Photosynthetic production and phytoplankton in the euphotic zone of some african and temperate lakes

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ABSTRACT

The relation $\Sigma\Sigma A = 0.14\ \Sigma B$, where $\Sigma\Sigma A$ ($g\ O_2\ m^{-2}\ d^{-1}$) is the daily gross production and ΣB (mg Chl a m^{-2}) is the euphotic zone content of phytoplankton, has been established for Lake Chad (Africa), where both $\Sigma\Sigma A$ and ΣB vary widely. This relationship may be considered representative of the situation in many African lakes and is quite different from $\Sigma\Sigma A = 0.052\ \Sigma B$ which can be derived from data for the growing season in North American lakes. The main cause of the difference is shown to be the assimilation index (or photosynthetic capacity) associated with higher temperatures in the African lakes.

KEY WORDS: Phytoplankton. Primary production.

RÉSUMÉ

PRODUCTION PHOTOSYNTHÉTIQUE ET PHYTOPLANCTON DE LA ZONE EUPHOTIQUE DANS QUELQUES LACS AFRICAINS ET TEMPÉRÉS

La relation $\Sigma\Sigma A = 0{,}14\ \Sigma B$ entre la production brute journalière $\Sigma\Sigma A$ ($g\ O_2\ m^{-2}\ d^{-1}$) et la quantité ΣB (mg Chl a m^{-2}) de phytoplancton contenu dans la zone euphotique a été établie pour le lac Tchad où $\Sigma\Sigma A$ et ΣB varient dans une large gamme. Cette relation peut être considérée comme représentative de nombreux lacs africains. Elle est par contre assez différente de $\Sigma\Sigma A = 0{,}052\ \Sigma B$ déduite des valeurs publiées pour les lacs nord-américains. Il est montré que la principale différence entre les deux types de lacs est due à un plus grand indice d'assimilation (capacité photosynthétique) associé aux températures plus élevées des lacs africains.

MOTS-CLÉS : Phytoplancton. Production primaire.

The photosynthetic activity of the phytoplankton in a lake depends mainly upon (1) the incident energy, (2) the part of this energy which is absorbed by the phytoplankton and (3) the efficiency of the transformation into chemical energy. The algal content of the euphotic zone, expressed by ΣB (mg Chl a m^{-2}), is an approximate index of the fraction of the incident energy which is available for photosynthesis. Furthermore, this variable integrates biomass and transparency values which are determined independently of the measurements of photosynthesis (TALLING, 1965 a).

In Lake Chad, where both water transparency and phytoplankton concentration vary widely, phytoplankton production measurements have been used to establish a relationship between ΣB and the daily photosynthetic activity $\Sigma\Sigma A$ ($g\ O_2\ m^{-2}\ d^{-1}$). This relationship may be regarded as representative of a number of African lakes, and is rather different from observations in temperate lakes.

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METHODS

A total of 132 results originating from five series of measurements in Lake Chad have been used: Bol (South-Eastern archipelago) during 1968-70 (a) and 1973-76 (b), Southern basin of the lake in December 1970 (c) and June 1971 (d), and April 1974 in the Northern basin (e).

As the vertical distribution of phytoplankton has been shown to be generally homogeneous in this shallow and windy lake, surface samples have been used to determine the concentration B (mg Chla m^{-3}) of chlorophyll a. Spectrophotometric measurements were determined on 90 % acetone extracts, after grinding, with no correction for degradation products, according to method 7.8.1 of the IBP manual n° 8 (GOLTERMAN, 1969).

The transparency SD (m) was usually measured with a Secchi disk. As the optical quality of the water changed with time and position in the lake, several different relationships have been observed between SD and ε, the mean vertical attenuation coefficient of photosynthetic available radiation (LEMOALLE, 1973, 1979). The depth Z_{eu} of the euphotic zone, defined by the 1 % level of incident energy, were estimated by:

Z_{eu}=2,79 SD in clay-laden waters
Z_{eu}=1,88 SD when dissolved organic matter dominated
and Z_{eu}=2,35 SD in phytoplankton rich (green) waters.

The photosynthetic activity of the phytoplankton was measured *in situ*, around midday, by means of the oxygen method after incubations lasting from 0.5 to 4 hours. For the series a to d, the hourly integrals

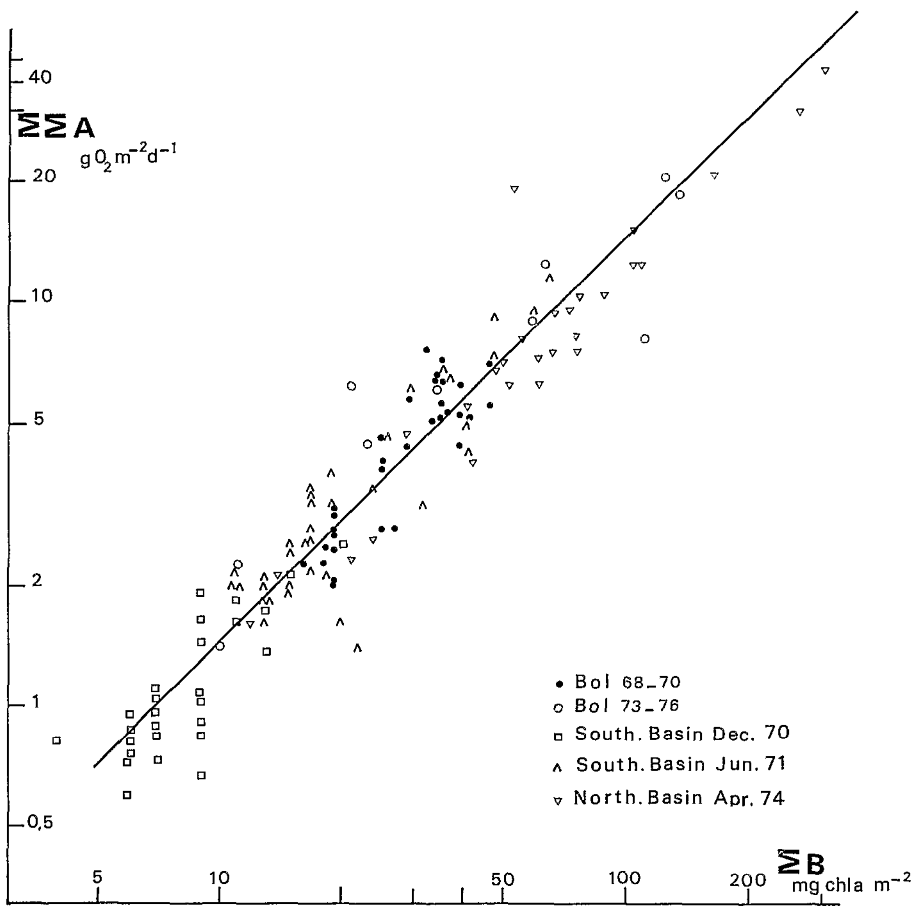

FIG. 1. — The relationship between daily gross production ΣΣA (g $O_2 m^{-2} d^{-1}$) and euphotic zone content (mg Chl *a*.m^{-2}) in Lake Chad. The straight line represents ΣΣA = 0.14 ΣB.

Relation entre la production journalière ΣΣA (g O_2 m^{-2} d^{-1}) et la quantité ΣB de phytoplancton contenu dans la zone euphotique (mg Chl a.m^{-2}) dans le lac Tchad. La droite représente la relation ΣΣA = 0,14 ΣB.

ΣA ($mg\ O_2\ h^{-1}$) have been estimated by planimetry. In the Northern basin (series e), only the upper part of the photosynthetic profile, and the optimum activity A_{opt} have been determined *in situ*. A relationship, established for the same optical type of water, in other regions of the lake, was then used to calculate ΣA.

All the daily figures used here have been calculated by:

$$\Sigma\Sigma A\ (g\ O_2\ m^{-2}\ d^{-1}) = 9{,}01\ \Sigma A\ (g\ O_2\ m^{-2}\ h^{-1})$$

a relationship established for clear weather from 28 measurements of $\Sigma\Sigma A$ obtained by successive *in situ* incubations during a whole day.

The other African data, originating from the literature or personal communications, have been converted when necessary by $1\ g\ C = 3\ g\ O_2$ (equivalent to a photosynthetic quotient of 1.12 as determined by *e.g.* Harris and Piccinin, 1977) and from midday hourly rates to daily rates by $\Sigma\Sigma A = 9\ \Sigma A$ (Talling, 1965 a).

RESULTS

The results from Lake Chad (fig. 1) were obtained from low transparency waters where either clay particles, dissolved organic matter or phytoplankton were the main factors of light attenuation. The three different types of water occur in the lake according to the region, the season and the long-term level changes (Lemoalle, 1979). The variation in transparency and chlorophyll concentration encountered in each series of measurements is given in table I, where *n* indicates the number of measurements.

Table I

Environmental characteristics

Serie	B $mg\ m^{-3}$	SD cm	water type	n
a Bol 1968-70	18-35	28-50	clay	32
b Bol 1973-76	9-295	12-65	variable	10
c Southern Basin Dec. 70	5-35	10-40	clay	27
d Southern Basin June 71	13-70	10-35	clay	36
e Northern Basin Apr. 74	60-1400	5-25	green	27

Futhermore, different conditions of temperature (18 to 32 °C), of conductivity (90 to 1700 $\mu S\ cm^{-1}$), of depth (0.4 to 4.0 m) are included in these results, where most of the lake's variability is thus encountered.

Phytoplankton concentration and water transparency varied widely during the period of study (1968-1976) and, most often, independently of each other (Lemoalle, 1979). This led to a wide variation of ΣB (see fig. 1) and to the determination of a rather strong relationship, where the variability of $\log \Sigma B$ accounts for 90 % of the variability of $\log \Sigma\Sigma A$. The other parameters of the daily production have a much lesser influence.

The regression equation for the 132 results is:

$$\log \Sigma\Sigma A = 0{,}988 \log \Sigma B - 0.827 \qquad r^2 = 0.914$$

after a logarithmic transform to homogeneize the two variances. This relationship is very similar to:

$$\Sigma\Sigma A = 0.140\ \Sigma B \qquad \text{when } \Sigma B \geqslant 5 \qquad (1)$$

the maximum difference between the two estimates being 4 % of $\Sigma\Sigma A$ for a given value of ΣB. This last equation is represented in figure 1, and will be used further in the discussion, being more conveniently compared with others.

Examples of photosynthetic production in some African lakes, as annual means or more occasional results, are given in table II and represented figure 2 in a log-log plot where the Chad results are summarized by equation (1).

In the high values of ΣB, four data appear to be relatively lower. Three of them originate from Lake Aranguadi and must be considered as underestimates of $\Sigma\Sigma A$ due to chlorophyll concentrations exceeding 900 $mg\ m^{-3}$ (Talling *et al.*, 1973, p. 62). The fourth is from Lake Hannington (Bogoria), with a φ_{opt} value of 9.9 (Källqvist, pers. comm.); the reason for such a low value is not known.

DISCUSSION

If we take into account that part of the scatter among African Lakes originates from the fact that different methods have been used in estimating the chlorophyll concentrations, the daily photosynthetic production and the depth of the euphotic zone, then equation (1) from Lake Chad may be regarded as roughly representative of tropical African Lakes. It is also very close to the results from lake Victoria where $\Sigma\Sigma A/\Sigma B$ lies between 0.135 and 0.180 (Talling, 1965 a).

The situation is quite different in temperate lakes. A relationship between $\Sigma\Sigma A$ and ΣB was calculated from 75 sets of data from 58 stations in North American lakes and published by Smith (1979). Using the values of $\Sigma\Sigma A/Z_{eu}$ and of the mean chlorophyll concentration in the euphotic zone, a mean value can be calculated:

$$\Sigma\Sigma A/\Sigma B = 0{,}052 \pm 0{,}009 \qquad (2)$$

TABLE II

African data used in figure 2: photosynthetic activity ΣΣA (g O_2 m^{-2} d^{-1}) and euphotic zone contents ΣB (mg Chl. a m^{-2}) in some African lakes.

	Period	ΣB	ΣΣA		Origin
Victoria	1960-61	43.5	7.4		TALLING, 1965
Pilkington Bay	07.02.61	71	10.2		TALLING, 1965
Pilkington Bay	27.04.61	57	11.0		TALLING, 1965
Kavirondo	05.12.60	51	10.7		TALLING, 1965
Kavirondo	12.76	35	5.7		KÄLLQVIST (pers. com.)
Kavirondo	22.12.73	42	6.2		MELACK, 1979 a
Sibaya	1973-74	33	2.36	ann. mean	ALLANSON and HART, 1975.
McIlwaine	1975-76	93	11.7	ann. mean	ROBARTS, 1979
George	1967-70	152	12	ann. mean	GANF, 1974
Sonachi	1973-74	55	4.9	mean	MELACK, 1976
Naivasha	1976-77	53	5.6	ann. mean	KÄLLQVIST (pers. com.)
Naivasha	16.06.73	44	3.7		MELACK, 1979 a
Naivasha	16.12.73	70	5.0		MELACK, 1979 a
Naivasha	25.01.74	42	5.3		MELACK, 1979 a
Oloidien	Dec. 73	84	8.4		MELACK, 1979 a
Crescent Is. Crater	Dec. 73	27	4.7		MELACK, 1979 a
Simbi	17.11.76.	200	19.2		MELACK, 1979 b
Hannington	1976	276	16.2	mean	KÄLLQVIST (pers. com.)
Tanganyika	Oct. Nov. 75	46	5.1	mean	HECKY *et al.*, 1978
Aranguadi	Jan. 66	325	16.4		TALLING *et al.*, 1973
Aranguadi		221	23.0		TALLING *et al.*, 1973
Aranguadi		248	16.1		TALLING *et al.*, 1973
Aranguadi		267	12.9		TALLING *et al.*, 1973
Kilotes	Dec. 65 Janv. 66	62	8.1	3 days	TALLING *et al.*, 1973
Kilotes	Feb. Mar. 64	185	16.3	4 days	TALLING *et al.*, 1973
Lubumbashi		34	5.8	ann. max.	FRESON, 1972
Kossou	Jan. 1977	34	7.0	ann. max.	KASSOUM, 1977
Connemara Dam 3	June 1975	15	2.3		NDUKU and ROBARTS (pers. com.)
Lagune Ébrié	1975	40	3.85	ann. mean	DUFOUR (pers. com.)

where ΣΣA is the mean daily photosynthesis during the growing season, exclusive of winter months. The confidence limits of the mean are for a 95 % probability (units: g O_2 (mg Chl.*a*)$^{-1}$ d^{-1}).

From the comparison of equations (1) and (2), for a given quantity ΣB of phytoplankton in the euphotic zone, tropical lakes have a daily production 2.7 times higher than that of temperate lakes during the growing season. Annual productions would be approximately 3.3 times higher. We thus have to consider which factors are responsible for such a difference.

Under the assumption that phytoplankton is homogeneously distributed with depth in the euphotic zone, and that the vertical variation in its photosynthesis is dependent on light only, the photosynthetic activity per unit area may be written as:

$$\Sigma A = \frac{A_{opt}}{\varepsilon} F(I) = \frac{B}{\varepsilon} \varphi_{opt} F(I)$$

where φ_{opt} (mg O_2 (mg Chl.*a*)$^{-1}$ h^{-1}) is the photosynthetic activity per unit of chlorophyll under saturating irradiance (or photosynthetic capacity *sensu* HARRIS, 1978), and F (I) a function of the photosynthetic incident light.

A good approximation of F (I) has been proposed by TALLING (1957):

$$F(I) = \ln I'_0 - \ln 0.5\ I_K$$

where I'_0 is the subsurface irradiance and I_K a measure of the onset of light saturation on photosynthesis. Using the same hourly rate φ_{opt}, the daily integral may be written as:

$$\Sigma\Sigma A = \frac{B}{\varepsilon} \varphi_{opt} H(I)$$

with $H(I) = 0.9 (\ln \bar{I}'_0 - \ln 0.5\ I_K) \Delta t$

and $\bar{I}'_0$ the mean hourly irradiance during the day whose length is Δ t hours.

In Lake Chad, φ_{opt} did not vary significantly during the year. Environmental conditions, such as high biomass during the warmer season, may have dampened the effects of temperature variations. The values of φ_{opt} were, for instance, 18.8 during December 1970 and 23.1 in June 1971 in the

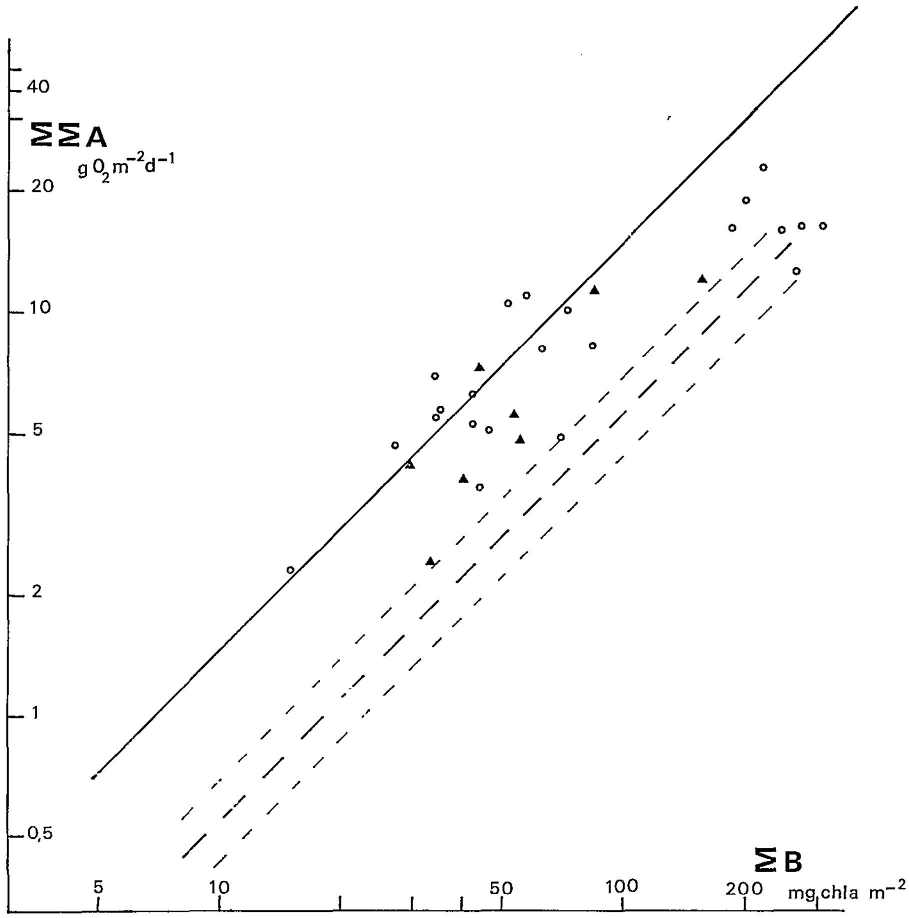

Fig. 2. — Examples of the relationship between ΣΣA and ΣB in some African lakes: annual means (▲) and occasionnal measurements (○). The full line was determined for lake Chad (fig. 1). The dashed line represents the relationship in North American lakes, with the 95 % confidence limits as calculated in the text.

Exemples de la relation ΣΣA = f (ΣB) dans quelques lacs africains: moyennes annuelles (▲) et mesures occasionnelles (○). En trait plein la droite définie figure 1; en tireté, la relation calculée pour les lacs nords américains, avec son intervalle de sécurité tel que défini dans le texte.

Southern basin of the lake, with water temperatures respectively 20 and 30.5 °C, close to the annual maximum and minimum.

A photosynthetic capacity φ_{opt} about 20 (mg O_2 (mg Chl.*a*)$^{-1}$ h^{-1}) may well be considered as representative of many African lakes (Talling, 1965 a; Talling *et al.*, 1973; Ganf, 1974; Robarts, 1979). With the exception of a mean value of 15 in marine coastal waters (Platt and Jassby, 1976), φ_{opt} values above 10 are quite uncommon in temperate waters and likely to be associated with summer temperatures and unusually high nutrient concentrations (Ichimura, 1958; Talling, 1965 b; Bindloss, 1974; Jewson, 1976; Lastein and Gargas, 1978).

This difference between photosynthetic capacities appears to be the main reason for the difference of productivity in the two categories of lakes (Talling, 1965 b). The second possible factor is F (I), with its daily integral H (I). The role of these two functions is to induce only moderate changes of photosynthesis when rapid and large variations of irradiance occur during the day or from one day to another.

Compared with production and biomass data, published results on F (I) are rather scarce but, usually, F (I) is close to 3; for instance 2.85 in Lake McIlwaine, as calculated from the data of Robarts (1979), 1.8 to 2.5 in lakes Kilotes and Aranguadi (Talling *et al.*, 1973), very close to 3 in L. George (Ganf, 1975), 3.46 as a mean for East African lakes (TALLING, 1965 a) and, for temperate lakes, 2.6 in Loch Leven (BINDLOSS, 1974). If a ceiling maximum value is attributed to I_K, due to phytoplankton physiology, high values of F (I) figures could occur in tropical lakes as a consequence of strong midday irradiances. However, this function is also dependent on other environmental characteristics such as the light climate and turbulence in the water mass. An example of such effects is found in Lough Neagh, where F (I) is higher in the open lake (2.6) than in a shallower eutrophic bay (2.2) (JEWSON, 1976). In L. Chad, F (I) does not vary significantly according to seasons, but is influenced by different turbulence and nutrient concentrations associated with different optical characteristics of the water masses: 2.85 in organically coloured waters and 3.45 in clay-laden areas (LEMOALLE, 1979).

The ratio H (I)/F (I), used to convert hourly to daily photosynthetic rates, has a value around 9 and 9.3 in tropical lakes (TALLING, 1965 a; LEMOALLE, 1979). In temperate lakes, its value varies according to day-length. Excluding four winter months, the mean H (I)/F (I) is 13 in Lough Neagh (54° N). In this same lake, for the same period, the mean value of H (I) is 28 or 35 in the bay and in the open lake, respectively. These figures are rather similar to tropical values obtained in L. Chad (26 to 32), in some East African lakes (32), and higher than for L. George (24) (GANF and VINER, 1973).

These examples of H (I) and F (I) values are in agreement with Talling's observations (1965 b). As far as a generalization can be drawn, H (I) does not bring any marked difference between tropical and temperate lakes, at least during the growing season of the latter. The photosynthetic capacity φ_{opt}, is significantly higher in tropical lakes and is responsible for the higher ratio of daily photosynthetic production ΣΣA to the euphotic zone content ΣB.

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