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The annual cycle of primary productivity in Laguna de Río Cuarto, a volcanic lake (maar) in Costa Rica.

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Abstract: The annual cycle of primary productivity of Laguna de Río Cuarto, a tropical lake formed by volcanic activity (maar) in Costa Rica, was measured using the oxygen method. Gross and net primary productivity amounted to 470 and 163 g C m^{-2} y^{-1} respectively. A distinct seasonal variation was observed. Maxima occurred in March / April and September / October, whereas minima were found in July and from December to February. The peak in primary productivity during March and April took place after a period of deeper circulation by which nutrients from the upper part of the hypolimnion were mixed into the photic zone. The carbon budget of the lake is imbalanced since the autochthonous primary productivity does not deliver the amount of organic material necessary to match the heterotrophic processes. The missing quantity, which amounts to at least 110 kg C per day for the whole lake, is transported mainly by leaves and litter from the densely forested rims of the lake.

Key words: Primary productivity, tropical lagoons, nutrient circulation.

Laguna de Río Cuarto is a tropical maar located at 360 m above sea level on the caribbean slope of the Cordillera Volcánica Central in Costa Rica, Central America (Fig. 1). The exact coordinates of the lake are 10° 21'N and 84° 13'W. The surroundings of Laguna de Río Cuarto consist of a rather flat area used mainly for cattle grazing. The lake itself lies in a small depression with very steep side walls of about 30 m height, which are densely covered by a tropical wet forest belonging to the premontane belt transition (Holdrige 1978). No rivers from outside enter the lake, but several small brooklets have their sources in the rim. Thus, the watershed of Laguna de Río Cuarto is less than the lake area itself. A small river originates from the lake and flows into the Río Cuarto.

Fig. 2 shows the shape and the depth isolines of the lake. As a common feature of most maars, the side walls are very steep, thus, the lake reaches great depth a few meters from the shore (Wetzel 1975). The area of Laguna de Río Cuarto amouts to 33.24 hectars and the

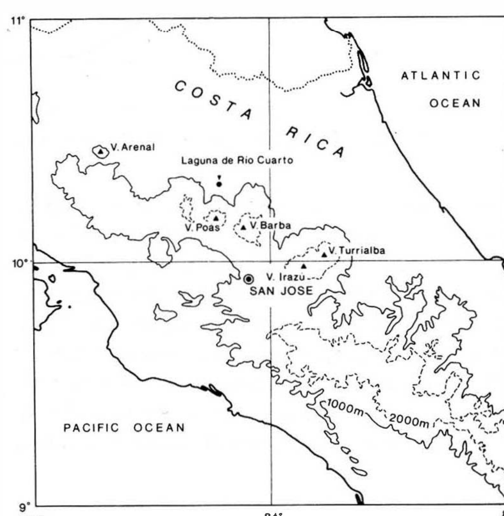

Fig. 1. Location of Laguna de Río Cuarto and main volcanic craters of Central Costa Rica.

greatest depth is 66 meters. A detailed description is given by Gocke *et al.* (1987).

Some information is already available about several limnological aspects of Laguna de Río Cuarto. M. Kohkemper was the first to per-

* CIMAR Contribution 159

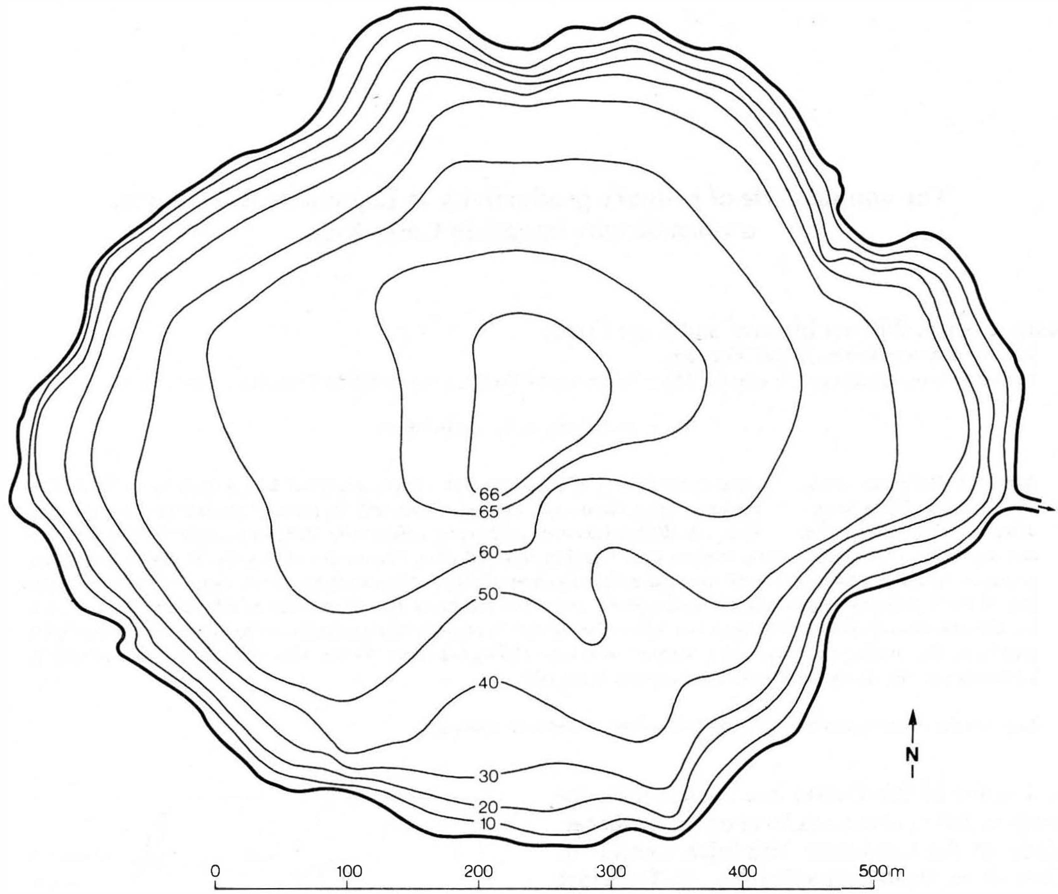

Fig. 2. Bathymetric map of Laguna de Río Cuarto. Depth isolines are given in meters.

form some studies, which were published in 1954 (Kohkemper 1954). Camacho (1985) studied the seasonal distribution of phytoplankton and Ramirez (1985) the zooplankton. Gocke *e t al.* (1987) described morphometric and basic limnological properties. The present paper is intented to add some information about the seasonal variation of the primary productivity in Laguna de Río Cuarto and the factors affecting it.

MATERIAL AND METHODS

Physico-chemical survey. Temperature, oxygen and oxygen deficiency measurements were always performed in the morning between 9:00 and 10:00 in order to minimize the effect of diurnal variations. The water temperature at various depths was determined with a reversible thermometer. Water samples for oxygen, primary productivity etc. were obtained with a Niskin sampler in the center of the lake.

The concentration of dissolved oxygen was measured by the Winkler technique. A highly precise microburette of 0.5 ml total volume allowed the titration to be done in the oxygen bottles themselves (100 ml nominal volume). This method is rapid and precise, since it minimizes the loss of volatile iodine (Green and Carrit 1966, Bryan *et al.* 1976). The 0_2 determinations were always done in duplicates.

The oxygen deficiency was determined according to Andersen and Foyn (1969). Since the technique is described in detail by Grasshoff *et al.* (1983), only a brief account will be given here. As in the oxygen determination, a Winkler bottle is carefully filled with the sample and the Winkler reagents added. In the presence of H_2S these reagents form a precipitate consisting of manganous sulphide instead of the higher valent manganese hydroxides, which are formed when O_2 is present. When the precipitate has settled, 12.5 ml of the clear supernatant liquid are removed. Then exactly 10 ml of a 0.01 n KIO_3 solution (the same, which is used in the Winkler technique for standardizing the thiosulfate solution) are carefully added (inmediately followed by 2 ml of H_2SO_4). From the liberated iodine a part is reduced by oxydizing the sulphides but also other reduced substances. The excess of iodine is then titrated as in the Winkler technique. This method has the advantage that it requires the same reagents as for the oxygen determination. As already stated, the technique not only measures the H_2S but also the concentration of other reduced substances and may therefore be of special interest in biological studies.

Primary productivity. The primary productivity was determined using the oxygen method, also known as "light and dark bottle technique" (Gaarder and Gran 1927). Two clear and one dark bottles (100 ml nominal volume) were incubated at the surface and at 1 m, 2 m, 4 m and 6 m depth. The initial O_2 concentration in these water depths was determined in duplicates. The differences in oxygen concentration due to photosynthesis or respiration were converted into units of organic carbon using a photosynthetic quotient (PQ) of 1.20 and a respiratory quotient (RQ) of 0.83, which means that 1 mg of O_2 produced or consumed equals 0.313 mg of C fixed or respired.

Problems regarding fixed PQ and RQ values are discussed in detail by Oviatt *et al.*. (1986). It is known that the PQ may be as high as 2, especially when nitrate is used as nitrogen source by the phytoplankton (Williams *et al.* 1979). Since, however, ammonia is present at much higher concentrations than nitrate in Laguna de Río Cuarto (Gocke *et al.* 1987) and therefore probably prevails as NH_4 and the low value can be considered to be justified (Parsons *et al.* 1984).

Since it is commonly accepted that the primary productivity between sunrise and noon surpasses that during the second half of the light day (Ohle 1961, Vollenweider and Nauwerck 1961), an incubation period was chosen as proposed by Vollenweider (1974). Accordingly, the time between sunrise and sunset was divided into 5 equal periods and the incubation was made during the second and third period. Since Laguna de Río Cuarto is located near 10^o N where the length of the light day is around 12 hours throughout the year, the exposure was always iniciated about 8:30 and lasted for 5 hours with only minor variations. Taking into consideration that the primary productivity is higher during the first half of the day, the result of 5 h incubation of the light bottles was multiplied only by 2 (instead of 2.4) to give the productivity per day.

Since the terminology of gross and net primary productivity is often quite confusing throughout the literature, a clarification of what is meant in this paper is given here: gross primary productivity per day (PP_G) is the difference in O_2 concentration between the light and dark bottles after 5 h incubation multiplied by 2. Community respiration per day (R) is the difference in O_2 concentration between the dark bottle after 5 h incubation and the initial amount of O_2 multiplied by 4.8 (4.8 is derived by dividing the length of the day by the length of the incubation period). Net primary productivity then is the difference between PP_G per day and R per day.

RESULTS

During the study period the surface temperature oscillated between 29.9 ^oC (May) and 26.4 °C (January). In January and February the upper 15 m were nearly homothermic, whereas between April and June the temperature profile showed a gradual decrease within the epilimnion (Fig. 3a).

Daily temperature fluctuations were measured on two occasions. In August on a cloudy day the surface temperature rose from 27.8 ^oC at 9:00 to 28.2 ^oC at 13:00. Below 4 m no temperature variation was detectable. In October, during a completely overcast day, the surface temperature rose from 26.6 ^oC at 6:00 to 27.5 ^oC at 15:00, after which it decreased. This shows that even though the temperature gradients are small, a slight separation of the epilimnion into two layers may occur during the day, and is probably destroyed during the night.

The temperature below 37 m always remained under 25 ^oC. The lowest value observed was 24.2 ^oC at 60 m. The low bottom water temperature must have originated during periods of anomalous cold weather. These may irregularly occur within intervals of several years. The total temperature range in the lake between surface and bottom is quite small. The vertical density differences due to temperature decrease and slight accumulation of inorganic constituents in the deep water layers (Gocke *et al.* 1987), however, are obviously sufficient to normally prevent a complete mixing of the lake. The wind cannot play a larger role in the mixing process, since the lake is well sheltered by its relatively high and steep rims. Normally, only the upper 25 m of the water column are involved in circulation. Thus, Laguna de Río Cuarto is classified as an oligomictic lake with tendency to meromixis (Gocke *et al.* 1987).

Usually the highest concentrations of dissolved oxygen were found at or near the surface (Fig. 3b). Only in May the highest amount was found at 6 m. During this month a slight thermocline had formed at about 4-5 m, which caused the oxygen produced by photosythesis (even if at 6 m the photosynthesis was quite small) to be trapped and accumulated temporarily.

The oxygen saturation fluctuated seasonally between 85 and 147 % at the surface (Fig. 3c). High values between March and May coincide with maximum primary productivity, whereas low values were observed in July and January, when primary productivity was low, and -at least in January- circulation reached deeper than normally.

Figs. 3b and 3c show that the oxygen concentration usually decreased sharply from high to very low values within a layer of a few meters thickness. The depht of the 75 % saturation

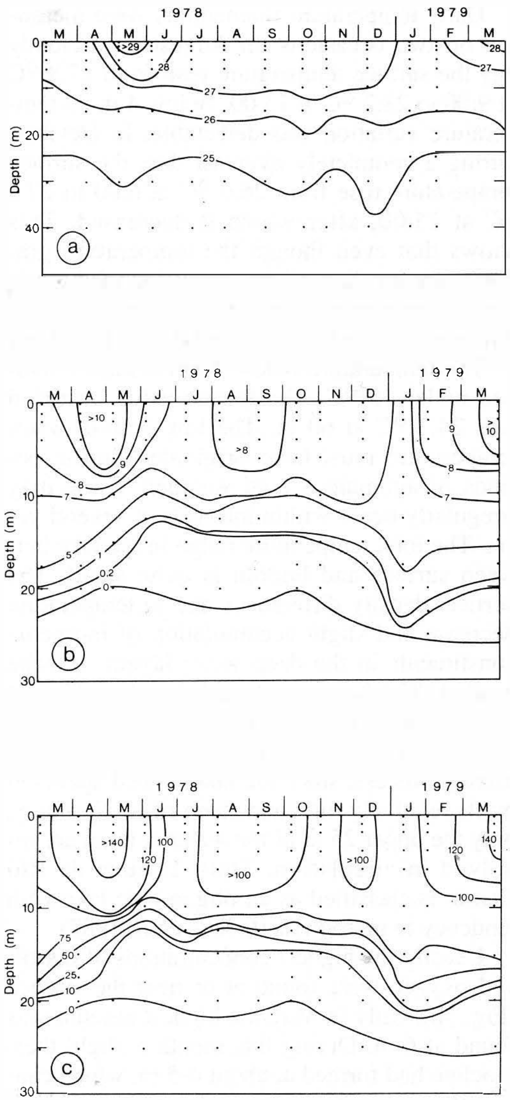

Fig. 3. Time-depth diagram of isotherms (given in ^{o}C) of Laguna de Río Cuarto (3a).
Time-depth diagram of isolines of oxygen (given in mg l^{-1}) of Laguna de Río Cuarto (3b).
Time-depth diagram of isolines of oxygen saturation (given in %) of Laguna de Río Cuarto (ec)

isoline between May and December was near 10m and that of 10 % saturation only about 4-5 m deeper. The depth of the interface between the oxic and anoxic water bodies oscillated seasonally between 20 and 26 m. Below 26 m oxygen was never found.

The oxygen deficiency (expressed in ml of oxygen) varied between 0.13 and 0.56 ml l^{-1} at 40 m and between 0.38 and 0.71 ml l^{-1} at 60 m. A distinct seasonal pattern was not found. The mean values were 0.36 (40 m) and 0.49 ml l^{-1} (60 m). This would be equivalent to 34 and 43 µmol l^{-1} H_2S respectively, if the method used would be specific for H_2S. In January 1986 the H_2S-concentration was measured using the methylene blue method as described by Grass- hoff *et al.* (1983), which is known to be both sensitive and specific. Concentrations of only 5.1 and 5.5 µmol l^{-1} H_2S were observed at 40 and 60m respectively. Even if these concentrations would be considered extremely low, there would be a large gap between the tritrimetrically obtained "H_2S" concentration and the photometrically measured one.Therefore, reducing agents other than H_2S must be present in higher quantities. Such substances, which are measured by the titrimetric method, may be of a different nature, including sulfite and thiosulfate (Broenkow and Cline 1969). Since these oxidized sulfur compounds are probably present in appreciable quantities only at the O_2 / H_2S interface, other substances must be considered. One of these could be ferrous compounds. Though Fe^{2+} was not measured during the cousrse of the study, its presence can be deduced from the heavy yellow-brownish precipitate observed in bottles of hypolimnetic water, which had been exposed to air for some time (Gocke *et al.* 1987).

Fig. 4 demonstrates the depth distribution of net primary productivity during the study period. It is shown that throughout the whole year a light inhibition of the primary productivity occurred at the surface and in most cases extended down to 1 m. Highest values of primary productivity were usually found between 2 and 3 m depth. Except in September the photic zone was not restricted to the first 6 m (where the incubations were performed), but may have extended down to about 8 m.

Mean vertical profiles of net primary productivity and community respiration are shown in Fig. 5. The bulk of the photosynthetic acti-

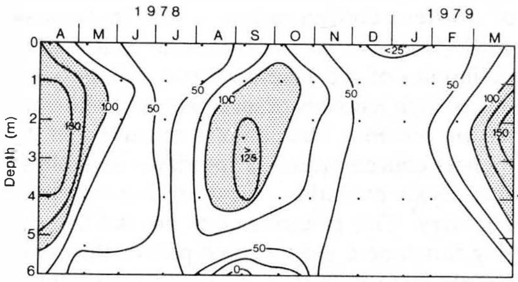

Fig. 4. Time depth diagram of isolines of net primary productivity during 5 h incubation (values are given in mg C m^{-3}).

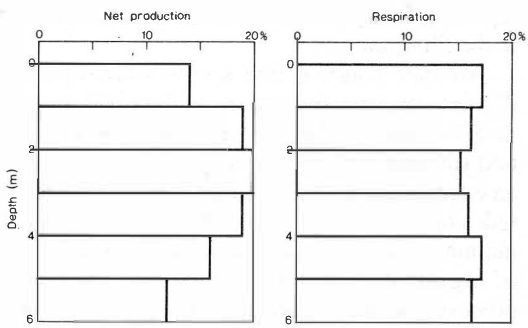

Fig. 5. Mean annual depth distribution of net primary productivity and respiration. The total production and respiration during 5 h incubation integrated for 6 m depth is taken as 100%.

vity was located between 1 and 4 m depth. It is also shown that the primary productivity may have been 7-8 % higher than measured, since the layers below 6 m depth received still a little light to allow at least a small production. The mean vertical profile of the respiration was relatively uniform showing a quite homogenous distribution of the planktonic organisms between the surface and 6 m of water depth.

The seasonal variation of the gross primary productivity per square meter and day is demostrated in Fig. 6, together with the values for community respiration. The latter are the integrated values given for the upper 6 m of the water column. The maximum production rates with values around 2 g C m^{-2} d^{-1} were encountered in March and April. After a gradual decrease and a short minimum in July, a second period of high values was observed from August to November. From December to

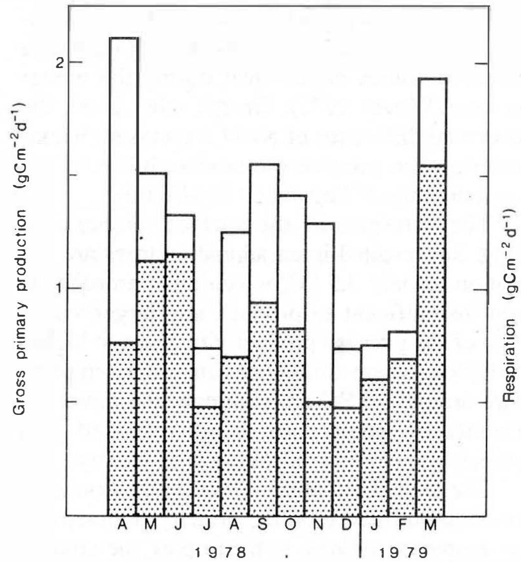

Fig. 6. Integrated gross primary productivity and respiration of the photic layer (down to 6 m). Gross primary produtivity is represented by the total length and respiration by the dotted part of the bars.

February the primary productivity was low again. During this period values around 0.75 g C m^{-2} d^{-1} were found. The community respiration followed the same seasonal pattern as the primary productivity. No fixed relation, however, between production and respiration was found. In April, only about 36 % of the material produced per day by photosynthesis was consumed within the upper 6 m, whereas in June it was 87 % (annual mean 65 %).

Annual gross primary productivity totaled 470 g C m^{-2} y^{-1} and net productivity 163 g C m^{-2} y^{-1}. Mean daily values were 1.29 and 0.45 g C m^{-2} d^{-1} respectively. The mean community respiration in the upper 6 m was 307 g C m^{-2} per year and 0.84 g C m^{-2} per day. Laguna de Río Cuarto can be classified as being eutrophic, but in the lower range of this trophic type.

DISCUSSION

The maximum values of primary productivity throughout the year surpassed the minimum ones by a factor of about 3. This difference is very small compared to that of lakes in the temperate regions, where the productivity during the spring phytoplankton bloom may be a hundred times higher than during the winter season (Wetzel 1975). On the other hand, the observed difference of about 3 seems high considering the relative climatic stability of the surroundings of Laguna de Río Cuarto.

The extremes of the surface temperature (Fig. 3a) resulted in an annual temperature variation of only 3.5 ^{o}C, which most probably is too insignificant to produce any larger variation of the primary productivity. Even at higher latitudes, where differences in water temperature around 20 ^{o}C are common, the direct influence of temperature is not regarded as a principal factor in controlling productivity.

The annual variation of solar radiation is of principal influence on the primary productivity in temperate regions. In the tropics, the amount of radiant energy received by the lake surface is less influenced by small changes in the angular height of the sun troughout the year and seasonal variations in cloud cover are more important. Unfortunately, due to the remotenes of Laguna de Río Cuarto, no data regarding radiant energy are available for the study period. Only the number of hours with sunshine per day measured in the nearby village of San Miguel (6 km distance from the lake, altitude about 100 m higher than the lake) are available. These are reported for 1984 / 85 by Camacho (1985). Number of hours with sunshine varied between < 1 h (minimum) from August to October and > 3 h (maximum values) from December to February. These values may indicate an extreme situation, since data published by the Instituto Meteorológico Nacional for comparable locations further away do not show periods with less than 1 h of daily sunshine. However, even if in 1978 / 79 such a relative great annual variation in sunshine had existed as for 1984 / 85, solar radiation cannot be the reason for the observed annual variation in primary productivity. This can be precluded since highest radiation values coincide with low ones of productivity and vice versa.

If temperature and light are excluded as principal factors in governing the seasonal variations in primary productivity of Laguna de Río Cuarto, it is possible that the availability of nutrients plays a major role. No determinations of nutrients could be performed during the study period. Nevertheless, the vertical profile of nutrient concentrations taken in January 1986 (Gocke *et al*. 1987) indicate that the hypolimnion of the lake acts as a a large sink, where high amounts of ammonia and phosphates are present. The authors conclude that the highest concentrations of nutrients avilable to the algae probably exist in January and February. This is attributed to the fact that during this time a considerable part of the upper hypolimnion with its high nutrient concentrations is mixed into the photic zone (see Figs. 3a and 3c). This then stimulates the phytoplankton and causes the highest primary productivity to occur in March and April. Lewis (1973, 1974) came to similar conclusions when studying the primary productivity of Lake Lindanao in the Philippines.

Another point, which seems worthwile to discuss concerns the carbon budget of Laguna de Río Cuarto. The light and dark bottle method (though not modern at first glance), offers an excellent opportunity to compare the magnitudes of the production and destruction of organic material in a lake. The mean daily amount of organic carbon produced by photosynthetic processes in the Laguna de Río Cuarto was determined as 1.29 g C per square meter down to 6 m depth.

Since the productive zone reached a little bit deeper (Fig. 5), the mean daily gross productivity will be about 1.38 g C m^{-2} d^{-1}. Due to the very steep shores of the lake the volume of the total photic zone is nearly identical with the product of the surface area of Laguna de Río Cuarto multiplied by the depth of its photic layer. This makes the calculation of the organic material produced in the whole lake quite simple, that is 458 kg C per day. Since the mean vertical distribution of respiration in Laguna de Río Cuarto is almost uniform between the surface and 6 m depth (Fig. 5), it seems safe to assume that this homogenous distribution is not restricted to only this layer but may reach further downwards. If this is presumed to reach the depth of 75 % oxygen saturation, which is situated at 12.2 m depth (annual mean), the amount of respired organic carbon would be 1.71 g C m^{-2} d^{-1}. Calculated for the whole lake 568 kg C is respired per day between the surface and 12.2 m. Our respiration measurements could not distinguish between O_2 consumption due to breakdown of organic material and chemical or microbiological oxydation of reduced inorganic substances. The latter process, however, is considered to be small. Therefore, even if the value of 568 kg C represents an overestimation, the error probably is relatively small. This means that the carbon budget is unbalanced since daily consumption by the plankton community exceeds phytoplankton daily production by 110 kg calculated for a year the difference would amount to 40 tons of organic carbon or to about 80 tons of organic dry matter. This is a very conservative figure since processes by which organic material is degraded are definitely not confined to the layer between the surface and the depth of the 75 % oxygen saturation but occur also in the anoxic hypolimnion and the sediment.

Such discrepancies between the amounts of material produced and consumed are a common feature within many lakes (Wetzel and Otsuki 1974, Overbeck 1982, Heyer and Babenzien 1985). In some cases a densely developed phytobenthos may fill the gap. This, however, is impossible in Laguna de Río Cuarto, since the phytobenthos, consisting almost entirely of *Chara* sp., is most probably not very significant in the lake due to the steep shores. Therefore, we assume that the carbon budget is balanced by dissolved and particulate organic material of terrestrial origin. This assumption is supported by the observation that a substancial part of the lake sediment consists of leaf and litter debris. Obviously this material is produced in the densely forested steep rims of the lake, from where it is easily washed in by the heavy rainstorms of the region. According to the concept developed by Odum (1956) and Cole (1975), Laguna de Río Cuarto belongs to the "heterotrophic" type, since, despite the relatively high autochthonous primary productivity, the "metabolism"of the lake depends partly on its surroundings.

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RESUMEN

Se estudió el ciclo anual de la productividad primaria en la Laguna de Río Cuarto, un maar tropical en Costa Rica, usando el método de las botellas claras y oscuras. La productividad primaria bruta ascendió a 470 y la neta a 163 g C m^{-2} a^{-1}. Se observó una variación estacional característica con picos en marzo / abril y setiembre / octubre. Valores mínimos se encontraron en julio y entre diciembre y febrero. El pico de la productividad primaria durante marzo y abril ocurrió después de un período de circulación más profunda de la laguna, la cual causó que los nutrientes de la parte superior del hipolimnion llegaron a la capa eufótica. El "carbon budget" de la Laguna de Río Cuarto no es balanceado, ya que la productividad primaria autóctona no puede suministrar la cantidad de materia orgánica necesaria para los procesos heterotróficos. Existe un déficit de por lo menos 110 kg de carbono orgánico por día para el lago entero y esta cantidad llega a la Laguna de Río Cuarto en forma de hojarasca originada de las orillas densamente arboladas.

REFERENCES

Andersen, A.T. & L. Foyn. 1969. Determination of hydrogen sulphide, p. 127-130 *In:* R. Lange (ed.). Chemical Oceanography, Universitetsforlaget, Oslo.

Broenkow, W.W. & J.D. Cline. 1969. Colorimetric determination of dissolved oxygen at low concentrations. Limnol. Oceanogr. 14: 450-453.

Bryan, J.R., J.P. Riley & P.J. leB. Williams. 1976. A Winkler procedure for making precise measurements of oxygen concentration for productivity and related studies. J. Exp. Mar. Biol. Ecol. 21: 191-197.

Camacho, V.L. 1985. Occurrencia y distribución vertical de las algas planctónicas del Lago de Río Cuarto, Alajuela, Costa Rica. Tesis de Licenciatura, Universidad de Costa Rica. 44 p.

Cole, G.A. 1975. Textbook of limnology. The C.V. Mosby Company. Saint Louis. 283 p.

Gaarder, T. & H.H. Gran. 1927. Investigations of the production of plankton in the Oslo Fjord. Rapp. et Proc. Verb., Cons. Internat. Explor. Mer. 42: 1-48.

Gocke, K., W. Bussing & J. Cortés. 1987. Morphometric and basic limnological properties of the Laguna de Río Cuarto, Costa Rica. Rev. Biol. Trop. 35: 227-285.

Grasshoff, K., M. Ehrhardt & K. Kremling. 1983. Methods of seawater analysis. Second revised and extended edition. Verlag Chemie, Weilheim. 419 p.

Green, E.J. & D.E. Carrit. 1966. An improved iodine determination flask for whole bottle titration. Analyst. 91: 207-208.

Heyer, J. & H.D. Babenzien. 1985. Untersuchungen des Methankreislaufes in einem oligotrophen See (Stechlinsee). Limnologica (Berlin) 16: 267-276.

Holdridge, L.R. 1978. Ecología basada en zonas de vida. IICA, San José, Costa Rica. 77 p.

Kohkemper, M.J. 1954. Bosquejo limnológico de la Laguna del Misterio. Tesis de Grado. Universidad de Costa Rica.

Lewis, W.M.Jr. 1973. The thermal regime of Lake Lindanao (Philippines) and its theoretical implications for tropical lakes. Limnol. Oceanogr. 18: 200-217.

Lewis, W.M.Jr. 1974. Primary production in the plankton community of a tropical lake. Ecol. Monogr. 44: 377-409.

Odum, H.T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102-117.

Ohle, W. 1961. Tagesrhythmen der Photosynthese von Planktonbiocoenosen. Verh. Int. Verein. Limnol. 14: 113-119.

Overbeck, J. 1982. Bakterien und Kohlenstoffumsatz im Pluss-See Probleme und Möglichkeiten der Mikrobenökologie. Forum microbiol. 5: 592-303.

Oviatt, C.A., D.T. Rudnick, A.A. Keller, P.A. Sampou & G.T. Almquist. 1986. A comparison of system (O_2 and CO_2) and C-14 measurements of metabolism in estuarine mesocosms. Mar. Ecol. Progr. Ser. 28: 57-67.

Parsons, T.R., M. Takahashi & B. Hargrave. 1984. Biological oceanographic processes. Pergamon Press, Oxford. 330 p.

Ramirez, R.E. 1985. Variaciones estacionales de la comunidad zooplanctónica del Lago de Río Cuarto, Alajuela, Costa Rica. Tesis de Licenciatura, Universidad de Costa Rica. 49 p.

Vollenweider, R.A. 1974. Methods for measuring production rates, p. 51-150. *In* R.A. Vollenweider (ed.). Primary production in aquatic environments. 2nd edit. IBP Handbook No. 12. Blackwell Scientific, Oxford. 225 p.

Vollenweider, R.A. & A. Nauwerck. 1961. Some observations on the C-14 method for measuring primary production. Ver. int. Ver. Limnol. 14: 134-139.

Wetzel, R.G. & A. Otsuki. 1974. Allochthonous organic carbon of a lake. Arch. Hydrobiol. 73: 31-56.

Wetzel, R.G. 1975. Limnology. Second Ed. Saunders, Philadelphia. 743 p.

Williams, P.J. leB, R.C.T. Raine & J.R. Bryan. 1979. Agreement between 14 C and oxygen methods of measuring phytoplankton production: reassessment of the photosynthetic quotient. Oceanol. Acta 2: 411-416.