Oxygen consumption patterns in a mangrove swamp on the Pacific coast of Costa Rica

by

Klaus Gocke*, **, Marcella Vitola* and Gilberto Rojas*

Abstract: Measurements of the oxygen consumption of the suspended organisms, the sediment biota and the prop root-epibiont system were made to determine the rate of decomposition of organic material in a mangrove swamp on the Pacific coast of Costa Rica. The tidal range in this area is about 2.5 m. The sediment consists mainly of clay with 12-15% organic material. The dominant mangrove species bordering the swamp channels was *Rhizophora mangle*. The O_2 consumption in the free water varies between 35 and 47 mg $m^{-3} h^{-1}$. The oxygen uptake of the sediment lies between 8.4 and 37.2 mg $m^{-2} h^{-1}$. The respiration of the root-epibiont system depends on the position of the root in relation to the low water line. Values between 0.65 and 29.5 mg $O_2 h^{-1}$ per 1000 cm^2 of root surface have been recorded.

In a transect between two tidal channels the O_2 consumption per sediment surface area and the percentage consumption by the three subsystems show a great range of variation depending mainly on the water depth at high tide and the period of water coverage. The mean oxygen uptake per square meter was 1310 mg per day. Of this 40.5% was consumed by the organisms suspended in the water column, 13.5% by the sediment biota and 46% by the epibiotic community on the prop roots. Thus, the decomposition of organic material would be about 410 mg $C m^{-2} day^{-1}$ (mean value).

Mangrove swamps are one ot the most fertile ecosystems (Golley *et al.,* 1962; Hicks and Burns, 1975, Hernández and Mullen, 1975; a summary of the literature has recently been published by Teas, 1979). A unique feature of this biotope is that there is very limited direct utilization of the produced plant material by terrestrial herbivores (Heald, 1969). It can be easily seen that only very few leaves of *Rhizophora mangle* are damaged by insects. The same holds true for the recently fallen leaves which are still floating on the channels of the swamps. Heald (1969) recorded the annual litterfall in a mangrove biotope of Florida as 352 g C m^{-2}. This material enters the aquatic food chain via stepwise decomposition and reduction in size to detritus particles and dissolved organic substances. Part of the leaf material is carried out of the mangrove system by currents and transported into the adjacent coastal zones. Golley *et al.* (1962) demonstrated a net export of particulate organic material from a Puerto Rican

---

* Centro de Investigaciones en Ciencias del Mar y Limnología, Universidad de Costa Rica.
** Present address: Institut für Meereskunde, 23 Kiel, West Germany.

mangrove swamp of 2.27 g dry weight per square meter of mangrove area per day. Odum and Heald (1972) found that at least half of the leaves produced in a Florida mangrove system is transported into the surrounding coastal zones in the form of detritus. Hence, as in many salt marshes (Odum and De la Cruz, 1967), the importance of the mangrove areas is partly due to the export of organic material produced in excess. These substances may influence the overall productivity of the coastal waters.

Even though a great part of the material produced by the mangroves is transported out of the system, sufficient material remains to support a high rate of decomposition activity in the mangrove swamp itself. This is clearly indicated by the temporal fluctuation of the oxygen concentration in the channels of the mangrove swamps (Walsh, 1967; Untawale et al., 1977). Measurements in the Estero de Morales revealed that the O_2 concentration of the water is related to the tides. The maxima and minima always run parallel to the high and low tide. This suggests that the oxygen production due to the primary production of the phytoplankton and the sessile algae cannot compensate the strong O_2 consumption due to decomposition processes. However, the influence of the aquatic primary production was evidenced by the differing O_2-maxima and minima of the tidal cycles for the light and dark periods.

The aim of the present study was to measure the total oxygen consumption per unit area in the *Rhizophora mangle* fringe of a mangrove swamp during the period of its submergence. In addition a determination should be attempted to find out how much of this consumption is due to the respiration of the organisms suspended in the water, how much to the sediment biota and how much to the epibiotic organisms on the prop roots of the mangroves (Fig. 1). From these data the decomposition of organic material per area can be calculated.

MATERIAL AND METHODS

Study area: The Estero de Morales, the main study area, is located on the east coast of the inner part of the Golfo de Nicoya ($10^{\circ}5'$ N and $84^{\circ}57'$ W, Fig. 2), a highly productive water basin on the Pacific coast of Costa Rica. The tide is semi-diurnal with a mean tidal range of 2.5 m. The general features of the Golfo are given by Peterson (1960).

About 2/3 of the shore line of the inner part of the Golfo is covered with mangrove swamps. The mangrove swamp of the Estero de Morales has an area of 327 ha (Fig. 2). The shore line of the outer region and the fringes of the entire channel system are occupied by *Rhizophora mangle,* and on the landward side, by *Avicennia nitida, Laguncularia racemosa* and *Conocarpus erectus* occur infrequently. With only few exceptions the mangroves of the Estero de Morales form a scrub vegetation not higher than 4-5 m. This is unusual for the mangrove swamps of the Golfo de Nicoya, where the mangroves are normally large trees (Pool et al., 1977).

Fresh water enters by the Quebrada Grande, a small creek which is nearly dry during the dry season. It responds rapidly to rainfalls rising and subsiding within a very short time. Thus, even during the rainy season the main influence of the Quebrada Grande on the salinity of the Estero is limited to short periods after heavy rainfall. The salinity values obtained lie between 25 and 35 $^{\circ}/oo$. In general the salinity of the mangrove swamp runs parallel to the salinity of the Golfo de Nicoya.
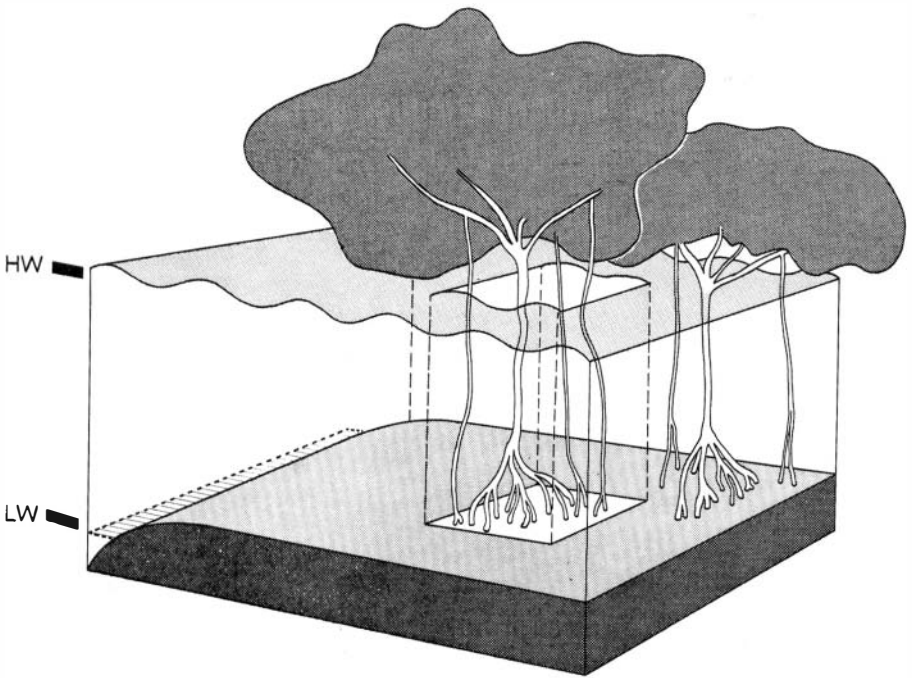
Fig. 1.   Diagrammatic section of a mangrove swamp showing the three subsystems: sediment, prop roots of *Rhizophora mangle*, and water column above a square meter. HW = high water mark, LW = low water mark.

The argillaceous sediments near the channels contain 12-15 % of organic material.

Chemical and biological methods: The oxygen concentrations of the water samples were determined by a micro-Winkler technique. Titration was performed by means of a micro-burette (0.5 ml) in the O_2-bottles (100 ml nominal volume) themselves. This is a rapid yet precise technique (Green and Carrit, 1966; Bryan *et al.*, 1976).

Oxygen uptake of suspended organisms: Oxygen uptake of the organisms suspended in the water column was measured in water bottles of 100 ml volume wrapped in black plastic and aluminum sheets to ensure total darkness. The samples were taken in the main channel of the mangrove swamp at different times of the tidal cycle thus accounting for the changing turbidity of the water. They were incubated *in situ* for 5 hours.

Oxygen uptake of the sediment biota: O_2-consumption of the total sediment community was determined by taking at least 3 cores of sediment per square meter by means of clear acrylic cylinders (Fig.3). The soft consistence of the substrate
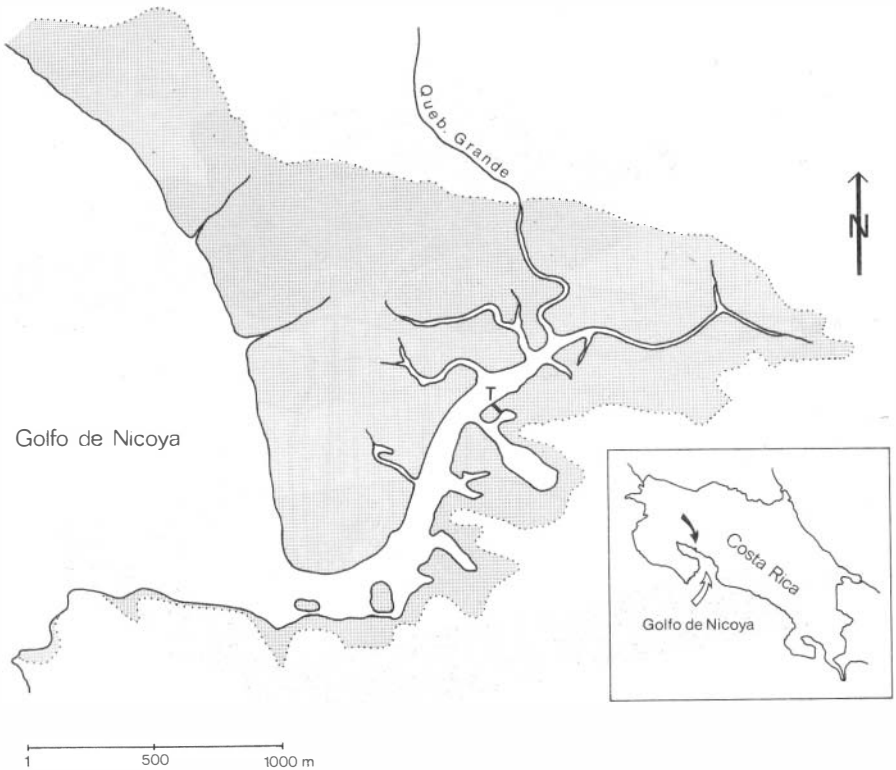
Fig. 2.   The mangrove swamp (shaded area) of the Estero de Morales showing the location
             of the transect (T). The black arrow on the map of Costa Rica points to Estero de
             Morales.

allowed cores to be taken without disturbing the sediment surface. All the cores
were taken at low tide when the sediment was exposed to air and were processed
within 1/2 hour in the laboratory. The sediment inside the cylinders was covered by
1-2 cm of water from the swamp and incubated for 1 hour at *in situ* temperature in
the dark. This pre-incubation proved to be necessary to fill the holes of the fiddler
crabs with water, so that during the following incubation escaping air would not
disturb the measurement. The water was then discarded. The cylinders were then
totally filled with water from the main channel. This entered gently through a
flexible tube immediately above the sediment surface. A second tube at the top
center of the acrylic cylinder served to pass the water into a glass bottle for
determination of the initial O_2 concentration. After sufficient flushing the cylinders
were sealed and incubated at *in situ* temperature in darkened insulation boxes filled
with sea water. After 5 hours of incubation the overlying water in the cylinders was
gently mixed by means of a propeller without disturbing the sediment surface. This
was necessary to destroy any possible oxygen concentration gradient (Hargrave,
1969). A second glass bottle for the final O_2 concentration determination was then
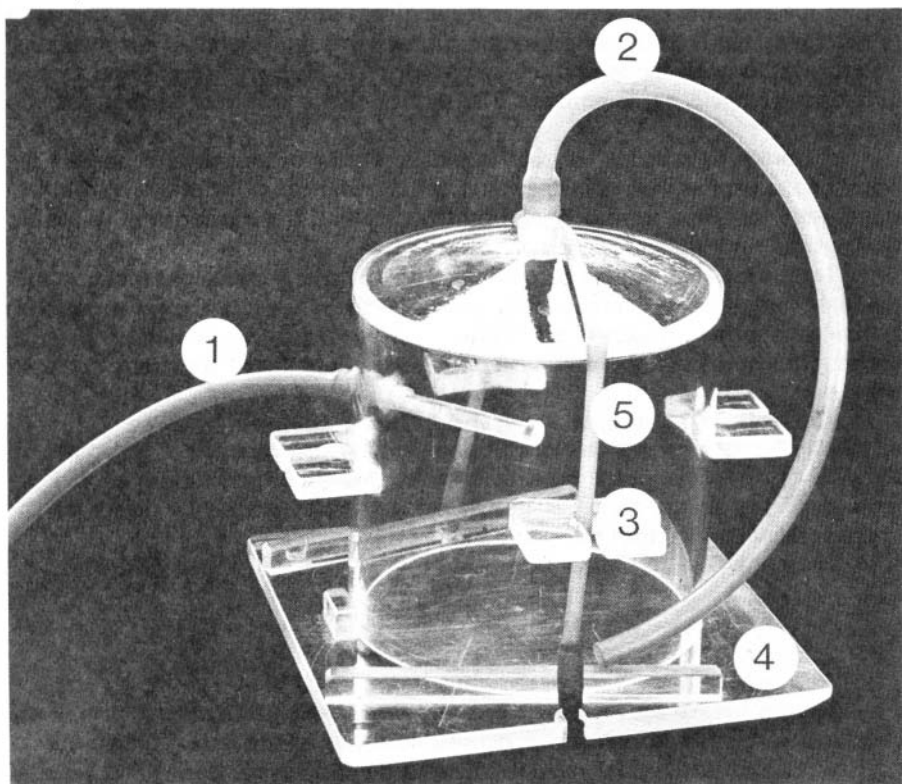decanted.

Fig. 3.   Sediment sampler designed to take and incubate undisturbed samples of sediment
1) inlet tube initially serving to gently fill the incubation chamber with water and
finally for taking the post incubation water sample;
2) removable outlet tube through which the initial water sample is taken. Upon
removal a propeller can be inserted through the vacated aperture for final water
mixing;
3) lugs serving as a depth guide;
4) base plate
5) rubber strap used to hold the base plate in a water-tight joint against the incu-
bation chamber.

Oxygen uptake of the epibiotic community: To measure the oxygen uptake
by the epibiotic organisms of the prop roots of *Rhizophora mangle*, sections of
these roots were carefully cut from different horizons between the bottom and the
high water mark. Horizon intervals of 0.5 m were used. At least 4 sections each
about 30 cm in length served as representatives of the total prop roots of each
horizon above 1 m^2 of sediment surface. The sections were held in a fixed position
in the water of the main channel for 12-24 h to prevent problems caused by
excretion of sap.

The sections were then put into separate black polyethylene bags which were
totally filled with water from the Estero. The bags were sealed and a subsample
taken out of each by means of a plastic tube fixed on the bottom of the bag in
order to determine the initial O_2 concentration. The bags were incubated in a
protected side channel for 3 hours. During the entire process care was taken not to

disturb the epibiotic organisms. After incubation a second water sample was taken to determine the final O_2 concentration. Considering the volume of the remaining water, together with the second subsample removed, the oxygen uptake per section of prop root could be determined. The surface of the prop root section was also measured.

In order to account for the O_2 uptake by the organisms suspended in the water of the bags as well as in the water of the sediment cylinders, oxygen uptake values were measured separately and subtracted from the consumption values for the bags and the sediment cylinders.

Total prop root surface per sediment surface area between the sediment and the high water line was determined by cutting all the prop roots above 1 m^2 at 6 m intervals along the transect (Fig. 2) after their position was recorded on a simple drawing. Subsequently the root surface area was determined separately for each horizon.

The total oxygen uptake by the epibiotic community above 1 m^2 of mangrove swamp area was calculated using the following parameters: O_2 uptake by the prop root sections in the bags, their surface area, the total surface area of the prop roots per square meter as determined for each horizon, the depth of the horizons related to the high water line and the tidal curve.

The study was undertaken from April to November 1979.

RESULTS AND DISCUSSION

Oxygen uptake by the suspended organisms (which include true planktonic organisms together with benthic organisms occurring in the water column due to tidal stirring) showed a clear relationship with the tidal cycle. During high tide the value was 0.035 mg $O_2 l^{-1} h^{-1}$. During low tide the uptake amounted to 0.047 mg $O_2 l^{-1} h^{-1}$. These values are similar to the means obtained from a year long study in the same area by the first author. The higher value is probably the result of a high turbidity combined with a heavy load of bacteria on the turbidity-causing particles. Intermediate uptake was found between the extremes of the tidal cycle.

The O_2 consumption by the sediment community was between 8.4 mg $m^{-2} h^{-1}$ and 37.2 mg $m^{-2} h^{-1}$. The uptake was greater on the higher parts of the transect. In general, the oxygen uptake by the sediment was quite low in spite of the high content of organic substances present and the high input of organic material by the mangrove vegetation. The values are lower than those obtained by Wieser and Kanwisher (1961) for a *Spartina* salt marsh (37-51 mg O_2 $m^{-2} h^{-1}$) or by Pamatmat (1968) for intertidal sandflats during the warm season (23-66 mg O_2 $m^{-2} h^{-1}$). The O_2 uptake by river mud was still higher (127 mg $m^{-2} h^{-1}$) as measured by Edwards and Rolley (1965). The low oxygen consumption values observed in this study may be due to the thin aerobic surface layer of the mud in the Estero de Morales. At locations with a large population of fiddler crabs the aerobic zone is increased as a result of the enlarged surface area available for gas exchange by means of the many crab holes. On the contrary, a very thin aerobic zone exists when the exchange of interstitial water is minimized by a layer of mangrove leaves.

As might be expected, the oxygen uptake per surface area of prop root depends mainly on the position of the root in relation to the low water line, since the density of the epibiotic biota is governed by the duration of the submersion period. Consumption per 1000 cm^2 of prop root surface area lies between 0.65 mg O_2/h and 29.2 mg O_2/h. The higher values are found for prop roots near the edges

of the channels immediately above the sediment. These roots are densely populated by barnacles, small bivalves, snails, polychaetes, anthozoans, algae, etc. Gerlach (1958) gives a comprehensive compilation of the variety of organisms found on prop roots in Brazil. It should be mentioned that at no site in the Estero de Morales were prop roots found submerged at low tide. This is probably due to the high tidal range which does not allow the growth of the mangroves near the low water line. Therefore the epibiotic community is much less developed than in other areas. Very low O_2 uptake values are found for prop roots near the high water level, which are free of macroscopic epibiotic organisms. Comparing the consumption by prop roots from the same depth in relation to the high water mark but from different heights above the sediment, those near the sediment generally show a much higher oxygen uptake. This is due to the fine sediment layer deposited by tidal currents on these roots.

Fig. 4 presents the diurnal variation of the O_2 consumption by the compartments: free water, sediment, and epibiotic community at different stations of a transect. The position of this transect between the main channel and a side channel is given in Fig. 2. Three areas were chosen to represent the depth profile of the transect. Site *a* is situated at the edge of the main channel. At this point the water depth at high tide is 2.30 m, the submersion period is 20 hrs per day. Site *b* is at a distance of 12 m from the border of the side channel, water depth and submersion time are 1 m and 10 hrs, respectively. Site *c* is at 24 m distance, depth and submersion time at this point are 0.56 m and 7 hrs 10 min., respectively.

The total surface area of the prop roots between the sediment and the high water mark varied considerably (Fig.5). At site *a* of the transect it was 2.9 m^2 per square meter of sediment surface area, i.e. the prop root surface area is larger than the sediment surface area beneath these roots. At higher sites along the transect the surface area of the prop roots decreases rapidly to as low as 0.45 m^2/m^2 of sediment surface area.

The pattern of the O_2 consumption parallels in general the tidal curve (Fig. 4). This is not surprising, because the total oxygen uptake per unit of sediment surface area by the suspended organisms and the epibiotic community depends largely on the height of the water column. The lack of an exact correlation between the O_2 consumption and the tidal curve is, however, due to several reasons. The surface area of the prop roots is generally larger at lower horizons. The same holds true for the density of the epibiotic community. For example at site *a* the prop root surface area per m^2 of sediment surface area amounted to 14,900 cm^2 for the lowest horizon and only 1020 cm^2 for the horizon between 1.5-2.0 m. The oxygen uptake per 1000 cm^2 of prop root surface area was 8.5 and 1.2 mg/h, respectively. Consequently, each subsequent increase in the water level results in a decreased O_2 uptake. Another reason that the O_2 consumption per unit of sediment surface area does not increase exactly parallel to the tidal curve, is the fact that the consumption by the sediment biota probably remains at the same level during the submersion period. This, however, may be a simplification.

Fig. 4 shows that not only the rate of the oxygen consumption, but also the duration of the uptake period depends on the location of the site. During low tide, when the sediment is exposed to air, the oxygen consumption of the total system was taken as zero. This is a simplification, at least for the sediment. Due to its structure and composition the sediment along the transect is always saturated with water and hence the O_2 uptake by the sediment organisms will continue. Teal and Kanwisher (1961) found no significant differences in oxygen uptake by sediments from a Georgia marsh whether measured in air or in water. However, since it was

the main aim of the present study to determine the uptake of dissolved oxygen, i.e. the rate of depletion of oxygen from the water, the total oxygen uptake by the three subsystems was taken as zero when the sediment was exposed to air.

The duration of a lag in time regarding the O_2 uptake by the epibiotic community remains as a further problem.
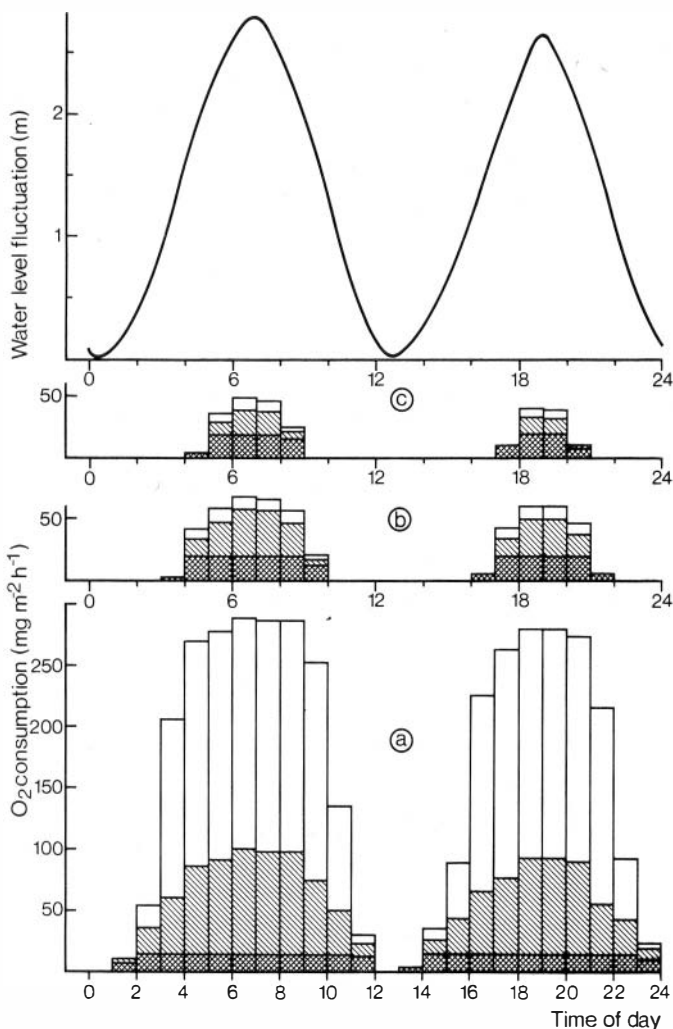

Fig. 4.   Tidal curve together with histograms of the oxygen uptake at three different stations along the transect. Station *a* near the border of the main channel, station *b* at 12 m distance and station *c* at 24 m distance from the side channel. Crossed sections of the bars indicate uptake by the sediment biota; diagonal sections, uptake by the suspended organisms; blank sections, uptake by the epibiotic community of the prop roots.

The oxygen consumption per unit area of the transect shown as the sum of the individual uptakes by the suspended organisms, the sediment community and the organisms living on the prop roots of the red mangroves is given in Fig. 5. Total oxygen consumption varies from 4.02 g $m^{-2} d^{-1}$ near the border of the main channel to 0.26 g $m^{-2} d^{-1}$ at the highest position of the transect. The oxygen uptake by the three compartments as a fraction of the total uptake per unit area is shown in Table 1. At the lower points of the transect the O_2 consumption is mainly caused by the suspended and by the epibiotic organisms. At the higher points the relative uptake by the sediment community increases rapidly, so that at the highest site of the transect nearly half of the total uptake is due to the respiration of the sediment organisms. Since the higher areas of the Estero de Morales occupy the greatest part of the mangrove swamp, it is quite probable that, considering the whole system, the activity of the sediment biota accounts for the greatest part of the total oxygen uptake.
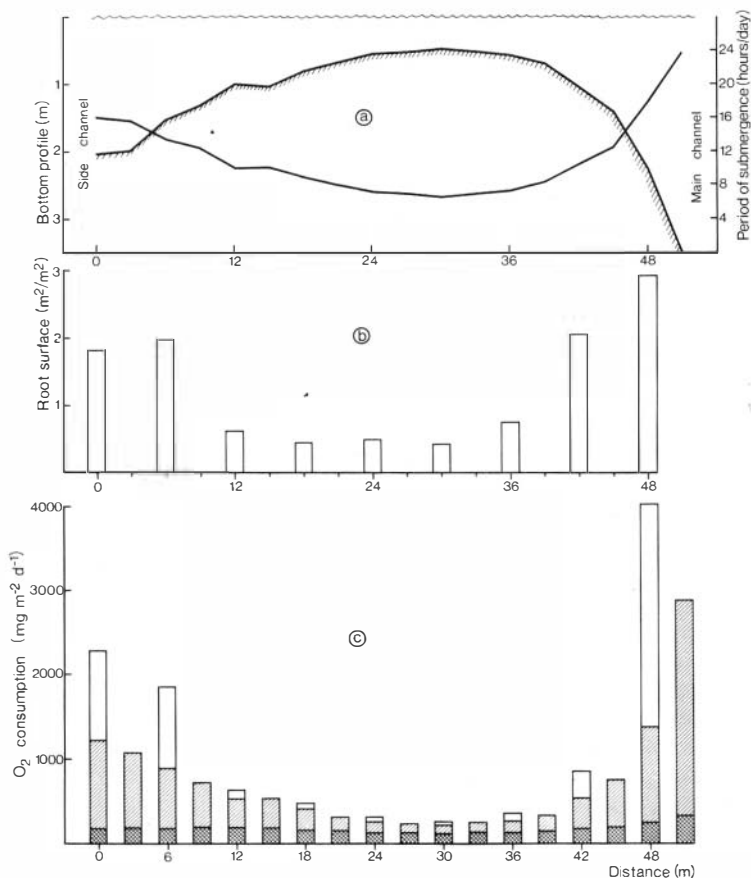

Fig. 5.　a. Bottom profile and submergence period for the transect; b, prop root surface area per square meter of sediment surface area; c, total oxygen uptake per square meter of sediment surface area.

TABLE I

Oxygen uptake by the organisms suspended in water,
the sediment biota and the epibiotic community
of the prop roots expressed as percentage

Distance (m) from the side channel	Water depth at high tide (m)	Oxygen uptake (%)		
		water	sediment	prop roots
0	2.05	46	8	46
6	1.53	33	9	58
12	1.00	55	31	14
18	0.82	53	34	12
24	0.56	40	41	19
30	0.47	37	44	19
36	0.58	37	38	25
42	1.06	42	21	37
48	2.24	28	6	66

The mean oxygen uptake of the transect per sediment surface area amounts to 1410 mg $m^{-2}d^{-1}$ in the *Rhizophora mangle* fringe of the Estero de Morales. The organisms suspended in the water account for 40.5%, the sediment community for 13.5 % and the epibiotic organisms for 46% of this value. From the 0_2 uptake values the decomposition of organic substances can be calculated. For this conversion an RQ-value of 0.85 was employed. Hence 410 mg C $m^{-2}d^{-1}$ of organic material was oxidized. The RQ value used is derived from the respiration of the plankton. A separate investigation would be necessary to study the validity of this value for the conversion calculations in a mangrove swamp. The bases of the food chain in such an ecosystem are detritus particles derived initially from fallen litter. Since the carbohydrate content of this material is higher than in plankton organisms, the RQ-value should be closer to unity.

The decomposition of 410 mg C $m^{-2}d^{-1}$ of organic material obviously is an underestimation. This is due to the fact that the decomposition process in the sediment proceeds during the period when the area is not covered by water (this has not been measured). It is also evident that decomposition processes are occurring in the anaerobic layers of the sediment. These are not reflected by changes in the oxygen concentrations. Desulfurication and denitrification permit a final oxidation of organic material with sulfate or nitrate as electron acceptors. Howarth and Teal (1979) have shown that in a salt marsh near Cape Cod the sulfate mediated respiration in the peat oxidizes perhaps 12 times as much organic matter as oxygen mediated respiration.

Determinations of the litterfall have not been performed so far for the Estero de Morales. However, if we accept about 1 g C $m^{-2}d^{-1}$ (Heald, 1969) as a probable value, about half of this material would be oxidized in the system itself.

ACKNOWLEDGEMENT

RESUMEN

Para determinar la descomposición de la materia orgánica en un manglar de la costa del Pacífico de Costa Rica (Estero de Morales) se hicieron mediciones del consumo de oxígeno para los organismos suspendidos en el agua, las comunidades de sedimento y el sistema epibióntico de las raíces de *Rhizophora mangle*. La amplitud de la marea en esta área es 2,5 metros. El sedimento consiste en su mayor parte de arcilla con 12-15 % de materia orgánica. La especie dominante en este manglar a la orilla de los canales, es *Rhizophora mangle* y en el interior, *Avicennia nitida*. El consumo de oxígeno por los organismos suspendidos varió entre 35 y 47 mg $m^{-3}h^{-1}$ y por las comunidades bentónicas entre 8,4 y 37,2 mg $m^{-2}h^{-1}$. La respiración de los organismos epibiónticos depende de la posición de las raíces en relación con el nivel del agua en marea baja. Se midieron valores del consumo de O_2/h por 1000 cm^2 de superficie de raíz entre 0,65 y 29,2 mg. Tanto el consumo total de O_2 por área, así como el porcentaje relativo de consumo por los tres subsistemas muestran una amplia variación, que depende sobre todo del nivel alcanzado por el agua y del período de la inmersión. En una sección entre dos canales del manglar, el promedio del consumo total de oxígeno por metro cuadrado fue de 1310 mg por día. El 40,5% de esa cantidad fue consumida por los organismos suspendidos en el agua, el 13,5% por los organismos del sedimento y el 46% por la comunidad epibióntica de las raíces. La descomposición del material orgánico resultó ser en promedio de 410 mg C m^{-2} por día.

LITERATURE CITED

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.

Edwards, R.W., & H.L. J.Rolley
1965.   Oxygen consumption of river mud. J. Ecol., 53: 1-19.

Gerlach, S.A.
1958.   Die Mangrovenregion tropischer Küsten als Lebensraum. Z. Morph. u. ökol. Tiere, 46: 636-730.

Golley, F.B., H.T. Odum, & R.F. Wilson
1962.   The structure and metabolism of a Puerto Rican red mangrove forest in May. Ecology, 43: 9-19.

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

Hargrave, B.T.
1969.   Epibenthic algal production and community respiration in the sediments of Marion Lake. J. Fish. Res. Board Can., 26: 2003-2026.

Heald, E.J.
1969.   The production of organic detritus in a south Florida estuary. Ph.D. dissertation,
               Univ. Miami, 111 p.

Hernández, A. & K.P. Mullen
1975.   Observaciones preliminares sobre la productividad primaria neta en un ecosistema
               de manglar-estuario (Guapi-Colombia). *In* II. Simposio latinoamericano sobre
               oceanografía biológica, Cumaná, Venezuela. Publ. Univ. Oriente, Venezuela.

Hicks, D.B., & L.A. Burns
1975.   Mangrove metabolic response to alteration of natural freshwater drainage in
               southwestern Florida estuaries, p. 238-255. *In* Proc. Int. Symp. on Biol. and
               Management of Mangroves.

Howarth, R.W., & J.M. Teal
1979.   Sulfate reduction in a New England salt marsh. Limnol. Oceanogr., 24: 999-1013.

Odum, E.P., & A.A. de la Cruz
1967.   Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem,
               p. 383-388. *In* G.H. Lauff (ed.), Estuaries. Amer. Ass. Adv. Sci. Publ., 83. Wash.,
               D.C.

Odum, W.E., & E.J. Heald
1972.   Trophic analyses of an estuarine mangrove community. Bull. Marine Sci., 22:
               671-738.

Pamatmat, M.M.
1968.   Ecology and metabolism of a benthic community on an intertidal sandflat. Int.
               Rev. Hydrobiol., 53: 211-298.

Peterson, C.L.
1960.   The physical oceanography of the Gulf of Nicoya, Costa Rica, a tropical estuary.
               Bull. Inter. Amer. Trop. Tuna Comm., 4: 139-214.

Pool, D.J., S.C. Snedaker, & A.E. Lugo
1977.   Structure of mangrove forests in Florida, Puerto Rico, Mexico and Costa Rica.
               Biotropica, 9: 195-212.

Teal, J.M., & J.W. Kanwisher
1961.   Gas exchange in a Georgia salt marsh. Limnol. Oceanogr., 6: 388-399.

Teas, H. J.
1979.   Silviculture with saline water. *In* Alexander Hollaender. (ed). The biosaline
               concept. Plenum, New York.

Untawale, A.G., T. Balasubramian, & M.V.M. Wafar
1977.   Structure and production in a detritus rich estuarine mangrove swamp. Mahasagar
               Bulletin of the National Institute of Oceanography, 10: 173-177.

Walsh, G.E.
1967.   An ecological study of a Hawaiian mangrove swamp. p. 420-431. *In* G.H. Lauff,
               (ed.) Estuaries, Amer. Assoc. Adv. Sci. Publ. 83, Wash., D.C.

Wieser, W., & J. Kanwisher
1961.   Ecological and physiological studies on marine nematodes from a small salt marsh
               near Wood's Hole, Massachusetts. Limnol. Oceanogr., 6: 262-270.