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Seasonal coupling of a tropical mangrove forest and an estuarine water column: enhancement of aquatic primary productivity

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Abstract

Seasonal and spatial patterns of aquatic primary production were compared in a tidal creek (Estero Pargo) bordered by mangroves and open waters of Terminos Lagoon, Mexico. Comparisions were made during a 17-month period in 1990–91 that spanned dry, rainy, and storm or 'Norte' seasons. Annual net primary productivity was 478 g C m^{-2} yr^{-1} in the lagoon and 285 g C m^{-2} yr^{-1} in the tidal creek. In some months, there were significant differences in primary production between the two sites. In both areas, the highest productivity occurred in summer at the start of the rainy season (June 1991), and the lowest production occurred during the dry season from February to May. Aquatic primary production was lower during the dry season of 1991 in comparison to 1990, possibly related to unusually low precipitation during 1991. Seasonal changes in water column productivity were correlated to variations in light and precipitation. The effect of runoff from mangrove forests was assessed by serial additions of surface water from a fringe forest to bottle incubations of lagoon water. Small additions of mangrove water stimulated primary production in lagoon waters during all seasons. The net productivity was extremely sensitive to aliquot volume; small amounts (0.3 and 1.7% of total volume) were stimulatory, increasing rates by $>$ 50% in 7 of 12 experiments. The greatest effect occurred in September, 1990, when productivity tripled after an amendment with 1 ml (0.3% by volume) of mangrove water. Additions greater than 3% of total volume generally led to reduction in net productivity probably due to the inhibitory effect of humic substances. In many tropical systems, tidal exchange of estuarine waters with mangrove forests is likely to be important to enhancing water column productivity by exporting organic nutrients and other growth-enhancing substances to the estuary.

Introduction

In many tropical estuaries there are strong inputs of nutrients and organic matter from adjacent mangrove ecosystems controlled by tides and river discharge (Boto & Bunt, 1981; Twilley, 1985; Robertson et al., 1988; Gong & Ong, 1990; Flores-Verdugo et al., 1990). In Terminos Lagoon, Rivera-Monroy et al. (1995) measured significant export of particulate material and dissolved organic nitrogen from fringe mangroves, potentially linking the mangrove and estuary subsystems. Most studies have focused on how these organic materials from mangrove forests support di-

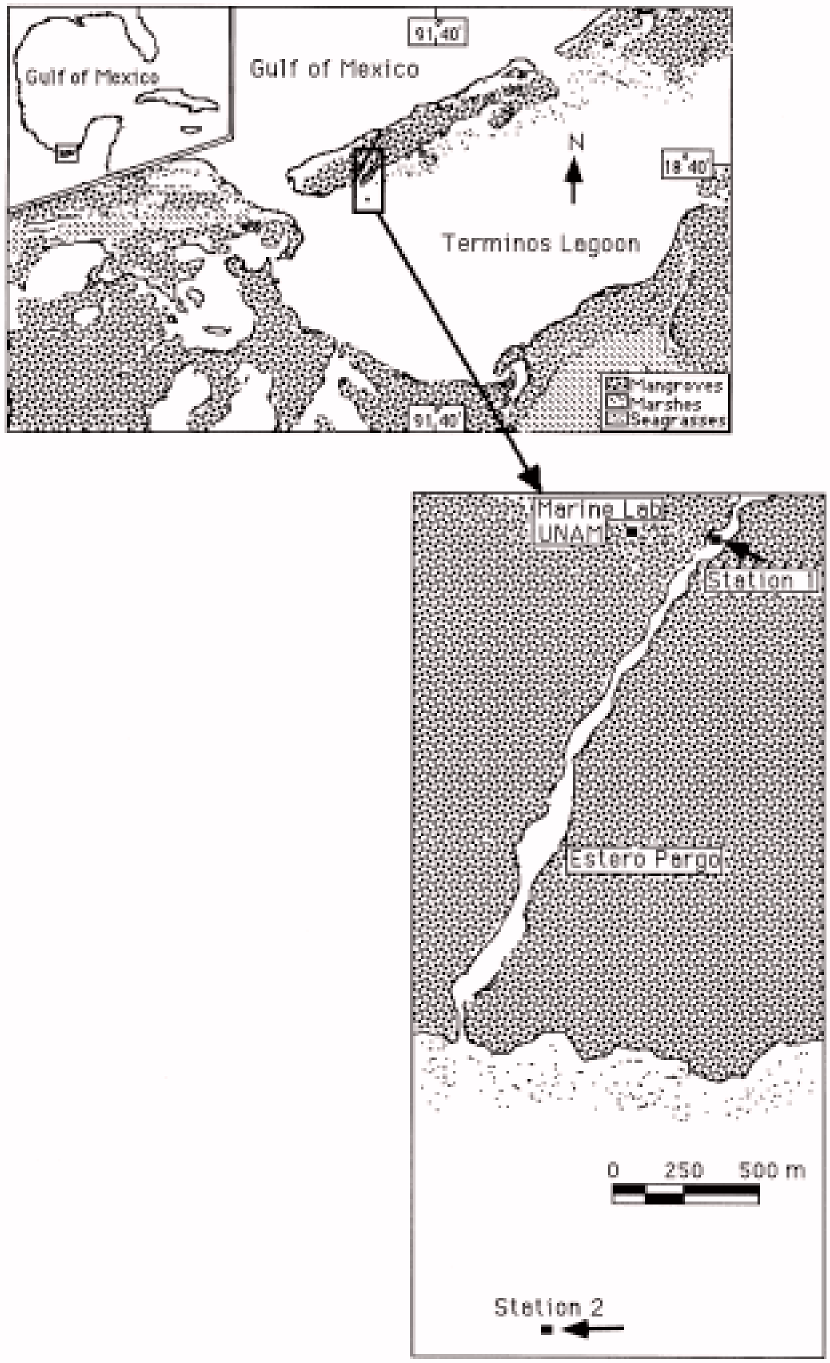

Figure 1. Map of study site, showing location of stations in Estero Pargo (Station 1) and Terminos Lagoon (Station 2).

verse food webs in coastal waters (e.g. Odum & Heald, 1972; Benner & Hodson, 1985; Morán et al., 1991). However, stimulation of primary production by exports of dissolved organic matter from mangroves has been demonstrated by Prakash & Rashid (1969) and Prakash (1971) in Jamaica, West Indies and Herrera-Silveira & Ramírez-Ramírez (1996) in Celestun Lagoon, Mexico. It is likely that organic carbon and nitrogen exported from mangrove forests can enhance aquatic primary productivity in addition to its effect on secondary productivity of tropical estuaries (Twilley, 1988).

In tropical and semi-tropical estuaries along the Gulf and Pacific coasts of Mexico and throughout the world, elevation or enhancement of aquatic primary productivity is often associated with periods of increased inputs of allochthonous material from seasonal patterns of rainfall and river flow (Flores-Verdugo et al., 1987; Rojas Galaviz et al., 1993). In Terminos Lagoon, a tropical estuary in the southern Gulf of Mexico and the site of this study, meteorological and hydrological cycles are characterized by a pronounced dry season in spring and a rainy season in summer. Previous work in this lagoon showed that chlorophyll *a* and aquatic primary productivity increased in the open waters of the lagoon during the rainy season and were highest during the passage of metereological fronts. Day et al. (1988) reported that in the rainy season runoff of mangrove water significantly increased respiration and net production of the estuarine water column. These observations suggest that either dissolved organic matter or nutrients exported from mangroves stimulated phytoplankton production. We report on the first direct studies of this relationship between runoff from mangrove forests and aquatic productivity in this tropical estuary. Relationships between seasonal environmental factors and rates of aquatic primary productivity were examined in two areas of Terminos Lagoon adjacent to and distant from a mangrove forest. Also investigated was the influence of surface runoff from fringing mangrove forests on estuarine water column metabolism. Our hypothesis was that primary productivity in the water column was highest during the wet season because of the stimulatory effect of high inputs of mangrove forest runoff at that time of the year.

Study area

Terminos Lagoon (18°40′ N, 91°30′ W) is a large (approximately 1800 km^2), shallow ($Z_{avg} = 3.5$ m) coastal embayment in the southern Gulf of Mexico. A barrier island (Isla del Carmen) separates the lagoon from the Gulf of Mexico. Tidal passes at each end of the island provide connection with the Gulf (Figure 1). Prevailing easterly trade winds force an east-to-west circulation of coastal waters, causing a net flux of marine water into the lagoon through the northeast pass and out of the lagoon through the southwest pass (Mancilla & Vargas, 1980; Graham et al., 1981). The lagoon is bordered by extensive mangrove swamps, dominated by *Rhizophora mangle* L. (red), *Avicennia germinans* L. (black), *Laguncularia racemosa* Gaertn. f. (white) (Day et al., 1987). Physical and biological processes of Terminos Lagoon are detailed in Phleger & Ayala-Castañares (1971) and Yáñez-Arancibia & Day (1982).

The climate of the region is tropical with average monthly air temperatures ranging from 18 °C to 30 °C. Annual precipitation averages 1680 mm yr^{-1}, but is concentrated during a rainy season that extends from June to October. During the storm or ‘Norte’ season from November to February, periodic northwesterly frontal passages bring high winds, clouds and occasionally substantial rainfall. The dry season extends from February to early June. Tides are mixed diurnal with a mean range of about 0.3 m. The Candelaria, Chumpán and Palizada Rivers are major sources of freshwater to the lagoon (Phleger & Ayala-Castañares, 1971) and peak discharge occurs in the second half of the rainy season from September through November.

Measurements for this study were made adjacent to Isla del Carmen in Estero Pargo, a narrow (14–200 m) tidal channel bordered by mangrove forest, and at a site in the open lagoon, approximately 1 km from the mouth of Estero Pargo (Figure 1). Estero Pargo is 5.9 km long (Ley-Lou, 1985) and during the Norte season, the mangrove forest is periodically flooded as strong north winds increase water levels in the lagoon. During the rainy season, frequent storms wash material from the mangrove forest floor into the channel, and during the dry season, high evaporation results in dry, hypersaline mangrove forest soils. The open water site is in the central basin of Terminos Lagoon, where mean depth is approximately 3 m. The site is close to shore and periodically influenced by drainage from the mangroves as evidenced by a zone of reddish

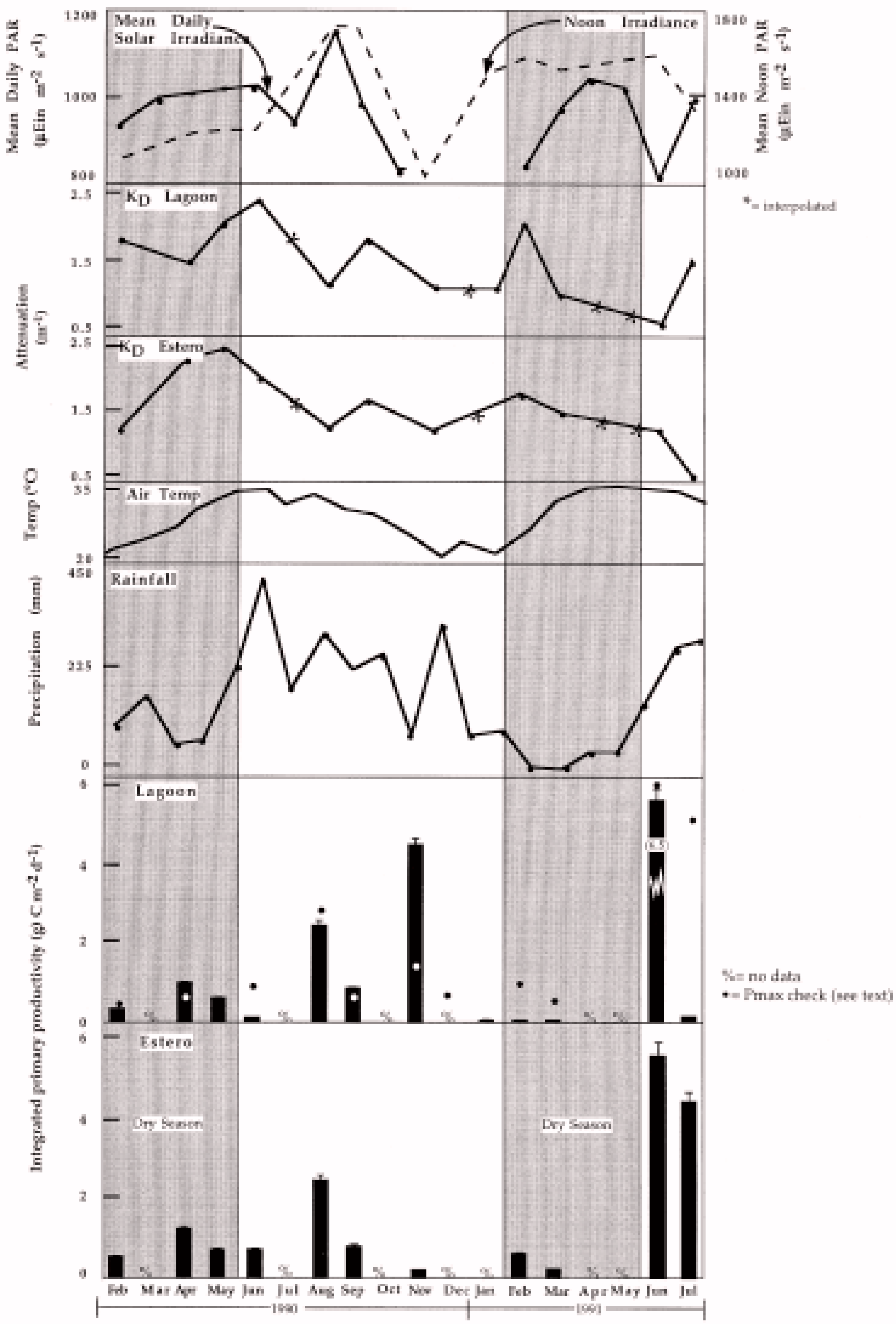

Figure 2. Environmental conditions and net productivity at Stations 1 and 2, February 1990–July 1991. Daily PAR (photosynthetically active radiation) at the study location is monthly average of continuous measurements. Noon PAR (dashed line) is surface irradiance during the incubation. Turbidity measurements (K_D) were made at time of sample collection. Air temperature and rainfall were collected at a meteorological station at the site. Bars on productivity histogram represent mean of three replicate measurements (error bars $\pm$ 1 sd). Points on lagoon graph are estimates from mangrove P_{max} incubations (see text). Shading indicates dry season.

brown dark mangrove water extending 1–2 km into the lagoon.

Material and methods

Sample collection and incubation

Primary productivity experiments
Water samples were collected near a fringe mangrove forest in Estero Pargo (Station 1) and a station in Terminos Lagoon (Station 2) nominally on a monthly schedule. Water was sampled from 15–25 cm depth in opaque 25 l carboys and incubated in situ at the Estero Pargo station as follows: clear and opaque 300 ml BOD bottles were filled under subdued light within 0.5 h after sampling and incubated using the light and dark bottle oxygen technique (Gaarder & Gran, 1927; Hall & Moll, 1975). Triplicate clear BOD bottles were placed in neutral density screen bags of one to four layers transmitting 75, 44, 27, and 14% of incident light. Three opaque bottles were filled and incubated in the dark to measure respiration. Screened bottles were suspended from a floating frame in the tidal creek at 15 cm depth for 3 h. Initial and final oxygen concentrations were measured with an Orbisphere® model 2607 oxygen meter (± 0.01 mg l^{-1}) with stirrer and a Clark temperature-compensated polarographic electrode (Kanwisher, 1960). Water column light profiles were taken at each station with a Licor® Li-1000 datalogger and Li-192SA underwater PAR (Photosynthetically Active Radiation) sensor. Water temperature and salinity were measured using a Beckman® (RS5-3) salinometer. Incident radiation was recorded continuously during incubations with a Licor® 190SA quantum sensor.

Bioassay experiments
Surface water from a fringe mangrove forest at Estero Pargo (Figure 1) was collected in a 500 ml plastic beaker, taking care not to disturb sediments, and transferred to 1 l acid washed (10% HCl v/v) plastic bottles. Samples were vacuum-filtered through preashed GF/F glass fiber filters. Aliquots of 0 (0%), 1 (0.3%), 5 (2%), 10 (3%), 20 (7%), and 50 (17%) ml were added to clear and opaque 300 ml BOD bottles and made up to 300 ml with water collected from the lagoon (Station 2). Triplicate BOD bottles were placed inside one-layer screen bags, transmitting 75% of incident light, and along with the dark bottles, fixed to a floating incubation frame at a depth of 20 cm. Oxygen concentration in bottles was measured before and after 3–4 h incubations around noon to determine water column production and respiration rate. A correction was made to account for dilution of lagoon water by specific volumes of mangrove water (Day et al., 1988). Air temperature, PAR and precipitation were measured continuously at a meteorological station at the study site.

Productivity calculations and statistical analysis

Relationships describing photosynthesis versus light intensity (*P–I* curves) and photosynthetic parameters were derived using a two-step curve fitting procedure (Jassby & Platt 1976). Oxygen production was fitted to the following function after Smith (1936) and Kirk (1983):

$$P = \frac{P_m \alpha E_d}{(P_m^2 + (\alpha E_d)^2)^{1/2}}; \qquad (1)$$

modified to include total production of the water parcel, where P_m is maximum photosynthetic rate, E_d is irradiance, and α is the photosynthetic efficiency (light-limited slope of the *P–I* curve). Photoinhibition was not observed in any of the incubations. P versus I relationships and vertical light profiles were used to calculate integrated productivity (Madden, 1992; Madden & Day, 1992) assuming homogeneous vertical distribution of phytoplankton (Gómez-Aguirre, 1974; Day et al., 1988). Hourly production was extrapolated to daily rates using continuous measures of incident light over time. Rates for months where no daily rate was available were estimated by interpolating existing values. Oxygen metabolism was converted to carbon values with a photosynthetic quotient of 1.2 (0.313 g C/g O_2) and expressed in mg C m^{-2} d^{-1} (Kirk, 1983).

Mangrove water addition incubations were performed with a single screen light treatment (75% ambient PAR), representing full saturation for the phytoplankton community, therefore reflecting the associated maximum productivity rate (P_{max}). Mangrove addition experiments were done nearly contemporaneously with *P–I* incubations (within 1 d), and used as a check on the repetitions of productivity measurements using full *P–I* curves. P_{max} measurements were multiplied by an average 10 h (daylength) and 1.5 m (euphotic depth) to yield an estimate of integrated daily carbon production in the water column (mg C m^{-2} d^{-1}). Differences among volume of mangrove water addition, sampling month, and an interaction term were tested using factorial general linear models. Differences in primary productivity between areas within each month were tested using a nested design with linear contrasts (SAS-JMP®, 1994).

Results

Seasonal and spatial patterns

Water salinity and temperature ranged from 25 to 30 ‰ and from 22.9 to 33 °C, respectively. Mean monthly air temperature ranged from 21–34 °C at the end of the dry season to 18–22 °C during the 'Norte' season. Maximum salinity values were observed on 12 June 1990 in Terminos Lagoon at the end of the dry season.

Photosynthesis versus irradiance (*P*–*I*) relationships closely followed a hyperbolic tangent model. Saturation onset (I_K) generally occurred between 200–300 μEin m^{-2} s^{-1}, regardless of season, which is high compared to other coastal systems. Irradiance was saturating in most incubations (with a few exceptions on cloudy days), and photoinhibition was not evident in any of the incubations. Photosynthetic parameters (P_{max} and alpha) differed significantly among months, but pairwise comparisons showed that between-site differences were not significant.

The magnitude and seasonality of net primary productivity were similar at both sites. Primary productivity ranged from 0.03 to 6.5 g C m^{-2} d^{-1} in the lagoon and from 0.09 to 5.2 g C m^{-2} d^{-1} in the tidal creek and followed a distinct seasonal pattern (Figure 2). At both sites, production was low during the dry season (February–May), averaging 0.49 g C m^{-2} d^{-1}, while rates were four times higher during both rainy and Norte seasons, averaging 2.22 g C m^{-2} d^{-1}. Seasonal differences in primary productivity were significant ($p < 0.02$, $F = 6.305$, $n = 22$ ANOVA). Maximum productivity for both sites was observed in June 1991 at the beginning of the rainy season when productivity averaged 6.5 g C m^{-2} d^{-1} in the lagoon and 5.2 g C m^{-2} d^{-1} in the tidal creek. Minimum rates of 0.05 g C m^{-2} d^{-1} occurred in March 1991 at both sites.

High average rates in the lagoon were strongly affected by two high measurements in November 1990 and June 1991. In seven of 11 paired incubations, productivity in the Estero was significantly higher than in the lagoon, while rates were higher in the lagoon only twice. In the dry season, productivity in the tidal creek always exceeded that in the lagoon ($n = 6$). During the wet and Norte seasons, rates at the two sites were either statistically similar (August–September, 1990) or higher in the lagoon (November, 1990; June, 1991). In the lagoon, dry season rates were much lower in 1991, averaging 0.1 g C m^{-2} d^{-1}, than in 1990, averaging 0.71 g C m^{-2} d^{-1}. While in the tidal creek, rates were about 70% lower in 1991 (0.25 g C m^{-2} d^{-1})

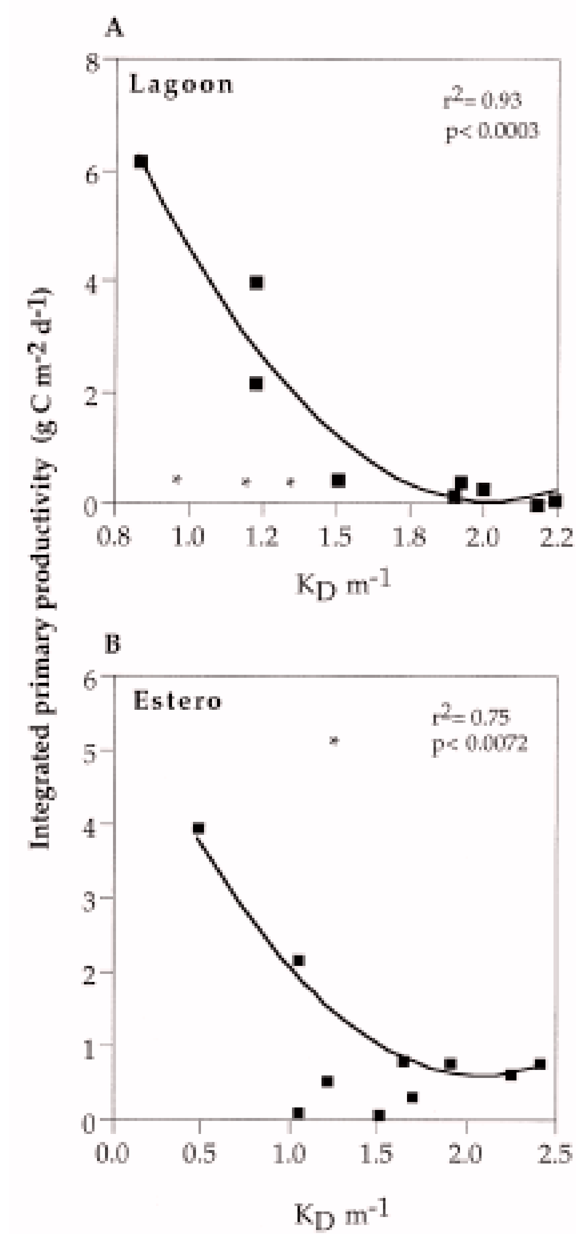

Figure 3. Relationship of integrated water column productivity and in situ turbidity (K_D) for lagoon and estero sites. Asterisks represent measurements not included in calculation of regression lines (see text).

Table 1. Environmental conditions, ratio of production to respiration (P:R), and salinity during sampling collection.

Date	$P_G:R$***		$P_N:R$****		Salinity (‰)		Weather	Season
	TL*	EP**	TL	EP		TL	EP	
1990								
February, 6	2.6	3.8	1.6	2.8	25.0	31.0	partially cloudy	'Norte'
April, 5	8.8	2.6	7.8	2.5	32.9	32.0	clear, sunny	Dry
May, 9	6.7	16.0	5.6	15.0	36.4	35.0	clear, sunny	Dry
June, 12	1.3	3.4	0.3	2.4	35.0	38.0	partially cloudy	Dry/Rainy
August, 15	11.2	3.1	10.2	2.1	28.0	26.0	clear, sunny	Rainy
September, 11	2.4	9.8	1.4	8.8	30.0	28.0	clear, sunny	Rainy
November, 3	8.6	5.5	7.6	4.5	26.2	25.8	partially cloudy	'Norte'
1991								
January, 6	1.0	nd	0.03	nd	26.8	27.2	clear, sunny	'Norte'
February, 19	1.1	1.8	0.11	0.8	25.9	32.0	clear, sunny	'Norte'
March, 29	1.2	1.1	0.17	0.2	33.5	34.7	clear, sunny	Dry
June, 6	5.0	3.1	4.01	2.1	36.4	36.2	sunny	Dry/Rainy
July, 18	1.1	3.4	0.05	2.4	30.5	35.0	clear, sunny	Rainy

* Terminos Lagoon.
** Estero Pargo.
*** Gross production/Respiration ratio.
**** Net production/Respiration ratio.
nd = no data.

compared to the dry season in 1990 (0.85 g C m^{-2} d^{-1}).

The ratios of net production to respiration (P_N:R) in the water columns of both sites were > 1 indicating autotrophy and ratios were generally higher in Estero Pargo than in the open lagoon. The ratio of gross primary production to respiration (P_G:R) in incubations ranged from 1.0–11.2 in Terminos Lagoon and 1.1–16.0 in Estero Pargo. Ratios of net production to respiration (P_N:R) ranged from 0.03–10.2 for the lagoon and 0.2–15 for Estero Pargo (Table 1). Average gross and net productivity ratios at both stations were consistently higher in 1990 (P_G:R and P_N:R = 6.4 and 4.5) than in 1991 (P_G:R and P_N:R = 0.87 and 2.4). The wider range in the *P*:*R* ratio in the tidal creek was predictable due to its proximity to a large source of organic input, resulting in a greater nutrient source for autotrophy, and an abundant carbon source for heterotrophy. The tidal creek system is thus also more likely to continue to have higher net productivity than the open lagoon during periods of low precipitation. In fact, during dry periods production was higher in the tidal creek than in the lagoon.

Light and productivity relationships

Water transparency was as variable monthly as it was seasonally at both sites (Figure 2). During the study, downwelling attenuation (K_D) averaged 1.5 m^{-1} at both sites, ranging from 0.48 to 2.40 m^{-1} in Estero Pargo and 0.83 to 2.24 m^{-1} in the lagoon. Extremes in turbidity corresponded to euphotic depths of less than 2 m to nearly 10 m, deeper than the water column (assuming Zeu = 1% of surface PAR). PAR at mid-day ranged from 1070 to 1675 μEin m^{-2} s^{-1} (Figure 2). Incubations were usually performed during clear and sunny conditions, although some days became hazy to partly cloudy during measurements. Average daytime irradiance ranged from 765 to 1100 μEin m^{-2} s^{-1} with a minimum in June 1991 and a maximum in August 1990 (Figure 2). Daily PAR was generally lowest during the Norte season (October–February), due to low solar zenith angle and overcast conditions during frontal passages. During the spring dry season, the sky was usually clear throughout the day, while during the summer rainy season cloudiness occurred in late afternoon, having minimal effect on average insolation.

Primary productivity was associated with water clarity and incident radiation (PAR). Rates of integrated net water column productivity declined expo-

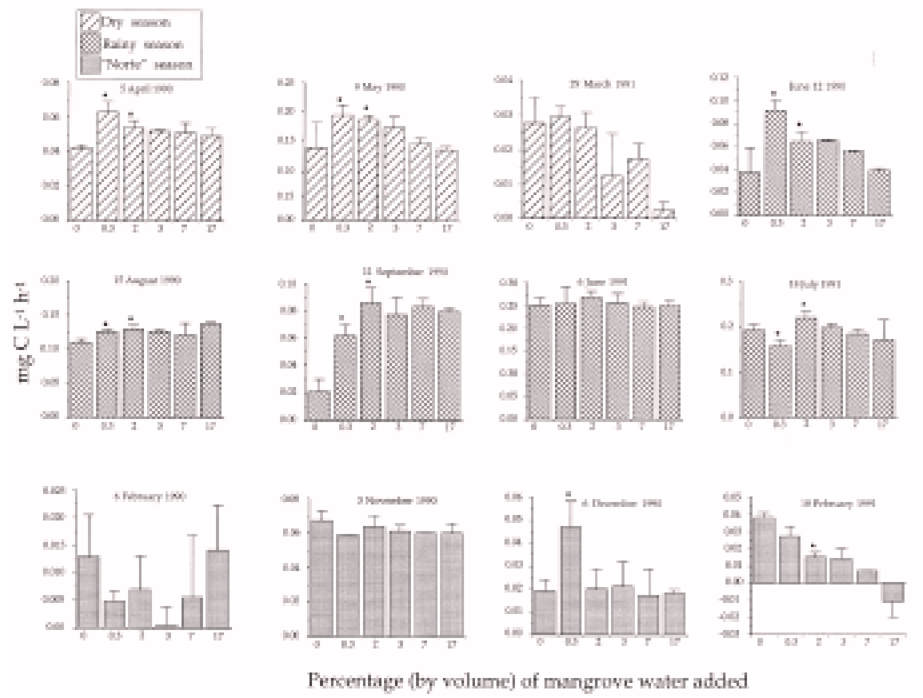

Figure 4. Seasonal net primary productivity of water from Terminos Lagoon treated with different percentages of filtered mangrove water. Percentages represent different aliquots (0, 1, 5, 10, 20, and 50 ml) added to BOD bottles (300 ml volume). Error bars are 1 standard deviation for means of 3 replicates. Asterisks indicate significant differences ($p < 0.05$) from the control treatment (0 ml).

nentially with increasing turbidity (K_D), described by quadratic regression (Figure 3), with correlation coefficients (r^2) of 0.35 for the lagoon ($n = 12$) and 0.65 for the tidal creek ($n = 11$). With the exclusion of three points from the lagoon regression, and one point from the tidal creek regression, r^2 increased to 0.93 and 0.75, respectively. The four excluded points occurred in 1991, an unusually dry year (see Figure 2). The three points from the lagoon with very low productivity relative to turbidity were in dry season conditions. The single outlying point from the tidal creek was from June 1991 in the early wet season, when production was unusually high.

Primary productivity patterns were also related to monthly rainfall, which provides a mechanism for the coupling of mangrove forests and tidal waters. Between 1988–1992, mean annual precipitation averaged about 1600 mm, and significant seasonal and interannual differences were observed. Precipitation during 1990 was greater than normal (1974 mm), while 1991 was drier than normal (1414 mm). Most of the rainfall deficit in 1991 occurred during the dry season, when precipitation totaled only 113 mm (dry season mean = 182 mm), about one-fourth that in the dry season of 1990 (424 mm), and almost half the level in a normal year. Precipitation for January through June in 1990 totaled 855 mm, versus 202 mm in 1991.

Enrichment studies

Small aliquots of surface water from a mangrove forest in Estero Pargo added to incubations of lagoon water stimulated primary productivity (Figure 4). Statistically significant differences in productivity were measured among the percentages of volume added (0, 0.3, 2, 3, 7, 17) ($p < 0.001$), months ($p < 0.001$), and the interaction volume$*$month ($p < 0.001$) treatments. Most significant increases were observed with low percentage of volume additions (0.3 and 2%), which significantly stimulated production in half of 24 experiments ($p < 0.05$) by 20 to 350%. Ten experiments showed no significant change and two of 24 measurements showed a significant decrease with 1 or 5 ml aliquots. The interaction term indicates that effects of additions on productivity were not constant throughout the year, but varied depending on month.

Stimulation of production was generally higher in incubations during the rainy season, with greatest increases in June and September 1990 and the smallest increases in March–June 1991. Mangrove water tended to inhibit productivity during the winter Norte season, even at low volume additions. Stimulation was consistently lower in 1991, a dry year, than in 1990, which had higher precipitation than normal. In two cases (August and September 1990, both during the rainy season), mangrove water additions = 3% resulted in significant stimulation. However, in all other cases the same additions did not affect net productivity or inhibited. In one case in March 1991, productivity decreased by more than an order of magnitude after adding 17% of mangrove water. Significant reductions in productivity were also observed in November 1990, February 1990, and February 1991, with even small percentage additions of 0.3 and 2.

Productivity of lagoon waters with no addition of mangrove water ranged from 0.001 to 0.27 mg C l^{-1} h^{-1}, and as in *P–I* curve incubations, highest rates were observed in June (0.25–0.27 mg C l^{-1} h^{-1}) and July 1991 (0.16–0.22 mg C l^{-1} $h^{-1)}$. The July 1991 P_{max} value estimated with zero mangrove water addition was significantly greater than the value derived from the complete *P–I* curve, and was close to the value we measured in the tidal creek. Similarly, the November 1990 value estimated from mangrove experiments was closer to the tidal creek result, 50% less than the net productivity from *P–I* incubation on the previous day. Overall P_{max} measurements and productivity calculated from *P–I* values were similar.

Discussion

Light as a control of production

Despite the lack of seasonality in the distribution of K_D (turbidity) a strong relationship between productivity, incident PAR and K_D was observed. Small variations in turbidity significantly altered total water column production as indicated by the exponential relationship demonstrated in Figure 3. Turbidity control of productivity has been demonstrated in systems with pulsed nutrient inputs due to the exponential relationship between light attenuation and depth (Cloern, 1987; Madden & Day, 1992). Both light and precipitation were better correlated in the tidal creek than in the open lagoon probably due to the proximity of the tidal creek to the mangrove forest, which is a source of particulate and dissolved organic nitrogen (Rivera-Monroy et al., 1995).

Coupling of mangroves with the estuary

Day et al. (1988) found that small additions of filtered mangrove water from Estero Pargo had a stimulatory effect on oxygen production in light bottles containing water from Terminos Lagoon. Yet, these studies were carried out only at the begining of the dry season. Our results show that this stimulation occurs during all seasons where addition of low percentages (0.3 and 2%) of surface water stimulated productivity by more than 50% in most of the experiments indicating that surface mangrove water can potentially stimulate aquatic primary productivity throughout the year. Overall, the magnitude of the stimulation was different between 1990 and 1991 suggesting an interannual variability.

In many tropical mangrove systems, complex organic compounds are quantitatively released during decomposition of mangrove litter. Approximately 30 to 50% of the organic matter in mangrove leaves are leachable water-soluble compounds such as tannins and sugars (Cundell et al., 1979). Morán et al. (1991) found high concentrations of lignin phenols in waters overlying a mangrove swamp. Humic substances and dissolved lignin phenols are formed during decomposition of red mangrove leaves. High concentrations of dissolved organic material exported from mangrove ecosystems may be a key factor supporting phytoplankton growth. For example, Twilley (1985) showed that leaching of dissolved organic carbon from mangrove leaf litter provided DOC to the surface of basin forests and later exported during rainfall. Previous studies have shown that substances exported from mangroves and other temperate wetlands, including organic nutrients and humic compunds, can stimulate phytoplankton production through a number of mechanisms (Prakash et al., 1973; Granéli et al., 1985; Gediorowska & Plinski, 1986; Moran et al., 1991; Carlsson et al., 1993; Carlsson & Granéli, 1993). It has been suggested that lignocellulose-derived humics are assimilated into microbial biomass (Benner & Hodson, 1985; Morán et al., 1991) enhancing remineralization and nutrient release. Also, organic matter stimulates marine phytoplankton (Toledo et al., 1980; Granéli et al., 1986) and benthic diatoms (Cooksey & Cooksey, 1978) by chelating toxic contaminants and trace metals, mitigating their toxic effects (Toledo et al., 1982; Mackey, 1984). Additionally, nitrogen in dissolved organic matter compounds may be directly available to some algal groups (Granéli et al., 1985; Carlsson & Granéli, 1993). Rivera-Monroy et al. (1995) found significant export of particulate (PN) and dissolved organic nitrogen (DON) from the fringe forest in Estero Pargo during the rainy and 'Norte' seasons. They reported PN export rates of 3.9 mg m^{-2} h^{-1} and 0.62 mg m^{-2} h^{-1} in August and November 1990, respectively. Also, significant export of DON was observed in November 1990 (1.3 mg m^{-2} h^{-1}) and June 1991 (0.075 mg m^{-2} h^{-1}). Export of nitrogen from the fringe forest coincides with high net aquatic primary production rates obtained for the same months in Estero Pargo indicating a potential direct relationship.

In our bioassay experiments, net primary productivity usually declined as gross productivity increased with additions of 3% or more of mangrove water. The inhibitory effects of humic substances have been noted in other locations where selective absorption of light by yellow color (Prakash & Rashid, 1968, 1969), excessive binding of iron or other metals (Prakash et al., 1973; Guildford et al., 1987), and reduced phosphate availability (Jackson & Hecky, 1980) caused lower rates of net productivity. Humics are also toxic to some microalgae (Craigie & McLachlan, 1974), and tannins released by mangroves can inhibit the growth of phytoplankton by reducing pH (Ricard, 1984).

Water column metabolism

The duration of this study over 18 months allowed us to estimate annual productivity and evaluate any patterns of seasonal variability. For the year beginning February 1990 overall means of 1.30 g C m^{-2} d^{-1} in the lagoon and 0.78 g C m^{-2} d^{-1} in Estero Pargo corresponded to annual rates of 474 g C m^{-2} and 285 g C m^{-2}, respectively. For the year beginning August 1990 similar rates were 1.54 and 1.2 g C m^{-2} d^{-1} for the Lagoon and Estero Pargo corresponding to 562 and 438 g C m^{-2} (Table 2). When data from the entire sampling period were included, annualized productivity was about 430 g C m^{-2} for Terminos Lagoon and 383 g C m^{-2} for Estero Pargo. Higher rates in Estero Pargo during the wet season in June and July 1991, elevated annual estimates of productivity. Annual integrated production for Terminos Lagoon in our study was significantly higher than in two earlier studies in the lagoon (Day et al., 1982; Day et al., 1987), which estimated 197 and 219 g C m^{-2} yr^{-1}, respectively. This may be related to our sampling scheme that covered the wet season period of highest production. Our results show that the water column was autotrophic in 1991 (average P:R = 1.4) and 1990 (average P:R = 5.6). Interestingly, we found lagoon productivity during the wet season to be 3–5 times higher than measured in earlier studies, but during the dry season rates were similar in both studies. More importantly, despite differences in magnitude between studies, the seasonal patterns of production we measured in the lagoon in 1990–91 closely matched those observed in the lagoon during 1986 by Day et al. (1988). In all years there is a clear pattern of higher production during the wet months, variably determined by inputs from the mangroves, a productivity peak in November, and low production in dry months.

High water column productivity is well documented in tropical coastal systems, and annual production > 400 g C m^{-2} for Terminos Lagoon is in the upper range reported for mangrove-dominated systems (Table 2). An annual rate of 232 g C m^{-2} yr^{-1} for estuarine waters on the Goa coast, India (Verlencar & Qasim1985) is similar to maximum rates of 292 and 321 g C m^{-2} yr^{-1} for the Cananeia mangrove region in Brazil and the Porto-Novo mangrove area in the Eastern Indian coast, respectively (Ricard, 1984). High rates of aquatic primary production occur in a coastal lagoon on the Pacific coast of Mexico at 522 g C m^{-2} yr^{-1} (Flores-Verdugo et al., 1988) and rates of up to 876 g C m^{-2} yr^{-1} in Phangha Bay in the southwest coast of Thailand (Wium-Andersen 1979). The high rates in Thailand are for an area surrounded by extensive mangrove forest.

Water column primary production in Estero Pargo and Terminos Lagoon followed a pronounced seasonal pattern related to precipitation and light. The period of highest water column productivity occurred during the summer rainy season, and minimum rates of productivity occurred in the spring dry season, despite higher temperatures and peak annual insolation. This is the first study we are aware directly addressing the coupling of mangrove forests and water column primary productivity in an estuary during an entire annual cycle. It is often difficult to obtain long-term ecological data for remote sites in the tropics and we are aware that this creates certain limitations in the data set. Nevertheless, our results strongly indicate that effluent from mangrove forest can enhance phytoplankton productivity in adjacent waters. By establishing effects of mangrove-estuary linkage on primary production at the system level in Terminos Lagoon, we hope to emphasize the importance of mangroves in sustaining productivity in tropical coastal ecosystems. It is important to recognize this ecological function in considering management of mangrove forests.

Table 2. Net primary production (NPP) of phytoplankton in mangrove-dominated tropical and semitropical coastal systems (modified from Ricard, 1984; and Flores-Verdugo et al., 1988).

Location	NPP range (g C m^{-2} yr^{-1})	Reference
Biscayne Bay, USA	13–46	Roman et al., 1983
Gulf of Tehuantepec, Mexico	25.5–522	Robles Jarero & Lara-Lara, 1993
Venezuelan Gulf, Venezuela	35–182	Curl, 1960
Cananeia Region, Brazil	36.5–292	Tundisi et al., 1973
Porto Novo Estuary, India	98–321	Sundararaj & Krishnamurthy, 1973
Cochin Estuary, India	128–310	Qasim, 1973
Phangha Bay, Thailand	182–876	Wium-Andersen, 1979
Mandovi Estuary, India	232	Verlencar & Qasim, 1985
Barra de Navidad Lagoon, Mexico	242	Sandoval-Rojo et al., 1988
Chautengo Lagoon, Mexico	248	Mee, 1978
Rookery Bay, USA	251	Twilley, 1982
Teacapan-Agua Brava Lagoon, Mexico	309	Flores-Verdugo et al., 1990
Mukue Lagoon, Africa	416	Kwei, 1977
Baie du Lévrier, Mauritania	511	Sevrin-Reyssac, 1980
El Verde Lagoon, Mexico	522	Flores-Verdugo et al., 1988
Huizache-Caimanero Lagoon, Mexico	894	Edwards, 1978
Terminos Lagoon, Mexico (entire Lagoon)	197	Day et al., 1988
Terminos Lagoon, Mexico (entire Lagoon)	219	Day et al., 1982
Terminos Lagoon, Mexico (nearshore station)	430–562	This study
Estero Pargo, Mexico	336	Ley-Lou, 1985
Estero Pargo, Mexico	285-438	This study

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