CARBON SINKS IN MANGROVES AND THEIR IMPLICATIONS TO CARBON BUDGET OF TROPICAL COASTAL ECOSYSTEMS.

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ABSTRACT. Nearly 50% of terrigenous materials delivered to the world's oceans are delivered through just twenty-one major river systems. These river-dominated coastal margins (including estuarine and shelf ecosystems) are thus important both to the regional enhancement of productivity and to the global flux of C that is observed in land-margin ecosystems. The tropical regions of the biosphere are the most biogeochemically active coastal regions and represent potentially important sinks of C in the biosphere. Rates of net primary productivity and biomass accumulation depend on a combination of global factors such as latitude and local factors such as hydrology. The global storage of C in mangrove biomass is estimated at 4.03 Pg C; and 70% of this C occurs in coastal margins from 0° to 10° latitude. The average rate of wood production is 12.08 Mg ha^{-1} yr^{-1}, which is equivalent to a global estimate of 0.16 Pg C/yr stored in mangrove biomass. Together with carbon accumulation in mangrove sediments (0.02 Pg C/yr), the net ecosystem production in mangroves is about 0.18 Pg C/yr. Global estimates of export from coastal wetlands is about 0.08 Pg C/yr compared to input of 0.36 Pg C/yr from rivers to coastal ecosystems. Total allochthonous input of 0.44 Pg C/yr is lower than in situ production of 6.65 Pg C/yr. The trophic condition of coastal ecosystems depends on the fate of this total supply of 7.09 Pg C/yr as either contributing to system respiration, or becoming permanently stored in sediments. Accumulation of carbon in coastal sediments is only 0.41 Pg C/yr; about 6% of the total input. The NEP of coastal wetlands also contribute to the C sink of coastal margins, but the source of this C is part of the terrestrial C exchange with the atmosphere. Accumulation of C in wood and sediments of coastal wetlands is 0.205 Pg C/yr, half the estimate for sequestering of C in coastal sediments. Burial of C in shelf sediments is probably underestimated, particularly in tropical river-dominated coastal margins. Better estimates of these two C sinks in the tropics, coastal wetlands and shelf sediments, is needed to better understand the contribution of coastal ecosystems to the global carbon budget.

1. Introduction

1.1 COASTAL MARGIN ECOSYSTEMS

The global flux of C is usually partitioned between terrestrial and oceanic compartments, assuming that terrigenous materials contribute to the budget of C in the oceans. However, there is a shallow transition region between terrestrial and deeper oceanic environments that represent less than 5 % of the earths surface, but is one of the most geochemically and biologically active areas of the biosphere (Figure 1). This coastal region includes

ecosystems from the upper intertidal regions (including tidal freshwater ecosystems) to the outer edges of the continental shelves. These areas are sites where terrigenous materials are introduced to the ocean, where productive wetlands have developed, and biogenic zones in nearshore waters are the most productive regions of the oceans. The elevated phytoplankton production of neritic waters are due in part to the fertile input of rivers and coastal boundary currents that promote primary productivity. Nearly 50% of terrigenous materials transported to the world's oceans are delivered through just twenty-one major river systems. These river-dominated coastal margins are thus important both to the regional enhancement of productivity and to the global flux of C that is observed in coastal ecosystems. River-dominated coastal margins may be key sites where geophysical and biogeochemical processes represent C sinks in the biosphere.

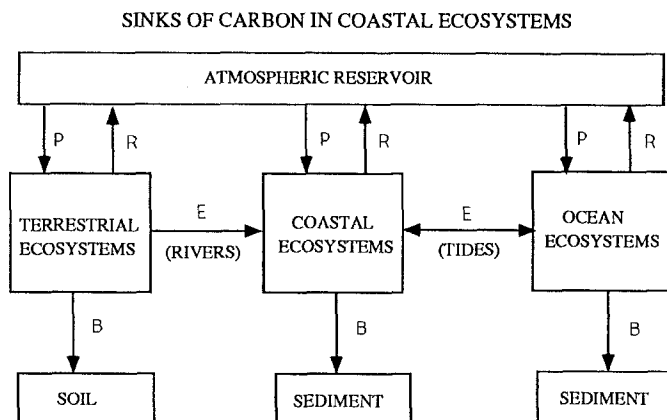SINKS OF CARBON IN COASTAL ECOSYSTEMS

Figure 1. Conceptual diagram of the three major compartments of the biosphere that influence the global cycle of C. P = production, R = respiration, E = exchange, B = burial.

This paper will focus on the factors that control the fate of C in coastal ecosystems of the tropics. Tropical coastal ecosystems are dominated by forested wetlands in the intertidal zone known as mangroves, shallow submersed coral reefs and seagrasses (macrophyte systems), and phytoplankton communities in the neritic waters of the tropical coastal oceans. The ecological processes of these three types of subsystems, together with the fate of riverine input, determine the role of tropical coastal ecosystems as C sinks in the biosphere. The fate of C as a sink in each of these subsystems can be evaluated using a mass balance approach to ecosystem dynamics (Hopkinson, 1988; Twilley, 1988). Net ecosystem production (NEP) of each of the three subsystems is a measure of the mass balance of in situ processes such that:

$$NEP = GPP - (Ra + Rh) - E \qquad\qquad (1)$$

where GPP is gross primary productivity, Ra is autotrophic respiration, Rh is heterotrophic respiration, and E is net export from the system. Ecosystem steady state (ESS) dynamics of C flux can be evaluated by a mass balance of gross C fixation (P) and allochthonous C inputs (I) against losses associated with total system respiration (R) and export (E) as follows:

$$ESS = (P + I) - (R + E) \qquad\qquad (2)$$

If C gains (P +I) are greater than losses (R + E) then the system is non steady state and there is net accumulation and a C sink.   If we consider river input to the coastal system as a whole, then ESS for each of the subsystems is equal to NEP. NEP may occur as increase in biomass annually or the accumulation of C in the sediment reservoirs of each respective subsystem. In phytoplankton ecosystems, there is little NEP (or permanent storage), most of the NPP is either respired or deposited to the seabed. However there are estimates that macrophyte ecosystems (including seagrasses and coral reefs) may be an important C sink in the tropics (Smith, 1981).

Mangroves may function as a sink of C in coastal margin ecosystems depending on the balance of production and decomposition within the forest, and net flux of C across the wetland boundary. Many mangrove ecosystems accumulate peat and this storage of C has not been evaluated on a global scale. These forested wetlands are also different from other subsystems of the coastal zone because of the potential for accumulation of C in wood that may be an important C sink. In addition, the export of organic C from mangroves may contribute to sedimentation or storage of C in coastal sediments. This review will synthesize existing information on biomass, wood production, sedimentation, and export of mangroves to make some preliminary estimates of the global scale of these ecological processes. These fluxes of C will be compared to the transport of terrigenous C to tropical waters as comparison to fate of C in these tropical coastal ecosystems. Particular attention will be focussed on the geographical distribution of these processes in the tropics, which should improve our estimates of these C fluxes. Thus we will start with a description of the forcing functions that influence the function of mangrove ecosystems.

1.2. GEOGRAPHICAL PROPERTIES

1.2.1 Regional classification: Thom (1982) proposed that the combination of geophysical energies with the geomorphology of the coastal zone is important to establishing the ecological characteristics of mangroves (Twilley, in press).   According to Thom, the landform characteristics of a coastal region together with environmental processes control the basic patterns in the structure of coastal forests.   He identified five basic types or classes of environmental settings where mangroves occur based on the relative influence of rainfall, river discharge, tidal amplitude, turbidity, and wave power. These geophysical energies are the dominate forcing functions of mangroves and collectively represent the energy signature of mangroves (Twilley, in press). The regional scale description of coastal environments using geomorphology and geophysical processes can be further separated into ecological classification systems. The ecological classification of mangroves as either fringe, basin, or dwarf forests describe the microtopographic effects of hydrology on the formation of forest types (Lugo and Snedaker, 1974). Within the regional boundaries of an environmental setting there may exist all three ecological types of mangrove forest depending on the local effects of tides, waves, and river flow.

The combination of geophysical energies, together with the regional geomorphology, explain the function of mangrove ecosystems.   Coastal geomorphology and hydrology have been used to classify the physiognomy and zonation of mangrove forests (Lugo and Snedaker, 1974; Watson, 1928).   Recently, the ecological processes or function of wetland ecosystems have also been related to coastal processes such as tides, rivers, and waves (Gosselink and Turner, 1978; Twilley, 1988).   Thus the productivity, sedimentation, and coupling of these ecological processes with coastal waters may be specific according to the geomorphology and geophysical characteristics of coastal ecosystems (Twilley, 1988).   The geomorphological type of coastal environments can constrain the function, as well as structure, of mangrove ecosystems. Linking ecological

function with specific types of environmental conditions of coastal ecosystems should develop greater generality in understanding the role of mangroves as C sinks.

1.2.3 *Global distribution of mangroves*: Information on the distribution of mangroves was gathered from World Resources 1986, a report by the World Resources Institute. This report claims there are 24.00 x 10^6 ha of mangroves in the tropics that dominate the river-dominated delta, lagoon and estuarine coastal environments. Other estimates of mangrove area range from 15.47 to 30 x 10^6 ha, with an average of 21.8 x 10^6 ha (Lugo et al. 1990, Table 4.1). The amount of mangrove area for each country was categorized into four latitudinal belts (0° to 10°, 10° to 20°, 20° to 30°, and 30° to 40°) combining north and south latitudes within each zone. The largest area of mangroves occurs in the 0° to 10° zone with 10.07 x 10^6 ha compared to only 0.25 x 10^6 ha in the 30° to 40° latitudes (Figure 2). The sum of mangrove area based on statistics for each country was short of the estimated total mangrove area of 24.00 x 10^6 ha by 5.81 x 10^6 ha. We distributed this mangrove area among the four latitudinal zones using the relative distribution of the areas given for each country. These distributions on mangrove area were used to develop global estimates of ecological processes within mangrove ecosystems.
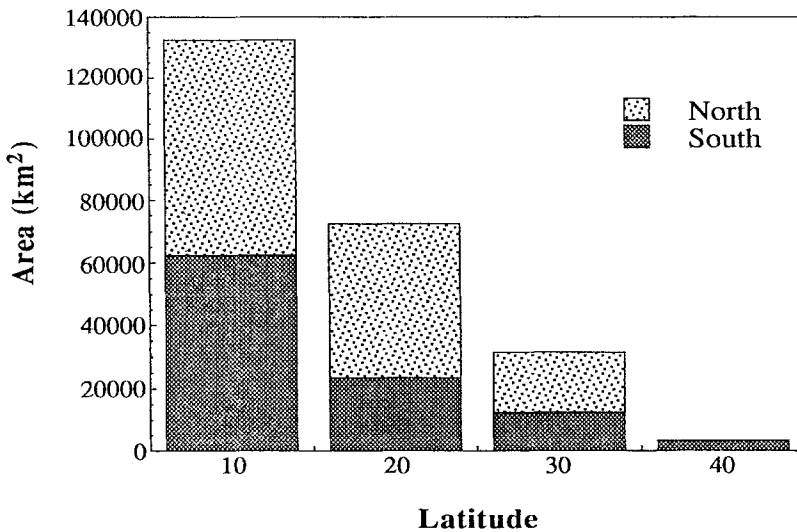

Figure 2. Global distribution of mangroves with latitude.

2. Carbon Sinks in Mangroves

2.1 BIOMASS

Estimates of mangrove biomass are usually restricted to aboveground structures and in many cases, only include the timber that can be harvested from the forest. The

distribution of biomass throughout the tropics indicate that higher values occur at lower latitudes (Figure 3). The model for biomass distribution with latitude in Figure 3 is Y = -7.291(X) + 298.5 (R = 0.75), where X is latitude and Y is biomass (Mg/ha). Cintrón and Schaeffer-Novelli (1984) found that mangrove tree height, which is a good indicator of forest biomass, increased at lower latitudes in the neotropics according to the model: Y = 45.8 - 1.28(X) (r^2 = 0.75); where Y is tree height (m) and X is latitude north or south. The sensitive response of mangrove biomass and tree height to relatively small changes in latitude is related to the influence of temperature and occurrence of frost on the structure of these ecosystems (Lugo and Patterson-Zucca, 1977). Thus, solar energy represents a major constraint on the distribution and maximum biomass of mangrove ecosystems.

There is much variation of mangrove biomass at any one latitude, particularly in the warmer tropics. Maximum potential biomass at 10° and 35° is about 400 and 100 Mg/ha, respectively, while values less than 50 Mg/ha may occur at either latitude (Figure 3). Thus while the upper limits of mangrove biomass may occur at lower latitudes, there are local effects that may limit the potential for forest development at all latitudes. These local effects include topography and hydrology, including the effects of river and tides on soil characteristics. Cintrón et al. (1978) found that with increasing salinity the values of a number of structural and functional parameters decreased. These included litterfall, tree density, basal area (total cross-sectional area of trunks), and tree height. For example, tree height (Y, m) of mangroves in Puerto Rico is inversely related to soil salinity by the equation Y= -0.20(X) + 16.58 (r^2 = 0.72), where X is soil salinity in ppt (Cintrón et al. 1978). Very few mangroves survive above a soil salinity of about 70 - 80 ppt.
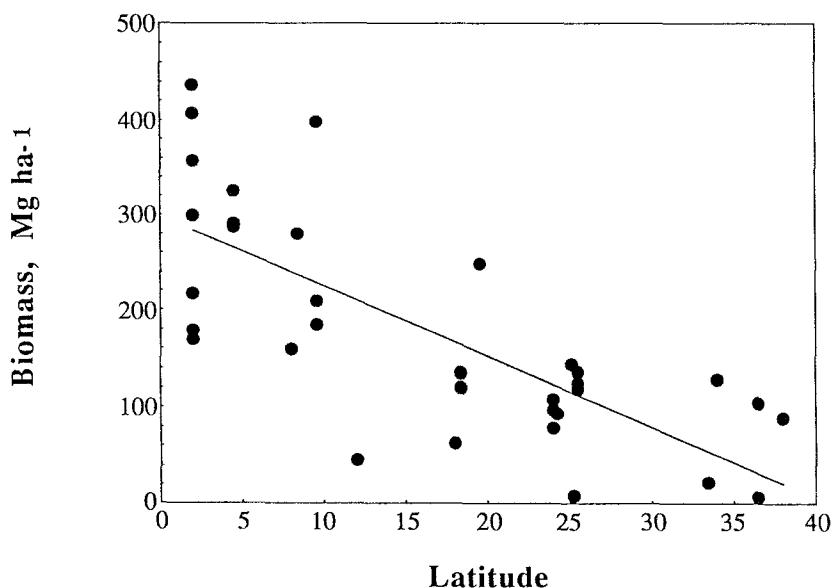

Figure 3. Distribution of aboveground biomass of mangroves with latitude.

Mean values of aboveground and belowground biomass for each of the latitudinal regions together with mangrove area were used to estimate mangrove biomass (Table 1). The average aboveground biomass ranged from 283.6 Mg/ha near the equator to 104.2 Mg/ha in the 30° to 40° zone. Belowground biomass was less and ranged from 171 Mg/ha near the equator to 96 Mg/ha at 30° to 40° latitude. There were fewer estimates of belowground biomass. The average estimate of aboveground (AG) and belowground (BG) biomass for all sites was 178.2 and 146.3 Mg/ha for a BG:AG ratio of about 0.82. Together with a decrease in mangrove area away from the central tropics, 70% of the total mangrove biomass occurs in the 0° to 10° zone (Table 1). Using a conversion of 45% C (per dry mass), the C storage in mangrove biomass at the equator was 2.72 Pg C compared to about 1 Pg C at the 10° to 20° zone. Total mangrove biomass was estimated at 4.03 Pg C.

Table 1. Global estimate of carbon stored in mangrove biomass based on 0.45 gC/g dry mass.

Component	Latitude				
	0° -10°	10° - 20°	20° - 30°	30° - 40°	Total
Area of Mangrove (x 10⁶ ha)	13.28	7.25	3.14	0.33	24.00
Biomass (Mg/ha)					
Aboveground	283.6	141.6	120.6	104.2	178.2
(Standard deviation)	(90.5)	(77.8)	(16.5)	(64.2)	(112.2)
Belowground	171.2	171.8	69.2	95.5	146.3
(Standard deviation)	(123.6)			(76.3)	(110.2)
Biomass (Pg dry mass)					
Aboveground	3.78	1.03	0.38	0.03	4.98
Belowground	2.27	1.25	0.22	0.03	3.71
Total	6.04	2.27	0.60	0.06	8.69
Biomass (Pg C)					
Aboveground	1.70	0.46	0.17	0.01	2.34
Belowground	1.02	0.56	0.10	0.01	1.69
Total	2.72	1.02	0.27	0.02	4.03

2.2 WOOD PRODUCTION

A variety of factors influences the productivity of coastal wetlands. Most factors are associated with changes in the physical or chemical environment, including solar radiation, temperature, tides, nutrient concentrations, soil type, drainage, oxygen concentration, and pH. The individual plant species present in the intertidal zone can also affect patterns of productivity, because some plants have growth rates that are intrinsically higher than others. Some of these factors cause a difference in productivity over a latitudinal range

within wetlands, while others operate at the local level.

Turnover rate of mangrove biomass ranged from 0.041 to 0.126 (Table 2). There was no apparent relationship of turnover rate with latitude. Shifts in ration of litterfall to biomass indicates less allocation of net productivity to wood production in higher latitudes (Warner 1990). Average wood production based on eleven estimates is 12.08 Mg ha^{-1} yr^{-1} (Table 2). Wood production decreased with latitude and a curve was fit to the data (Y = -0.449 X + 19.88, R = 0.60) . This curve was used to apply a weighted rate of wood production for each of the four latitudinal zones. Most of the wood production occurs in the 0° to 10° zone at about 0.1 Pg C/yr (Figure 4). Total wood production for mangroves is estimated at 0.16 Pg C/yr.

Table 2. Wood production (growth) of mangroves relative to biomass and latitude and the turnover rate of mangrove biomass at each location.

Site	Latitude	Biomass (B) (Mg/ha)	Growth (G) (Mg ha^{-1} yr^{-1})	G:B (yr^{-1})	Reference
Malaysia	4° 50' N	286.8	11.8	0.041	Ong et al. 1979
Malaysia		257.4	24.1	0.094	Ong et al. 1979
Phuket, Thailand	8° N	159	20	0.126	Christensen 1978
Puerto Rico	18° N	62.8	3.07	0.049	Golley et al. 1962
Estero Pargo, Mexico	18° 35' N	120	7.72	0.064	Day et al. 1987
Boca Chica, Mexico	18° 35' N	135	12.06	0.089	Day et al. 1987
Florida, USA			7.31		Sell 1977
Florida, USA			13.33		Sell 1977
Hainan, China	19° 53' N	248.5	11.5	0.046	Lin et al. 1990
Fujian, China	24° 24' N	93.4	8.69	0.093	Lin et al. 1985
Hong Kong	23° N	129.1	13.3	0.103	Lee 1990

2.3 BURIAL

Trapping of particulate materials by wetland plants is an important sedimentary and biogeochemical process in accretionary wetlands (Frey and Basan, 1978). Sedimentation rates in wetland sediments have previously been measured by various methods, including the use of natural and man-made radionuclides, such as ^{137}Cs and ^{210}Pb (Armentano and Woodwell, 1975; Hatton et al., 1983; Sharma et al. ,1987). Lynch et al. 1989 used these techniques to estimate the accretion rates in mangrove forests in southwest Florida and Terminos Lagoon, Mexico. Recent accretion rates based on these techniques ranged from 1.6 to 2.4 mm/yr (Table 3). Higher rates were observed for riverine mangroves in Mexico compared to basin mangroves in Rookery Bay, Florida. Estimates of accretion in mangroves based on aging deep peat cores (6,000 yr time scales) range from 0.3 to 1.88 mm/yr (Table 3). These rates are nearly all for reef mangroves, with little terrigenous inputs. It is surprising that the two techniques give similar estimates for the accretion of material in mangrove sediments. It is possible to suggest from this pattern, that accretion in reef mangroves is less than 1 mm/yr, basin mangroves 1 to 2 mm/yr, and riverine mangroves greater than 2 mm/yr.
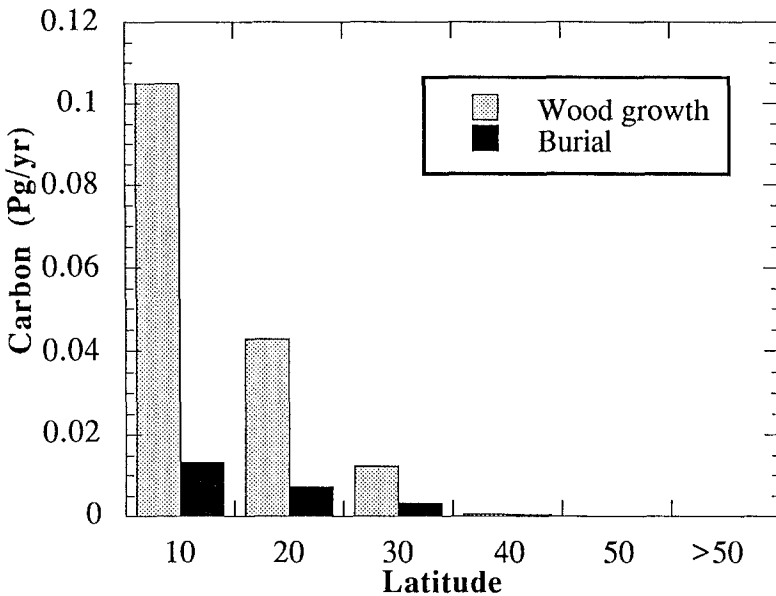
Figure 4. Estimates of annual carbon storage in mangrove wood and sediments.

Sediments suspended in the water column are deposited in mangroves during flooding and this material enriches mangrove soils.   The extensive root system of mangroves enhances this trapping process and retards the forces of erosion along the shoreline (Scoffin, 1970).   Although this function has been overstated to the extent of calling mangroves "walking trees", roots do contribute to sedimentation in estuaries (Lynch et al., 1989).   The accumulation of organic matter in the five sites investigated in Florida and Mexico by Lynch et al. (1989) ranged from 130 to 409 g m^{-2} yr $^{-1}$ (Figure 5).   Levels of organic matter accumulation were not correlated with amount of litter production.   The higher amount of organic matter accumulation relative to litterfall occurred in basin forests, possibly due to less export at these sites (Twilley et al., 1986).   Another source of organic matter is belowground productivity, which has seldom been included in C budgets of mangrove ecosystems.   The contribution of inorganic material varied greatly among the five sites and ranged from 133 to 1404 g m^{-2} yr $^{-1}$ (Figure 5).   The higher values occurred in the riverine mangrove forest in Terminos Lagoon in Mexico where the Candelaria, Chumpan, and Palizada rivers discharge more than 190 m^3/s of freshwater. The ratio of inorganic to organic material in the sedimentation process was 0.70 and 1.9 for the basin forests in Estero Pargo and Rookery Bay, compared to 4.5 for the riverine forest in Boca Chica.   These ratios indicate that the sequestering of C among mangroves in different environmental settings is not as different as the total sedimentation rate.   This indicates that the ecological processes associated with C accumulation in mangrove sediments is about 100 gC m^{-2} yr^{-1} among different types of mangrove ecosystems (Figure 5).

Table 3.   Critical rates of mangrove peat accretion based on deep cores and ^{14}C ages for low and high islands (from Ellison and Stoddart 1991). Rates for lagoon mangroves from Lynch et al. 1989.

Location	Rate (mm/yr)	Source
	Low Islands	
Taongatapu	0.77	Ellison 1989
Grand Cayman	0.88-0.90	Woodroffe 1981
	High Islands	
Fiji	1.17	Southern 1986
	0.76	Matsushima et al. 1984
	1.31	Latham 1979
Caroline Islands	1.34 - 1.40	Ward 1988
	1.37	Matsumoto et al. 1986
	0.30	Bloom 1970
Samoa	0.99 - 1.05	Matsushima et al. 1984
	1.88	Bloom 1980
South Florida	0.46	Scholl et al. 1969
	Lagoons	
Rookery Bay	1.6	Lynch et al. 1989
Terminos Lagoon, Mexico	2.4	Lynch et al. 1989

Based on an average C burial rate of 100 gC m^{-2} yr^{-1} for all four latitudinal zones, the global estimate of C accumulation in mangrove sediments was much less than in wood (Figure 4). Total C sequestered in mangrove peat is about 0.02 Pg/yr. Thus the global NEP of mangroves based on wood production and burial is estimated at about 0.18 Pg C/yr.

2.4 LITTER DYNAMICS

Litter produced in the canopy of mangrove forests represents a major source of organic matter and nutrients for outwelling to adjacent coastal waters (Odum and Heald, 1972; Twilley, 1988). Thus the dynamics of mangrove litter including productivity, decomposition, and export influence the coupling of mangroves to coastal ecosystems (Twilley, 1988). Litter productivity values for mangrove forests worldwide range from about 2 to 16 Mg ha^{-1} yr^{-1} and also decrease with latitude (Figure 6). Based on the mangrove sites represented in Figure 6, the maximum level of litterfall is about 14 Mg ha^{-1} yr^{-1} from 0° to 20° latitude. Above this latitude, litterfall decreases to less than 10 Mg ha^{-1} yr^{-1}. The lower limit of productivity is 8 Mg ha^{-1} yr^{-1} in the lower latitudes, compared to less than 2 Mg ha^{-1} yr^{-1} in the subtropical zones. This trend indicates that litter productivity is less sensitive to changes in latitude than observed for biomass.
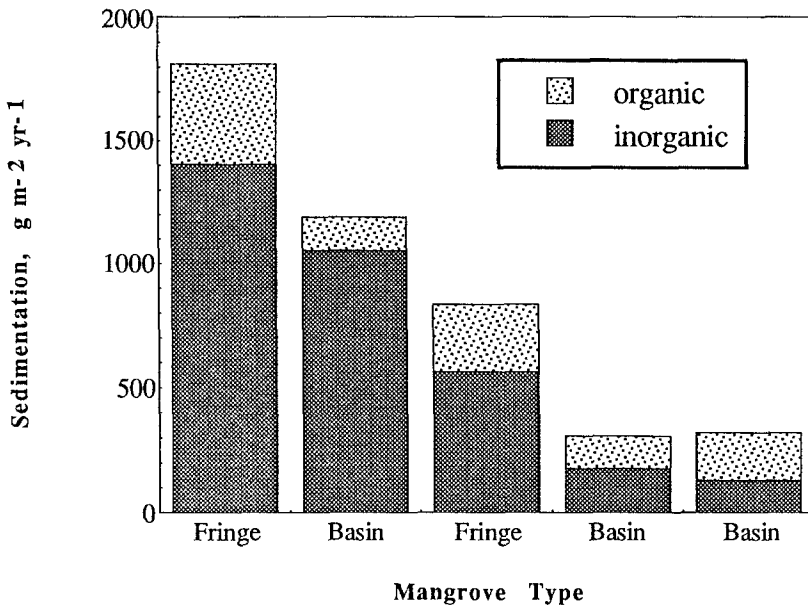
Mangrove Type

Figure 5.   Estimates of sedimentation (organic and inorganic) in mangrove sites in southwest Florida and Mexico (from Lynch 1989). Sites are arranged in order of river discharge.

Export of leaf litter and detritus from mangroves is linked to the hydrology of mangrove forests. Rates of organic C export from basin mangroves are dependent on the volume of tidal water inundating the forest each month, and accordingly export rates are seasonal in response to the seasonal fluctuation in sea level. Rainfall events may also increase organic C export from mangroves (Twilley, 1985), especially dissolved organic C (DOC).   Total organic C (TOC) export from infrequently flooded basin mangroves in southwest Florida is 64 gC m^{-2} yr^{-1} , and nearly 75% of this material is DOC (Twilley, 1985). Particulate detritus export from fringe mangroves in south Florida was estimated at 186 gC m^{-2} yr^{-1} (Heald, 1971), compared to 420 gC m^{-2} yr^{-1} for a riverine mangrove forest in Australia (Boto and Bunt, 1981). Estimates of average tidal amplitude in these three forests types are 0.08 m, 0.5 m and 3 m, respectively. Accordingly, as tidal amplitude increased, the magnitude of organic material exchanged at the boundary of the forests increased (Twilley, 1985).   Trends for litter productivity and export suggest that as geophysical energy increase, the exchange of organic matter between mangroves and adjacent estuarine waters also increase.

Litter productivity in a riverine forest in Ecuador is similar to a riverine forest in south Florida at about 10 Mg ha^{-1} yr^{-1}.   However, the riverine forest in Ecuador has a 3 m tidal amplitude, while the tides in the riverine forests in south Florida are 0.5 m.   Leaf litter on the forest floor in Ecuador is absent except for 3 mo of the year (Twilley et al., 1990).

This may be expected to be associated with greater export owing to the effect of tides on the transport of leaf litter from the forest . Yet observations in the mangroves in Ecuador suggest that most of the leaf litter on the forest floor is harvested by the mangrove crab, *Ucides occidentalis*, and transported to sediment burrows (Twilley et al., 1990). During September and October, when the crab aestivates, the standing crop of leaf litter increases on the forest floor. The levels of leaf litter during these 2 mo are still much lower than expected based on daily rates of leaf fall suggesting that leaf export is significant. The influence of mangrove crabs on litter dynamics has been described in other mangrove ecosystems with high geophysical energies and rates of litter turnover above 5 yr^{-1} (Malley, 1978; Leh and Sasekumar, 1985; Robertson and Daniel, 1989). Thus, the use of geophysical forcing functions such as tides to predict export of leaf litter is limited by consideration of ecological factors within the ecosystem such as crabs. In these examples, high rates of litter turnover do not reflect the coupling of mangrove to coastal waters, but the conservation of organic matter within the forest.
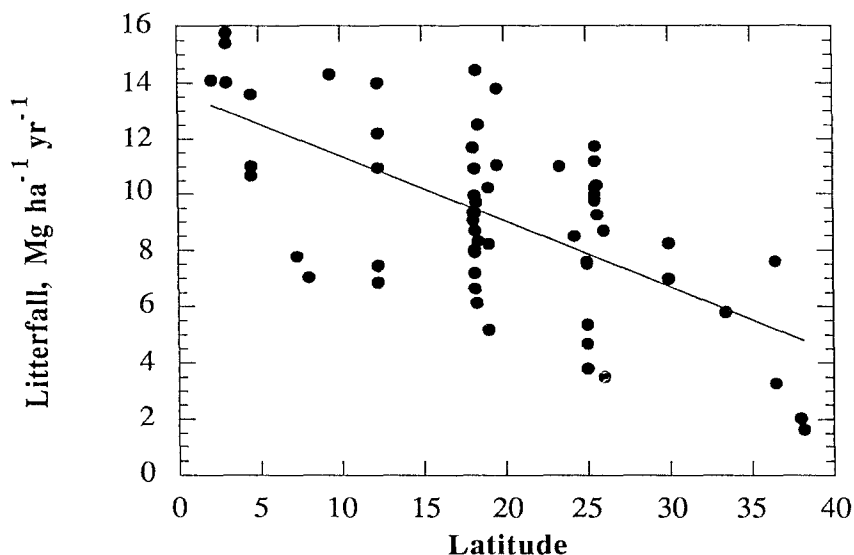

Figure 6. Survey of litterfall of mangrove forests with latitude.

There are now ten estimates of C flux from mangrove ecosystems that range from 1.86 to 401 gC m[-2] yr^{-1} (Table 4). An average export of C for mangrove ecosystems is about 200 gC m[-2] yr^{-1}. Nixon (1980) estimated that the average C net export from salt marshes is about 100 gC m[-2] yr^{-1}. There have been several suggestions to explain why the transport of organic C from mangroves is greater than for coastal marshes, including the buoyancy of mangrove leaf litter and the hydrology of these tropical coastal wetlands (Twilley, 1988). This average export value can be applied to the areal distribution of mangroves to estimate global contribution of mangroves to tropical coastal waters (Figure 7).

Table 4. Export of organic carbon from mangrove forests (gC m^{-2} yr^{-1}).

Site	Export	Reference
Florida, USA	91.2	Lugo and Snedaker 1974
Florida, USA	292	Odum and Heald 1972
Florida, USA	186	Heald 1969
Florida, USA	64	Twilley 1985
Puerto Rico	401	Golley et al. 1962
Hichinbrook, Australia	340	Robertson et al. 1986
Hichinbrook, Australia	420	Boto and Bunt 1981
Matang, Malaysia	193.5	Gong et al. 1990
New Zealand	109.5	Woodroffe 1985
Hong Kong	1.9	Lee 1989
Average	210	

The export of organic C from mangroves ranges from 10 to 50% of litterfall (Twilley 1985). Using an average of 25% and the latitudinal distribution of litterfall in Figure 6, a second estimate of C export from mangrove ecosystems is given in Figure 7. This value of C export is consistently lower than the areal average of 200 gC m^{-2} yr^{-1}. Using the higher estimate, the contribution of organic C from mangroves to coastal waters is 0.05 Pg C/yr.
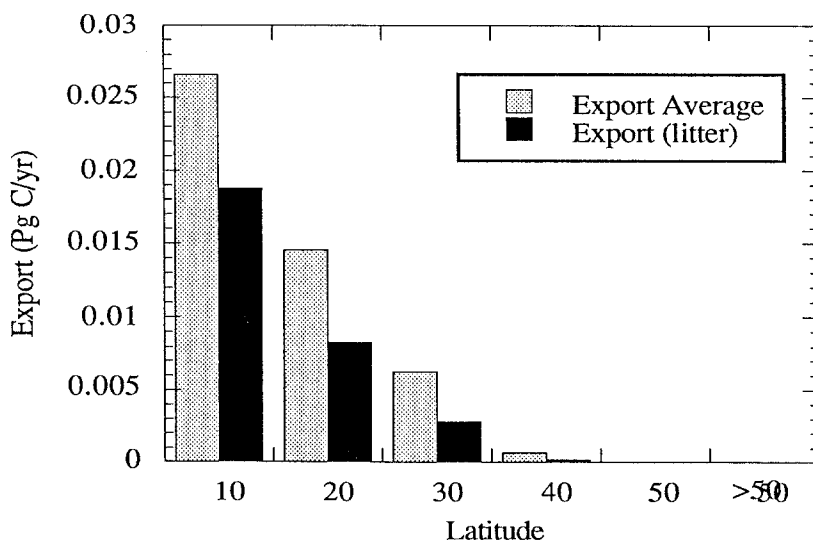

Figure 7. Global estimates of carbon export from mangrove ecosystems with latitude.

3. Carbon Budget Of Coastal Ecosystems

Rivers discharge about 13.5 x 10^9 tons of particulate material annually to the coastal oceans, over half of which is supplied by the world's 21 largest rivers (Milliman and Meade, 1983). Besides their POC load, rivers carry an approximately equal load of DOC - about 200 x 10^{12} g per year. In addition, the nutrient load of rivers may enhance the primary productivity of neritic waters, and some of this C may accumulate in the sediments of continental margins. Present estimates suggest that there is much more organic matter coming down the rivers than can be accounted for in annual accumulation of sediment C in the ocean. And few estimates have synoptically accounted for the other sources of in situ C, such as mangrove, seagrasses, and coral reefs, that may accumulate in coastal ecosystems. Where does all this C go? Or have we grossly underestimated the global C sinks in these ecosystems? The following section is a summary of some mass balances of coastal ecosystems, with emphasis of the tropical regions of the biosphere.

3.1 CARBON SOURCES IN COASTAL ECOSYSTEMS

The drainage area and discharge of the major rivers of the world in Figure 8 are distributed along ten degree latitudinal zones, based on the geographic location of the river mouth. Most of the freshwater input to coastal ecosystems occur in the tropical latitudes; in fact seven of the top ten rivers in discharge empty in the 0° to 30° latitudes. The greater proportion of discharge from watersheds in this region is related to more abundant rainfall. This analysis is important in the consideration of how C export from rivers to coastal margins is estimated. Estimates based on sediment discharge using a ratio of 0.45% of the sediment is particulate organic C are low at only 0.1 Pg C/yr (Walsh, 1983). Rates of organic C transport based on an average export of 6.5 gC m^{-2} (of watershed) yr^{-1} are about 0.2 Pg C/yr (Meybeck, 1982). We feel a more accurate estimate of C export is
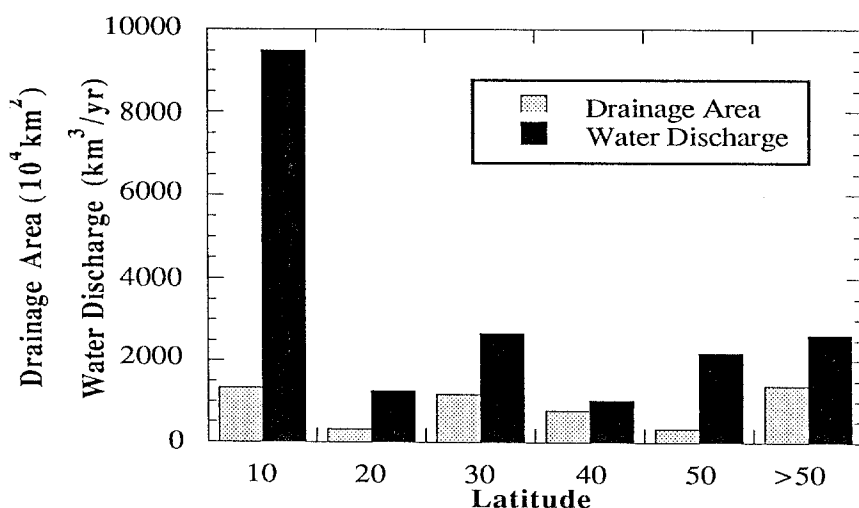

Figure 8. Discharge characteristics of the major river systems in the world with latitude.

based on actual river discharge and an average dissolved plus particulate organic carbon concentration of 20 mg/L (Meybeck, 1982; Milliman and Meade, 1983). This method estimates the delivery of organic C to coastal regions of the world at 0.36 Pg C/yr (Figure 9), similar to the average for recent estimates of river input (Table 5). This value may still underestimate total organic carbon input since the larger particulate pool transported by these rivers is not considered.

Table 5. Estimates of delivery of total organic carbon from the major river systems of the world to coastal ecosystems.

Total Organic Carbon (Pg C/yr)	Reference
0.37	Schlesinger and Melack 1981
0.383	Meybeck 1981
0.302	Meybeck 1988
0.33	Degens et al. 1991
0.35	Average

The contributions of C to coastal ecosystems from terrigenous and mangrove sources are compared in Figure 9. It is interesting to note that nearly 0.26 Pg C/yr of the estimated 0.36 Pg C/yr export from rivers occurs in the 0° to 10° latitude (Figure 9). In the 0° to 10° latitudinal zone, river contribution of TOC is much higher than for mangroves. However, in the 10° to 20° region of the tropics, C input to coastal waters from mangrove is nearly 75% of river contribution.

Global estimates of C sources in coastal ecosystems in Table 6 are identified as either allochthonous or in situ depending on whether the source of CO_2 is from the atmosphere or of ocean origin. River input is terrigenous organic carbon fixed by terrestrial vegetation. TOC export from coastal wetlands also represents C fixed by vegetation directly from the atmosphere, but these are included as part of coastal ecosystems (Figure 10). Coastal wetlands thus should be carefully evaluated in developing carbon budgets of coastal ecosystems since they exchange C directly with the atmosphere and with coastal waters. C export from mangroves is estimated in this study at 0.05 Pg C/yr. Lugo et al. (1990) estimated marsh export at 0.03 Pg C/yr using a mean export of 95 gC m^{-2} yr^{-1}. This is near the average rate of C export suggested by Nixon (1980). Based on this rate of C export for salt marshes, the total contribution of C from coastal wetlands is estimated at 0.08 Pg C/yr. Together with estimate of river input, the total allochthonous input of organic carbon into coastal ecosystems is 0.44 Pg C/yr (Table 6).

Estimates of primary production in coastal environments range from approximately 1.0-7.0 Pg C /yr (Deuser, 1979; Smith and Mackenzie, 1987; Walsh, 1988). Walsh (1984) classified coastal production among macrophyte, estuarine, and shelf systems for total in situ production of 6.65 Pg C/yr (Table 6). Based on these estimates of net primary productivity of coastal waters, the total input of organic C to coastal ecosystems is 7.09 Pg/yr (Table 6).
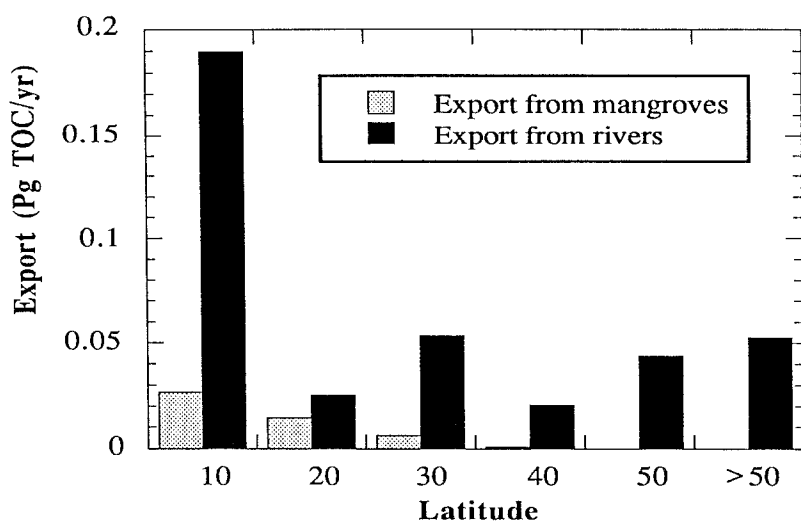
Figure 9. Relative contribution of organic carbon from river transport and mangrove export to tropical continental margins.

Table 6. Estimates of carbon sources and sinks in coastal ecosystems (Pg C/yr)

SOURCES		
Allochthonous	0.44	
Rivers	0.36	This study
Wetlands	0.08	This study
Net Primary Production	6.65	
Shelf Waters	5.40	Walsh 1984
Estuaries/Deltas	0.92	Walsh 1984
Macrophytes	0.33	Walsh 1984
TOTAL	7.09	
SEDIMENT SINKS		
Coral Reefs	0.01	Walsh 1984
Shelf	0.2	Berner 1982
Estuaries	0.20	Walsh 1984
TOTAL	0.41	
WETLAND SINKS		
Mangroves	0.18	This study
Marshes	0.025	Hopkinson 1988
TOTAL	0.205	

3.2 CARBON SINKS IN COASTAL ECOSYSTEMS

Continental margins are important depositories of organic matter for three reasons: (1) the input of terrigenous organic C and the production of marine C result in an abundant supply of organic C to these environments; (2) high sedimentation rates lead to rapid removal of organic material below the oxidized zone near the sediment-water interface causing preferential burial of organic matter (Berner, 1982; Deuser, 1988; Dagg et al. 1991), and (3) coastal wetland sediments and biomass represent large reservoirs of organic C (this study). Most of the 5 to 10 Pg of organic matter ultimately reaching the oceans annually is deposited in estuaries and on continental margins. Shelf sediments may play an important role as a short-term sink for anthropogenic CO_2, accounting for as much as 40% of the total oceanic sink (Smith and MacKenzie, 1987; Wollast and MacKenzie, 1989; Tans et al. 1990). However, estimates of C burial on continental shelves are about 0.2 Pg C /yr; a small fraction of the C supplied (Berner, 1982). There is apparent discrepancy in the estimates of supply and removal of C in coastal environments regarding the magnitude of C export from shelf environments (Walsh et al., 1985; Rowe et al., 1986). Evidence from natural abundance of isotopes in sediments of river-dominated shelf ecosystems such as the Mississippi River indicates that most of the terrigenous C entering coastal margins is deposited in the proximal areas of river plumes (Shultz and Calder, 1976; Gearing et al. 1977; Thayer et al. 1983). In addition, estimates of recent deposition and accumulation of terrigenous materials on the Louisiana shelf in vicinity of the Mississippi River plume demonstrate the strong seasonal nature of these inputs (Dagg et al., 1991). Short term events of extremely high deposition may cause preferential burial of terrigenous C in river-dominated shelf ecosystems. This suggests that in coastal regions dominated by strong rivers, very little of the terrigenous C may be transported to deep water oceanic environments (Figure 10).
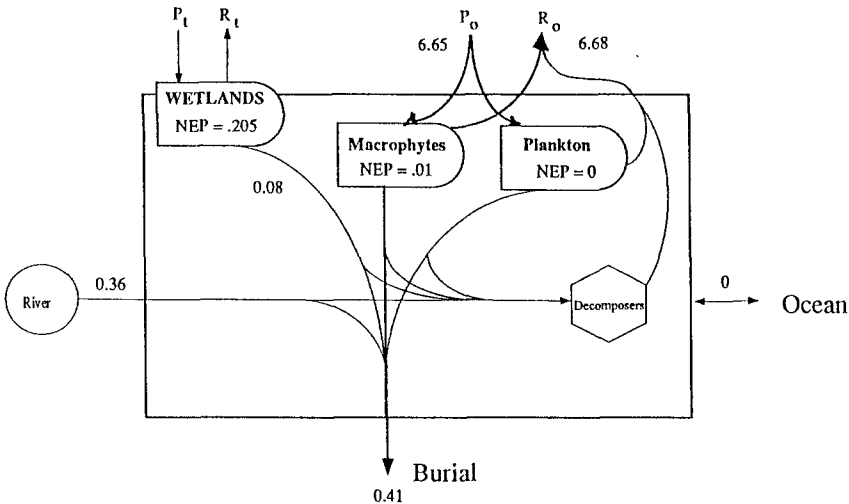

Figure 10. Mass balance of C for coastal ecosystems based on estimates of in situ net production and allochthonous inputs, minus losses associated with burial in coastal sediments. P and R represent net production and heterotrophic respiration, respectively, with exchange of CO_2 directly with atmosphere (t) or coastal waters (o).

In addition, estuaries are considered efficient traps of allochthonous and in situ C with estimates of 0.2 Pg C/yr (Walsh 1984) buried in estuarine sediments (Table 6). Coral reefs may contribute only 0.01 Pg/yr to C sinks in coastal ecosystems. It is unknown what role other macrophyte communities may serve in sequestering C in coastal waters, although biomass and turnover estimates suggest that they may be significant (Smith, 1981). Total sinks in coastal ecosystems is estimated at 0.41 Pg C/yr (Table 6). This is only 6% of the total inputs from allochthonous and in situ sources of C.

Coastal or nearshore environments are considered by some to be net heterotrophic (net respiration exceeds primary production of organic matter), which implies that the high biological activity of coastal ecosystems relies on terrigenous organic C (Smith and MacKenzie, 1987). Smith and Mackenzie (1987) assumed there was no exchange between coastal and oceanic systems and using a mass balance analysis of ecosystem processes (such as equation 2 above), solved for system respiration given inputs and burial. Using the same approach, the respiration of coastal ecosystems in our analysis is about 6.68 Pg C/yr (Figure 10). This gives a P:R ratio (net production to heterotrophic respiration) of about 1.0, symbolic of a steady state system. Smith and Mackenzie assumed that 64% of terrigenous organic carbon is respired and only 1% of the total C input was buried, causing shelf systems to be heterotrophic. Such perspectives of coastal systems rely on accurate estimates of C burial in sediments, which may be underestimated in many shelf environments, particularly in the tropics. Thus the trophic nature of many coastal ecosystems will depend on the relative contribution of respiration and burial to the fate of allochthonous and in situ C sources (Figure 10).

Another sink of C in coastal environments is wetlands. The NEP of mangroves in this study is estimated at 0.18 Pg C/yr, most of which is sequestered in annual increment of wood biomass. Average sedimentation of C in salt marshes along the Atlantic and Gulf coast is 83 gC m^{-2} yr^{-1} (Hopkinson 1988), compared to 100 gC m^{-2} yr^{-1} used in this study for mangrove sedimentation of C. Based on an areal coverage of 0.3 x 10^{12} m^2 (Lugo et al. 1990), the global sink of C in salt marsh sediments is 0.025 Pg/yr. Walsh (1984) estimated C burial in salt marshes at 0.05 Pg/yr. The annual accumulation of C in plant biomass in salt marshes is considered negligible (Hopkinson 1988). Together with mangrove C accumulation in sediments and wood, the total C sequestered in coastal wetlands is 0.205 Pg/yr (Table 6). This is half of the C buried in coastal sediments and represents a major C sink in coastal environments. However, as mentioned above, the source of this C is directly from the atmosphere, and does not influence the balance of C in coastal waters.

3.3. PERTURBATIONS TO CARBON SINKS

This analysis of C sinks in mangrove and coastal ecosystems is based on wide geographic averages of ecological processes. These ecosystems are consistently responding to alterations in the forcing functions that control the ecological processes responsible for the nature of these C sinks. Perturbations, both natural and anthropogenic, can alter the net balance of C in mangrove and coastal ecosystems. These include tropical storms, evolution of landscapes, forest reclamation, and eutrophication.

3.3.1 *Tropical Cyclones*. Another important constraint on the development of biomass in mangroves, particularly in areas such as the Caribbean, is the frequency of hurricanes. It is interesting that of those sites from the Gulf coast and Caribbean islands in Figure 3 (25° latitude), those with the highest biomass are located on west coast of Yucatan peninsula where hurricanes seldom occur (Ruffner, 1978). A basin mangrove forest in Rookery Bay was apparently damaged by a hurricane in 1965, and the regeneration of this forest

resulted in high density and low biomass of trees in 1971 compared to 1987. A decline in density and increase in basal area is typical of a developing forest. Biomass was stable by 1987, indicating that a mature forest had developed within 25 yrs following the hurricane disturbance (Warner, 1990). Flores-Verdugo et al. (1986) attributed the poorly developed forest structure in el Verde Lagoon on the Pacific coast of Mexico to frequent hurricanes. Most mangroves in the tropics that are susceptible to damage from high winds and hurricanes are considered young successional forests.

The time scale for a mangrove forest to reach maturity based on steady state levels of biomass is dependant on the regional and local attributes of the environmental setting. Forests in lower latitudes with no natural or human disturbance may reach biomass levels over 250 Mg/ha. For example, biomass of mature forests in the protected areas of Malaysia is 350-400 Mg/ha (Putz and Chan, 1986). Yet forests in higher latitudes do not have the potential for maximum levels of biomass as observed in lower latitude forests (Figure 3). Thus mature levels of biomass in these mangroves may be obtained in less time than in the lower latitudes, given similar rates in wood production. In the Caribbean and Gulf of Mexico, 25 -30 years may be enough time for forests to reach maturity given the maximum biomass that can be supported in these areas. Time scales for recovery and net accumulation of C may occur over longer time scales in warmer tropical regions.

3.3.2 *Mangrove Reclamation.* The destruction of mangroves occurs throughout the tropics for charcoal production, mariculture (shrimp ponds), agriculture, urban development, and dams. In Ecuador there is recently one of the more extreme examples of mangrove reclamation for the production of shrimp ponds. Mangrove loss from 1984 to 1987 ranged from less than 500 to more than 2,500 ha/yr. These are permanent loss of mangrove resources from the coastal zone. The biomass in these forests was largely converted to charcoal, so the C stored was not completely loss. But the wood production, sediment burial and export processes in this coastal environment has diminished in the last 10 yrs. The cumulative impact of mangrove reclamation projects on the global importance of these natural resources has not been evaluated.

3.3.3 *Coastal Geomorphology.* Geomorphology, together with tidal amplitude, will determine the extent of the intertidal zone of a coastal region. Thus geomorphology will to a large extent control the areal distribution of wetlands in any coastal system. The ratio of wetland area to the area of coastal waters has been suggested as important to the ecological function of a coastal wetland (Mann, 1975; Welsh et al., 1982). For example, the Mississippi Deltaic Plain has about 2,500,000 ha of marshes that account for 60% of the coastal wetlands in the lower 48 states (Turner and Gosselink, 1975). However, losses of coastal wetlands in some regions of the delta have been as high as 100 km^2 per year (Gagliano et al., 1981). This has resulted in the conversion of vegetated areas to open water decreasing the wetland:water area ratio. Much of this wetland loss is associated with a high rate of regional subsidence and erosion characteristic of degrading deltas. At the mouth of the Atchafalaya River, however, a wetland system representing the early progradational stages of delta formation is evolving (van Heerden et al., 1983). Here the levels of sediment discharge compensate for the relative increase in water levels due to subsidence and sea level rise. Therefore the Mississippi Deltaic Plain is an environment where the wetland:water ratio is changing due to successional stages in the development of delta ecosystems. A shift in this ratio to less wetland and more water means proportionately less of the organic matter supply will be buried in wetlands. Thus the development of deltas and shifts in the wetland:water ratio in coastal ecosystems will influence the magnitude of C sinks in coastal ecosystems.

3.3.4 *Coastal Eutrophication.* A major change that has occurred, especially during the last 30 to 40 years, is the increase in concentration of nitrogen in river waters, particularly dissolved nitrate (Walsh et al., 1981). Prior to leveeing of the Mississippi River a large portion of this new nitrogen was not transported directly to the shelf system but was processed by coastal bays and marshes before reaching the Gulf. The increase in nitrate concentration has thus occurred simultaneously with changes in how materials from the river are processed in coastal ecosystems along the Louisiana coast. Utilization of nitrate includes assimilation by primary producers in the water column and exchange with wetlands and benthic sediments, where it is either assimilated into biomass or dissimilated to nitrogen gas. A portion of the assimilated nitrate may be buried in wetland and/or benthic sediments, and together with the dissimilated nitrate, represent losses of this nutrient from community metabolism. The direct discharge of nitrate to the shelf is dramatically different from that of an unleveed river, and likely has major impacts on the distribution of biological productivity within the coastal regions of the northern Gulf of Mexico. This region of the Gulf of Mexico has thus been the focus of scientific interests in the coupling of eutrophication of coastal waters with the C balance of the biosphere (Walsh et al., 1981).

4. Conclusions And Recommendations

We propose that a three compartment conceptual model (Figure 1) is needed to focus attention on ecological processes (Figure 10) that influence the global C cycle. This three compartment model includes coastal margin ecosystems in addition to the present terrestrial and oceanic (deep water) ecosystems that are presently being evaluated. These coastal margin ecosystems include the wetland, estuarine, littoral, and shelf environments from the tidal freshwater region to the continental slope. This area is less than 5% of the total land area, but the biogeochemical processes warrant more complete investigations into potential C sinks in the biosphere. For example, the influence of river discharge on coastal margin ecosystems is twofold: 1) the discharge of particulate and dissolved organic C and the fate of this terrigenous C needs more thorough analysis; 2) the nutrients transported to the coastal margins from the ten major river systems in the world (most of which are in the tropics) may enhance the new production of the biogenic regions of these river plumes. In addition, there has not been an integrated approach to the evaluation of these coastal margins to include the synoptic analysis of wetlands (including marshes and mangroves), littoral subsystems (such as seagrasses and coral reefs), together with the fate of new production in phytoplankton communities. This analysis is particularly warranted in the tropical and subtropical regions of the biosphere. This effort should include a hierarchial modelling effort, similar in magnitude to terrestrial and oceanic components, to predict the influence of perturbations to the coastal margins (such as wetland loss, nutrient enrichment, rise in sea level, etc.) on future predictions of global climate change.

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