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Seasonal Trends in Gas Exchange Characteristics of Three Mangrove Species*

R. T. MOORE, P. C. MILLER, J. EHLERINGER and W. LAWRENCE

Biology Department, California State University, San Diego, California 92115, U.S.A.

Abstract

Net photosynthesis, dark respiration, and transpiration of three mangrove species (*Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa*) were measured in February, May, and October in southern Florida. The data indicated sizeable seasonal shifts in the photosynthetic and transpirational behavior of *Rhizophora* with less marked changes in the other tow species. The temperature optima in all three species were higher during the summer than they had been in the winter. Peak net photosynthetic rates ranged from 3.7 to 6.8 mg dm^{-2} h^{-1} for *Rhizophora*, 4.2 to 6.1 for *Avicennia*, and 5.9 to 6.8 for *Laguncularia*, with the highest values occurring in May and October.

Net photosynthesis (P_N), transpiration (E), and dark respiration (R_D) measurements were made on three mangrove species in southern Florida three times during the year. The species were *Rhizophora mangle* L. (red mangrove), *Avicennia germinans* L. (black mangrove), and *Laguncularia racemosa* GAERTN. (white mangrove). Throughout this paper they will be referred to as *Rhi ophora*, *Avicennia*, and *Laguncularia*. The first data, collected during January and February, have been presented in detail in an earlier paper (MOORE *et al.* 1972). This paper presents data collected during May and October and an overall comparison for all three periods.

Although the three tropical and subtropical mangrove species exhibit distinct habitat preferences within the int tidal zone, they commonly occur sympatrically in southern Florida. Other studies have shown that they differ in their water relations (MILLER and EHLERINGER, unpublished) and in their winter photosynthetic behavior (MOORE *et al.* 1972). The objective of this study was to determine whether the differences observed during the winter continued through the year and to establish a basis for estimating annual production for each species. GOLLEY *et al.* (1962) have estimated daily production rates for *Rhizophora mangle* from measurements in May in Puerto Rico, but no such estimates are available for the other species. A model simulating the annual course of production and water relations based on our data will be presented in a later paper.

METHODS

In May gas exchange rates of three *Rhizophora*, one *Avicennia*, and one *Laguncularia* were measured at different temperatures and irradiances in a cuvette. These were plants that had

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been sampled in February. In October four *Rhizophora*, three *Avicennia* and three *Laguncularia* were measured. Mechanical injury of several individuals used in February and May necessitated selection of new plants in October. All measurements were made at Turkey Point near Homestead, Florida.

Gas exchange rates were measured with a *Siemens "Sirigor"* cuvette system, a *Beckman 215A* infra-red gas analyser, and *Cambridge* dew point hygrometers in an open system. This system and the procedures for measurements were described by Moore *et al.* (1972). The temperature response experiments involved step changes in cuvette temperature of approximately 5 °C from 20 °C to 40 °C while total irradiation was maintained near 70 mW cm^{-2}. The irradiance response experiments involved four and five levels of irradiance intensity from 15 to 100 mW cm^{-2} while leaf temperatures were held at 25 ± 2 °C. Humidity within the system was controlled only to avoid condensation. Vapor density within the cuvette was normally above ambient due to transpiration.

Irradiation was provided by diffuse solar radiation supplemented by two *Sylvania* 300 W "*Cool lux*" incandescent lamps. Irradiance was regulated by changing the solar shading, the distance to the lamps, and the layers of cheesecloth filter. To avoid confounding by endogenous rhythms, the temperature and light response measurements were conducted during normal daylight hours.

Irradiance values presented here are for visible and near infra-red radiation measured with a thermopile pyranometer. Later laboratory tests showed that a filter of 2.5 cm of acrylic plastic and 7.5 cm of water would have reduced the irradiance by 25 to 30% indicating that there was a substantial red and far red component.

Due to limitations in equipment and time the February carbon dioxide compensation data were used for calculating internal resistances in May and October, rather than repeating the measurements.

Water vapor diffusion resistances (r_{H_2O}), mesophyll resistances (r_m, Gaastra 1959), and intracellular resistances (r_{int}, Slatyer 1971), were calculated with the equations (Moore *et al.* 1972):

$$r_{H_2O} = 360(\chi_l - \chi_a)/E \qquad (1)$$

$$r_m = 0.6522(C_a - \Delta C)/P_N - 1.56\, r_{H_2O} \qquad (2)$$

$$r_{int} = 0.6522(C_a - \Delta C - \Gamma)/P_N - 1.56\, r_{H_2O} \qquad (3)$$

where: r_{H_2O}, r_m, and r_{int} [s cm^{-1}], χ_l is the saturation vapor density at leaf temperature and χ_a is vapor density of the air exiting from the cuvette [mg l^{-1}], E [mg H_2O dm^{-2} h^{-1}], C_a is the ambient carbon dioxide concentration [vpm], ΔC is the depletion of carbon dioxide within the cuvette [vpm], Γ is the light saturated CO_2 compensation point [vpm] for the species at the same leaf temperature, P_N [mg CO_2 dm^{-2} h^{-1}], and 360 and 0.6522 are constants for conversion of units. The ambient carbon dioxide concentration was measured as about 370 vpm in May and 330 vpm in October.

The r_{int} resistance approximates the intracellular CO_2 transfer resistances in the liquid phase within the mesophyll, assuming that under light saturated conditions Γ is the best estimate of CO_2 concentration at the effective carboxylation/decarboxylation surface (Slatyer 1971). The remaining factors associated with the change in CO_2 concentration from Γ at the effective carboxylation/decarboxylation surface to zero within the chloroplast are viewed as biochemical or carboxylation "resistances" and would include photorespiratory effects.

This treatment is an oversimplification of the actual physiological processes since all three species apparently possess photorespiration (indicated by their high Γ values and oxygen inhibition of net photosynthesis) and have anisolateral stomatal distributions. Both of these factors

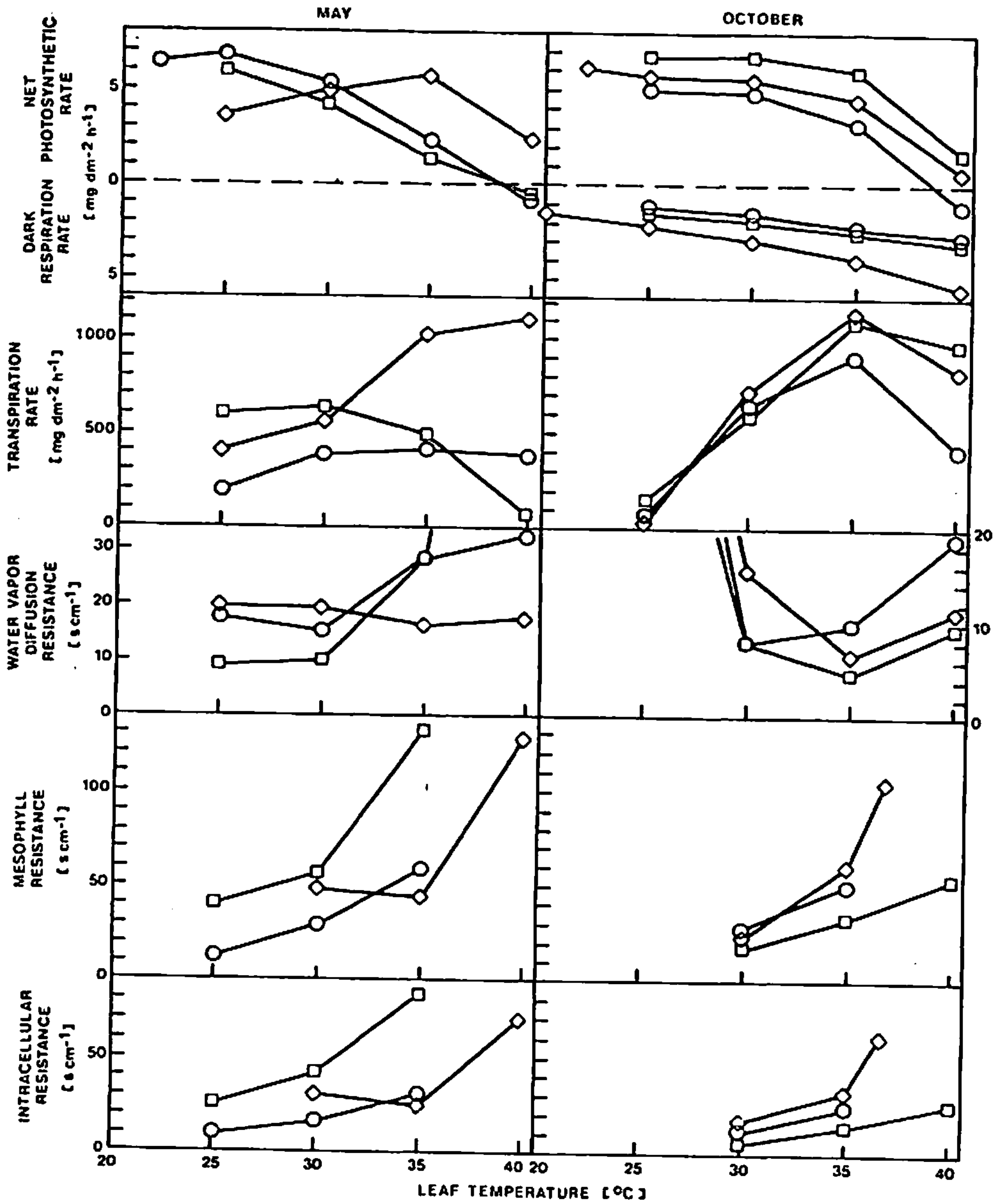

Fig. 1. Net photosynthesis (P_N), dark respiration (R_D), transpiration (E), water vapor diffusion resistances (r_{H_2O}), mesophyll resistances (r_m) and intracellular resistances (r_{int}) in relation to leaf temperature for ○ *Rhizophora mangle*, ◊ *Avicennia germinans*, and □ *Laguncularia racemosa* during May and October. 95% confidence intervals for October were approximately ±2 to 4 mg dm^{-2} h^{-1} for P_N, ±1 to 2 mg dm^{-2} h^{-1} for R_D, and ±100 to 300 mg dm^{-2} h^{-1} for E.

bias the estimates of internal CO_2 resistances as derived above (LAKE 1967a,b; GALE and POLJAKOFF-MAYBER 1968; MORESHET *et al.* 1968; ŠESTÁK *et al.* 1971). However, the simplified scheme provides a group of measurable parameters which allow seasonal and species comparisons. The parameters also characterize the physiological processes for a productivity simulation model. JONES and SLATYER (1972) showed that estimates of intracellular resistances based on overall gas exchange measurements may overestimate the actual resistances by less than 10%.

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RESULTS

Temperature relations

Net photosynthesis: In May P_N of *Rhizophora* and *Laguncularia* was similar, with maximum rates of 6.8 and 5.9 mg dm^{-2} h^{-1} respectively near or below 25 °C and an upper thermal compensation point of about 39 °C (Fig. 1). Maximum P_N of the *Avicennia* plant was 5.7 mg dm^{-2} h^{-1} near 35 °C and was still positive at 40 °C. Its upper thermal compensation point probably would have exceeded 42 °C. In October the response of P_N to temperature was similar among the three species, with maximum rates of 5.2, 5.7, and 6.8 mg dm^{-2} h^{-1} at temperatures of 25, 25, and 30 °C and upper temperature compensation points of 39, 41, and 42 °C for *Rhizophora*, *Avicennia*, and *Laguncularia* respectively. The maximum P_N, the temperature optima and the upper temperature compensation points were higher in May and October than in February in all three species.

Dark respiration: In May R_D was not measured; in October R_D rates of *Rhizophora* and *Laguncularia* were similar and approximated the rates for all three species in February (Fig. 1). R_D of *Avicennia* in October was almost twice that in February.

Transpiration: Maximum E rates in February, May, and October were lowest in *Rhizophora* and highest in *Avicennia*. In May maximum E of *Rhizophora* occurred between 30 and 40 °C, of *Laguncularia* between 25 and 30 °C, and of *Avicennia* above 40 °C (Fig. 1). In October maximum E of all species occurred at about 35 °C.

Leaf resistance to water loss: In May at temperatures between 25 and 30 °C, *Laguncularia* had the lowest leaf resistance, and *Avicennia* the highest. Between 35 and 40 °C *Laguncularia* had the highest resistances and *Avicennia* the lowest. Resistances of *Avicennia* hardly changed with temperatures, but those of *Rhizophora* and *Laguncularia* increased with temperature. In October all species had their lowest resistances at temperatures between 30 and 35 °C. Above 35 °C resistances in *Rhizophora* increased more rapidly than those in the other species.

Mesophyll and intracellular resistances: In May the r_{int} values corresponding to peak photosynthesis for each species were lowest for *Rhizophora* and highest for *Avicennia* (Fig. 1). In the three species, resistances of *Laguncularia* were most sensitive to temperature increases below 35 °C. During October r_m values of *Rhizophora* and *Avicennia* were similar below 35 °C. Above 35 °C the resistances of *Rhizophora* probably increased more rapidly than those for *Avicennia* since *Rhizophora* had a lower thermal compensation point. *Laguncularia* had the lowest r_{int} of the three species throughout the entire temperature range tested. The r_{int} of *Laguncularia* would probably have increased abruptly near the thermal compensation point.

Light relations

Net photosynthesis: Irradiance response curves in May showed that *Rhizophora* and *Avicennia* were light saturated at about 50 mW cm^{-2} (Fig. 2). Data on *Laguncularia* were insufficient to characterize its response. In October, *Avicennia* was light saturated at about 55 mW cm^{-2}, and *Rhizophora* and *Laguncularia* were not saturated at 70 mW cm^{-2}. Extrapolating from the irradiance response curves and the peak P_N values in Fig. 1, *Rhizophora* and *Laguncularia* should have reached saturation by irradiance at 70 to 80 mW cm^{-2} and 85 to 100 mW cm^{-2} respectively.

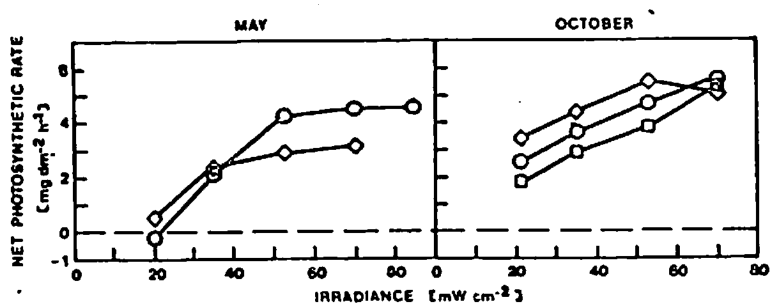

Fig. 2. Net photosynthetic rate (P_N) in relation to irradiance for ○ *Rhizophora mangle*, ◇ *Avicennia germinans*, and □ *Laguncularia racemosa* during May and October.

Transpiration: Because the irradiance response experiments were conducted at leaf temperatures of 25 °C, transpiration levels were low. During both sampling periods most individuals of *Rhizophora* and *Avicennia* showed decreasing transpiration rates as irradiance increased beyond approximately 50 mW cm^{-2}. Transpiration rates of *Laguncularia*, however, remained relatively stable or increased with increasing irradiance above 50 mW cm^{-2}.

Leaf resistance: Minimum transpiration resistances in *Rhizophora* and *Avicennia* occurred at irradiance levels between 20 and 40 mW cm^{-2} in October. Resistance data for *Laguncularia* in October were quite scattered without a consistent pattern. Minimum resistances for *Rhizophora* in May occurred at about 40 to 50 mW cm^{-2}.

DISCUSSION

Seasonal comparisons

Several seasonal shifts in gas exchange characteristics appeared in the three species (Table 1). For *Rhizophora*, net photosynthetic rates and the thermal compensation point were higher in May and October than in February. Peak P_N and thermal compensation points for *Laguncularia* and *Avicennia*, on the other hand, were similar or only slightly higher during the summer. *Avicennia*, in May and October, and *Rhizophora* and *Laguncularia* in October showed a shift to higher optimum temperatures for photosynthesis. In October P_N of all species was relatively insensitive to temperature within the ambient temperature range.

The relation of R_D to temperature for *Rhizophora* and *Laguncularia* was similar in February and October, but R_D rates of *Avicennia* were almost doubled in October. Since *Avicennia* actively excretes salts in the leaves, the higher summer R_D may be related to increased salt excretion because of increased transpiration and salt uptake.

Table 1

Seasonal comparisons in gas exchange characteristics.

	Rhizophora			*Avicennia*			*Laguncularia*		
	February	May	October	February	May	October	February	May	October
n	5	3	4	4	1	3	4	1	3
$T\ opt$*	20	25	25	25	35	25	25	25	30
$P_N(T\ opt)$**	2.7	6.8	5.2	4.1	5.7	5.7	6.0	5.9	6.8
R_D (25 °C)**	0.7	—	1.1	1.1	—	2.1	0.8	—	1.5
$E(T\ opt)$**	160	190	50	350	1020	10	430	590	590
$r_{H_2O}\cdot(T\ opt)$***	17.4	17.2	39	9.6	14.7	70	10.8	7.0	7.7
$r_m(T\ opt)$***	40	17	—	59	43	—	28	34	16
$r_{int}\cdot(T\ opt)$***	27	6	—	30	24	—	19	23	8
$E\ max$**	580	410	910	800	1100	1150	610	620	1100

* [°C]
** [mg dm^{-2} h^{-1}]
*** [s cm^{-1}]

Rhizophora had higher P_N at all irradiances in May and October than in February and appeared to require higher irradiances for saturation in the summer. *Avicennia*, likewise, had higher P_N rates and reached saturation at higher irradiances in October than in February. P_N of *Laguncularia* in October, however, was only 50 to 60% of February rates at irradiance levels below 70 mW cm^{-2}. *Laguncularia* was saturated by irradiance at about 50 to 60 mW cm^{-2} in February, but not at irradiances up to 70 mW cm^{-2} in October. At irradiance levels of 70 to 85 mW cm^{-2} in October, P_N of *Laguncularia* was at or above the February level.

Transpiration rates of *Rhizophora* and *Avicennia* were higher in May and October than in February at most temperatures. Transpiration rates of *Laguncularia* were higher in October than in February except at temperatures below 25 °C. Leaf resistances to water loss of *Rhizophora* were lower in May and October (minima of 11.7 s cm^{-1}) than in February (minima of 17.4 s cm^{-1}). Transpiration resistances were similar for all species in October, whereas in February *Rhizophora* had far higher resistances than the other species above 20 °C. Minimum leaf resistances for all species occurred at higher temperatures in October than in May and February.

The internal resistances for *Rhizophora* were similar in May and October and far lower than in February. Internal resistances for *Avicennia* were lower in October and May than in February for temperatures below 30 °C, but higher at temperatures above 30 °C. Internal resistances of *Laguncularia* were lower in October than in February and May. All resistances of *Rhizophora* changed much more through the year than did those of *Avicennia* and *Laguncularia*.

Comparison with other species

The peak P_N rates of the three mangrove species appear to be slightly lower than those for temperate zone broad-leaved evergreen trees. LARCHER (1963) reported rates of 10 to 16 mg dm^{-2} h^{-1} for sun leaves and 3 to 8 mg dm^{-2} h^{-1} for shade leaves of broad-leaved evergreen trees. These are only about one-half the rates he reported for deciduous trees. HESKETH (1963), however, reported rates of 6 and 10 mg dm^{-2} h^{-1} for maple and oak, respectively. The senior author and others found P_N up to 5 and 9 mg dm^{-2} h^{-1} for *Eurotia lanata* and *Atriplex confertifolia* growing in a cold salt desert environment in Utah (R. S. WHITE, R. T. MOORE, and M. M. CALDWELL, unpublished). Due to soil salt accumulations the water stress conditions encountered by these shrubs during the period of peak photosynthesis would correspond roughly to the mangrove swamp environment. GOLLEY *et al.* (1962) measured P_N of 5 to 20 mg dm^{-2} h^{-1} by *Rhizophora* plants in Puerto Rico. Like the measurements reported here, their data show a high degree of variability among gas exchange rates of different branches.

During both the winter (February) and summer (October), *Rhizophora* had lower P_N than either *Avicennia* or *Laguncularia*; however, in this environment, where all three species are capable of growing, *Rhizophora* is by far the most abundant. In this instance dominance cannot be implied from potential P_N. Admittedly, we have no estimates of root and stem respiration for each species, which could easily reverse the order of productivity potentials. However, the research area is near the northern limit for each species. *Rhizophora* extends farther north than the other two suggesting a greater degree of winter hardiness. While our results cannot be construed as proof of such, perhaps the seasonal acclimation of photosynthetic mechanisms helps render *Rhizophora* less susceptible to low winter temperatures.

Acclimation of photosynthetic mechanisms to changing climatic conditions has been demonstrated in several other species. MOONEY and SHROPSHIRE (1967) and MOONEY and HARRISON (1970) found very rapid temperature acclimation in *Encelia*. MOONEY and WEST (1964) found that acclimation of several shrubs could occur within a few weeks. Thus, seasonal acclimation in evergreen species is probably common.

In summary, it appears that all three species exhibit a seasonal acclimation in terms of photosynthesis and stomatal behavior but this seasonal shift from high stomatal and internal resistances during the winter to low resistances in the summer was most conspicuous in *Rhizophora*.

REFERENCES

GAASTRA, P.: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. — Meded. Landbouwhogeschool (Wageningen) 59: 1—68, 1959.

GALE, J. A., POLJAKOFF-MAYBER, A.: Resistances to the diffusion of gas and vapor in leaves. — Physiol. Plant 21: 1170—1176, 1968.

GOLLEY, F. B., ODUM, H. T., WILSON, R. F.: The structure and metabolism of a Puerto Rican red mangrove forest in May. — Ecology 43: 9—19, 1962.

HESKETH, J. D.: Limitations to photosynthesis responsible for differences among species. — Crop Sci. 3: 493—496, 1963.

JONES, H. G., SLATYER, R. O.: Effects of intercellular resistances on estimates of the intracellular resistance to CO_2 uptake by plant leaves. — Aust. J. biol. Sci. 25: 443—453, 1972.

LAKE, J. V.: Respiration of leaves during photosynthesis. I. Estimates from an electrical analogue. — Aust. J. biol. Sci. 20: 487—493, 1967a.

LAKE, J. V.: Respiration of leaves during photosynthesis. II. Effects on the estimation of mesophyll resistance. — Aust. J. biol. Sci. 20: 495—499, 1967b.

LARCHER, W.: Die Leistungsfähigkeit der CO_2-Assimilation höherer Pflanzen unter Laboratoriumsbedingungen und am natürlichen Standort. — Mitt. flor.-soziolog. Arbeitsgemeinsch., N. F. 10: 20—34, 1963.

MOONEY, H. A., HARRISON, A. T.: The influence of conditioning temperature on subsequent temperature-related photosynthetic capacity in higher plants. — In: Prediction and Measurement of Photosynthetic Productivity. Pp. 411—417. PUDOC, Wageningen 1970.

MOONEY, H. A., SHROPSHIRE, F.: Population variability in temperature related photosynthetic acclimation. — Oecol. Plant. 2: 1—13, 1967.

MOONEY, H. A., WEST, M.: Photosynthetic acclimation of plants of diverse origin. — Amer. J. Bot. 51: 825—827, 1964.

MOORE, R. T., MILLER, P. C., ALBRIGHT, D., TIESZEN, L. L.: Comparative gas exchange characteristics of three mangrove species during the winter. — Photosynthetica 6: 387—393, 1972.

MORESHET, S., KOLLER, D., STANHILL, G.: The partitioning of resistances to gaseous diffusion in the leaf epidermis and the boundary layer. — Ann. Bot. 32: 695—701, 1968.

ŠESTÁK, Z., ČATSKÝ, J., JARVIS, P. G. (ed.): Plant Photosynthetic Production. Manual of Methods. — Dr. W. Junk N. V. Publishers, The Hague 1971.

SLATYER, R. O.: Effect of errors in measuring leaf temperature and ambient gas concentration on calculated resistances to CO_2 and water vapor exchanges in plant leaves. — Plant Physiol. 47: 269—274, 1971.