-1} (Talling et al. 1973);
— Alkaline lakes in Kenya and Tanzania, 84–168 mé l^{-1} (Melack and Kilham 1974).

Only Lake George (Uganda) has high production (12 g O_2 m^{-2} d^{-1}) with rather low alkalinity of 2 mé l^{-1} (Ganf 1972).

11.4 Changes in the phytoplankton in relationship to environmental conditions

The physico-chemical conditions of the environment interact with the three main elements of the primary level: the phytoplankton concentration, the portion of the solar energy effectively used by this phytoplankton (gross production) and the fraction of this energy which may be used by the other trophic levels (net production). From the results obtained in Lake Chad it is possible to show some of the relationships between environmental factors and the phytoplankton (Fig. 9), and the variations in the level Z which strongly influence the other parameters.

In relation to past and present variations in the lake level, the emergent macrophytes are more or less abundant and, as seen in Chapter 5 their action involves four main variables. Amongst these are the chlorophyll concentration B (1) and the water transparency (3) because of their filtration effects on the clay or algal particles in the water. The optical quality of the water is also modified when the inorganic particles are replaced by dissolved organic matter, resulting in a modification of the coefficient k of the relation Z_i: k SD (2). Moreover, macrophytes limit the fetch, damping the short-term variations in water level, and act as a true barrier for the water supply in the northern basin. This is shown by the interaction between the water level and the macrophytes (4). These influences are significant for phytoplankton development and can be used to distinguish two periods in the evolution of the lake: before and after the development of the macrophytes. The general relationships given earlier were valid only for the water areas where the macrophyte had limited influence. When the influence was stronger one has to consider a series of particular cases which were dependent upon the water circulation through the swamps.

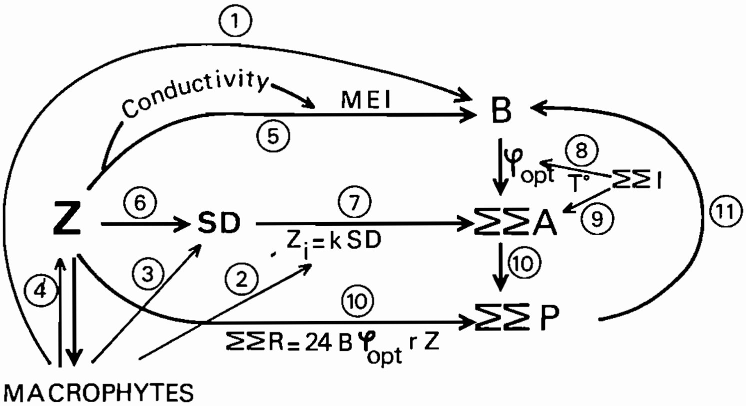

Fig. 9 Diagram of the interrelations between environmental conditions and the parameters of phytoplankton production.

11.4.1 *Phytoplankton concentration*

An increase in the chlorophyll concentration B was observed during a lowering of the water level in different regions of the lake. An increase in the total dissolved solids was generally associated with this lower level as indicated by the conductivity C.

The variations in B (mg Chl. *a*. m^{-3}) are represented in relation to the conductivity C (μS. cm^{-1}, 25°C) on Fig. 11, in the form: log B = f (log C).

In the open waters of the southern basin, the average relationship for the period 1973–76 was expressed by:

$$\log B = 5 \log C - 8.0$$

As the conductivity and the mean level of this region remained fairly constant during the period under consideration, this relationship describes the seasonal variations in a heterogeneous body of water, rather than long-term changes.

In Bol archipelago, chlorophyll increased with conductivity during the concentration phase. After the macrophytes developed, the filtration through the mats of macrophytes disturbed the possible relations between the two parameters (Fig. 10). The B versus C curve at Bol is representative of other stations of the archipelago (Fig. 10) during the concentration period (August 1972–July 1973). The data for the period 1968–1970 which are drawn on the same figure are situated in the continuation of the first cluster of points.

In the northern basin, the measurements have also been divided into two groups: during the concentration phase — from January 1973 to December 1974 — there was a clear relation between chlorophyll and conductivity (Fig. 11). After a first small flood in early 1975, the chlorophyll concentrations remained rather high while the conductivity strongly decreased. The data from Kindjéria during the two years of concentration fit quite well with the data from the whole basin (Fig. 11) and will be used later to represent the phenomena observed in this region.

In addition to our Lake Chad results, the data from the permanent alkaline ponds in Kanem (Iltis 1974) are given in Fig. 12 which summarizes the above mentioned relationships. The upper limit of the chlorophyll concentrations measured in Lake Chad is also shown by a broken line and compared with the limits observed by Talling (1970) in carbonated lakes having alkalinity ranging from 0.5 to 1000 mé l^{-1} (dotted line).

These results lead to several observations:

— during a concentration phase, there was a clear relationship between the conductivity and the chlorophyll concentration in the Bol archipelago and the northern basin. The stations at Bol and Kindjéria were representative of these changes;

— in the open water of the southern basin where there was no real concentra-

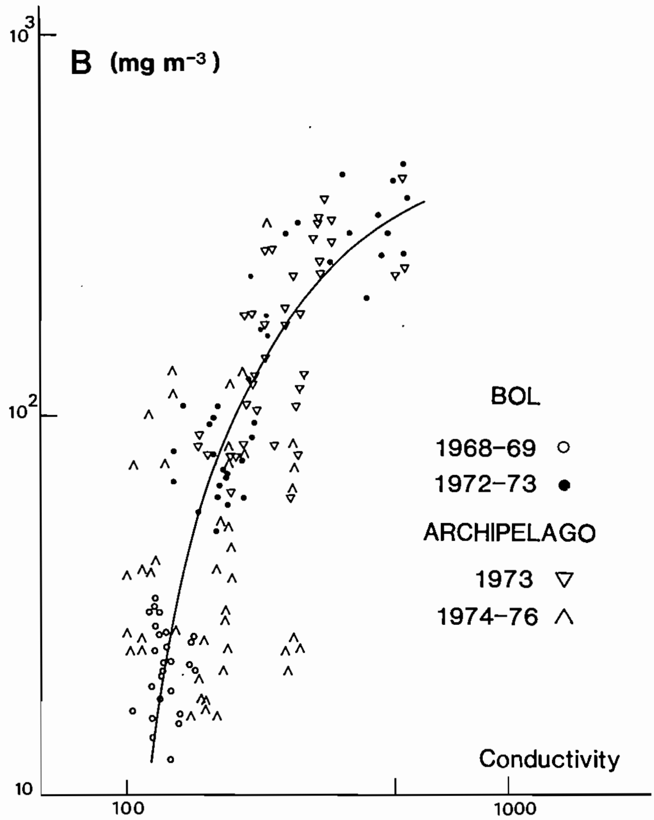

Fig. 10 Relationship between chlorophyll *a* concentration and conductivity at Bol in 1968–69 (○) and in 1972–73 (●) as well as in the archipelago before the development of macrophytes in 1973 (▽) and in the presence of macrophytes in 1974–76 (△).

tion of dissolved solids the seasonal changes in B and C leads to a similar relationship;

— the relationships shown were different for each environment observed;

— an upper limit of B versus C can be determined, which includes all the data from the different regions of the lake (Fig. 12).

The first two points suggest a causal relationship between chlorophyll and conductivity. Actually conductivity itself varied in relation to several other environmental factors.

In the open water of the southern basin, the conductivity varied with the water level and the season: the level was low during the warm season before the occurrence of the flood. After the end of the Shari flood, an increase in temperature, a decrease in the level and in the water transparency (which was

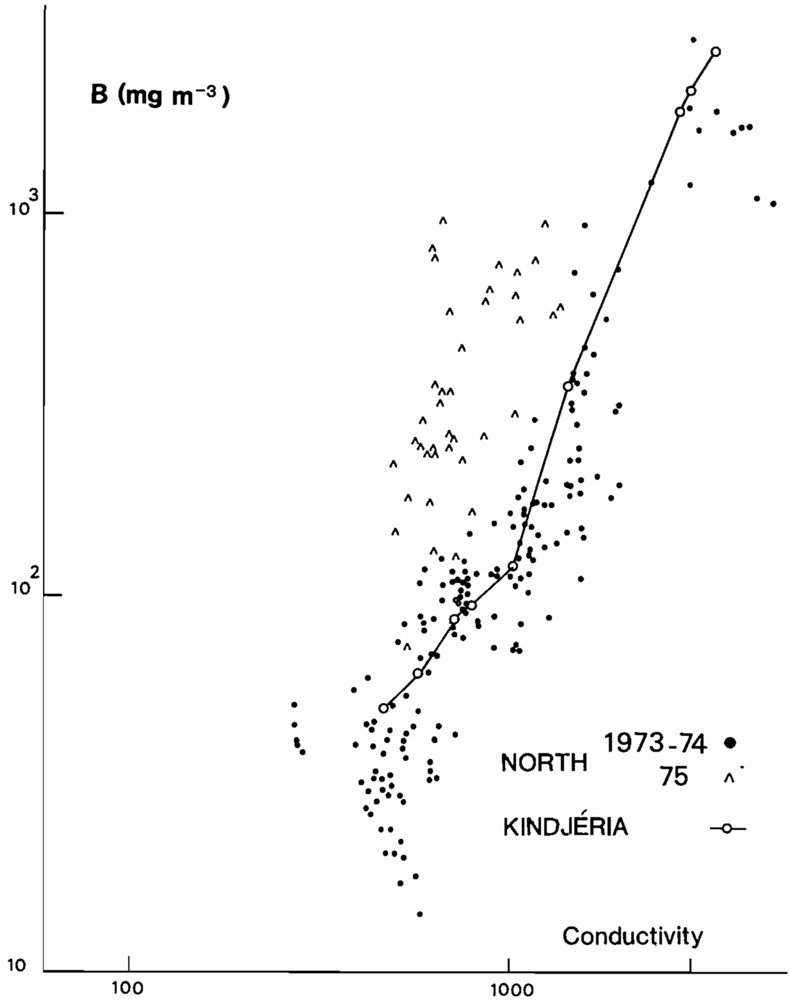

Fig. 11 Relationship between chlorophyll *a* concentration and conductivity in the northern basin. At Kindjéria, the relationship is indicated by the line.

often related to an increase of B in 1975–76) corresponded to the seasonal increase in conductivity.

In the northern basin, the seasonal variations did not appear during the two year drying up phase under consideration. Therefore, the possible influence of temperature may have been overlooked. When the dissolved salt concentration increased, the alkalinity increased and permitted high photosynthetic activity of the high biomass; as the available carbon increased, so did the buffer capacity which reduced the pH fluctuations which resulted from variations in total CO_2.

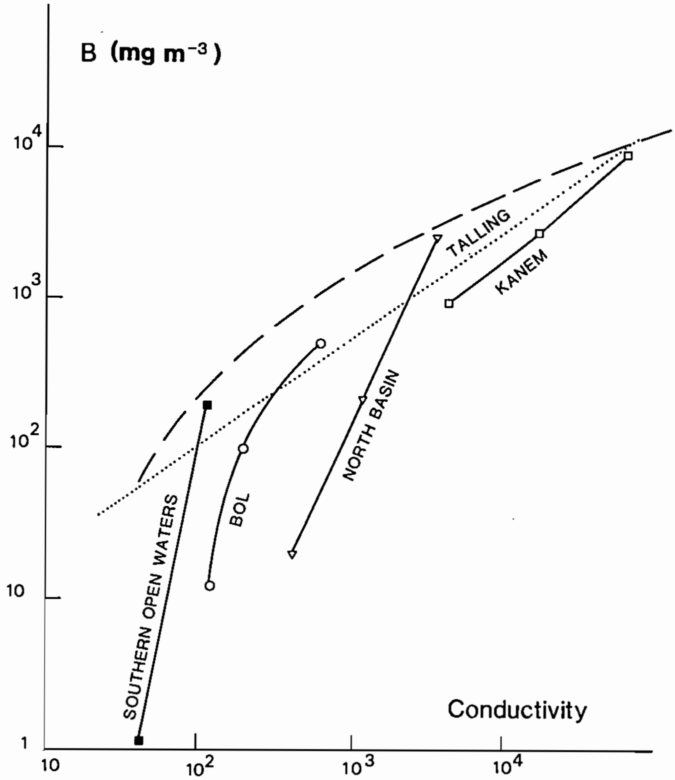

Fig. 12 The change in chlorophyll concentration in relationship of conductivity in the different environments, in the absence of macrophytes. The dotted line indicates the approximate limit of the maximum biomasses observed by Talling in lakes of various alkalinity. The broken line indicates the limit observed in Chad.

Since changes in conductivity and water depth were two related phenomena, a variable including these two parameters may be used: the morpho-edaphic index of Ryder (Rawson 1955; Moyle 1956; Ryder 1972; Henderson et al. 1973). It was applied to the different stations of the lake:

$$\mathrm{MEI} = \frac{\text{conductivity } (\mu\text{S cm}^{-1} \text{ at } 25°\text{C})}{\text{depth (m)}}$$

During the drying up period, before the macrophyte development the regression equations of B with C and MEI were, respectively:

$$\begin{array}{ll} \log \mathrm{B} = 0.410 + 0.866 \log \mathrm{C} & r_1 = 0.705 \\ \log \mathrm{B} = 0.062 + 0.736 \log (\mathrm{MEI}) & r_2 = 0.80 \end{array} \quad n = 244$$

The use of the morpho-edaphic index thus improved the description of the phytoplanktonic concentration (path 5 of Fig. 9).

11.4.2 *Photosynthetic activity (gross production)*

If the phytoplankton concentration, B, and the water transparency are the only variable parameters, the production per unit area is proportional to p, the percentage of the light attenuation which results from phytoplankton absorbance. This value is directly related to the amount of phytoplankton per unit area in the euphotic layer.

In the case of Lake Chad where the water transparency SD was measured with a Secchi disc, the following general relationship was proposed (Lemoalle 1979):

$$1/SD = \gamma_W + \gamma_{Fe} + \gamma_B B$$

Then the parameter, p, is expressed as:

$$p = 100\ \gamma_B . B\ (SD)$$

Using B and SD results, P was calculated for the southern basin in December 1970 and June 1971, for the northern basin in April 1974, and for Bol during the period 1968–70 and from March 1973 to May 1976. For each series, the relationship between ΣA and p are presented in a diagram $\log \Sigma A = f(\log P)$ in Fig. 13, which shows that ΣA was proportional to p.

For the northern basin some values of p were close to 100 and the three highest even exceeded this figure. These high values indicated that the coefficient γ_B used was too high for the phytoplankton considered.

The results obtained in Lake Chad support the above-mentioned theory that production depends upon the proportion of light absorbed by the phytoplankton independently of the absolute concentrations of phytoplankton, mineral particles or dissolved elements.

Concurrently, we observed an increase in photosynthetic activity per unit area at Bol as well as in the northern basin during the reduction in water level. This indicates that, in spite of the increased turbulence at the sediment interface, the increase in phytoplankton concentration resulted in an increase in p; the decrease in SD was proportionally less important than the increase in B.

The photosynthetic yield, E_{tot}, was expressed by the ratio of the assimilated energy (supposing that 1 g O_2 is equal to 3.33 kcal) to the total incident energy over a day. For all the *in situ* measurements in Lake Chad, E_{tot} ranged from 0.04% to 1.80% and was proportional to the percentage, p, which thus appeared as the main factor of variation. The percentage, p, ranged from 3 to 100% according to the stations and to the period of measurement.

The value $E_{tot} = 0.26\%$ which was calculated for Bol during the year 1969 must be considered only as representative of this region during this period. The variability of the lake did not allow extrapolation as was sometimes done elsewhere.

Given the assimilation index φ_{opt} of the phytoplankton in Lake Chad and the

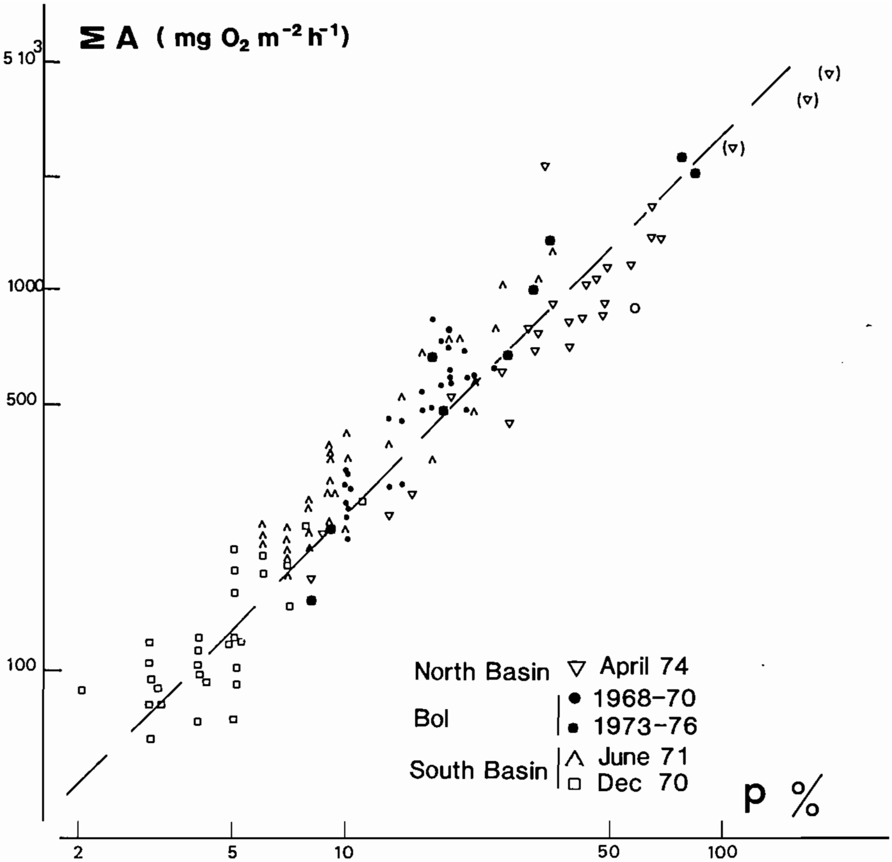

Fig. 13 Relationship between ΣA and p (percentage of the attenuation resulting from the phytoplankton) for various measurements made in Lake Chad (logarithmic scales).

relative constancy of the daily irradiation, gross production depended mainly upon B and SD. However, there was a maximum limit to the phytoplankton concentration beyond which the respiration of the water column becomes higher than the production in the euphotic zone. This boundary condition was defined in relation to the respiration coefficient, r, and to the ratio of the water transparency to the depth, SD/Z (Talling 1970) where $r = R/A_{opt}$, R being the hourly respiration per unit volume. Respiration thus appeared to limit net production and the biomass (path 10 and 11 in Fig. 9).

With the symbols used and the mean conditions for Lake Chad, daily net production ΣΣP is expressed as follows:

$$\Sigma\Sigma P = \Sigma\Sigma A \left(1 - 2.64\,\frac{r\,.\,Z}{k_1\,.\,DS}\right)$$

The mean values observed in different parts of the lake imply that $r = 0.05$ can be considered as a lower limit, while $r = 0.9$ seems to be the upper limit of the respiration coefficient. Moreover, we noticed that the ratio SD/Z increased when the lake changed from 'Normal Chad' (clay water) to 'Lesser Chad' (organic water) at Bol as well as in the northern basin. Concurrently, I_K of Talling was lower in clay water than in water with dissolved organic matter, as if the phytoplankton adapted to their environment, and the algae likely to use a low irradiance were found when relative water transparency was low and vice versa.

11.5 Comparison with other lakes

The variability of Lake Chad makes it difficult to make a comparison with other more stable environments. It has the same characteristics as Lake Chilwa, as it is shallow, endorheic and unstable. In both lakes, the variations in water level with drying up as the ultimate phase, lead to the same increase in salt and phytoplankton concentration, growth of macrophytes, mortality and recolonization by fishes (Howard-Williams and Lenton 1975, Bénech et al. 1976).

In the previous paragraphs, some temporal variations in the parameters of primary production in the various regions of Lake Chad, have been described. This constitutes a comparison of the lake with itself at different moments of its development. The range of variations observed in gross production (from 1.4 $gO_2\ m^{-2}\ day^{-1}$ in the peri-deltaic region during 1970–71, to 30 g $O_2\ m^{-2}\ day^{-1}$ in the northern archipelago of the northern basin during 1974) is equivalent to that observed by Brylinski and Mann (1973) in their first synthesis of the I.B.P. results from 55 lakes distributed from 0 to 65° latitude.

Since biomass and phytoplankton production resulted from the interaction of numerous environmental conditions, we have compared the main parameters measured in some representative environments.

With the introduction of the morpho-edaphic index the variations in the chlorophyll concentration in relation to the environmental conditions could be described for Lake Chad and other water bodies such as the Kanem lakes and Lake Fitri. These lakes constitute a type of tropical carbonated lake whose suspended solids decrease when conductivity increases.

In a graph of log B = f (log MEI), the points representative of Lake George (MEI 87, $B = 200$ mg/m^3) or Lake Mariut in Egypt (MEI50 resulting from alkalinity, a very considerable biomass) (Aleem and Samaan 1969) have much higher biomasses than Lake Chad as compared with their morpho-edaphic index. The same holds true for Loch Leven in Scotland whose mean biomass is, moreover, sensitive to the climatic variations. In comparison with Lake Chad, these three shallow lakes have a common feature: light absorption in the water results mainly from the phytoplankton as shown by the close relationship between B and SD or K (Aleem and Samaan 1969; Bindloss 1974; Ganf 1972).

If we consider the morpho-edaphic index, Lake Chad was characterized by a low biomass during the normal period as compared with the tropical shallow lakes for which data are available. The suspended minerals were responsible for this situation and brought Lake Chad closer to lakes where turbulence is considerable at the bottom level: Lake Balaton (Entz 1964), IJsselmeer (Lijklema 1976) Neusiedlersee (Dokulil 1973) some lakes in Australia (Kirk 1977). As stated by Henderson et al. (1973), who found it necessary to use corrective terms in the MEI when dealing with fish production, it also appears that the MEI needs the same type of correction when applied to phytoplankton biomass.

The results obtained in Chad for the photosynthetic activity per unit area have shown the importance of the percentage of light attenuation resulting from the phytoplankton itself. In this respect, the points representative of shallow lakes varying in latitudes combine with the data from Lake Chad in the graph log $E_{tot} = f$ (log p) of Fig. 14, although the seasonal variations in irradiance and production are much more important under temperate conditions.

The values of φ_{opt} observed in the different environments confirm the distinction made by Talling (1965b) between temperate and tropical lakes. More recently, Lastein and Gargas (1978) showed that, for 18 shallow lakes in Denmark, φ_{opt} and I_K were mainly dependent upon the temperature, the difference between eutrophic and oligotrophic lakes being of lesser importance. If the impact of the temperature on φ_{opt} seems clear cut, the same does not hold true for I_K which depends upon the attenuation per unit of pigments. In Lake Chad, I_K was estimated at 8.8 J cm^{-2} h^{-1} (400–700 nm) in clay water and at 15.9 J cm^{-2} h^{-1} in organic water, which emphasizes the importance of the phytoplankton adaptation.

In shallow lakes, maximum biomass and production depend upon the light climate defined by the ratio of the water transparency to the depth, as well as by the features of the phytoplankton, I_K and K_B. In a discussion about the influence of the morphometry on lake productivity, Richardson (1975) and Horne et al. (1975) put forward opposite arguments on shallow lake productivity. Nutrient cycling is faster in shallow lakes, as a result of the absence of stratification (Richardson), but they can be placed in an unfavourable position by the suspended minerals and a shallow euphotic layer (Horne et al.). Of course, some examples support both views.

The influence of the nutrients and especially of nitrogen and phosphorus was not considered in this study as concentration measurements alone are insufficient, and it would have been necessary to deal with the dynamics of the various forms of these two elements. However, the values of φ_{opt} observed in Lake Chad suggest that these nutrients may not be limiting optimal photosynthetic activity.

We noticed that highest biomass and production rates were usually observed

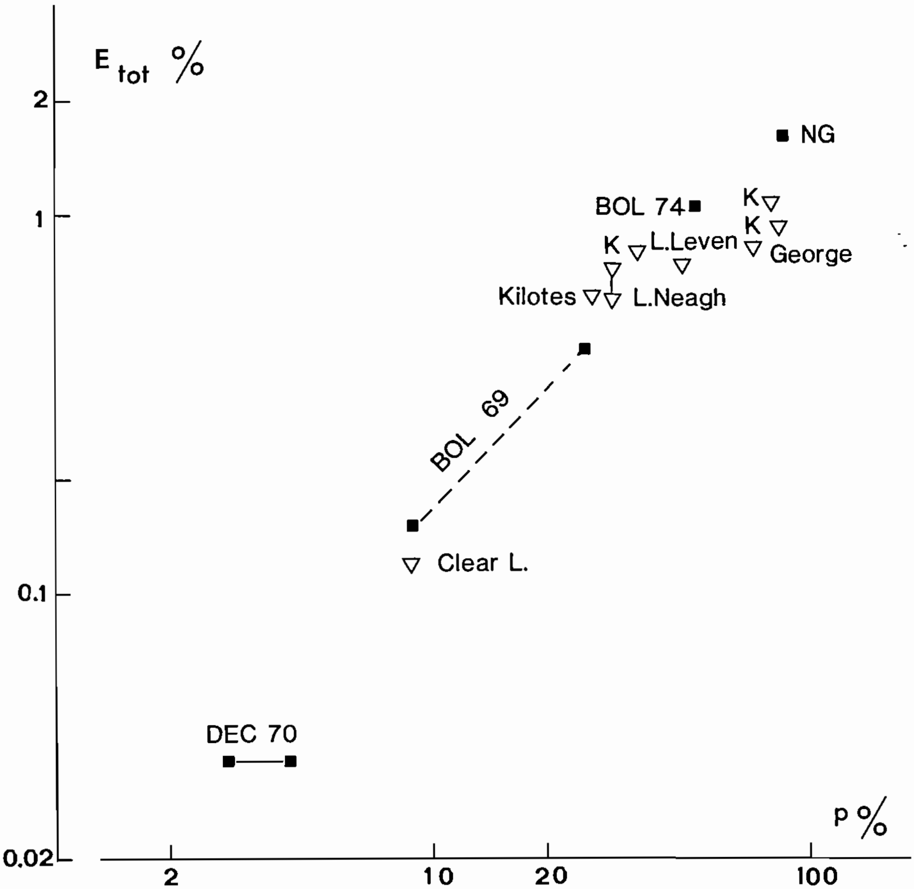

Fig. 14 Relationship between the total photosynthetic yield E_{tot} and the percentage, p, of light attenuation resulting from the phytoplankton. Measurements made in Lake Chad (■) and in other shallow lakes (▽).

when the environmental conditions (SD/Z) were most favourable to positive net production. There was however, an exception, when the filtration effect resulting from the water circulation through the macrophytes limited the phytoplankton concentration. Apart from this case, the photosynthetic yields equalled the highest values observed in other eutrophic environments.

If different parameters of the primary production are considered separately, we may conclude that Lake Chad did not show any particular feature. However, the suspended clay turbidity during the period of 'Normal Chad', and the filtration effect through the macrophyte mats during the period of 'Lesser Chad', largely contributed to its individuality when considering phytoplanktonic biomass and production together.

It thus appears that the biological development of a lake depends upon its physical features when the nutrients are not strictly limiting, and that turbulence is of prime importance in shallow lakes.

11.6 Comments on the use of remote sensing

Landsat satellites which make observations of the earth carry multispectral scanners with four bands: MSS4 from 500 to 600 nm, MSS5 from 600 to 700 nm, MSS6 from 700 to 800 nm and MSS7 from 800 to 1100 nm in the near infra-red. The data from these satellites were used to extrapolate to larger water areas the discrete field measurements made along a single route (Lemoalle 1979).

The water column could be considered as homogeneous, especially in the morning at about 9.30 a.m. when the satellite data were acquired. With a clear sky, the surface radiance, L (energy reflected by the lake surface) was representative of the water column and depends upon the optical properties of the water (Morel and Prieur 1977). If a relationship existed between the MSS radiance in band X and the field data, it was possible to extrapolate this relationship to the whole surface and estimate the distribution of the field parameter from the distribution of radiances.

Generally, there is a simple relation between the radiance L_X, as it is observed by the satellite, and the reciprocal of the water transparency as measured with the Secchi disc, 1/SD. This relationship can be extrapolated if the body of water is composed of only one type of water, that is to say that the relative proportions of the different substances playing a significant part in the light attenuation must remain constant. For instance, the relationship between the transparency of clay or organic waters and the luminance were clearly different.

For a lake of a given type of water, it is therefore possible to estimate the distribution of water transparency. If, moreover, there is a relationship between 1/SD and the chlorophyll concentration B, it is also possible to estimate the distribution of the phytoplankton, and for each picture element the photosynthetic activity which is proportional to the product $B \times (SD)$, may also be computed.

Such conditions are not always met. But, when they are, a synoptic picture of the distribution of the useful parameters over a large area provides information that cannot be obtained by field measurements only, given the size of the lake.

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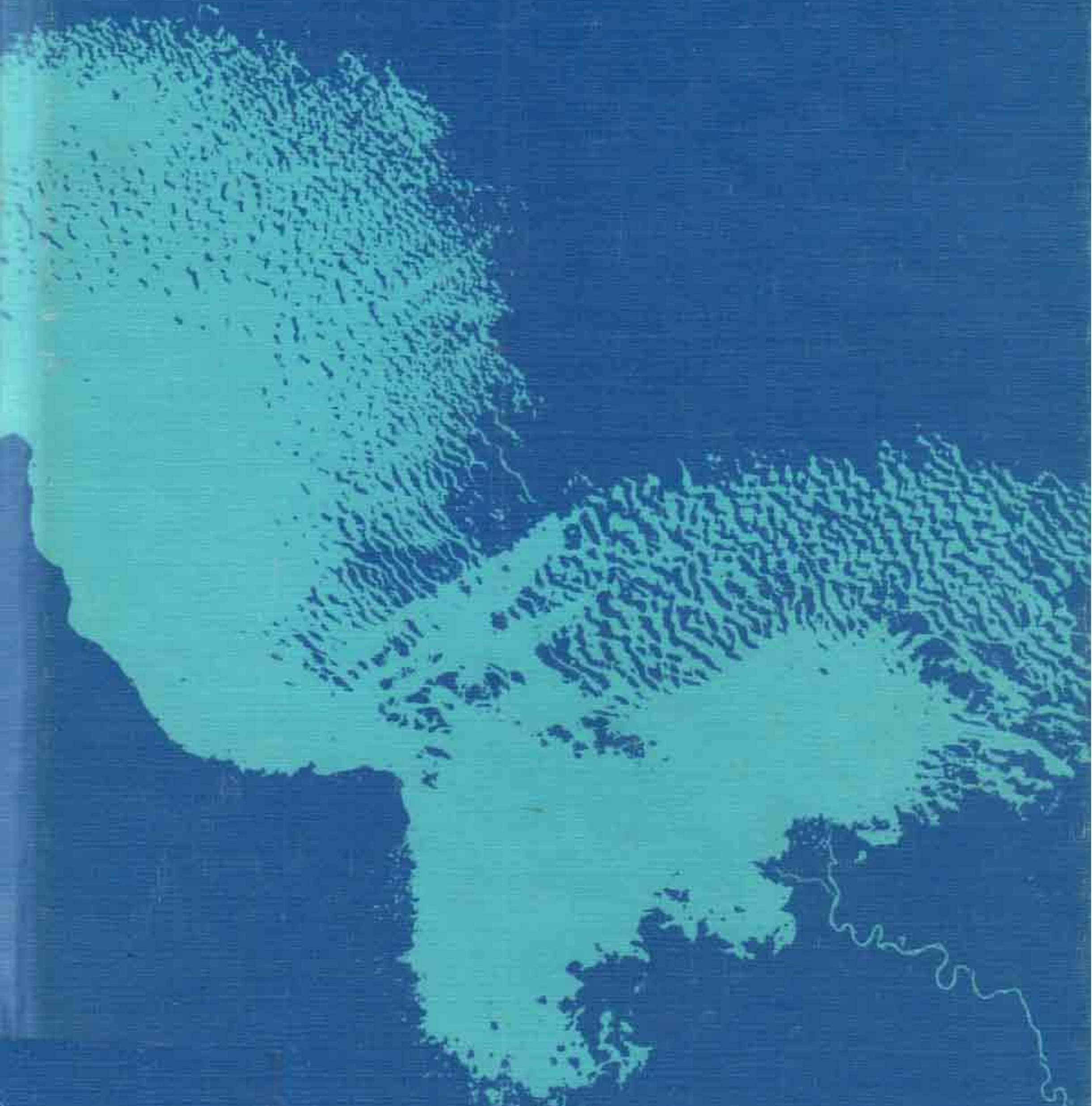

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