

SENSITIVITY ANALYSIS OF A MANGROVE ECOSYSTEM MODEL

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ABSTRACT

Mangrove ecosystems represent one of the most important ecosystems in terms of commercial use, inasmuch as their productivity is comparable to that of coral reefs and sea grass beds. In the present article, a comparative analysis is presented for delineating the ecological significance of mangrove ecosystems. Then, a mangrove ecosystem computer model is analyzed, and sensitivity analyses identify key parameters in the design of environmental management plans aimed at optimal and judicious use of mangroves. Analytical expressions are derived for steady state conditions. Moreover, conditions for ecological feasibility are also ascertained. Tidal action and nutrient inputs from terrestrial run-off turn out to be one of the most important controlling factors with respect to detritus export and nutrient cycling.

INTRODUCTION

The intertidal mud flat zones of tropical seas and estuaries are occupied by trees and shrubs known as mangroves. They constitute one of the most important tropical marine ecosystems, the productivity of which is comparable to that of coral reefs and sea grass beds [1]. The major portion of production is the mangrove vegetation itself. Organic matter production in a mangrove ecosystem has been reported to be very high [2, 3]. Litter fall and detritus decomposition are

one of the most important processes which distinguish mangroves from other ecosystems [3, 4].

Detritus decomposition enhances nutrient regeneration and recycling. This is mainly because of the fact that plants, microbes, and animal components are so inextricably interwoven that nutrients are very rapidly reabsorbed soon after they are released.

Mangrove swamps develop on the margins of estuarine and coastal regions, and they play the dual role of land builders and protectors of coastal areas during periods of high tides and strong winds. Hence they function as solar-powered, tidally-subsidized, pulse-stabilized ecosystems. They also serve as an important exporter of organic matter to adjacent bays and assume significance mainly for the following reasons [1, 5]:

1. in fisheries, they serve as a source of very rich nutrients and highly useful tannin;
2. they act as an erosion barrier and land builder;
3. they aid in soil formation by trapping debris;
4. they filter land run-off and thus control terrestrial organic matter;
5. they serve as a habitat for many species of fish, invertebrates, and birds;
6. they are a major producer of the detritus that contributes to offshore productivity; and
7. they are also used in honey and charcoal production.

However, due to several anthropogenic activities, the mangroves, in general, are being continuously exploited and destroyed. Manufacturing of coal and mining of economically important mineral resources such as tin, iron, and manganese are few of the activities by which mangroves are being continuously exploited. Hence, ways and means have to be strategically framed in order to conserve and protect such ecologically important zones [6].

For their healthy ecological functioning, it is important for mangroves to receive a steady input of terrestrial nutrients so as to maintain their characteristic rates of growth. Thus, among other things, mangrove management requires maintenance of terrestrial run-off patterns. This necessitates studying the sensitivity of mangrove ecosystems in terms of various controlling and forcing functions. Factors such as dissolved oxygen, tidal effects, and solar radiation constitute important regulatory forcing functions [7]. Sensitivity studies of forest biomass [8], detritus, and nutrient cycling with respect to these factors helps immensely in the ecological analysis by helping to understand and quantify their roles in the management of ecosystem. In the present article, a mangrove ecosystem model is analyzed [7] to reveal the sensitivity of state variables with respect to ecologically significant parameters [9].

SEA GRASSES, CORAL REEFS, AND MANGROVES

A common topographical feature of Asian ocean areas are the enclosed coastal seas dominated by two highly productive ecosystems [1, 10], sea grass beds and mangrove forests. The strategic coastal position of these ecosystems makes them highly vulnerable to natural and man-made stresses. In tropical latitudes, sea grass systems are found between mangroves and coral reefs. This topographical position ensures functionally strong interlinking with the adjacent ecosystems.

Sea grass beds act as hydrodynamic barriers by creating a low energy zone favorable to the mangrove forests. The beds prevent abrasion and burial of the "breathing" mechanisms of the mangroves by trapping and thereby stabilizing the sediments. Otherwise, these sediments would smother the sea grasses. In this way they also regulate fresh water flow and buffer salinity changes that may be unfavorable to plant growth.

Tropical sea grasses are concentrated in two large areas: the Indo—West Pacific, where all seven characteristically tropical species occur, viz. *Enhalus*, *Thalassia*, *Halophila*, *Halodule*, *Syringodium*, *Cymodocea*, and *Thalassodendron*; and the Caribbean and the Pacific Coast of Central America, which also has *Halodule*, *Syringodium*, *Thalassia*, *Halophila*, and other species.

Although the number of sea grass species is small, their number belies their ecological and economic importance. Their significance accrues largely because of their quantities. They form dense beds which cover large areas of coastal waters and perform a wide spectrum of biophysical functions in the marine environment. They stabilize the substrate, produce sediments, and serve as habitats, nurseries, and primary food sources for fish, many invertebrates, turtles, and dugongs. They also provide alternative feeding sites for commercial and forage organisms. Because of their strategic position between coral reefs and mangroves, tropical sea grass beds act as effective buffers, reducing wave energy and exporting nutrients to nearby ecosystems.

Mangroves thrive best where tidal regime is normal and amplitude is significant, mixing sea waters with fresh water from land run-off. They comprise a functional grouping of intertidal biota dominated by evergreen broad-leaved trees that remain partly submerged. Their main ecological roles are:

1. promoting soil formation by trapping debris,
2. filtering land run-off and removing terrestrial organic matter,
3. providing habitat for many fish and bird species, and
4. enhancing offshore productivity generally.

Natural stresses to the vegetation take the form of tropical cyclones, typhoons, tidal waves, volcanic activity, pests, and diseases. Human-induced stresses come from mining, felling of trees, road construction, and dumping of waste materials.

PHOTOSYNTHESIS AND NUTRIENT CYCLING IN MANGROVE ECOSYSTEMS

Mangroves exhibit a type C_4 photosynthesis path [3]. They minimize water loss by opening of stomata wide only in the early hours of the day. The presence of trichomes and thick cuticles also check and control the water loss.

Most of the nutrients flowing into mangroves have terrestrial origin. The growth and vigor of mangrove stands is highest in riverine conditions where detritus accumulation is low. For example, red mangroves exposed to riverine inputs exhibit rates of photosynthesis which are nearly twice as high as those of white mangroves [7].

A wide variety of plant-waste-material enters the soil and water of mangrove ecosystems. This helps establish a mixed heterogeneous microflora which keeps interacting with the organic constituents of plants. Decaying dead tissues are transformed into a vast heterogeneous group of carbon compounds.

Nitrogen enters the mangrove through 1) rainfall and fresh water run-off from surrounding land forests and from rivers, 2) agricultural land drainage, sewage, and industrial effluents, and 3) decomposition of organic matter. Phosphorus is second only to nitrogen as an inorganic nutrient required by both plants and microorganisms, and is essential to the accumulation and release of energy.

As is ever evident from the smell of H_2S and the formation of black sulfides in the mangrove region, sulfur cycling is one of the important processes that take place in mangrove ecosystems. This mainly involves the following principal steps: 1) alter the solubility of organic phosphorus compounds, 2) mineralize organic compounds with the release of organic phosphate, and 3) oxidize or reduce inorganic phosphorus compounds.

MODEL APPLICATION AND SENSITIVITY ANALYSIS

Gross photosynthesis of mangrove ecosystems is sensitive primarily to terrestrial inputs of nutrients. Zonation and vigor are functions of nutrient availability and salinity. During periods of succession, mangrove ecosystems significantly control and regulate the flow of nutrients to adjacent ecosystems.

The storage of organic detritus in the forest and its export to adjacent zones is a function of tidal amplitude. Tides do not seem to affect gross photosynthetic rates significantly. Mangrove forests appear to reach a steady state, with respect to their biomass, almost in phase with the frequency of tropical hurricanes in the regions where they occur. As noted, mangroves protect coastal areas during high tides and storms, export organic matter to adjacent waters, and function as nursery grounds for commercially important fish and shrimp species [11]. This mangrove-dependent commercial development creates several socio-economic conflicts. In order to assess tradeoffs and management alternatives,

ecosystem analysis and computer simulation modeling are valuable tools. A three-compartment non-linear model developed in [7], with mangrove biomass, detritus, and nutrient concentrations as state variables, is extended to evaluate the impacts of terrestrial run-off and tidal flushing, with dissolved oxygen, tidal amplitude, and solar radiation as the main exogenous forcing functions. Additional nutrient inputs from terrestrial run-off also are included as an external forcing function.

The main goals of our modeling exercise are to compare the effects of terrestrial run-off and tides on nutrient cycling and mangrove forest productivity, to study the impact of tidal flushing on accumulation and export of detritus in and from mangrove forests, and to characterize the impact of mangroves on water quality.

In the model (Figure 1) detritus, under tidal action, is exported from the forest floor to the estuary. Some is lost through the processes of grazing and decomposition. Intercompartmental transfers and interactions have been modeled as linear or non-linear depending upon the relevant processes involved [7, 9]. The values used for the state variables and coefficients are shown in Tables 1 through 5.

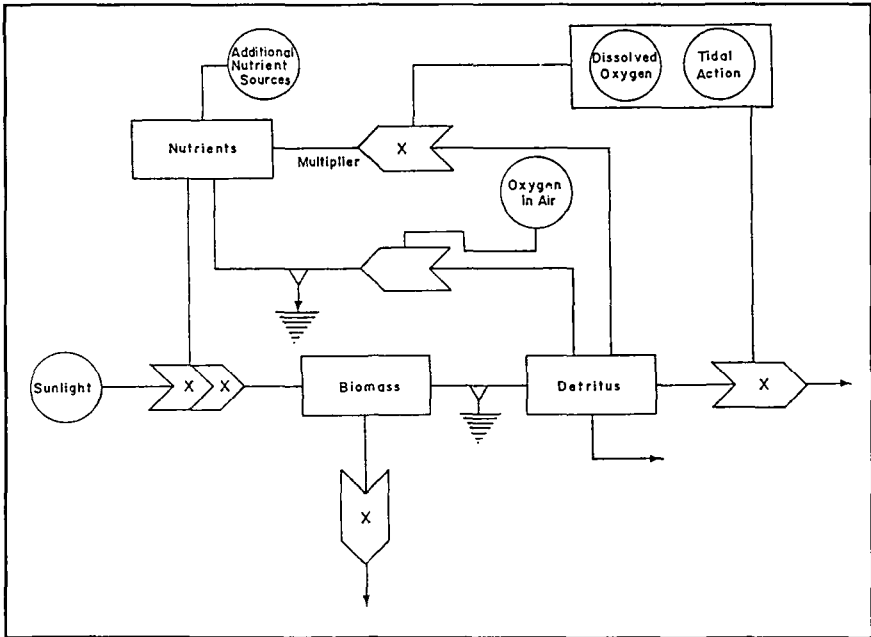


Figure 1. Mangrove ecosystem model (after Lugo et al. [7]).

Table 1. Rate Coefficients Used in the Model

Coefficients	Values
c1	
High metabolism, low nutrients	$2.55 \times 10^{-9} \text{ m}^4/[\text{Kcal g (nutrients)}]$
High metabolism, high nutrients	$4.25 \times 10^{-11} \text{ m}^4/[\text{Kcal g (nutrients)}]$
Mean metabolism, low nutrients	$1.32 \times 10^{-9} \text{ m}^4/[\text{Kcal g (nutrients)}]$
Mean metabolism, high nutrients	$2.20 \times 10^{-11} \text{ m}^4/[\text{Kcal g (nutrients)}]$
c2 ----->	$8.4 \times 10^{-2} \text{ y}^{-1}$
c3	
High metabolism ----->	$1.68 \times 10^{-5} \text{ m}^2/[\text{g (carbon) y}]$
Mean metabolism ----->	$1.25 \times 10^{-5} \text{ m}^2/[\text{g (carbon) y}]$
c4 ----->	$5.12 \text{ m}^{-1} \text{ y}^{-1}$
c5 ----->	$1.8 \times 10^{-2} \text{ m}^2/[\text{g (carbon) y}]$
c5' ----->	$1.44 \times 10^{-3} \text{ m}^2/[\text{g (carbon) y}]$
c6 ----->	$1.02 \times 10^{-2} \text{ m}^3/[\text{g (O}_2\text{) y}]$
c6' ----->	$8.2 \times 10^{-4} /[\text{g (O}_2\text{) y}]$
c8	
High metabolism, low nutrients	$3.5 \times 10^{-1} \text{ y}^{-1}$
High metabolism, high nutrients	$5.8 \times 10^{-1} \text{ y}^{-1}$
Mean metabolism, low nutrients	1.88 y^{-1}
Mean metabolism, high nutrients	$3.13 \times 10^{-2} \text{ y}^{-1}$
c9	
High metabolism, low nutrients	$2.05 \times 10^{-10} \text{ m}^4/[\text{Kcal g nutrients}]$
High metabolism, high nutrients	$3.40 \times 10^{-12} \text{ m}^4/[\text{Kcal g nutrients}]$
Mean metabolism, low nutrients	$1.05 \times 10^{-10} \text{ m}^4/[\text{Kcal g nutrients}]$
Mean metabolism, high nutrients	$1.75 \times 10^{-12} \text{ m}^4/[\text{Kcal g nutrients}]$
c10 ----->	$3.68 \times 10^{-1} \text{ y}^{-1}$

Where y = year

Source: Lugo et al. [7]

Steady State Values

Steady state values have been derived [9] on the basis of time-derivatives for the three variables mangrove biomass [Biomang], detritus [Det], and Nutrients [Nut]. The relevant equations are as follows:

$$[\text{Biomang}] = \{ (c1/c3) * (\text{Sun}) * [\text{Nut}] - (c2/c3) \} \tag{1}$$

$$[\text{Det}] = \{ c1 * (\text{Sun}) * [\text{Nut}] - c2 \} * [(c2/c3 * \{ c4 * (\text{Tid}) + c5 + c6 * (\text{Disso}) + c10 \}] \tag{2}$$

$$[\text{Nut}] = \{ \text{sqrt} (B^2 - 4 A * C) - B \} / 2A \tag{3}$$

Table 2. State Variables and Forcing Functions

Functions and Variables	Initial Value	Maximum Value
Forcing Functions		
Sunlight (Sun)	4000.0 Kcal m ⁻² day ⁻¹	10000.0 Kcal m ⁻² day ⁻¹
Tidal Action (Tid)	10.0 Cm	2 m
Dissolved Oxygen (Disso)	4.0 g m ⁻³	8.0 g m ⁻³
State Variables		
Mangrove Biomass (Biomang)	10500.0 g (carbon) m ⁻²	30000.0 g (carbon) m ⁻²
Detritus (Det)	780.0 g (carbon) m ⁻²	10000.0 g (carbon) m ⁻²
Nutrients (Nut)		
Low Nutrients	100.0 g m ⁻²	800.0 g m ⁻²
High Nutrients	6000.0 g m ⁻²	8000.0 g m ⁻²

Source: Lugo et al. [7]

Where,

$$A = (c1*c9/c3)*(Sun)^2 \quad (4)$$

$$B = c8 - (c2*c9/c3)*(Sun) - \{c1*c2*(Sun)*(c5' + c6'*(Disso))\} / \{c3*(c4*(Tid) + c5 + c6*(Disso) + c10)\} \quad (5)$$

$$C = \{c2^2(c5' + c6'*(Disso))\} / \{c3*(c4*(Tid) + c5 + c6*(Disso) + c10) - (Nuttra)\} \quad (6)$$

(Sun), (Nuttra), (Disso), and (Tid) denote solar radiation, extra nutrient sources through terrestrial run-off, dissolved oxygen, and tidal action respectively.

Condition for Ecological Feasibility

The ecological feasibility [9, 12] of the model is judged by the following criteria: 1) there is at least one mathematically and ecologically satisfactory steady state equilibrium in which all the compartments and flows have positive finite values; 2) if a system had no steady state, it could not persist; and 3) steady state involving infinite, zero, negative, or imaginary values for the compartments and flows, though mathematically sound, are ecologically non-feasible.

$$\begin{aligned} & [c8 - (c2*c9(Sun))/c3 - \{c1*c2*(Sun)*(c5' + c6'*(Disso))\} \\ & / \{c3*(c4*T+c5+c6*(Disso) + c10)\}^2 - 4.0*c1*c9*(Sun)^2(c5' + c6' \\ & *(Disso)) / \{c3^2*(c4*(Tid) + c5 + c6*(Disso) + c10)\} - \\ & c1*c9*(Sun)^2 * (Nuttra) / c3 > 0 \end{aligned} \quad (7)$$

Table 3. Ecosystem Flows

Gross Photosynthesis ($c1 \cdot \text{Sun} \cdot \text{Biomang} \cdot \text{Nut}$)	Max. 10.72 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ Mean 5.54 g (carbon) $\text{m}^{-2} \text{day}^{-1}$
Respiration of mangroves ($c3 \cdot \text{Biomang}^2$)	Max. 5.07 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ Mean 3.79 g (carbon) $\text{m}^{-2} \text{day}^{-1}$
Litter Fall ($c2 \cdot \text{Biomang}$)	Max. 2.41 g (carbon) $\text{m}^{-2} \text{day}^{-1}$
Export of detritus by tidal flushing ($c4 \cdot \text{Det} \cdot \text{Tid}$)	Max. 1.1 g (carbon) $\text{m}^{-2} \text{day}^{-1}$
Decomposition of detritus when mangroves are dry ($c4 \cdot \text{Det}$)	0.16 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ (only 3 months of year)
Decomposition of detritus when mangrove forest floor is water-covered ($c6 \cdot \text{Det}^2$)	0.12 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ (during 3 months of dry season) 0.12 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ (during 6 months of wet season)
Grazing of detritus and other losses ($c10 \cdot \text{Det}$)	0.786 g (carbon) $\text{m}^{-2} \text{day}^{-1}$
Nutrients derived from decay of:	
a) detritus ($c5 \cdot \text{Det}$)	0.0128 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ (during 3 months of dry season)
b) detritus ($c6 \cdot \text{Oxy} \cdot \text{Det}$)	0.0336 g (carbon) $\text{m}^{-2} \text{day}^{-1}$ (during 3 months of dry season + 6 months of wet season)
Nutrients from other sources (Nuttra)	0.940 g (nutrients) $\text{m}^{-2} \text{day}^{-1}$
Nutrient uptake by mangroves ($c9 \cdot \text{Sun} \cdot \text{Biomang} \cdot \text{Nut}$)	0.846 g (nutrients) $\text{m}^{-2} \text{day}^{-1}$
Nutrient uptake by mangroves ($c8 \cdot \text{Nut}$)	0.094 g (nutrients) $\text{m}^{-2} \text{day}^{-1}$

Source: Lugo et al. [7]

Table 4. Rate Coefficients Used for Sensitivity Analysis

Coefficients	Values
c1	
High metabolism, low nutrients	$2.55 \times 10^{-9} \text{ m}^4/[\text{Kcal g (nutrients)}]$
c2 ----->	$8.4 \times 10^{-2} \text{ y}^{-1}$
c3	
High metabolism ----->	$1.68 \times 10^{-5} \text{ m}^2/[\text{g (carbon) y}]$
c4 ----->	$5.12 \text{ m}^{-1} \text{ y}^{-1}$
c5 ----->	$1.8 \times 10^{-2} \text{ m}^2/[\text{g (carbon) y}]$
c5' ----->	$1.44 \times 10^{-3} \text{ m}^2/[\text{g (carbon) y}]$
c6 ----->	$1.02 \times 10^{-2} \text{ m}^3/[\text{g (O}_2\text{) y}]$
c6' ----->	$8.2 \times 10^{-4} /[\text{g (O}_2\text{) y}]$
c8	
High metabolism, low nutrients	$3.5 \times 10^{-1} \text{ y}^{-1}$
c9	
High metabolism, low nutrients	$2.05 \times 10^{-10} \text{ m}^4/[\text{Kcal g (nutrients)}]$
c10 ----->	$3.68 \times 10^{-1} \text{ y}^{-1}$

Where y = year

Table 5. State Variables and Forcing Functions Used for Sensitivity Analysis

Functions and Variables	Initial Value
Forcing Functions	
Sunlight (Sun)	$1460.0 \text{ Kcal m}^{-2} \text{ day}^{-1}$
Tidal Action (Tid)	10.0 cm
Dissolved Oxygen (Disso)	4.0 g m^{-3}
Extra Nutrient Input (Through Terrestrial Run-off etc.)	343.7 (Lugo et al. [7])
State Variables	
(initial values used by Lugo et al. [7])	
Mangrove Biomass (Biomang)	$10500.0 \text{ g (carbon) m}^{-2}$
Detritus (Det)	$780.0 \text{ g (carbon) m}^{-2}$
Nutrients (Nut)	
Low Nutrients	100.0 g m^{-2}

Sensitivity Expressions

Expressions for sensitivity to solar radiation (Sun), extra nutrient sources (Nuttra), dissolved oxygen (Disso), and tidal action (Tid) have been derived and denoted by expressions of the form A_B [9], where A refers to state variable under consideration and B to the parameter with respect to which sensitivity is being studied. Some typical expressions are shown below:

Sensitivity to Solar Radiation

$$(\text{Nut_Sun}) = \left\{ \frac{[\text{Nut}]^2 * (\text{A_Sun}) + [\text{Nut}] * (\text{B_Sun})}{2\text{A} * [\text{Nut}] + \text{B}} \right\} \quad (8)$$

$$(\text{Biomang_Sun}) = \left\{ \frac{1}{c_3 * [\text{Nut}]} \right\} + \left\{ \frac{1}{c_3} * (\text{Sun}) * (\text{Nut} - \text{Sun}) \right\} \quad (9)$$

$$(\text{Det_Sun}) = \left\{ \frac{c_1 * c_2 * [\text{Nut}] + c_1 * c_2 * (\text{Sun}) * (\text{Nut} - \text{Sun})}{c_3 * \{c_4 * (\text{Tid}) + c_5 + c_6 * (\text{Disso}) + c_{10}\}} \right\} \quad (10)$$

Where,

$$\text{A_Sun} = (2.0 * c_1 * c_2 / c_3) * (\text{Sun}) \quad (11)$$

$$\text{B_Sun} = \frac{-(c_2 * c_9 / c_3) - c_1 * c_2 * \{c_5' + c_6' * (\text{Disso})\}}{c_3 \{c_4 * (\text{Tid}) + c_5 + c_6 * (\text{Disso}) + c_{10}\}} \quad (12)$$

Sensitivity to Nutrient Sources

$$(\text{Nut_Nuttra}) = 1.0 / \{2\text{A} [\text{Nut}] + \text{B}\} \quad (13)$$

$$(\text{Biomang_Nuttra}) = \left\{ \frac{c_1 * (\text{Sun})}{c_3} \right\} * \left\{ \frac{1.0}{2\text{A} * (\text{Nut}) + \text{B}} \right\} \quad (14)$$

$$(\text{Det_Nuttra}) = \left\{ \frac{c_1 * c_2 * (\text{Sun})}{c_3 * \{c_4 * (\text{Tid}) + c_5 + c_6 * (\text{Disso}) + c_{10}\}} \right\} * \left\{ \frac{1.0}{2\text{A} * [\text{Nut}] + \text{B}} \right\} \quad (15)$$

Sensitivity to Dissolved Oxygen

$$(\text{Nut_Disso}) = (\text{B_Disso} + \text{C_Disso}) / (2.0 * \text{A} * \text{Nut} + \text{B}) \quad (16)$$

$$(\text{Biomang_Disso}) = (c_1 * (\text{Sun}) / c_3) * (\text{Nut}) - (\text{Disso}) \quad (17)$$

$$(\text{Det_Disso}) = \left\{ \frac{c_2}{c_3 * \{c_4 * \text{T} + c_5 + c_6 * (\text{Disso}) + c_{10}\}} \right\} * \left\{ \frac{c_1 * (\text{Sun}) * (\text{Nut} - \text{Disso}) - \{c_6 * (c_1 * (\text{Sun}) * [\text{Nut}] - c_2)}{c_4 * \text{T} + c_5 + c_6 * \text{Disso} + c_{10}} \right\} \quad (18)$$

Where,

$$B_Disso = B1_Disso * B2_Disso \quad (19)$$

$$B1_Disso = \{c1 * c2 * (Sun) / \{c3 * (c4 * (Tid) + c5 + c6 * (Disso) + c10)\}\} \quad (20)$$

$$B2_Disso = c6 * (c5' + c6' * (Disso)) / \{c4 * (Tid) + c5 + c6 * (Disso) + c10 - c6'\} \quad (21)$$

$$C_Disso = C1_Disso * C2_Disso \quad (22)$$

$$C1_Disso = c2^2 / c3 * \{c4 * (Tid) + c5 + c6 * (Disso) + c10\} \quad (23)$$

$$C2_Disso = c6' - c6' * \{c5' + c6' * (Disso)\} / \{c4 * (Tid) + c5 + c6 * (Disso) + c10\} \quad (24)$$

Sensitivity to Tidal Action (Tid)

$$(Nut_Tid) = -\{[Nut] * B_Tid + C_Tid\} / \{2A * [Nut] + B\} \quad (25)$$

$$(Biomang_Tid) = (c1 * (Sun) / c3) * (Nut_Tid) \quad (26)$$

$$(Det_Tid) = Det1_Tid * Det2_Tid \quad (27)$$

Where,

$$Det1_Tid = -c2 * \{c1 * (Sun) * [Nut] - c2\} * c4 \quad (28)$$

$$Det2_Tid = c3 * \{c4 * (Tid) + c5 + c6 * (Disso) + c10\}^2 \quad (29)$$

$$B_Tid = B1_Tid / B2_Tid \quad (30)$$

$$B1_Tid = c1 * c2 * (Sun) * (c5' + c6' * (Disso)) * c4 \quad (31)$$

$$B2_Tid = c3 * \{c4 * (Tid) + c5 + c6 * (Disso) + c10\}^2 \quad (32)$$

$$C_Tid = C1_Tid / C2_Tid \quad (33)$$

$$C1_Tid = -c2^2 * (c5' + c6' * (Disso)) * c4 \quad (34)$$

$$C2_Tid = c3 * \{c4 * (Tid) + c5 + c6 * (Disso) + c10\} \quad (35)$$

RESULTS AND DISCUSSION

Steady state values for mangrove biomass, detritus, and nutrient have been derived and expressed [equations 1 through 6] in terms of coefficients and parameters listed in Tables 1 through 5. The expression for nutrient (variable) turns out to be a quadratic function of radiation, dissolved oxygen, tidal amplitude, and terrestrial run-off through incorporation of appropriate coefficients. Conditions for ecological feasibility [9] demand that all solutions be real. As a result, equation (7) follows.

Simulations have been carried out under the assumptions of high metabolism and low nutrient availability, with appropriate corresponding values of state variables and coefficients [Tables 4 and 5]. Steady state values for mangrove biomass, detritus, and nutrient compartments turn out to be 11312.6, 1012.2, and 73.6 g/m² respectively. Thus mangrove biomass and detritus significantly deviate from the initial values, i.e., 10500.0 and 780.0 g/m² respectively as reported by Lugo et al. [7]. However, in the case of the nutrient compartment, there is only a small deviation of some 26.4 g/m².

Sensitivity analysis [13, 14] helps in resolving issues of understanding uncertainties and offers insight into the structure and internal functioning of the ecosystem. It also offers a tool for investigating the relationships between state variables and system parameters. With y being a state variable dependent on the parameter x , (dy/dx) has been taken as the measure of absolute sensitivity and $[(dy/dx)*(x/y)_{\text{equilibrium}}]$ as that of the relative sensitivity [9, 12]. Absolute and relative sensitivity values are plotted in Figures 2 and 3.

The computer simulation reveals that tidal action is the parameter with respect to which almost all state variables are highly sensitive. This particular observation justifies the structure of the model. The most pronounced impact of the tidal action is on detritus (Table 6). Solar radiation has the least influence on detritus (Tables 6 and 7), as expected. Terrestrial run-off has strongest influence on mangrove biomass (Table 6). The strong influence of tidal action on detritus export is confirmed by the very high relative sensitivity value of -0.545 (Table 6), a negative value signifying an adverse impact and export of detritus.

The coefficients representing interactions among different state variables have been assumed to be constant in the simulation. This simplification does not take into account additional environmental and management variables influencing the mangrove ecosystem. The coefficients also will change depending on whether one is dealing with a high metabolic or a low metabolic situation. Therefore, investigations into the dynamics of turn-over rates and ecological efficiencies would be especially valuable.

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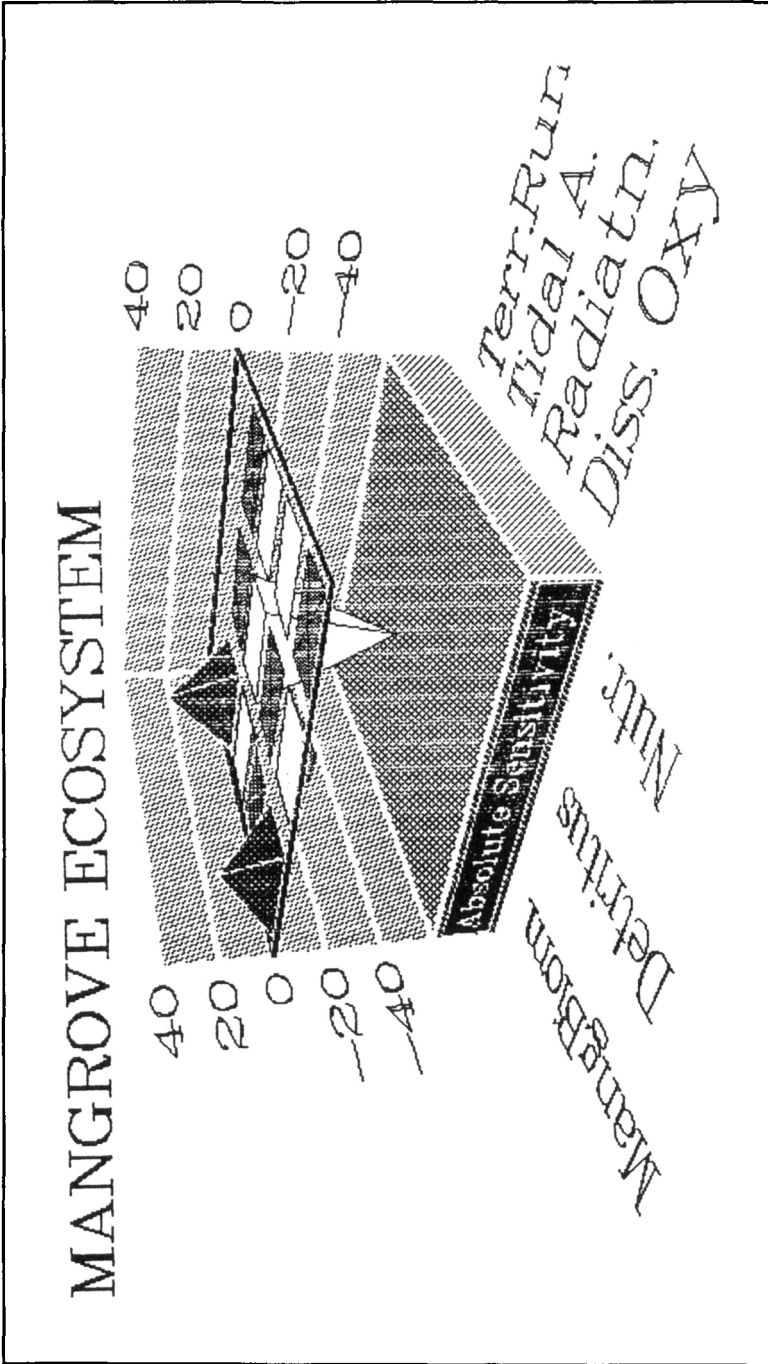


Figure 2. Absolute sensitivity values of mangrove biomass, detritus, and nutrients with respect to dissolved oxygen, solar radiation (values are multiplied by 10⁴), tidal action (values are multiplied by 10⁵), and terrestrial run-off.

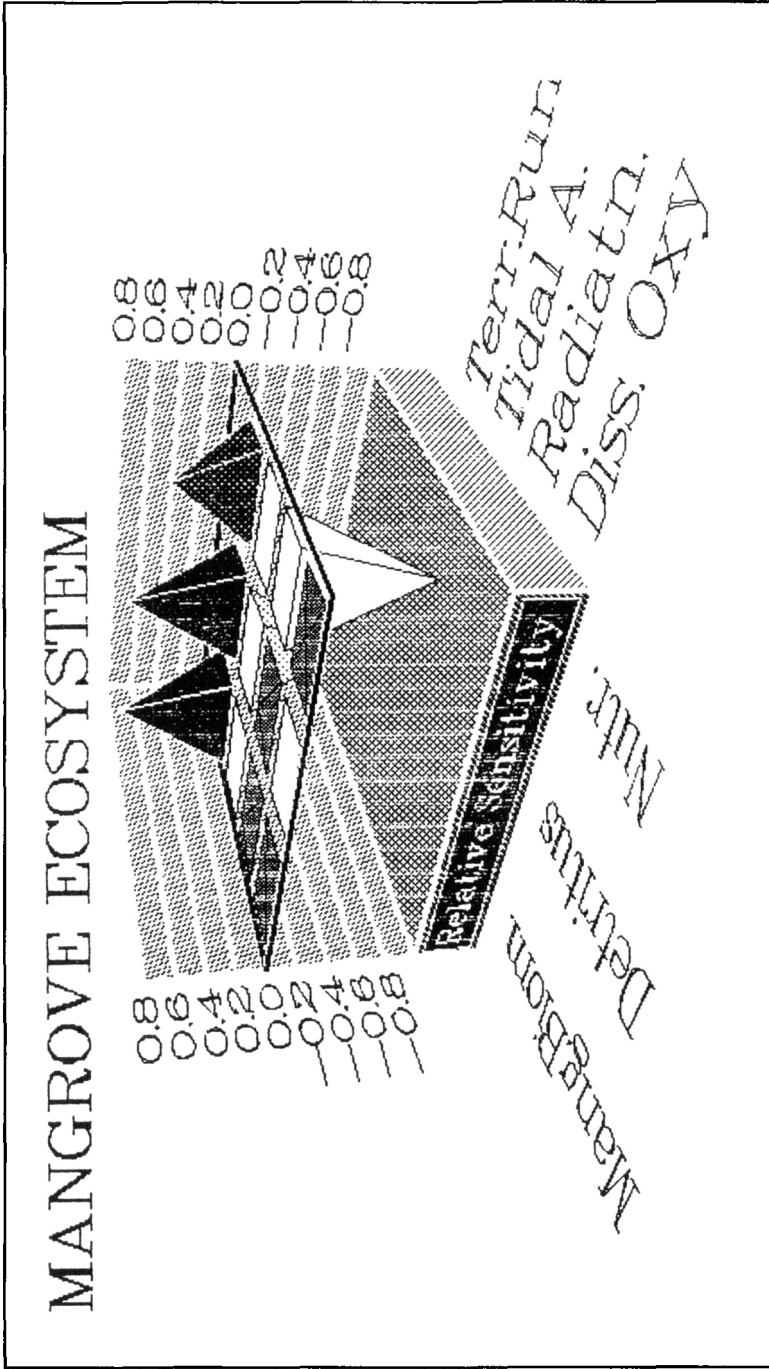


Figure 3. Relative sensitivity values of mangrove biomass, detritus, and nutrients with respect to dissolved oxygen, solar radiation, tidal action, and terrestrial run-off.

Table 6. Sensitivity Analysis

S. No.	State Variables	Steady State Values (g/m ²)	Sensitivity w.r.t.			
			Dissolved Oxygen	Radiation	Tidal Action	Terrestrial Run-off
Absolute Sensitivity						
1.	Mangrove Biomass	11312.6	20.2	4.6×10^{-4}	-695.7	25.9
2.	Detritus	1012.2	-9.2	4.1×10^{-5}	-5520.3	2.3
3.	Nutrients	73.61	0.09	-4.8×10^{-5}	-3.1	0.1
Relative Sensitivity						
1.	Mangrove Biomass	11312.6	0.007	0.059	-0.006	0.789
2.	Detritus	1012.2	-0.03	0.059	-0.545	0.789
3.	Nutrients	73.61	0.004	-0.958	-0.004	0.547

Table 7. Sensitivity Analysis

S. No.	Parameters	State Variables Which are Maximum and Minimum Sensitive	
		Maximum	Minimum
Absolute Sensitivity			
1.	Dissolved Oxygen	Mangrove Biomass (+20.22)	Nutrients (+0.091)
2.	Radiation	Mangrove Biomass (+0.00045)	Detritus (+0.000041)
3.	Tidal Action	Detritus (-5520.3)	Nutrients (-3.1)
4.	Terrestrial Run-off	Mangrove Biomass (+25.9)	Nutrients (+0.11)
Relative Sensitivity			
1.	Dissolved Oxygen	Detritus (-0.036)	Nutrients (+0.004)
2.	Radiation	Nutrients (+0.95)	Detritus (+0.059)
3.	Tidal Action	Detritus (-0.545)	Nutrients (-0.004)
4.	Terrestrial Run-off	Mangrove Biomass (0.789)	Nutrients (0.547)

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