

7. Photosynthetic activity of phytoplankton in tropical African soda lakes

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Introduction

The soda lakes of tropical Africa are recognized as among the world's most productive ecosystems (e.g., Likens 1975; Cole 1979) largely on the basis of the work of Talling *et al.* (1973) and Melack & Kilham (1974). These investigators reported exceptionally high rates of photosynthesis derived from dissolved oxygen changes in bottles and in free water. For example, the maximal photosynthetic rate measured by Talling *et al.* in Lake Aranguadi (Ethiopia) was $30 \text{ g O}_2 \text{ m}^{-3}\text{h}^{-1}$, and a rate of $36 \text{ g O}_2 \text{ m}^{-2}\text{d}^{-1}$ was calculated by Melack & Kilham from diel free water analyses in Lake Nakuru (Kenya). More recently, Melack (1979a) reported similar rates for the phytoplankton of Lake Simbi (Kenya).

As impressive as these reports of high photosynthetic rates are, they include few of the numerous soda lakes of tropical Africa, and do not adequately indicate diurnal, seasonal and annual variability. The purpose of this paper is a comparative analysis of the variability of photosynthetic activity during an 18-month period in four Kenyan soda lakes. Three aspects of the photosynthetic activity of phytoplankton will be presented. First, the diurnal and month-to-month changes in photosynthetic activity in two contrasting lakes, Elmenteita and Sonachi, will be summarized. Second, the photosynthetic rates and phytoplankton abundances in these two lakes and in additional tropical African soda lakes will be compared. Third, the relations among photosynthetic activity, insolation and efficiency of light utilization for tropical soda lakes will be examined.

General features of Kenyan soda lakes

Large, shallow soda lakes occupy the rift valleys

in Ethiopia, Kenya and Tanzania and occur in southern Africa. Small but numerous soda lakes stretch northeast from Lake Chad and are scattered through the eastern and western rift valleys of eastern Africa especially in northern Tanzania and Uganda. In Table 7.1 the major soda lakes or lake districts in tropical Africa are listed by country and, if possible, designated as to broad categories of depth and area. A general description of saline African lakes is available in Beadle (1974). Livingstone & Melack (1981) update Beadle's text and include a summary of biological response to evaporative concentration and of nutrient dynamics in Kenyan soda lakes. Geochemical aspects of saline lakes including those in Africa are treated by Eugster & Hardie (1978).

Geographic and limnological features of the Kenyan soda lakes emphasized in this paper are presented in Fig. 7.1 and Table 7.2. Among these four lakes are represented conditions found in most of the soda lakes of Africa with the exception of the large, deep lakes (e.g., Lake Shala), the seasonal pans and the brines (e.g., Lake Magadi). Lakes Elmenteita and Bogoria are broad, shallow lakes lying in tectonic basins associated with fault scarps. Lakes Simbi and Sonachi occupy small, moderately deep volcanic explosion craters. All four lakes lie in semi-arid basins of internal drainage, and their levels can fluctuate considerably in response to wet and dry seasons and annual differences in rainfall. Long-term rainfall records for Nakuru, a town located near Lakes Elmenteita, Bogoria and Sonachi, indicate the annual variability in water supply (Fig. 7.2). The oscillations in Lake Elmenteita's level from 1958 to 1974 are illustrated in Fig. 7.3. Long-term detailed records of water level are not available for Lakes Bogoria, Sonachi or Simbi.

Table 7.1 Tropical African soda lakes and lake districts. The criteria to include a lake are a pH >9, an alkalinity >20 meq l⁻¹, an electrical conductivity >3 mmho cm⁻¹, and Na⁺ and HCO₃⁻ + CO₃ the predominant ions.

Morphometric divisions: shallow Z_m < 2 m, (sh); intermediate 2 m < Z_m < 15 m, (in); deep Z_m > 15 m, (d); large A > 5 km², (1); small A < 5 km² (sm).

Pans in southern Africa (e.g. Namibia, Zimbabwe-Rhodesia, Botswana, South Africa) are not included.

ETHIOPIA

Bishoftu craters¹: Lakes Aranguadi (sm, d) and Kilotes (sm, in)

Danakil and Afar region: Lake Hertale², Lake Metahara^{3, 4} (sm, sh)

Rift Valley: Lakes Abiata³ (l, in)⁵, Shala³ (l, d)⁵, Chiltu⁶ (sm, d)

SUDAN

Jebel Mara: Large (sm, in) and Small (sm, d) Dariba Lakes^{3, 7}

KENYA

Eastern Rift Valley^{3, 8}: Lake Turkana (l, d); Central Island Crater Lakes (L. Turkana); Lakes Bogoria (l, in); Nakuru (l, sh); Elmenteita (l, sh), Sonachi (sm, in), Magadi (l, sh) Lake Simbi (sm, d)⁹

TANZANIA

Eastern Rift Valley^{3, 8}: Lakes Natron (l, sh), Embagi (sm, d), Magad (Ngorongoro) (l, sh)¹⁰, Manyara (l, in), Balangida, Basotu Crater Lakes⁸, e.g., Ghamar and Gidaburk

Momela Lakes⁸: Kusare, Tulusia, El Kekhotoito, Small Momela, Big Momela (sm, d)¹⁰, Lekandiro, Reshitani (sm, d)¹⁰

Serengeti Lakes⁸: Lgarya (sm, sh) and Ndutu (sm, sh)

Lake Rukwa⁸ North (l, sh)

UGANDA

Katwe - Kikorongo Crater Lakes^{3, 8, 11}: Kikorongo (sm, in), Nyamunuka (sm, sh), Munyanyange (sm, sh), Murumuli (sm, sh)

CHAD

Lake Chad region¹²: e.g., Lakes Bodou, Rombou, Djikare, Mombolo

Sahara¹³: e.g., Lakes in Ounianga Serir and Ounianga Kebir (e.g., Lake Yoan)¹⁴

¹ Prosser *et al.* (1968).

² Pitwell (1971).

³ Talling and Talling (1965).

⁴ Luther and Rzoska (1971).

⁵ Baxter *et al.* (1965).

⁶ Wood (personal communication).

⁷ Hammerton (1968).

⁸ Kilham (1971).

⁹ Melack (1979a).

¹⁰ Melack and Kilham (1974).

¹¹ Arad and Morton (1969).

¹² Maglione (1969).

¹³ Beadle (1974).

¹⁴ Leonard and Compère (1967).

The four lakes lie at moderate altitudes within one degree of the equator and receive consistently high insolation during nearly constant periods of daylight. For example, in 1973 the mean daily insulations \pm one standard deviation in Nakuru and Kisumu, a town near Lake Simbi, were 513 ly \pm 91 ly and 556 ly \pm 74 ly, respectively (calculated from East African Meteorological Dept. data). The water temperatures are warm, and the daily changes are similar to the seasonal variations. A diel cycle of stratification and mixing occurs in Lakes Elmenteita and Bogoria and in the upper two to four meters of Lakes Sonachi (Fig. 7.4) and Simbi. The latter two lakes are meromictic at deeper depths. The lakes' alkaline, saline waters all are above pH 9.5 but vary in electrical conductance and alkalinity by an order of magnitude. Sodium is the principal cation, and SiO₂ and F concentrations are high (Hecky & Kilham 1973). Orthophosphate concentrations in the euphotic zones of the four lakes vary from below detection to several milligrams per liter. In the monimolimnion of Lakes Simbi and Sonachi, 7 mg PO₄ - P · l⁻¹ and 200 µg PO₄ - P · l⁻¹ can occur, respectively. Ammonia concentrations were <50 µg NH₃ - N · l⁻¹ on the few days euphotic zone measurements were made in Lakes Elmenteita, Sonachi and Simbi. In the monimolimnion of Lakes Simbi and Sonachi, 700 µg NH₄ - N · l⁻¹ and 31 000 µg NH₄ - N · l⁻¹ can occur, respectively.

All four lakes were turbid as indicated by the limited Secchi disk visibilities (Table 7.2). In both the deep and the shallow lakes phytoplankton were an important component of the turbidity. For example, Melack (1979a) presented laboratory and field data to show that about 60% of attenuation of photosynthetically available irradiance was caused by *Spirulina platensis* in Lake Simbi.

The biota of African soda lakes includes few species (see Livingstone & Melack 1981, and Beadle 1974), and phytoplankton usually are the major primary producer. Aquatic vascular plants are limited to patches of *Cyperus laevigatus*, but at times, benthic algae can make a substantial contribution to productivity in shallow lakes such as Lake Elmenteita (Melack 1976). *Spirulina platensis* (Norst.) Geitl. occurred as an almost unialgal population in Lakes Simbi and Bogoria, and in a mixed assemblage in Lake Elmenteita. Other numerically important species in Lake Elmenteita included *Anabaenopsis arnoldii* Aptekarj, *Spirulina laxis-*

Table 7.2 Geographic and limnological features of Lakes Elmenteita, Bogoria, Sonachi and Simbi.

	Elmenteita	Bogoria ^a	Sonachi ^b	Simbi
Location	0°27'S 36°15'E	0°15'N 36°06'E	0°47'S 36°16'E	0°22'S 34°38'E
Altitude (m)	1 776	963	1 891	1 142
Area (km ²)	20 ^c	33 ^d	0.18 ^e	0.29 ^f
Zm (m)	1.1 ^g	9 ^h	7 ⁱ	23 ^j
Z̄ (m)	0.9 ^k	5.4 ^h	4 ⁱ	13 ^j
mmho · cm ^{-1(o)} (20 °C)	38 ^l	72 ^m	9.7 ⁿ	18 ^j
Alkalinity ^o (meq · l ⁻¹)	400 ^l	1 500 ^m	105 ⁿ	260 ^j
NH ₄ -N ^o (μg · l ⁻¹)	tr-50 ^p	-	tr ^q	(30) ^j
PO ₄ -P ^o (μg · l ⁻¹)	<3 ^r	3 300 ^s	<3 ^r	2 000 ^j
pH ^o	9.85 ^l	10.2 ^m	9.6 ⁿ	10.55 ^j
Near Surface Water				
Temp. Range	15-28 ^t	24-31 ^u	19-26 ^t	26-30 ^v
Secchi Disk				
Visibility (cm)	12->100 ^w (bottom 100)	28-45 ^x	30-120 ^y	21-70 ^j

^a Previously published descriptions of the lake used the name, Lake Hannington. Name changed by Kenya Government.

^b Previously published descriptions of the lake used the name Naivasha Crater Lake. The Survey of Kenya (Longont, 1:50 000 (Series Y731, sheet 133/4, edition 6-SK), Kenya Government, 1966) refers to the lake as Crater Lake. The local Maasai name for the lake is Sonachi, meaning barren bull but not in the sense of a castrated bull (S. Njuguna, personal communication). To avoid confusion with the Crescent Island Crater in Lake Naivasha and with other crater lakes in Kenya, the name, Lake Sonachi, is recommended.

^c Planimetry of Survey of Kenya maps: Gilgil, 1:50 000 (Series Y731, sheet 119/4, edition 6-SK, Kenya Government, 1971) and Nakuru, 1:50 000 (Series Y731, sheet 119/3, edition 7-SK, Kenya Government, 1970). Same maps used for location and altitude.

^d Planimetry of Survey of Kenya maps: Solai, 1:50 000 (Series Y731, sheet 105/3, edition 5-SK, Kenya Government, 1966) and Ngelesha 1:50 000 (Series Y731, sheet 105/1, edition 6-SK, Kenya Government, 1966). Same maps used for location and altitude.

^e Planimetry of Survey of Kenya aerial photograph V13B-RAF 596 No. 116 taken in 1967.

^f Planimetry of Survey of Kenya map: Kendu Bay, 1:50 000 (Series Y731, sheet 116/3 edition 4-D.O.S., Directorate of Overseas Surveys, 1963). Same map used for location and altitude.

^g Approximate range form February 1973 to August 1974, 0.85 to 1.35 m (Melack, 1976).

^h East African Plunge Project 1972.

ⁱ February 1973 (Melack, 1976).

^j Melack (1979a).

^k Range from February 1973 to August 1974, 0.65 to 1.1 m.

^l 20 April 1974.

^m 13 May 1974.

ⁿ 28 February 1974.

^o Euphotic zone values.

^p May and June 1974; tr means trace, near detection limit.

^q May 1974.

^r Peters and MacIntyre (1976).

^s S. MacIntyre (personal communication), 7 July 1974.

^t Range based on diel measurements each month for 13 months (Elmenteita) spanning 16 months or 10 months (Sonachi) spanning 15 months.

^u Range based on three diel studies and mid-morning to mid-afternoon measurements during one month.

^v Range based on mid-morning to mid-afternoon measurements in five months.

^w Range based on measurements in 16 months spanning 18 months.

^x Range based on measurements in four months spanning 17 months.

^y Range based on measurements in 13 months spanning 17 months.

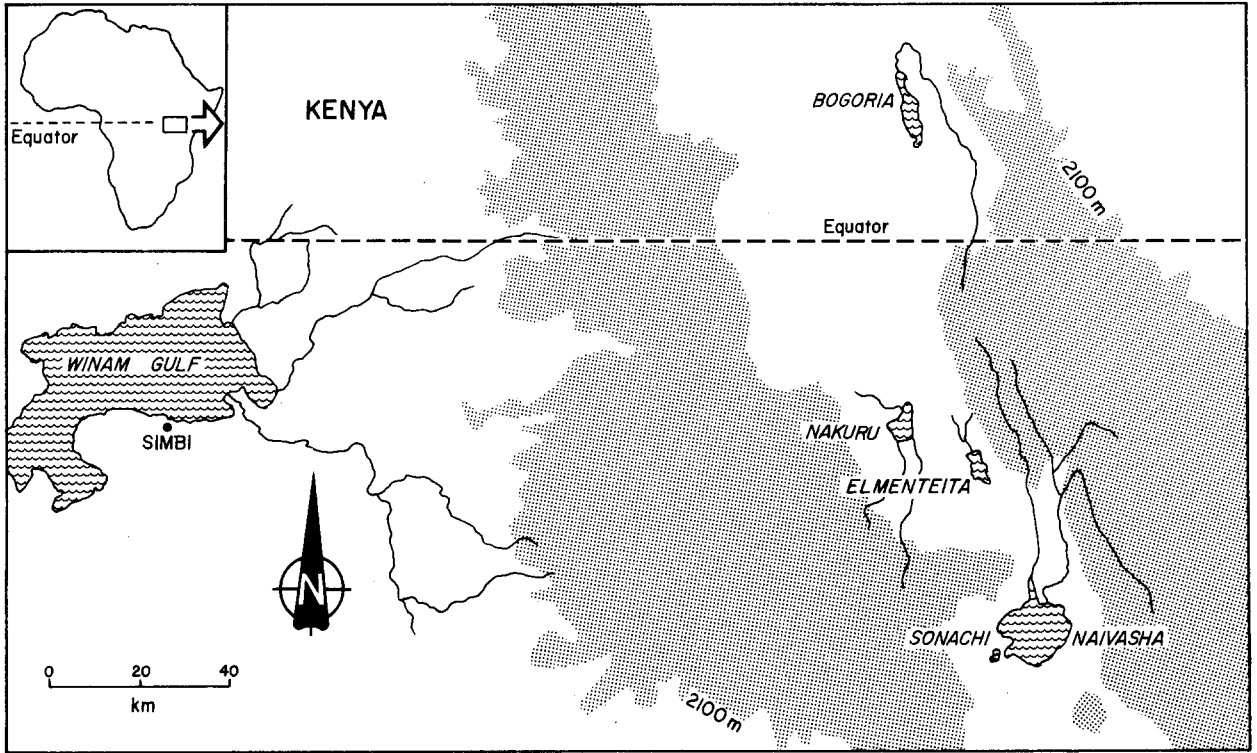


Fig. 7.1 Map of central Kenya with lakes named and major rivers shown. Areas above 2 100 m (stippled) delimit the rift valley; horizontal line bisecting map is the equator. Rectangle in insert locates map on African continent.

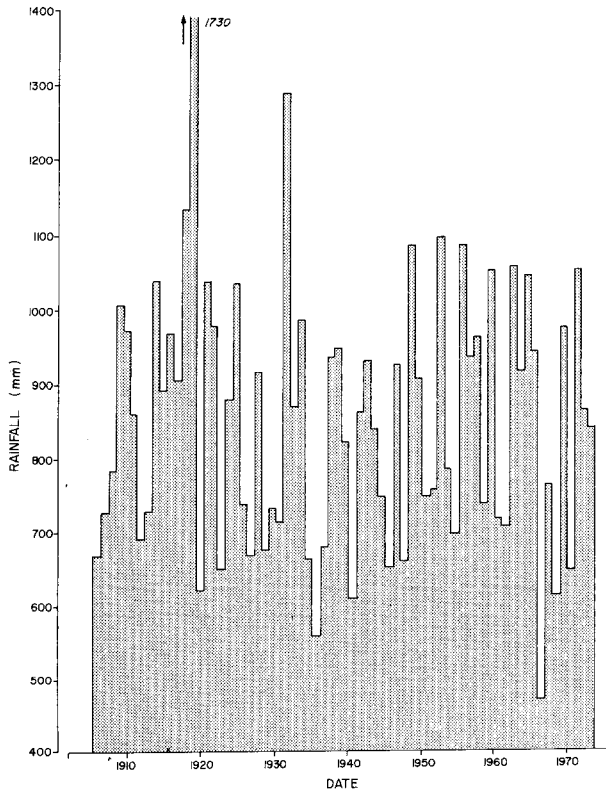


Fig. 7.2 Annual rainfall (1904 to 1972) recorded at Nakuru railroad station (0° 17'S, 36° 04'E; 1 851 m above sea level).

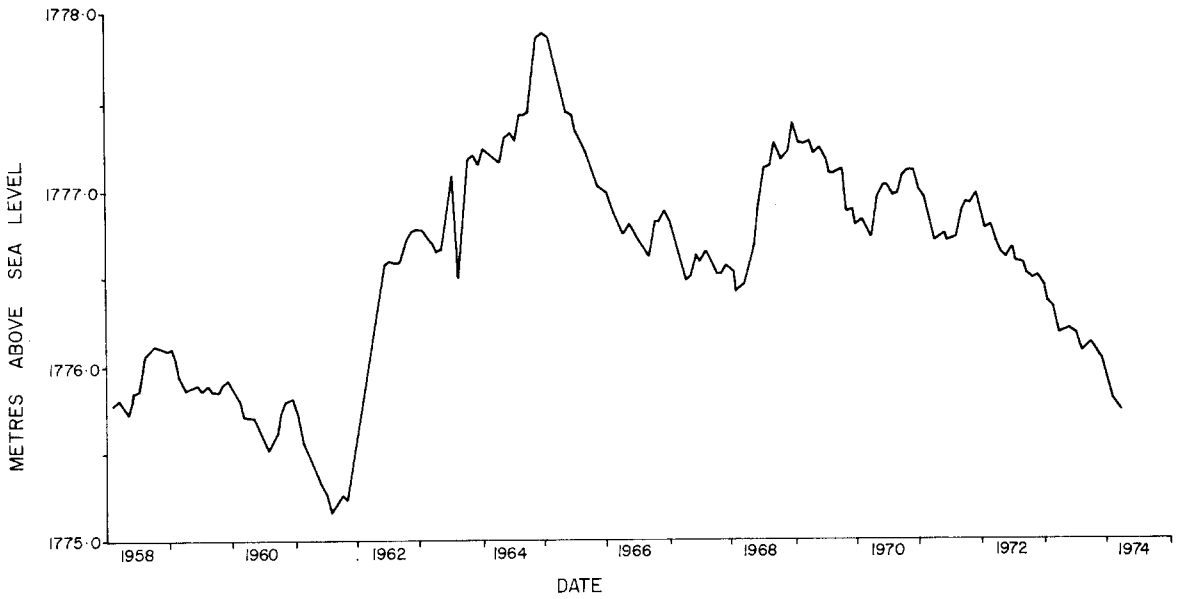


Fig. 7.3 Lake Elmenteita levels, 1958 to 1974. Gauge 2 FA9, Kenya Ministry of Works, Hydrology Section.

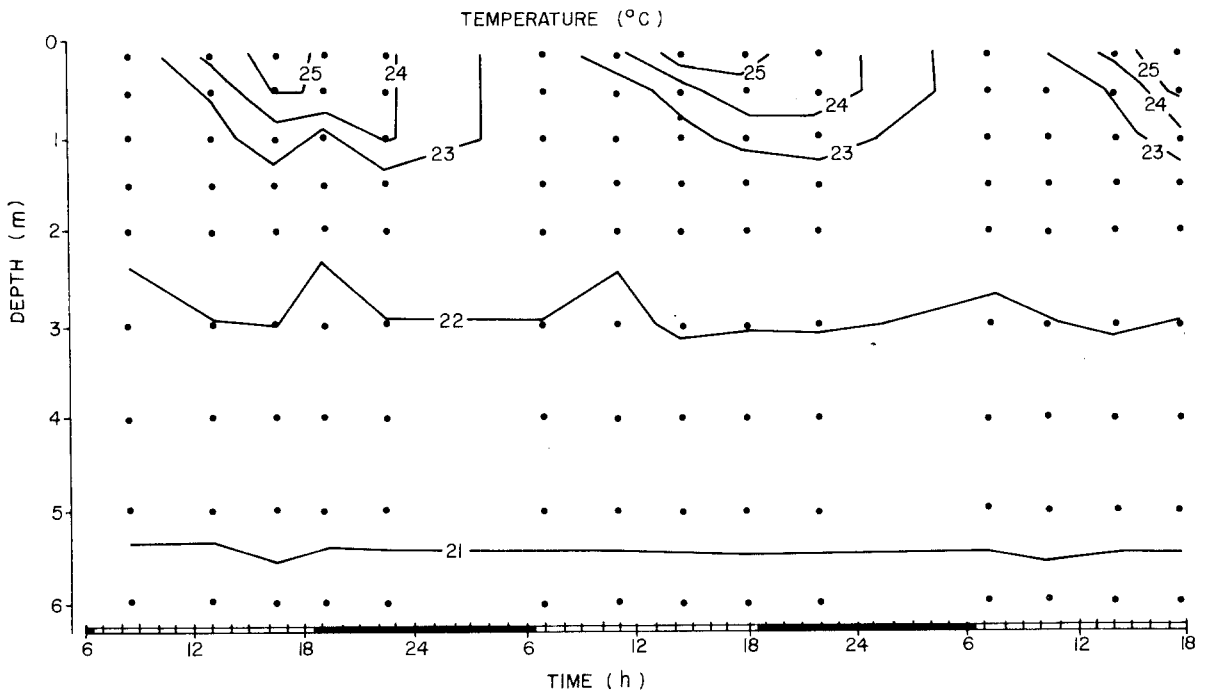


Fig. 7.4 Time depth diagram of temperature, 5 to 7 March 1973, Lake Sonachi.

sima West, G. S., *Selenastrum* sp., *Nitzschia* sp. cf. *latens* Hust., *Nitzschia sigma* (Kutz.) W. Sm., and *Navicula elkab* O. Mull. Lake Bogoria sometimes is dominated by coccoid cyanobacteria (*Aphanocapsa* sp?). Lake Sonachi is numerically dominated by coccoid cyanobacteria and *Spirulina laxissima*.

Methods

Photosynthetic rates were measured as the difference in dissolved oxygen concentration between transparent and opaque bottles. Phytoplankton samples were collected with an opaque, plastic, 2 liter van Dorn sampler modified for horizontal suspension and closure. Two transparent and one opaque borosilicate glass bottles of 300 or 125 ml capacity were suspended horizontally at several depths through the euphotic zone. Dissolved oxygen was measured immediately after the end of an incubation with a Clark polarographic electrode and Yellow Springs Instrument Model 51A meter. The electrode and a battery operated stirrer was inserted directly into each bottle. To improve the accuracy of the dissolved oxygen values other methods were used to calibrate the polarographic electrode. A modification of the Winkler method which reduced the problem of effervescence because a portion of the sample was removed after the manganic hydroxide precipitate had settled but before acidification was used in Lakes Simbi and Sonachi. An improved Miller method (Ellis & Kanamori 1973) was used in Lake Elmenteita. For Lake Bogoria, the modified Winkler and the Scholander microgasometric (Scholander *et al.* 1955) methods were attempted but gave unsatisfactory results, and the improved Miller method did not perform sufficiently well to warrant altering the polarographic electrode's values.

Chlorophyll *a* was determined in 90% acetone extracts of seston collected on Gelman A glass fiber filters following homogenization with a Teflon tissue grinder and a 15 minute extraction in the dark at ca. 20 °C. The optical densities of the extracts were read with a Pye Unicam Model S.P. 600 spectrophotometer and converted to concentrations of chlorophyll *a* using the formulae given in Golterman (1969). Attempts to determine phaeopigments by a acidification with 100 μ l of 4 N HCl (Golterman 1969) usually gave negative phaeopig-

ment values; the reason for these spurious values is explained by Moed & Hallegraeff (1978). Extraction with 90% methanol was also tried but turbidity was excessive after filters were homogenized and extraction was less complete and values were less precise than with acetone.

Incident photosynthetically available irradiance (400–700 nm) was measured with a specially filtered, cosine corrected silicon photodiode (Lambda Instruments Model LI-190S). The millivolt output of the sensor was recorded on a portable chart recorder (Cole-Parmer Mark VII) and calibrated to read in μ Einstein's $m^{-2}s^{-1}$. The chart records were integrated with a digitizer connected to a programmable calculator (Hewlett Packard Model 9864A digitizer and Model 9820A calculator).

Results and discussion

Diurnal and monthly changes in Lakes Sonachi and Elmenteita

The diurnal variations of photosynthetic rates assessed with a series of short term incubations for a full day each month for 11 months in Lake Elmenteita and for 7 months in Lake Sonachi are summarized in Table 7.3. In Lake Sonachi the period from mid-morning to early afternoon (Period A) received more irradiance and had higher but more variable photosynthetic rates than the mid-afternoon (Period B). Afternoon cloudiness is a common feature of the region and may be only cumulus cover but sometimes includes storm clouds and rain. As expected from the well-known non-linear relation between light and photosynthesis (e.g. Jassby & Platt 1976), the variation in photosynthesis is less than the variation in insolation.

The diurnal variations in Lake Elmenteita are subdivided into three intervals and again reflect the tendency for afternoons to be cloudy. During the late afternoon (Period C), light was lower and more variable than earlier in the day, and consequently photosynthetic rates were lower. The two periods that span the time from early morning to mid-afternoon have similar photosynthetic rates, although insolation was higher in Period B.

The month-to-month changes in photosynthesis in Lake Sonachi are illustrated in Fig. 7.5. The rates in March, April and May 1973 were similar, but the

Table 7.3 Diurnal differences in photosynthetic rates in Lakes Sonachi and Elmenteita. Units for insolation are Einsteins per m^2 per h; S.D. means standard deviation. The seven days with photosynthesis data and six days with light data for Lake Sonachi span the period from May 1973–May 1974. The photosynthesis data (A, 10 days; B and C, 11 days) and light data (A and B, 9 days; C, 10 days) for Lake Elmenteita span the period from April 1973–May 1974.

	Period	Time interval		Photosynthesis			Insolation		
		Midpoint	Duration (hr)	ΣA, $mg O_2 m^{-2} \cdot h^{-1}$	Mean	(S.D.)	Range	Mean	(S.D.)
Sonachi	A	1 100	3.7	180–870	520	(210)	4.4–6.4	5.7	(0.8)
	B	1 510	3.8	180–480	330	(100)	0.9–5.3	3.6	(1.7)
Elmenteita	A	0 930	3.1	190–940	475	(260)	2.9–4.8	4.1	(0.7)
	B	1 305	2.7	200–940	460	(240)	6.1–7.7	6.7	(0.5)
	C	1 605	2.7	160–410	290	(100)	1.2–5.3	3.1	(1.3)

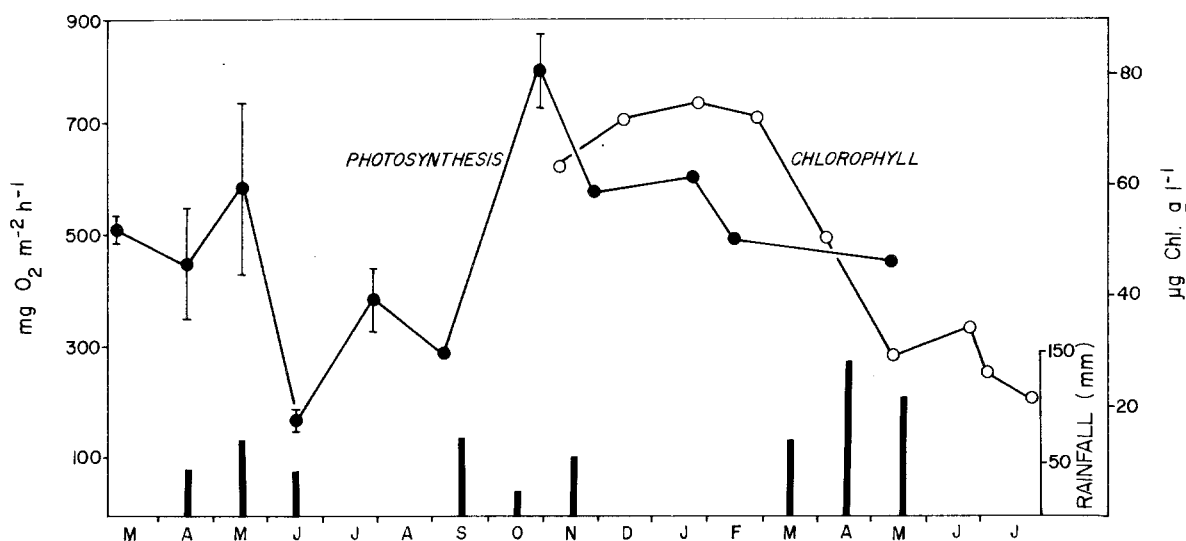


Fig. 7.5 Seasonal variations of photosynthetic rates of phytoplankton ($mg O_2 m^{-2} \cdot h^{-1}$), chlorophyll *a* concentrations ($\mu g chl a l^{-1}$) and rainfall near lake, Lake Sonachi. Vertical bars indicate range of values on adjoining days.

rates declined to only $165 mg O_2 m^{-2} \cdot h^{-1}$ in June before rising to a peak in October 1973. A steady, gradual decline occurred from October 1973 to May 1974. The depth profiles of photosynthesis usually had a maximum in subsurface water and a regular decline in the lower portion of the euphotic zone (Fig. 7.6). Maximum rates of photosynthesis varied from 130 to $850 mg O_2 m^{-3} \cdot h^{-1}$ during the 26 measurements spanning 14 months (Table 7.4).

The chlorophyll *a* concentration in the euphotic zone of Lake Sonachi varied from 29 to $74 mg$ chlorophyll *a* m^{-3} from October 1973 to June 1974.

The vertical distribution of chlorophyll in the mixolimnion usually had less than a two-fold variation during this period. In July and August 1974, the euphotic zone deepened and, as the chlorophyll decreased in the upper water, a deep pigment maximum developed at $4 m$.

In Lake Elmenteita the initiation of a major biological change (Melack 1976; Livingstone & Melack 1981) coincided with a period of rapid lake level decline and evaporative concentration in 1973 (February to April). The conditions continued to change during the subsequent four months. Photo-

Table 7.4 Photosynthetic rates and phytoplankton abundances in tropical African soda lakes. Photosynthetic rates expressed as maximum rates per hour (A_{\max} , $\text{mg O}_2 \text{ m}^{-3} \cdot \text{h}^{-1}$) and areal rates per hour (ΣA , $\text{mg O}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$). Phytoplankton abundances expressed as chlorophyll *a* concentrations (B, $\text{mg chlorophyll } a \cdot \text{m}^{-3}$). Numbers in parenthesis are the number of measurements.

	A_{\max} Range, Mean	ΣA Range, Mean	B Range, Mean
Elmenteita ^{1, 2}	270–5 540, 1 230 (50)	110–1 740, 500 (50)	16–310, 97 (16)
Bogoria ^{1, 3}	640–6 000, 1 900 (7)	280–3 000, 960 (7)	150–800, 350 (4)
Sonachi ¹	130–850, 425 (24)	150–870, 440 (24)	21–68, 45 (9)
Simbi ⁴	950–12 900, 4 200 (8)	620–5 220, 1 900 (8)	120–970, 570 (5)
Nakuru ^{1, 2, 5}	1 100–2 300 (3)	500–800 (3)	140–960, 330 (17)
Aranguadi ^{6, 7}	10 000–30 000 (4)	1 430–2 560 (4)	500–5 000, 2 500 (44)
Kilotes ⁶	4 000–10 000, 6 600 (10)	470–2 400, 1 350 (10)	205–412, 330 (6)
Magad ⁵	1 900 (1)	700 (1)	–
Manyara ⁵	1 300–1 900 (2)	300–600 (2)	–
Reshitani ⁵	2 300 (1)	2 000 (1)	–
Big Momela ⁵	1 900 (1)	1 300 (1)	–

¹ Melack (1976).

² Melack (1979b).

³ E. Vareschi (personal communication).

⁴ Melack (1979a).

⁵ Melack & Kilham (1974).

⁶ Talling *et al.* (1973).

⁷ B. Wood (personal communication).

synthetic rates of phytoplankton declined from $4\,670 \text{ mg O}_2 \text{ m}^{-3} \cdot \text{h}^{-1}$ in February to a nadir of $410 \text{ mg O}_2 \text{ m}^{-3} \cdot \text{h}^{-1}$ in November (Fig. 7.7). Parallel declines in integral photosynthesis ($1\,230$ to $240 \text{ mg O}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$) and chlorophyll *a* concentrations (310 to $16 \text{ mg chlorophyll } a \text{ m}^{-3}$) also occurred. Monthly samples from stations located throughout the lake indicated that the changes were lake-wide. During this period the depth distribution of photosynthesis shifted from profiles with conspicuous subsurface

maxima and narrow euphotic zones to flatter profiles without obvious maxima and with photosynthesis occurring to the bottom (Fig. 7.8). From August 1973 to August 1974 photosynthetic rates and chlorophyll *a* concentrations changed only slightly in comparison to the preceding six months, but a peak in photosynthesis did occur at the onset of the rains in March 1974.

To appreciate fully the amplitude and patterns of variability in photosynthetic activity and to deter-

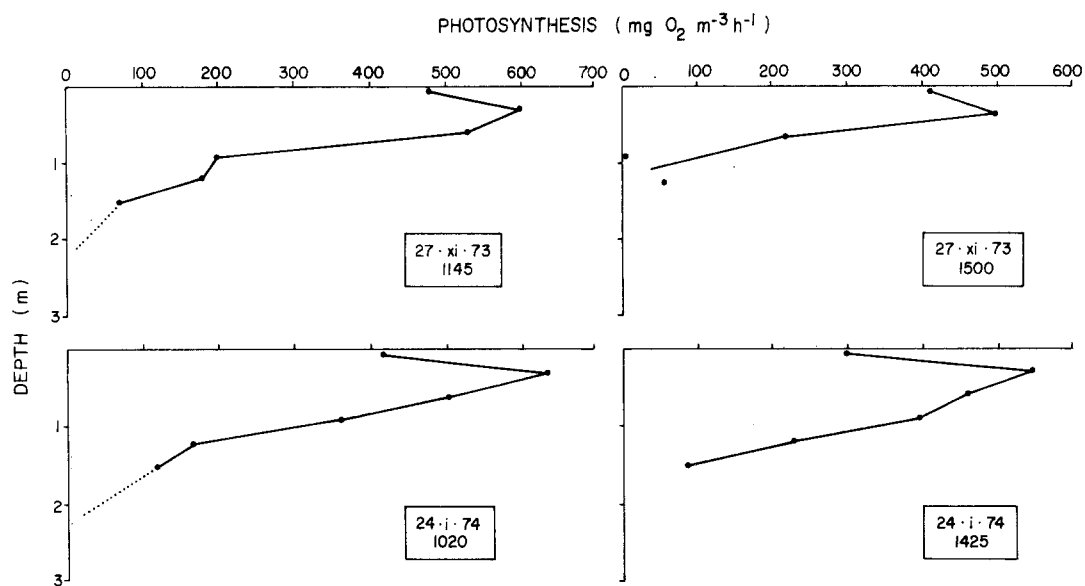


Fig. 7.6 Photosynthesis profiles, Lake Sonachi. Time at midpoint of incubation is listed below date.

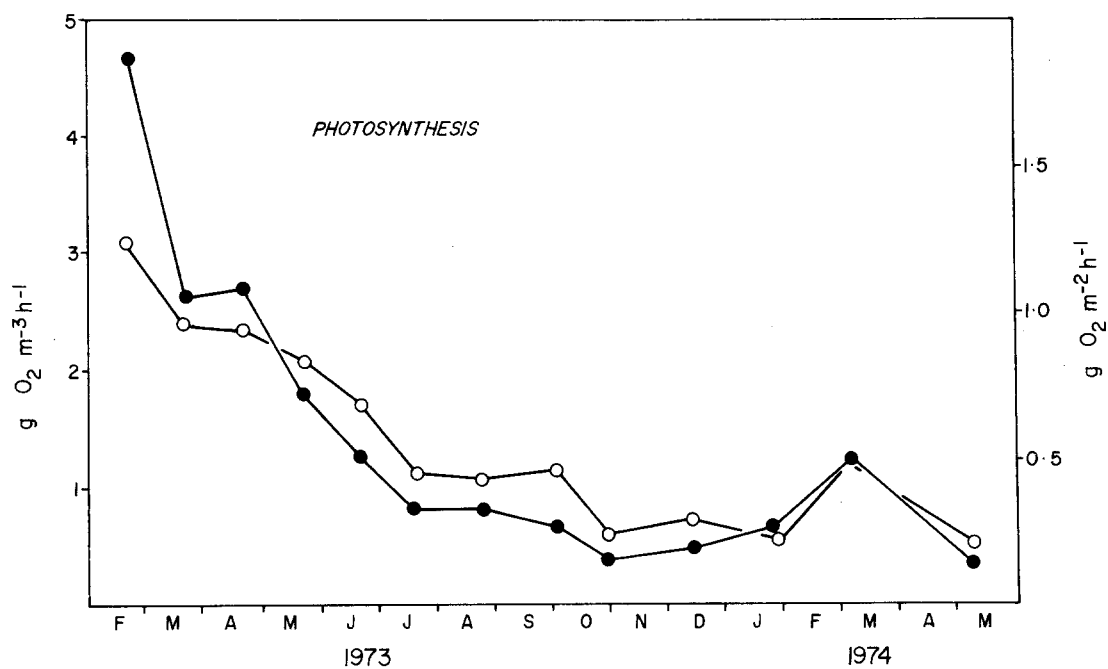


Fig. 7.7 Temporal changes in photosynthetic rates of phytoplankton in Lake Elmenteita. Volumetric rates ($\text{g O}_2 \text{ m}^{-3} \cdot \text{h}^{-1}$, ●) are maximal rates measured during midmorning incubation. Areal rates ($\text{g O}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$, ○) were measured during the same midmorning incubation.

mine how ecological factors influence photosynthesis requires measurements on time scales from minutes to years. The results from Lakes Elmenteita and Sonachi include only time intervals of hours, days and months, but clearly indicate significant variability on these times scales. Melack (1979b) statistically analysed the magnitude of monthly variability in photosynthetic rates in tropical lakes. Among the 26 tropical lakes analysed, the coefficient of variation (CV, standard deviation/mean) ranged from 15% to 86% and no latitudinal trend was apparent. Lakes Elmenteita (CV = 58%) and Sonachi (CV = 37%) are the only two soda lakes

Table 7.5 Efficiency of light utilization (Q, mmoles O₂/Einsteins of Ph.A.R.) by phytoplanktonic photosynthesis in tropical African soda lakes. An Einstein is one mole of photons. The number in parenthesis is the number of measurements.

	Range	Mean
Elmenteita	0.8-12.4 (41)	3.7
Sonachi	1.0-7.2 (18)	3.2
Aranguadi	5.8-16 (3)	
Kilotes	2.4-7.5 (6)	5.7

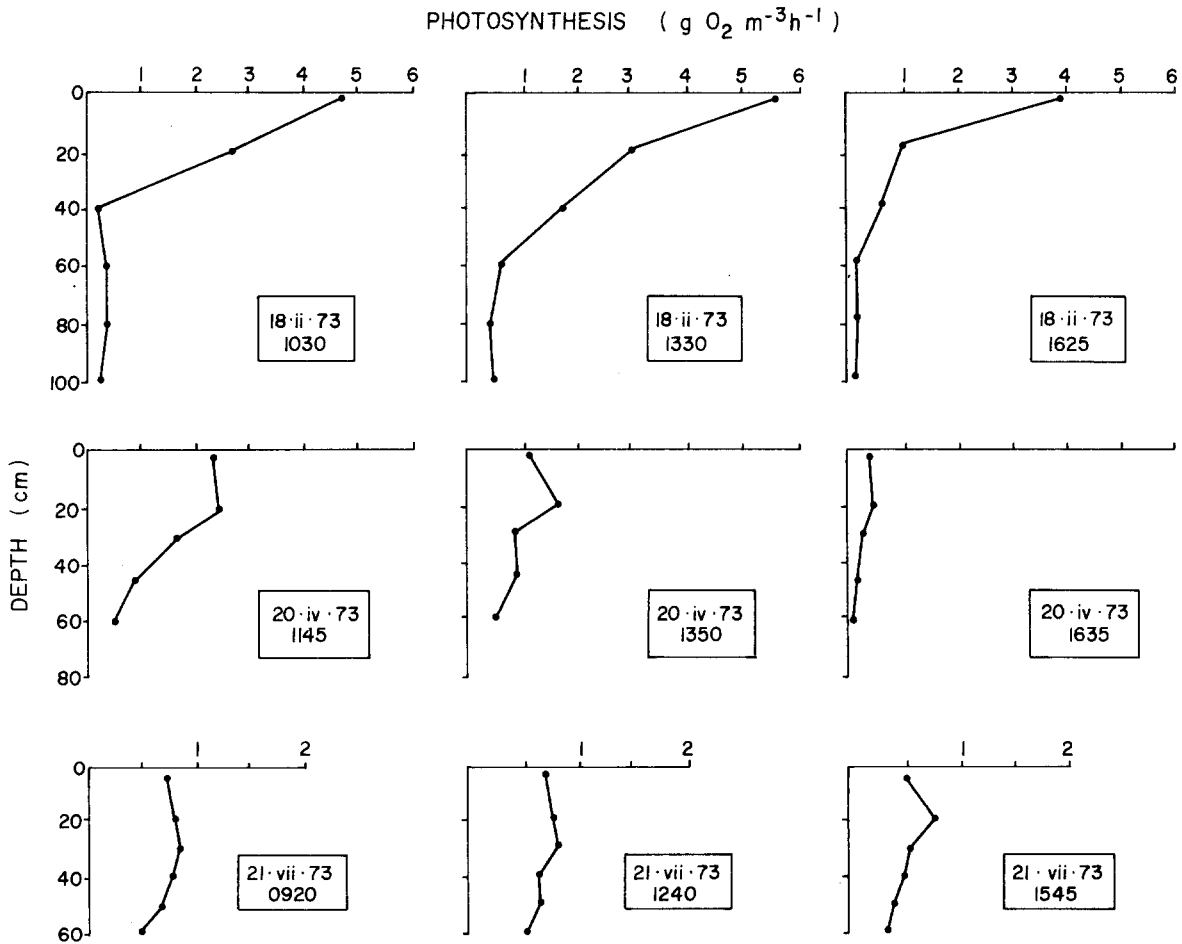


Fig. 7.8 Photosynthesis profiles, Lake Elmenteita. Time at midpoint of incubation is listed below date.

included in this analysis and their CV's are of intermediate value.

Melack (1979b) also included CV's for chlorophyll *a* from nine tropical lakes; the values range from 18% to 108%. Lakes Sonachi (CV = 44%) and Nakuru (CV = 85%) had intermediate to high values. The CV for Lake Elmenteita (108%), if recalculated based on chlorophyll *a* values uncorrected for phaeopigments, is 97% and remains the highest value. If Wood's data for Lake Aranguadi (CV = 51%) are included (Talling *et al.* 1973), a fourth soda lake can be added. If these four CV's for African soda lakes are compared with the CV's for six other tropical lakes (mean CV = 34%), the soda lakes appear more variable.

Photosynthetic activity in tropical African soda lakes

Table 7.4 summarizes the published measurements of photosynthetic rates of phytoplankton in tropical African soda lakes. These data are based on short (ca. 0.5–4 hr) *in situ* incubations of bottled samples. Many of the incubations were within three hours of noon but some were during early morning or late afternoon. If the 89 measurements of Amax made in Lakes Elmenteita, Bogoria, Sonachi and Simbi are compared with the 22 measurements reported in Talling *et al.* (1973) and Melack & Kilham (1974), the latter data appear slightly biased toward high values. The range among the four Kenyan lakes was 130 to 12 900 mg O₂ m⁻³ · h⁻¹, while the range among the other lakes was 1 100 to 30 000 mg O₂ m⁻³ h⁻¹. However, if the integral rates (ΣA) are compared, the values for the four Kenyan lakes bracket the values for the other lakes. Although tropical soda lakes can attain exceptionally high rates of photosynthesis, the low values that occurred in Lakes Elmenteita and Sonachi illustrate that long periods with modest rates of photosynthesis are not uncommon.

One source of variability of these data stems from day-to-day and time of day differences in irradiance. Unfortunately, only a portion of the measurements for four of the lakes (Elmenteita, Sonachi, Aranguadi and Kilotes) included concurrent records of irradiance and permit calculation of the photosynthetic rates per unit insolation. The efficiency of utilization of photosynthetically available irradiance (Ph.A.R.) by photosynthesis was calcu-

lated on a molar basis, i.e. moles of oxygen evolved/ moles of photons of Ph.A.R. incident on the lake surface (Melack 1979c). The advantages of molar units, instead of the usual use of energy units, are that the photosynthetic rates need not be converted by an approximate factor to caloric values, and that the photochemical reactions of photosynthesis depend on the absorption of quanta. Table 7.5 lists the efficiencies of light utilization for the phytoplankton of the four lakes. Although individual values ranged 20-fold among the lakes, the mean efficiencies were similar, especially for Lakes Sonachi and Elmenteita. Relationships among efficiency, light and photosynthesis are presented below.

Unfortunately, all the measurements of photosynthetic rates summarized in Table 7.4 may be systematically biased underestimates. Support for this contention is provided by Talling *et al.* (1973), Melack & Kilham (1974) and Melack (1976, 1979a). These investigators of African soda lakes reported estimates of photosynthesis based on changes in dissolved oxygen in free water substantially in excess of those based on changes in bottles. For example, in nine comparisons of the two methods in Lake Sonachi, free water estimates of daily photosynthetic rates were higher, as much as four times higher, than measurements based on bottled samples. Explanation of such disparities is outside the scope of this paper and remains a controversial area in phytoplankton production ecology (cf. Harris & Piccinin 1977).

The chlorophyll *a* concentrations summarized in Table 7.4 vary over 200-fold. These data are derived from near surface collections and are representative of euphotic zone values but not complete vertical profiles (cf. Melack 1979a). The very high values for Lake Aranguadi may be due to sampling surface scums. However, the consistently high values during a three year period support Wood's contention (personal communication) that the abundance of *Spirulina platensis* seldom was below 1 000 mg chlorophyll *a* m⁻³ in Lake Aranguadi. Among the other lakes the high chlorophyll *a* values (>500 mg chlorophyll *a* m⁻³) were also associated with near unialgal *Spirulina platensis* blooms. Mean chlorophyll concentrations in all the lakes are well above the values usually considered indicative of eutrophic lakes.

Photosynthetic activity in two volcanic crater lakes, Lakes Sonachi and Simbi

In contrast to the low rate of photosynthesis typical of Lake Sonachi, Lake Simbi had exceptionally high rates. A proximate explanation for the disparity is the lower chlorophyll *a* concentrations in Lake Sonachi, and a probable cause for less chlorophyll *a* is a lower rate of supply of nutrients (Schindler 1978). No measurements of nutrient supply are available for either lake, but the large disparity in orthophosphate concentrations (Table 7.2) suggests a difference is likely. Unfortunately, the reason for the probable difference in phosphorus supply is not apparent from the available hydrologic and petrologic information. In 1973, rainfall totalled 1 134 mm at Lake Simbi and 369 mm at Lake Sonachi, but the catchment area of the former is 42 ha (69% of lake's area) and of the latter it is 84 ha (21% of lake's area). The volume of Lake Simbi ($360 \times 10^4 \text{ m}^3$) is greater than that of Lake Sonachi ($65 \times 10^4 \text{ m}^3$). Detailed petrology has not been done in either basin, but the common minerals in the sediment are similar (Table 7.6). Lake Simbi is a fluidisation crater puncturing weathered lacustrine sediments, and Lake Sonachi occupies a volcanic crater formed of an agglomerate.

An alternative or supplement to different rates of nutrient supply from the catchment is different rates of internal regeneration and mixing. Vertical profiles of electrical conductivity, ammonia and phosphate indicated that both lakes were chemically stratified; chemoclines separated monimolimnia rich in dissolved nutrients from the mixolimnia. However, the chemoclines in Lake Simbi were less

Table 7.6 Qualitative X-ray diffraction analyses of surface sediment samples from Lakes Simbi and Sonachi. X-ray diffraction analyses done by Dr. Peter Stoffers. Samples collected by J. M. Melack: Lake Simbi, 21 July 1973, offshore in 14 m deep water; Lake Sonachi, 3 July 1974, offshore in 5 m deep water.

Mineral	Simbi	Sonachi
Quartz	+	+
Microcline	+	+
Orthoclase	+	+
Plagioclase	+	+
Calcite	+	+
Mg-Calcite	+	-
Dolomite	+	-
Illite	+	-

Table 7.7 A morphometric index of mixing potential applied to Lakes Simbi and Sonachi: Mixing Potential (MP) = [(maximum diameter of lake, D)/(minimum height of crater rim above lake, C)] ÷ (maximum depth of lake, Z_m). Z_m for Lakes Simbi and Sonachi is depth of steepest chemocline, not maximum depth. All units are meters, except MP is meters⁻¹.

	Simbi	Sonachi
D	740	625
C	15	50
Z_m	4	4
MP	12	3

steep and relative to the maximum depth were nearer to the surface, and the lake was less protected from winds. The largest waves observed on Lake Sonachi were only about 10 cm high, but 30 cm waves were common in the afternoon in Lake Simbi. Furthermore, the mixing potential (Melack 1978) of Lake Simbi was four times greater than that of Lake Sonachi (Table 7.7).

Although the higher chlorophyll *a* concentrations in Lake Simbi are a satisfactory cause for the higher volumetric rates of photosynthesis, the higher chlorophyll *a* values need not effect higher integral rates of photosynthesis. Two factors could tend to equalize the integral rates in the two lakes. Evidence exists for an inverse relation between the chlorophyll *a* concentration and the photosynthetic

Table 7.8 Depths of euphotic zone (Z_{eu}) and chlorophyll *a* contents of euphotic zone (ΣB) in Lakes Sonachi and Simbi. Columns designated Z_{eu} are based on depth (cm) of 1% of incident light as measured by CdS sensor with peak sensitivity of 550 nm (ΣB) and by quantum sensor which measures photosynthetically available irradiance (Ph.A.R.). Columns designated ΣB (mg chlorophyll *a* m^{-2}) correspond to euphotic zone depth columns with same abbreviations for sensors. Data for Lake Simbi from Melack (1979a).

Lake/date	Z_{eu} 550	Z_{eu} Ph.A.R.	ΣB 550	ΣB Ph.A.R.
Sonachi				
10 Oct. 73	210	150	130	95
16 Dec. 73	210	150	150	110
25 Jan. 74	225	150	160	110
28 Feb. 74	210	145	150	110
12 May 74	330	240	120	90
Simbi				
21 Dec. 73	75	-	650	-
15 May 74	-	37	-	320
17 Nov. 76	-	154	-	200

capacity (i.e. $\text{mg O}_2 \text{ mg chl } a^{-1} \cdot \text{h}^{-1}$) (Findenegg 1965; Wright 1960), but no such inverse relation was observed. The photosynthetic capacity ranged from 7 to 15 in Lake Simbi and from 8 to 14 in Lake Sonachi. Second, the depth of the euphotic zone should become shallower as the chlorophyll *a* concentration increases, especially if the chlorophyll *a* is the principal cause for the attenuation of the light. The euphotic zone was determined as the depth of 1% of the light measured with a CdS photoresistor with peak sensitivity at 550 nm and/or the depth of 1% of the light measured with a silicon photodiode filtered to record photosynthetically available irradiance. An average chlorophyll *a* concentration in the euphotic zone was then used to compute the chlorophyll *a* content of the euphotic zone (ΣB_{eu}). By all criteria for the euphotic zone depth, the values of ΣB_{eu} in Lake Simbi were larger than those in Lake Sonachi (Table 7.8). This difference is owed, in part, to the greater attenuation by non-photosynthetic seston and dissolved substances in Lake Sonachi. Another reason may be that *Spirulina platensis* causes less attenuation per unit increment in density than other types of seston. Melack (1979a) presented laboratory data that do indicate a low attenuation of light per unit chlorophyll for *Spirulina platensis*.

Interrelationships among photosynthetic activity, insolation and efficiency of light utilization

In general, in both aquatic and terrestrial communities, a direct correlation exists between photosynthetic efficiency of light utilization and photosynthetic rates. Based on a comparative analysis of 54 lakes distributed from the Arctic to the tropics, Brylinsky & Mann (1973) reported a correlation coefficient of 0.83 between phytoplankton photosynthetic efficiency (annual gross production/visible incident radiation) and phytoplankton production in the growing season. Based on data from woody and herbaceous terrestrial plant communities distributed from high to low latitudes, McNaughton & Wolf (1973) found the annual primary productivity was directly related to the efficiency of light utilization. In other words, the efficiency of energy transfer increases as primary productivity increases. Regression equations that relate efficiency and photosynthesis in Lakes

Elmenteita, Sonachi, Kilotes and Aranguadi are listed in Table 7.9. A direct relation between ΣA and Q does occur, but the relation is weak for Lake Sonachi (1c), and not strong for the four lakes (1a), the three crater lakes (1b) or Lake Elmenteita alone (1d).

Vertical profiles of efficiency of light utilization usually have a region of increasing efficiency as irradiance decreases (Tilzer *et al.* 1975; Tyler 1975), and the efficiency of integral photosynthesis can show an inverse relation with insolation (Melack 1979c; Hickman & Jenkerson 1978). The efficiency (Q) in the four soda lakes is inversely related to insolation but the regression coefficients are low (Table 7.9, 2a–c). In fact, the only convincing inverse relations are present for the Lake Sonachi (2b) and perhaps Lake Elmenteita if the period of rapid change in February and April 1973 is excluded (2c (1)).

In dense phytoplankton suspensions, such as those typical of African soda lakes, high efficiencies

Table 7.9 Regression equations relating photosynthetic activity, insolation and efficiency of light utilization in Lakes Elmenteita, Sonachi, Kilotes and Aranguadi:

ΣA , integral photosynthetic rate, $\text{mg O}_2 \text{ m}^{-2} \cdot \text{h}^{-1}$.

Q , efficiency of utilization of photosynthetically available irradiance, $\text{mmoles O}_2 \text{ Einstein}^{-1}$.

E , photosynthetically available irradiance (Ph.A.R.), $\text{Einsteins m}^{-2}\text{h}^{-1}$.

ΣB_{eu} , chlorophyll *a* content of the euphotic zone, $\text{mg chlorophyll } a \text{ m}^{-2}$. Euphotic zone measured as the 1% level of the Ph.A.R.

	Equation	Lake
(1a)	$\ln(\Sigma A) = 0.73 \ln Q + 5.24$ $r^2 = 0.51, n = 68$	Elmenteita, Sonachi, Kilotes, Aranguadi
(1b)	$\ln(\Sigma A) = 0.88 \ln Q + 5.14$ $r^2 = 0.58, n = 27$	Sonachi, Kilotes, Aranguadi
(1c)	$\ln(\Sigma A) = 0.46 \ln Q + 5.45$ $r^2 = 0.19, n = 18$	Sonachi
(1d)	$\ln(\Sigma A) = 0.6 \ln Q + 5.3$ $r^2 = 0.44, n = 41$	Elmenteita
(2a)	$Q = -1.82 \ln E + 6.68$ $r^2 = 0.09, n = 68$	Elmenteita, Sonachi, Kilotes, Aranguadi
(2b)	$Q = -1.89 \ln E + 5.88$ $r^2 = 0.46, n = 18$	Sonachi
(2c) (1)	$Q = -2.56 \ln E + 7.17$ $r^2 = 0.20, n = 41$	Elmenteita
(2) (2)	$Q = -1.55 \ln E + 4.91$ $r^2 = 0.38, n = 36$	(excluding Feb. and April 1973)
(3)	$Q = 0.03 (\Sigma B_{\text{eu}}) + 2.0$ $r^2 = 0.34, n = 36$	Elmenteita, Sonachi, Kilotes, Aranguadi

of light utilization are possible because a large proportion of the insolation is absorbed by photosynthetic pigments, and because both surface inhibition and light limitation at depth are reduced per cell as the phytoplankton circulate through the steep light gradient (Tilzer *et al.* 1975). To test for the influence of phytoplankton abundance on efficiency, the chlorophyll *a* content of the euphotic zone was regressed against the efficiency (Table 7.9, 3). In the range of ΣB_{eu} values (12 to 267 mg chlorophyll *a* m⁻²) included in this analysis, no convincing evidence for increased efficiency as ΣB_{eu} increases is present. Unfortunately, the influence of fluctuation in irradiance due to vertical mixing through a light gradient on efficiency cannot be tested based on the measurements of photosynthesis for the soda lakes derived from changes in bottles suspended at a static sequence of depths. However, the importance of vertical mixing even in less dense phytoplankton suspensions is documented (e.g. Marra 1978). Marra reported that vertically cycled bottles gave estimates of integral photosynthesis 19 to 87% higher than estimates from a static series.

Overall, the highest and most efficient photosynthetic rates in tropical African soda lakes occur during blooms of the cyanophyte, *Spirulina platensis*. To understand the ecological constraints on these exceptional photosynthetic rates will require elucidation of the influence of vertical mixing of the phytoplankton through light gradients and of the mechanisms and rates of nutrient supply. Furthermore, actual growth rates and loss rates of the phytoplankton must be measured and integrated into a model of the dynamics of the population abundances.

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