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$$\text{Actual evapotranspiration from successional vegetation} = \left(1 + \frac{\text{Actual Ht. of second growth}}{\text{Ht. of mature vegetation}}\right) \times \left(\frac{\text{Actual evapotranspiration from mature vegetation}}{2}\right)$$

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THE STRUCTURE AND METABOLISM OF A PUERTO RICAN RED MANGROVE FOREST IN MAY[1]

FRANK GOLLEY,[2] HOWARD T. ODUM[3] AND RONALD F. WILSON[3]

INTRODUCTION

To develop a comparative science of world ecosystems, measurements of holistic properties are needed for all the important types of communities. Diverse ecosystems on land and water may differ widely in floristic and faunistic composition and in environmental conditions, but the basic function of communities may be placed on a comparable basis with measurements of photosynthesis, respiration, efficiency, biomass, and assimilation number. One major community type little studied from the functional viewpoint is the tropical mangrove swamp. According to a recent atlas of shore systems (McGill 1958), mangroves dominate about 75% of the world's coastlines between 25°N and 25°S latitude. This study reports measurements of structure and metabolism for a representative red mangrove community of the terrestrial type on the southern shores of Puerto Rico.

In the American tropics the mangrove swamp forest consists of a series of zones each dominated by one species of tree (Holdridge 1940, Davis 1940, Dansereau 1947). From open water and extending through the area which is covered by maximum high tides the red mangrove, *Rhizophora mangle* Roxb., is dominant. In this community the trees are supported by high, arching prop-roots, which make travel by an observer exceedingly difficult. Except for prop roots and the red mangrove seedlings, the forest floor is devoid of higher plant life. The next zone toward land is typically dominated by the black mangrove, *Avicennia tomentosa* Jacg., which characteristically sends up myriads of breathing roots 10-15 cm above the mud surface. The innermost zone is usually dominated by the white mangrove, *Laguncularia racemosa* Gaertn. Few herbaceous plants or epiphytes are associated with the mangrove trees in the first and second zones, but ferns and grasses may grow under the white mangroves. Animal life in the above-water parts of the mangrove forest is not abundant, but where the roots are submerged, as in tidal channels, massive epifauna are numerous, and include

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oysters, tunicates, and sponges. This underwater fauna does not derive food directly from the mangrove trees.

In January, 1958, May, 1959, and May, 1960, intensive studies over one to 2 wk periods were made in a red mangrove forest on the southern shore of Puerto Rico (18°N Lat, 67° W Long). Brief additional studies were made by Golley in June, 1961, while a visiting professor at the University of Puerto Rico at Mayaguez. The study area was on a peninsula of Magueyes Island, the location of the Institute of Marine Biology of the University of Puerto Rico. The peripheral red mangove forest occupied the greatest area on the peninsula, while a combination of red, black, white, and button (*Conocarpus erectus* Linn.) mangroves occupied a higher, central area. The study forest had not been disturbed since 1954 but evidences of earlier cutting were discovered. The forest is typical in this respect and is representative of other red mangrove forests in Puerto Rico as described by Holdridge (1940).

Methods

Environmental properties, vegetational structure, animal densities, and metabolism of principal components were investigated and a metabolic budget for one average day in May was compiled. The study of these quantities was facilitated by a boardwalk constructed through the swamp by the Marine Institute, which provided easy access to all zones of the forest. The area of the forest was surveyed by running measured lines from the boardwalk to the open water.

Environmental measurements.—Peat depth, temperature, light, wind movement, and depth and rate of tide movement were measured. To determine the depth of the peat 6 cores (5 cm in diameter) were taken on a transect from the mainland to the edge of open water. Temperature was measured on the mud surface and in the air above the mud at the study plots. Light measurements were taken vertically at one meter intervals from the mud surface to a point above the crown of the trees with a General Electric light meter, calibrated in foot-candles. The depth and cycle of the tides in May were measured and related to annual records obtained from Coker and Gonzalez (1960). Wind speed was measured with a Taylor anemometer at various strata within the center of the forest. Five min readings were taken at each level.

The biomass structure of the vegetation.—This was investigated in 2 plots in the center of the red mangrove community away from edge conditions. In 1959, on a 25m² quadrat all trees were harvested and the area and biomass of leaves, and number of roots were determined for meter strata from the mud to the crown. Leaf area was measured by tracing leaves on graph paper and then counting the number of cm² within the tracing. In 1960, on a 100 m² quadrat adjacent to the 25 m² quadrat, another method of estimating biomass was used. The diameter at breast height (dbh) was measured for all trees in the plot. Ten trees representing the most abundant diameter classes were harvested and the biomass of roots, trunks, branches, and leaves was determined (Tables I and II). Samples of fresh leaves, wood, and roots were dried at 100°C for 24 hrs in an oven to estimate dry weight biomass. The curves of biomass per dbh class from the harvested trees (Fig. 1) were used to estimate the biomass of the trees of known dbh on the entire 100 m² plot. The average biomass for the midpoint of a dbh class (1.5, 2.5, etc.) was read from the curves and multiplied by the number of trees in the class. The values of biomass of the dbh classes were summed to obtain the biomass of

Table I. Biomass of harvested red mangrove (in grams)

DBH Class cm	Height meters	Roots		Branches		Leaves		Trunk Dry Wt	Total Tree Dry Wt
		No.	Dry Wt	No.	Dry Wt	No.	Dry Wt		
1.2	3.6	5	159	9	136	143	109	374	778
1.5	3.7	4	131	8	136	123	99	409	775
1.5	3.7	5	134	9	187	179	123	438	882
1.7	3.6	6	293	9	239	173	133	596	1261
2.0	4.1	9	439	10	392	212	153	851	1835
2.4	6.0	8	622	15	438	243*	184	1255	2499
2.7	5.2	7	1379	17	851	529*	399	1856	4485
2.8	5.1	10	988	23	727	473*	357	1856	3928
3.7	6.0	6	2001	23	1056	691*	522	3575	7154
5.3	8.6	16	3514	40	4358	2375*	1608	6810	16290

* Number estimated from samples.

Table II. Biomass of red mangrove based on curves of biomass versus dbh. Average biomass per dbh class and per square-meter considered separately

DBH Class cm	Number of Trees	Roots		Leaves		Branches		Trunk	
		Per DBH Class	Per m²	Per DBH Class	Per m²	Per DBH Class	Per m²	Per DBH Class	Per m²
		Biomass in grams dry weight							
1- 2	67	180	121	110	74	180	121	440	295
2- 3	35	680	238	250	88	500	175	1250	438
3- 4	16	1700	272	510	82	1100	176	3100	496
4- 5	7	2700	189	900	63	2500	175	5200	364
5- 6	4	3840	154	1340	54	3900	156	7400	296
6- 7	3	4850	146	1760	53	5000	150	9500	285
7- 8	2	5840	117	2200	44	5950	119	11400	228
11-12	2	10000	200	3900	78	10100	202	19700	394
Total			1437		536		1274		2796

all trees on the plot. The few trees harvested in the 5+ cm dbh classes were insufficient to determine the shape of the curve in the larger size classes. The curves were extended in a straight-line through the 11-12 cm class (not shown in Fig. 1) to estimate the biomass of the few large

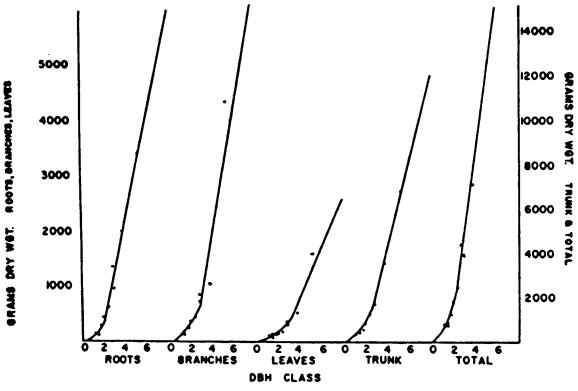

FIG. 1. Dry weight biomass in grams for roots, branches, leaves, trunks, and total trees from ten harvested red mangrove trees with dbh from 1 to 5 cm.

trees on the plot. Since Holdridge (1942) stated that red mangrove in Puerto Rico may reach 30 m in maximum height and 90 cm in maximum diameter, straight-line extension of the curves is probably reasonable.

Chlorophyll a was measured in sun and shade leaves from trees on the 25 m^2 plot in 1959. Values were multiplied by leaf area measurements to determine total chlorophyll. The method of chlorophyll extraction and analysis is described in Odum *et al.* (1958).

Growth of wood.—This was measured by determining the increase in the dbh of trees on the 100 m^2 study area from 1959 to 1960. From the 10 harvested trees a regression coefficient of wood biomass on dbh was calculated to be 3.39 x 10^3 g/cm. The increase in tree diameter was converted to grams of wood by multiplying the regression coefficient of wood biomass on dbh by the number of trees in each class and by the average dbh for each class. The wood deposition for each class was summed to obtain the total wood production during the year.

Photosynthesis and respiration.—These functions of the leaves were measured with a Liston-Becker infra-red CO_2 analyzer (Model 15A) operating in the field from a 500 watt Kohler gasoline generator in 1959 and from a 900 ft extension wire from the electrical supply of the Institute of Marine Biology in 1960. Initially, air was drawn over a bundle of leaves in a plastic bag at the rate of 2 l/min. The CO_2 readings were taken alternately from the bags and from free air outside the bags. After a series of measurements, the leaves were collected and their area and dry weight were determined.

In 1959, it was found that at high light intensities temperature increased in the bags during the mid-part of the day, affecting respiration and photosynthesis measurements. This was noticeable in the large discrepancy between respiration and gross photosynthesis of the forest, based on the 1959 balance sheet. Since respiration was about 6 times as great as photosynthesis, either photosynthesis was depressed or respiration was accelerated under the system of measurement.

In 1960, a plexiglass leaf chamber was constructed with a double wall. Ice water was circulated between the walls by an electric pump from a bucket containing fresh water and ice. Values were somewhat higher but still too small to match respiration data. During experiments with the cooled chamber CO_2 production was also influenced by the rate of air flow through the chamber. Measurements at 2 to 15 l/min flow rates showed CO_2 production increased to a flow rate between 10 and 15 l/min (Fig. 2). At these

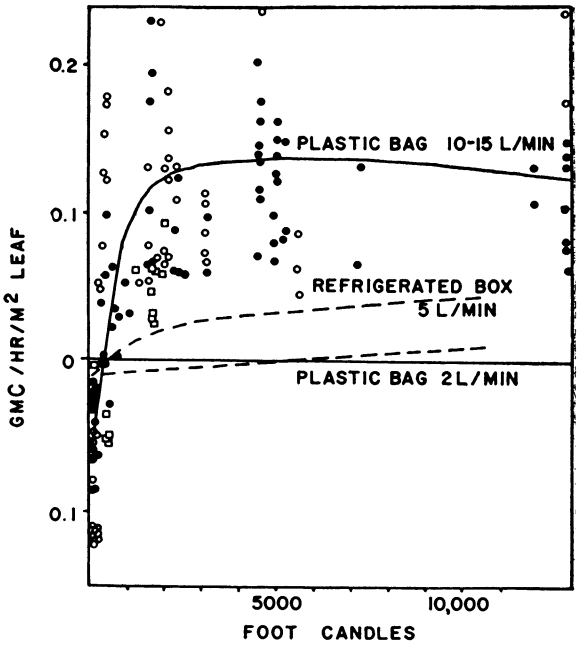

FIG. 2. Metabolism in gram carbon per hour per m^2 leaf surface of sun, shade, and seedling leaves of *Rhizophora mangle* measured at 10-15 l/m in one liter bags. Seedling data are indicated by dark circles, shade leaves by squares, sun leaves by open circles. Dashed lines summarize experiments at 2 and 5 l/m.

high rates there was no need for refrigeration of the plant chamber.

Earlier data were discarded and the data for calculation of metabolism were taken at flow rates

between 10 to 15 l/min. In the field, the infra-red gas-analyzer was standardized by injection of CO_2 gas with a syringe into a a closed system of 20 l volume, previously cleared of CO_2 by absorption with NaOH.

Respiration of leaves was investigated at night by comparing CO_2 production of leaves in plastic bags with CO_2 content of free air. For budget computations we have assumed that night and day leaf respiration are equal. Respiration of prop roots was measured by enclosing the air exchange portion of the root (zone of pores) in plastic and drawing air over the root surface.

Respiration of the peat floor of the forest during low tide when the peat was exposed to air was measured by placing an aluminum sheet on the peat and drawing air under the sheet to an intake tube. The CO_2 production of the peat also varied with air flow, reading highest at the highest rates of flow available with field equipment (15 l/min). Thus soil respiration was a function of ground air flow. To calculate soil respiration it was necessary to know the rates of air movement over the forest floor.

Underwater respiration of the peat during high tide was measured by enclosing tidal water under a bell jar in the field and then measuring the O_2 change by the Winkler method.

Export of particulate organic matter.—Such export was estimated by pouring a measured volume of incoming and outgoing tidal water through a #10 plankton net. Water at the end of the boardwalk on incoming tide was sampled as representative of incoming water. Water on the study quadrat on outgoing tide was taken as representative of outflowing water. The organic matter collected was dried in an oven at 100°C for 24 hrs and weighed.

Biochemical oxygen demand.—Bottles were filled with incoming and outgoing water and the oxygen was measured by the Winkler method. After 6 days duplicate bottles were measured for oxygen content. The oxygen changes over 6 days were measured to estimate the magnitude of labile organic matter. Studies of decomposition of organic matter in sea water have shown that in 6 days between 60% and 80% of the organic matter is decomposed of that which will decompose over several months (See curves for sea waters in Sargent and Austin 1949, Fox, Oppenheimer, and Kittredge 1953, Rakestraw 1947). Thus the grams carbon in the labile organic matter can be estimated from 6 day oxygen decreases by dividing the grams O_2 consumed by .70.

Densities of animals.—Animal densities were determined by a variety of methods depending on the activity period and the habitat of the various taxa. There appeared to be 3 major habitats for animals in the forest: (1) areas containing mostly prop roots and seedlings, shaded by a few large trees; (2) dense thickets of small mangroves; and (3) areas of prop roots, seedlings, and a moderate number of medium sized trees (dbh 2-5 cm). Animal activity was partly influenced by time of day and partly by the tidal cycles. Square-meter quadrats were placed in each of the 3 types of habitats, twice during the day and once at night, to obtain estimates of animals living on the forest floor. In these surveys the observer sat motionless on the mangrove roots and observed the plot for one hour. All animals seen and the time each spent on the plot were recorded. Because the animals were active at different periods of the day, the census during the time of maximum activity was used to calculate densities. For instance, the snail, *Melampus coffeus,* was present throughout the day but ascended the roots and seedlings at high tide (occurring at night in May) (Golley 1960). Thus the night counts of these snails provided the most accurate estimates of density on the quadrats.

Many animals were censused on a 2 m wide transect beside the boardwalk (termed boardwalk census, Table III). There it was possible to move rapidly through the forest, with a minimum disturbance to the animal life. Traverses made by climbing over and under prop roots were mainly effective for these forms that could not move rapidly (such as the web spiders) or for going to a quadrat which would be under observation for a long time.

Flying insects were most difficult to census since it was not possible to use a sweep net or a similar device in the red mangrove forest. All insects flying across or along the boardwalk (in a cross-section area approximately 2 x 9 m) were recorded during day and night observation periods in 1959 and 1960. In 1960, volumes of air were examined visually at night by repeatedly flashing a spotlight into the forest for a few seconds, followed by a minute interval of darkness. Small flies (*Amphineuridae*) and gnats which remained on the mud or in the air above the m^2 quadrats for as long as 15 min were counted at 5 min intervals during the observation periods. The average count for the afternoon period (when these forms were most active) was used as an estimate of their density.

Leaf and branch dwellers were censused by carefully examining leaves, branches, and trunks of

TABLE III. Density and biomass of mangrove animals Abbreviations: weight, wt; individual, ind; quadrat, quad.

Taxa		Density per m²	Biomass per m²
SNAILS			
Melampus coffeus	6m² quad at night (1959: 23,35,41) (1960: 31,37,19) wt 0.0047/ind	31	0.15
Littorina anglepifera	4 in 100m² (0.04/m²) 4 per 20 tree stems (0.27/m²) wt 0.1025/ind	0.2	0.02
CRABS			
Aratus pisonii	8/20 trees, 7/21 trees, 7/9m² quad 1959, 5/9m² quad 1960. wt 0.3638/ind	0.6	0.218
Eurytium limosum	4 per 5m² quads; wt 0.948/ind	0.8	0.759
Uca mordax	4m² quad (6,9,3,1); wt 0.53/ind	5.0	2.65
Ucides cordatus and *Goniopsis eventata*	4 large crabs seen. Mangrove crabs within 8m of each other. Assume one per 16m² wt 24/ind.	0.06	1.44
INSECTS			
Aglaopteryx diaphana	6 night, m² quad (1959: 3,2,0) (1960: 1,1,0) ave 1.2/m² 15/21 trees, 9/20 trees, 1.36 trees/m²; wt 0.0025/ind	1.1	0.003
Gryllidae	18m² quad (1959: 0,2,3,0,0,4,0,1,4) (1960: 4,0,1,3,0,1,4,0,4) wt 0.003/ind	1.8	0.005
Amphinumidae	12m² quad (1959: 2,1,1,1,1,0,0) (1960: 3,1,1,2,0,1) wt 0.001/ind	2.1	0.021
Sarcophagidae	12m² quad (1959: 2,1,1,1,1,0,0) (1960: 1,1,0,0,1,1) wt 0.003/ind	0.8	0.002
Unidentified forest floor insects	18m² quad (1959: 0,1,26,0,1,4,0,2,1) (1960: 0,1,0,4,1,2,0,0,1) est wt 0 002/ind	2.5	0.050
Rhagovelia plumbea	3m² night quad (6,6,0) est wt 0.0005/ind	4.0	0.002
Flying gnats	3m² quad (4,4,12) est wt 0.0001/ind	6.7	0.001
Flying insects	Boardwalk census, area 118 x 2m (0,9,14,16,13,8,11,2,11) est wt 0.003/ind	1.4	0.004
MISC. tree arthropods (incl crickets, ants, scorpions)	7/1031 leaves (1065 leaves/m²) 7.4/m² 3/20 trees, 3/21 trees 1.36 trees/m² est wt 0.002/ind	7.6	0.015
SPIDERS			
Olios antiguensis	6/100m²—0.06/m²		
Gasteracantha tetracantha	2/100m²—0.02/m²		
Tree spiders	2/20 trees, 3/21 trees —0.16/m²		
Spider webs	Boardwalk census, area 118 x 2m (1959: 71,58,48) (1960: 5,5)—.16/m² wt 0.003/ind	0.2	0.001
VERTEBRATES			
Fish	5m² night quad (1,1,2,0,0) est wt 1.3/ind	0.8	1.0
Anolis cristatellus	2/100m² area, 2 on 8 boardwalk censuses, est wt 0.60 gm	0.01	0.006
Birds (residents)			
Yellow warbler	1959: 4,3,0; 1960: 3,2,3.		
Grassquit	1959: 2,2,0; 1960: 3,2,3.		
Dove	1959: 1,2,2; 1960: 2,0,0.		
(Nonresidents)			
Rail	1959: 0,0,1; 1960: 1 1,2.		
Crow	1959: 0,0,0; 1960: 1,1,1.		
Hummingbird	1959: 1,0,0; 1960: 1,0,0.		
Vireo	1959: 0,0,0; 1960: 1,0,0.		
Green heron	1959: 0,0,0; 1960: 1,0,0.		
Unid	1959: 0,1,0; 1960: 2,2,1.		
	est 22 birds in forest or 0.003/m² est wt 10/ind	0.003	0.03
Total.....		66.673	6.377

20-25 trees along the boardwalk and in the forest at night and during the day.

Birds were censused by making bird walks along the boardwalk at about 6:30AM 3 days in 1959 and 1960. Some of the dry land species on Magueyes Island utilized the edge of the mangrove forest for roosting and cover. Other birds, especially the larger water forms such as rails and green herons, mainly used the edge near open water and flew between several stands of mangroves. Actual time these transients spent in the forest was not estimated; actual counts of individuals were used in the density estimates. Resident birds were those seen or heard regularly and for which nests were located. These included the yellow warbler (*Dendroica petechia*), black-faced grass-quit (*Tiaris bicolor*) and the ground dove (*Columbigallina passerina*). Singing birds were counted as representing a pair of birds.

Specimens of the most abundant animals were collected, stored in formalin and later dried in an oven at 100°C for 24 hrs to determine dry weight biomass.

We have not attempted to obtain a complete species list of the fauna of the red mangrove forest. Our major objective was to outline the structure and function of the community, and this required identification of the dominant animals and determination of their density and biomass. Not all measurements are equally accurate; estimates of flying insects are probably least accurate, while estimates of mud dwellers, crabs and spiders are probably more accurate. Micro-organisms were not studied.

Animal respiration.—Respiration of a few medium-sized animals was measured in a simple variable respirometer (described in Teal 1959). Duplicate measurements were made at 26-27°C and the readings were corrected with a thermobarometer. Since the animals were quiet in the respirometer the metabolic rates should be considered minimal estimates of actual field respiration. Some approximations of oxygen consumption of forms too small or large to fit into the respirometer were taken from Spector (1957). Oxygen consumption of small arthropods was estimated as 1.0 ml O_2/g/hr and for vertebrates as 3.0 ml O_2/g/hr. The biomass estimates were multiplied by the oxygen consumption per gram dry weight to estimate the respiration of the animal population.

RESULTS

The Environment

The peninsula containing the mangrove study area was approximately 7400 m², with red mangrove occupying 4600 m², and a complex of red, black, white and button mangrove occupying 2800 m². The mangrove forest was protected

from the open sea by a coral reef about 6 m from the forest, and separated from the forest by a narrow bed of *Thallasia testudinum* mixed with coral.

The swamp floor consisted of a layer of mangrove peat and roots about one meter thick in the center of the forest and graded to 1.2 m at the water edge and 0.8 m at the land edge. The peat rested on a coral platform. Samples of peat from the peat cores taken near the water edge were burned in a muffle furnace at 600°C for 6 hrs to determine the per cent ash. The first 3 sections (25 cm long) contained 54.7, 47.9 and 32.7% ash and the last section, from the coral base, contained 91% ash. These samples did not include sections of large roots. The limited data indicate that almost one-half of the mass of the peat is inorganic.

During May high tide occurred at night and reached a depth, on the study quadrats, of about 5-17 cm depending on wind conditions. On one night no tide reached the quadrat floor. According to the regime described by Coker and Gonzalez (1960), there is only one low and one high tide daily, each occurring at the same time of day over extended periods. High tide occurs at night in late spring and summer and at noon in winter. Changes in sea level between tides are small. The mean monthly annual changes in tide is 21.0 cm. Salinity of water flowing over the peat is 29.1 $^0/_{00}$.

Light intensity curves for different depths of the forest and times of day are plotted in Figure 3. On May 28, 1959, the temperatures on the mud surface in the shade, 2 cm in the mud, 60 cm in the air, and in the water during high tide were as follows:

	AM					PM	
	8:50	9:30	10:40	12:25	2:45	3:45	10:30
60 cm in air..	26	27	28	30	29	30	—
mud surface..	27	28	31	35	35	32	—
2 cm in mud..	27	28	30	31	35	32	—
water			no water				29

The temperature on the mud surface, the habitat of many of the mangrove animals, reaches slightly higher levels than the other temperatures. On June 24, 1961, wind speed was measured on the study plots and at one meter above sea level in the ocean before the forest, at 9:00 and 11:00AM and 3:00PM. Average wind speeds in the direction of the prevailing wind in ft/min were: 1.5 at ground, 57.7 at 1m, 71.6 at 3.5m, 104 at 5.5m, and 736 at sea.

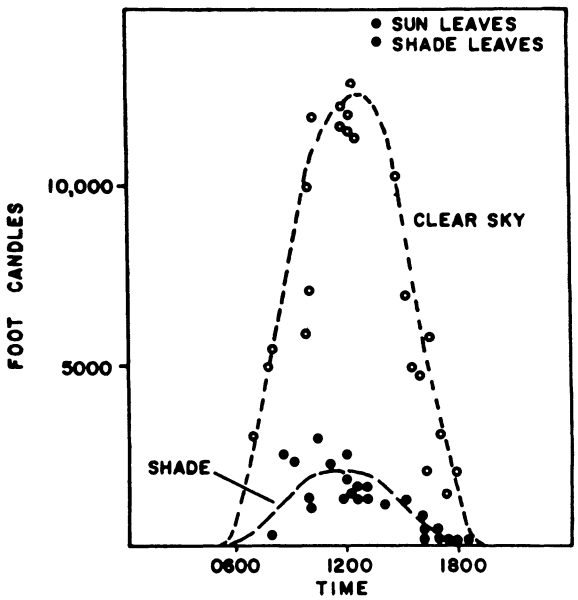

FIG. 3. The diurnal sequence of light intensity in the top of the forest (sun leaves) and under the forest canopy (shade leaves) in May, 1960.

Structure of the Red Mangrove Forest

A vertical section through the forest shows distinct stratification (Fig. 4). In the lowest meter the arching roots (18 roots/m^2) form an intricate tangle. At the base of each root are conspicuous lenticels shown by Scholander to be used for oxygen respiration (Kramer and Kozlowski 1960). In dense profusion among the roots are seedlings (an average of 17/m^2 on 3 plots with 27, 4, and 19 seedlings) which sprout from their "viviparous embryos" dropped from the canopy into the soft mud. Above the lower meter of roots is the stratum of principal trunks with leaves less dense than above in the canopy or below in the seedling-root zone. Leaves in this stratum are of the shade type. Above the trunk zone at about 5 m is the area of maximum leaf biomass, with sun and shade leaves in profusion. All leaves in the upper 2 m exhibit the smaller size and thicker texture of sun leaves. Measurements of vertical structure are graphed in Figure 4.

The frequency distribution of dbh of red mangrove trees on the 100m^2 plot containing thickets, medium and large trees, is shown in Table II. Small trees from one to 4 cm dbh were most abundant. Dry weight biomass calculated from tree harvest (Table I) totaled 536 g in leaves, 1274 g in branches, 2796 g in trunks, and 1437 g above ground in prop roots per m^2 (Table II). Combining the leaf estimates made in 1959 and 1960 the average biomass of leaves is 778 g per m^2 for the forest. Underground portions of the vegetation, the peat and roots, totaled about 45,000 g dry weight/m^2. Small (0.5-1 cm diameter) and large (2+ cm diameter) roots were

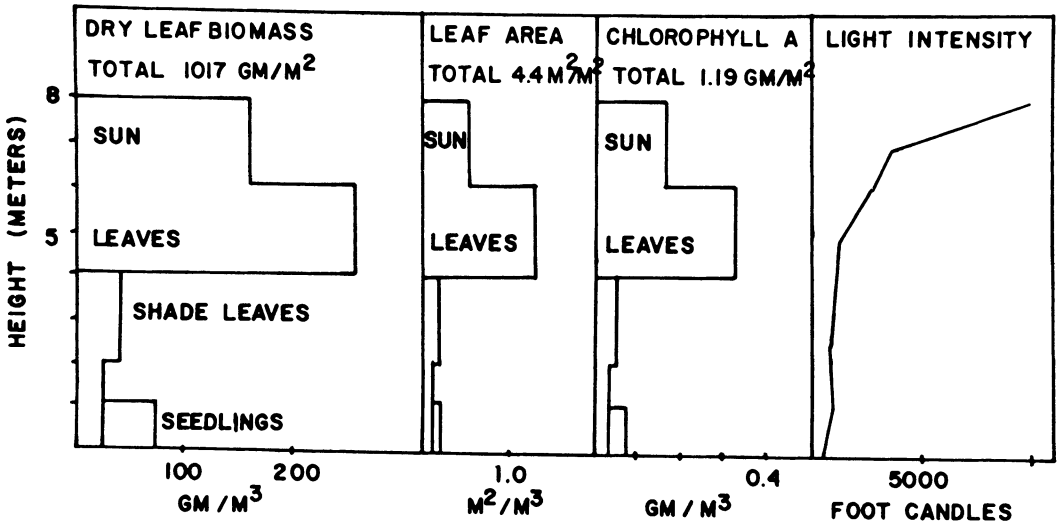

FIG. 4. Vertical distribution of leaf biomass, leaf area, chlorophyll *a*, and light intensity in the red mangrove forest, based on measurements and counts of all leaves on a 25m² quadrat in May, 1959.

taken from the core samples; large roots weighed 997 g and small roots 4000 g/m². A few large roots were also taken from the coral sections, indicating that mangrove roots extend into the coral substrate. These latter roots are not included in the estimates.

Chlorophyll *a*

Chlorophyll *a* was measured in sun and shade leaves of *Rhizophora mangle* and in the mangrove litter on the mud. In January, 1958, the following vertical sequence was measured in grams of Chlorophyll *a* per m² of leaf area: 6m, 0.25; 5m, 0.19; 4m, 0.32; 3m, 0.35; 2m, 0.23; 1m, 0.25; mud, 0.18 g/m² mud surface. In May, 1959, shade leaves contained 0.24 and 0.29 g/m² of leaf area; sun leaves contained 0.31 and 0.33 g/m² of leaf area in two different collections of leaves. Using mean values for shade and sun leaves and leaf area data in Figure 4, Chlorophyll *a* computed for each stratum is reported in Figure 4. Chlorophyll *a* for the whole quadrat was 1.19 g/m².

Animal Populations

Each stratum of the forest had its characteristic fauna. On the forest floor the dominant animals were the fiddler crab (*Uca mordax*) and the mud crab (*Eurytium limosum*), the snail (*Melampus coffeus*) and crickets (*Gryllidae*). On the trees the crab (*Aratus pisonii*), the snail (*Littorina angelifera*), roaches (*Aglaopteryx diaphana*), spiders (*Gasteracantha tetracantha,* and *Olios antiguensis*), lizards (*Anolis cristatellus*), and birds were encountered. Flying among the trees were various flies (Ephydridae and Sarcophagidae), gnats, butterflies, moths, and birds. When the forest was covered with water, fish, water striders, and large crabs emerged from burrows and entered from the sea edge.

The total fauna in May consisted of about 67 animals per m², which weighed a total of about 6.4 g dry weight (Table III). In terms of biomass the crabs were of greatest importance.

Photosynthesis of the Red Mangrove Forest

Rates of CO_2 uptake during the day determined for sun, shade, and seedling leaves of measured area at various light intensities are reported in Figure 2. A curve corresponding to the mean values of CO_2 output at the measured light intensities was fitted to the data by eye. Confidence limits of 95% were computed for sun, shade and seedling leaf data. At this level, the average confidence limits were 29% of the mean value for sun and seedling and 23% for shade leaves; this means that the confidence limits for the photosynthesis and respiration estimates based on the curve are within about 25% of the estimated value.

The number of hours at each 1000 ft-c light intensity during an average day was estimated from the light intensity curves for sun and shade leaves (Fig. 3). The CO_2 production per square meter of leaf for the daylight hours was calculated for seedlings, shade and sun leaves from the curve in Figure 2 and leaf area in Figure 4. Net daytime photosynthesis totaled 0.12 g C/m²/day for seedlings, 0.24 g C/m²/day for shade leaves, and 5.2 g C/m²/day for sun leaves.

Respiration

Based on night measurements, the average respiration per area of leaf surface was computed for sun leaves as 0.0449 g $C/m^2/hr$, for shade leaves as 0.0465 g $C/m^2/hr$, and for seedling leaves as 0.1470 g $C/m^2/hr$. Respiration rates for seedlings were slightly higher than those of other leaves. These estimates were multiplied by the area of leaves by strata (Fig. 4) to obtain the estimates of respiration by strata for 24 hrs (Fig. 5). Total leaf respiration of all strata was 5.4 g $C/m^2/day$.

The mean respiration of the lenticel zones of the prop-roots was 0.0046 g C/root/hr (based on the following measurements: horizontal zone, 0.0016; seedling, 0.0032; average sized roots, 0.0049, 0.0033, 0.0028, 0.0013, 0.0025, 0.0037, 0.0049, 0.0067, 0.0066; and large roots, 0.0098, 0.0085).

Measurement of the respiration of the forest floor was complicated since the mud was covered with water for about 10 hrs of each 24 hr period (at night). Based on the result of bell jar measurements (Table IV) made during high tide,

TABLE IV. Oxygen utilization of water covering forest floor by bell jar experiments

Unit	Initial Oxygen mg/l	Time Lapse hours	Final Oxygen mg/l	Mean Oxygen Change mg/l	Respiration g $O_2/m^2/hr$
A	2.92 2.75		1.60 1.40		
	2.82	3.3	1.50	−1.32	0.047
B	5.43 5.81 5.40		4.73 4.95		
	5.55	3.6	4.85	−0.70	0.039
C	5.43 5.81 5.40		5.00 5.15		
	5.55	3.7	5.07	−0.48	0.034
mean value					0.040

A Bell jar volume, 4.0 liters; area, 380cm².
B Bell jar volume, 3.54 liters; area, 177cm².
C Bell jar volume, 1.0 liters; area, 39cm².

respiration of the soil under water was about 0.04 g $O_2/m^2/hr$ or about 0.02 $C/m^2/hr$. The respiration of the soil during air exposure varied from 0.005 g $C/m^2/hr$ at air flow 0.1 cm/sec to 0.20 g $C/m^2/hr$ at air flow 3 cm/sec, as recorded in 41 measurements. Since the average wind velocity at ground level was 1.5 ft/min or .76 cm/sec, the soil respiration was about 0.012 g $C/m^2/hr$ or 0.168 g $C/m^2/14hr$. Whether peat was accumulating or decreasing during May is not known. The peat layer of a mangrove forest tends to develop a fairly constant inter-tidal equilibrium level (Chapman and Ronaldson 1958).

Respiration of the medium-sized animals (snails, crabs, and spiders) as measured in the field is presented in Table V, together with esti-

TABLE V. Estimate of oxygen consumption of mangrove fauna

Taxa	Dry Wt/m²	ml O_2/g/hr	ml $O_2/m^2/hr$
Snails	0.170	1.49	0.253
Crabs	5.070	0.26	1.318
Insects	0.103	1.00	0.103
Spiders	0.001	7.67	0.008
Vertebrates	1.036	3.00	3.108
			4.790

mated values for insects and vertebrates. These values of oxygen consumption per gram body weight were multiplied by estimates of biomass (Table III) to obtain the total metabolism of the fauna—0.164 g $O_2/m^2/day$ or 0.082 gm $C/m^2/day$. These data indicate that the macrofauna account for only a small portion of the total consumption of the community.

Export

Every evening in May there was a gentle and gradual rise and fall of the tide. At night over a 10 hr period, 10 cm or 100 l/m^2 of water moved onto the quadrat and out again without perceptible turbulence or easily recognizable current. Data in Table VI indicate that the water moves

TABLE VI. Estimate of export of particulate organic matter in tidal water[1]

Sample	Incoming Water mg/l	Outgoing Water mg/l	Change mg/l
1	1.36	38.20	36.4
2	1.87	10.60	8.7
average	1.62	24.40	22.7

[1] 100 liters of tidal water flow over one square-meter/day.

out with 22.7 mg net dry particulate matter in each liter per day. Thus the particulate matter carried out in May is estimated at 2.27 g/m^2 or 1.14 g $C/m^2/day$.

Data in Table VII indicate that the outgoing water carries more labile organic matter than the incoming water since there was 1.61 mgO_2/l water oxygen consumption in 6 days or 0.23 g $C/m^2/day$ labile organic matter exported, much less than the particulate value.

TABLE VII. Oxygen changes in biochemical oxygen demand bottles over a 6 day period in the dark at 28° C. Data as mg/1, oxygen

	Start	After 6 days	Change
Incoming Water	5.90 5.89	5.13 5.40	
	5.90	5.26	−0.64
Outgoing Water	4.88 4.53	2.40 2.50	
	4.70	2.45	−2.25
Difference	—	—	1.61 mg/1/6 days

Apparently the particulate matter includes a large proportion of non-labile organic matter. Bottles containing swamp water were still visibly full of particulate matter after one year. The only fraction of organic matter not included was the non-labile matter smaller than the net mesh.

Comparison of Gains and Losses

The various estimates of photosynthetic gain and loss due to respiratory consumption and export are included in one budget graph in Figure 5. The gains due to photosynthesis are plotted on the right. These include the observed daytime net photosynthesis plus an estimate of daytime photosynthesis that is consumed by concurrent daytime respiration. Thus the total length of bars to the right of the center line represents estimates of gross production. The bars to the left include day and night respiration and estimates of export as indicated. The graph in Figure 5 represents a synoptic view of the processes in the mangrove forest during an average day in May.

Apparently a large proportion of the gross photosynthesis is immediately used in plant respiration during the day and night. The estimates of gross photosynthesis and total attrition are sufficiently close to suggest that this forest is not in rapid succession. Without data from other

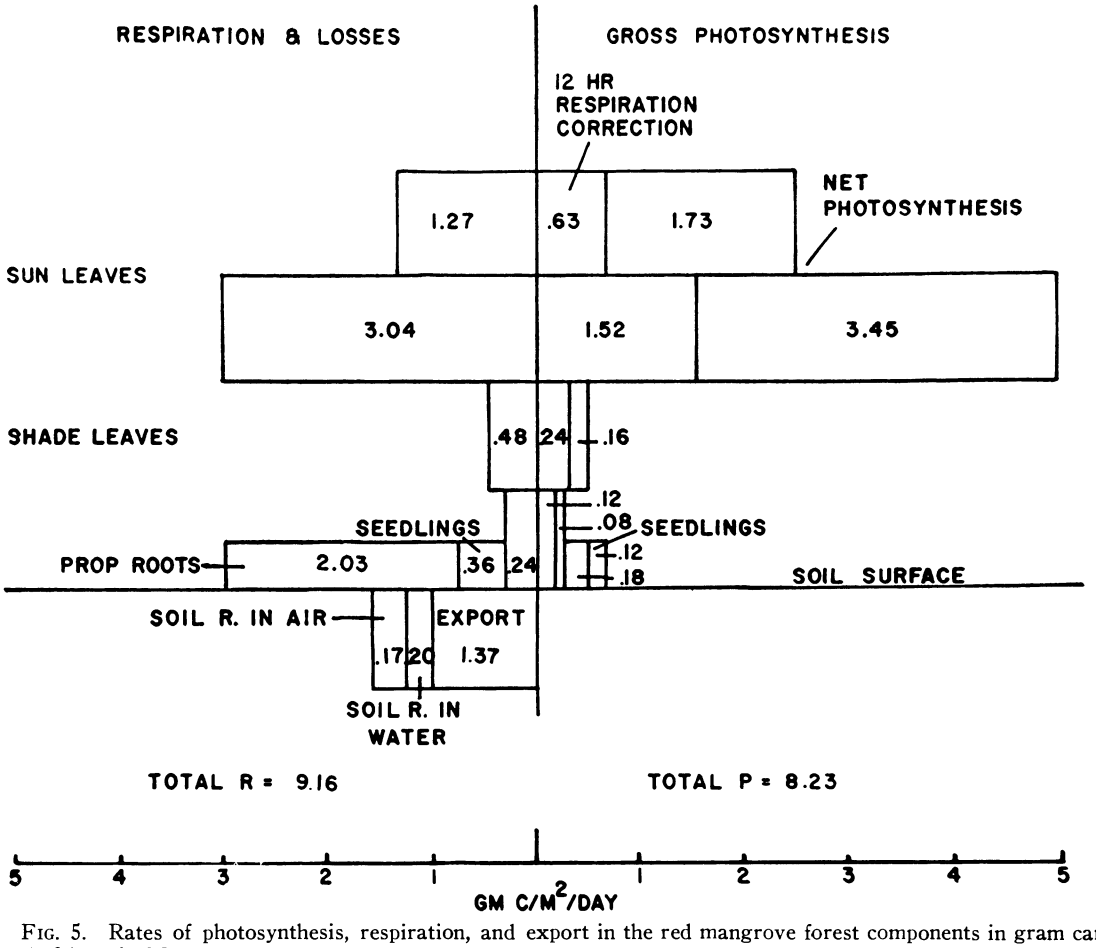

FIG. 5. Rates of photosynthesis, respiration, and export in the red mangrove forest components in gram carbon/m²/day in May.

seasons and other years, and further replications the results cannot be interpreted in too great detail.

Net estimates of annual growth of wood totaled 0.84 g/m²/day or about 0.42 g C/m²/day (Table VIII). Since there are some sites with an open canopy in the forest and no trees which approach the maximum size for red mangrove (dbh, 90 cm), this forest may still be growing. Noakes (1955) in Malaya reported 130-140 cu ft/acre (14 g C/m²/day) yield of timber based on mean annual increment over 25 yrs in growing red mangrove (*Rhizophora mucronata*) forest. Holdridge (1940) reported 2 in. diameter growth in 5 yrs on red mangrove plantations. These growth rates are much higher than those measured in our plot.

TABLE VIII. Net growth of wood of red mangrove on 100m² plot

DBH Class cm	Number Trees 1959	DBH Increase cm/tree	Increase in Class* g/tree	Total Increase
0-1.....	4	.58	1965.0	7860
1-2.....	65	.08	271.0	17615
2-3.....	38	.00	0.0	
3-4.....	12	.00	0.0	
4-5.....	7	.19	643.7	4506
5+.....	10	.02	67.8	678
Totals...	136			30659/100m²
average growth of 306.6 g/m²/yr or .84 g/m²/day				

* Based on regression of 3388 g wood per cm dbh.

The organic matter supplying the soil falls as leaves from the euphotic zone above at a rate of about 1.3 gm/m²/day or 0.65 g C/m²/day (measured on a total of 24 m² in 4 replications as 1.4, 0.1, 1.9 and 2.8 g organic matter/m²/day). Since export of particulate matter (1.1 g C/m²/day) and soil respiration (0.37 g C/m²/day) together are more than twice the estimates of the leaves, some other sources of organic matter to the mud may be present. Students of the field biology course at the University of Puerto Rico at Mayaguez set up a one hour plastic bell jar experiment to determine mangrove soil respiration in June, 1961. CO_2 was absorbed in KOH and each series contained a control, a clear plastic and a aluminum-foil covered box. Gross production of algae associated with the mud (calculated as the difference between covered and clear boxes) was 2.70 and 0.90 ml CO_2/hr or 1.134 and 0.378 g C/m²/14 hours. Gains to the mud, the leaf fall plus the difference between gross production of the algae (using the highest value) and soil respiration in air, of 1.61 g C/m²/day were close to total losses to soil respiration and export of 1.74 g C/m²/day. Although these are very preliminary data, they suggest that algae may be important producers in the mangrove community.

Comparison of Metabolism with Other Communities

With a total gross production and respiration exceeding 8 g C/m²/day or about 16 g organic matter/m²/day, the red mangrove community is more fertile than most marine and terrestrial communities (Summarized by Odum and Odum 1959). The montane rain-forest, studied in the Luquillo Mountains, Puerto Rico, (Odum, Abbott, Selander, Golley, and Wilson, in manuscript; 17 g C/m²/day) and the coral reefs, studied near Magueyes Island, Puerto Rico (Odum, Burkholder, and Rivero 1959); up to 22 g C/m²/day) have greater gross production rates than the mangrove forest. The Puerto Rican red mangrove forest, although well adapted to survive on tropical shores, is not as efficient as the montane rainforest or the coral reef in the conversion of sunlight into organic matter in a similar light regime.

The ratio of gross photosynthesis per 12 hrs of day (0.68 g C/m²/hr) to Chlorophyll a (1.19 g/m²) is the assimilation ratio of the community (0.57 g C/g Chlorophyll a/hr or about 1.2 g O_2/g Chlorophyll a/hr). This ratio falls within the range (0.4 to 4.0 g O_2/g Chlorophyll a/hr) reported for other whole communities by Odum, McConnell and Abbott (1958).

SUMMARY

Measurements of structure and metabolism are reported from a stand of red mangrove (*Rhizophora mangle*) in southeastern Puerto Rico during May, 1959 and 1960 as follows: leaf biomass dry weight, 778 g/m²; wood dry weight, 5507 g/m²; peat and roots, 45,000 g/m²; community chlorophyll *a*, 1.19 g/m²; and animal biomass, 6.4 g/m². Total photosynthesis and leaf respiration were each estimated from measurements with a CO_2 analyzer and were about 8 g C/m²/day. The forest respiration from air exchange holes in the prop root bases was 2.03 g C/m²/day. Smaller magnitudes were found with estimates of leaf fall (1.3 g C/m²/day), trunk growth (0.4 g C/m²/day), tidal export of particulate matter (1.1 g C/m²/day), underwater respiration of the soil (0.2 g C/m²/day) and soil respiration in air (0.168 g C/m²/day). For animals a small metabolism (0.082 g C/m²/day) indicates a minor role in the ecosystem.

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THE MICROCLIMATE OF SUGAR MAPLE STANDS IN OKLAHOMA[1]

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INTRODUCTION

A study of the microclimate of a relict stand of *Acer saccharum*,[2] sugar maple, in Devils Canyon in west central Oklahoma including a review of the literature on microclimates was reported earlier (Rice 1960). Sugar maple occurs in Devils Canyon and in several similar canyons in an area about 185 miles west of the more continuous range of sugar maple in eastern Oklahoma. Near Devils Canyon, tall-grass prairie occurs on soils derived from shales while 3 types of scrubby upland forest communities, blackjack-red cedar, blackjack, and blackjack-post oak, occur on soils derived from sandstone. To help explain why sugar maple has survived in such a dry climate, Rice (1960) compared certain environmental factors in Devils Canyon with those outside. Air temperature, evaporation, insolation, air movement, and soil temperature were consistently higher outside the canyon than inside. Relative humidity was generally much higher in the canyon; soil moisture was depleted much faster outside it. During unusually moist, cool periods the differences were not very great but in relatively dry, hot periods they were pronounced. It was concluded that the pronounced ameliorating effects of the canyon on certain climatic factors were probably responsible for the survival of sugar maple.

The results of the project described above suggested the desirability of comparing the microclimate of Devils Canyon with that of a stand of sugar maple in the more continuous distributional

[1] This project was sponsored by the Oklahoma Biological Survey, Carl D. Riggs, Director, and was supported in part by grants from the University of Oklahoma Faculty Research Fund. Part of the equipment used was originally obtained under Contract No. G-4815 with the National Science Foundation.

[2] Nomenclature follows Fernald (1950).