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Adapting an Ecological Mangrove Model to Simulate Trajectories in Restoration Ecology

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We used an ecological model to simulate the trajectories of mangrove attributes according to different restoration criteria at geographically specific conditions and at decadal time scales. This model can contribute to the design and implementation of restoration projects, and also be used to verify key mechanisms controlling ecosystem attributes during the recovery period. An existing gap model of mangrove wetlands, FORMAN, was used to simulate restoration trajectories in one of the largest estuary rehabilitation projects (128 000 ha) in South America, Ciénaga Grande de Santa Marta, Colombia (CGSM). Recovery of a disturbed mangrove forest based on simulations of basal area following reductions of salinity to 40 g/kg within 2 yr or 10 yr time periods suggests that in both cases dominance would reach about 75% of that in the reference site (80 m^2/ha) in 40 yr. Both forests are > 80% dominated by *Avicennia*, and *Laguncularia* has greater basal area than *Rhizophora* in the remaining structure. Simulations of forest recovery with a 25 yr target for salinity reduction show that only about 50% of the basal area in the reference site is recovered after 40 yr. After 40 yr of recovery, both the 2 and 10 yr salinity targets produce higher basal area and different patterns of community composition (*Laguncularia* becomes the dominant species) under enhanced recruitment (planting program) than observed under more natural recruitment. Ecological models can be used to establish trajectories of mangrove response to a variety of initial site conditions at spatially explicit locations that can improve engineering designs, project operation, and more clearly define monitoring programs and natural resource valuation. Modelling techniques can be used to identify the appropriate spatial and temporal scales of problems associated with mangrove restoration projects that could improve our ability to conserve and manage one of the most valuable forested wetlands in the tropical coastal zone. © 1999 Elsevier Science Ltd. All rights reserved

Introduction

Degradation of natural resources is a major environmental issue that societies around the world are currently facing (Ehrlich and Mooney, 1983; Houghton, 1994; Dobson *et al.*, 1997). Limited information on how specific mechanisms regulate the structure and function of ecosystems has restricted the development of management plans that govern the use, conservation and restoration of natural resources. During the last 10 yr ecological restoration has been strongly advocated as a measure to minimize ecological damage and to compensate for widespread urban development (Brown and Lugo, 1994). However, restoration of natural systems requires an integration of disciplines (e.g. ecology, hydrology, engineering, economics) across a wide variety of scales (Allen and Hoekstra, 1987). These disciplines generally have not been interfaced at the landscape and regional level in the solution of environmental problems (Sklar and Costanza, 1990; Naveh and Lieberman, 1994). Moreover, the magnitude of human impacts on ecosystems and landscapes has forced the ecological sciences to include humans as a fundamental constraint on ecological processes and acknowledge land use as a decisive factor of habitat change (Ojima *et al.*, 1994; Riebsame *et al.*, 1994). Restoration ecology includes both the development and application of fundamental ecological concepts together with policy constraints of social sciences to rehabilitate degraded landscapes (Twilley *et al.*, 1998).

Landscapes that represent transition zones, or ecotones, between distinct environmental settings are usually more sensitive to human disturbance and recovery (di Castri and Hansen, 1992; Wiens, 1992; Fortin, 1995; Holland, 1996). Coastal wetlands are ecotones at the interface between terrestrial and aquatic landscapes whose boundaries and functions may shift in response to natural and human disturbances (Mitsch and Gosselink, 1993). Changes in the environmental settings that regulate the exchange of water, energy and materials across coastal landscapes can control levels of biological diversity as well as primary and secondary productivity (Risser, 1995; Carter *et al.*, 1994). These features are sensitive to changes in regional hydrology, and any large modification at the landscape scale can alter wetland functions (Mitsch and Wilson, 1996; Blom *et al.*, 1996). One of the most difficult tasks in restoring ecological systems such as coastal wetlands is to use proper spatial scales from regional to habitat levels when selecting site criteria that will promote some specific goal or endpoint (Pickett, 1987; Pickett, 1994; Aronson *et al.*, 1995). The success of a restoration project is qualified by the trajectories and endpoints selected, which are rarely defined operationally and usually based on the perceptions of 'the original indigenous state' (Brown and Lugo, 1994; White and Walker, 1997). Given the complex biotic and abiotic interrelationships at different hierarchical scales in a ecosystem (Allen and Hoekstra, 1987; Pickett, 1994; Luan *et al.*, 1996), there are few diagnostics that anticipate the trajectories and endpoints related to specific site criteria.

Ecological restoration represents manipulations of landscapes that provide 'natural experiments' from which we can obtain information about ecological functions that vary at different spatial and temporal scales (Urban *et al.*, 1987; Michener, 1997). Accumulating, interpreting and applying information on rehabilitated landscapes at diverse scales can be accomplished through the construction of ecological models. These models can help us to understand the relative significance of ecological processes at different scales in projecting the trajectories of natural resource response to rehabilitation projects (Shugart, 1989; Conroy *et al.*, 1995). Models can be used to synthesize results of field studies (Eberhardt and Thomas, 1991; Conroy *et al.*, 1995; Michener, 1997), direct research efforts to test specific hypotheses about ecological processes (Kadlec and Hammer, 1988; Jørgensen, 1994), and provide assistance in management decision process (Birkett, 1994; Constanza *et al.*, 1990). However, there are few examples of either conceptual frameworks or specific techniques whereby ecological modelling can be used in restoration ecology (Michener, 1997). The use of models in forecasting trajectories of change in community and ecosystem attributes under different restoration criteria deserves more attention (Shugart, 1989; Conroy *et al.*, 1995).

In this paper we discuss the application of a classification scheme and a modelling approach to direct the rehabilitation of mangrove wetlands. This approach is developed using conceptual constructs from both hierarchy and disturbance theories and landscape ecology to forecast potential scenarios of mangrove species composition and structure in a tropical coastal region. The use and development of ecological models within a restoration context is a recent component in the management of coastal regions (e.g., Madden and Kemp, 1996), therefore we propose scenarios as a set of hypotheses to be tested during a restoration project. By using this approach we propose a theoretical framework to establish the interactions among boundary constraints and ecological processes for the restoration and rehabilitation of mangrove ecosystems. First we describe an ecogeomorphic classification of mangrove wetlands that can be used to define constraints at different scales of the landscape that regulate mangrove structure and function. We then discuss the use of individual-based models to simulate the ecological processes within a specific environmental setting that explain the response of mangroves under different rehabilitation scenarios. Finally, we describe a case study, the largest mangrove rehabilitation project in the new world tropics, where ecosystem modelling can be used to test hypotheses concerning the selection of site criteria to evaluate specific endpoints in the rehabilitation process.

Theoretical Framework and Approach

Applying hierarchy and disturbance theories to mangrove wetlands

Hierarchy theory addresses the understanding of systems with a certain type of organized complexity (Allen and Starr, 1982; O'Neill *et al.*, 1989; Urban *et al.*, 1987; Müller 1992). This theory can be used to test hypotheses related to the complexity of multilevel systems particularly in restoration projects (Allen and Hoekstra, 1987). A process at a particular level of organization (the focus) in a hierarchy can be explained by constraints at higher levels (boundary conditions) along with mechanisms at lower levels of organization (the components) (Risser, 1987; Pickett *et al.*, 1989). Therefore, lower levels provide data for testing hypotheses and the search for causality (Meentemeyer, 1989). Processes are regulated at levels of organization above and below the focus of a mangrove restoration project. And there are linkages and feedbacks among these levels, requiring some attention to these diverse spatial constraints. The ecogeomorphic and ecological classifications of mangrove wetlands, which are clearly delimited by natural boundaries, reflects a combination of large spatial hierarchical levels that represent an upper limit constraint on ecological processes at the level of the mangrove wetland (Fig. 1).

The ecogeomorphic classification of mangroves describes the nature of geophysical processes of coastal environments that along with ecological processes account for the biological and functional diversity of mangrove wetlands (Thom, 1984; Woodroffe, 1992; Twilley, 1995; Twilley *et al.*, 1996; Twilley, 1997). The climate and landform characteristics of a coastal region together with local ecological processes control the basic properties of mangrove wetlands (Thom, 1984; Twilley, 1995). The two basic types of geomorphic settings are those with terrigenous inputs of sediments and those with in situ sedimentary processes that form carbonate sediments (Fig. 1). These coastal geomorphic settings

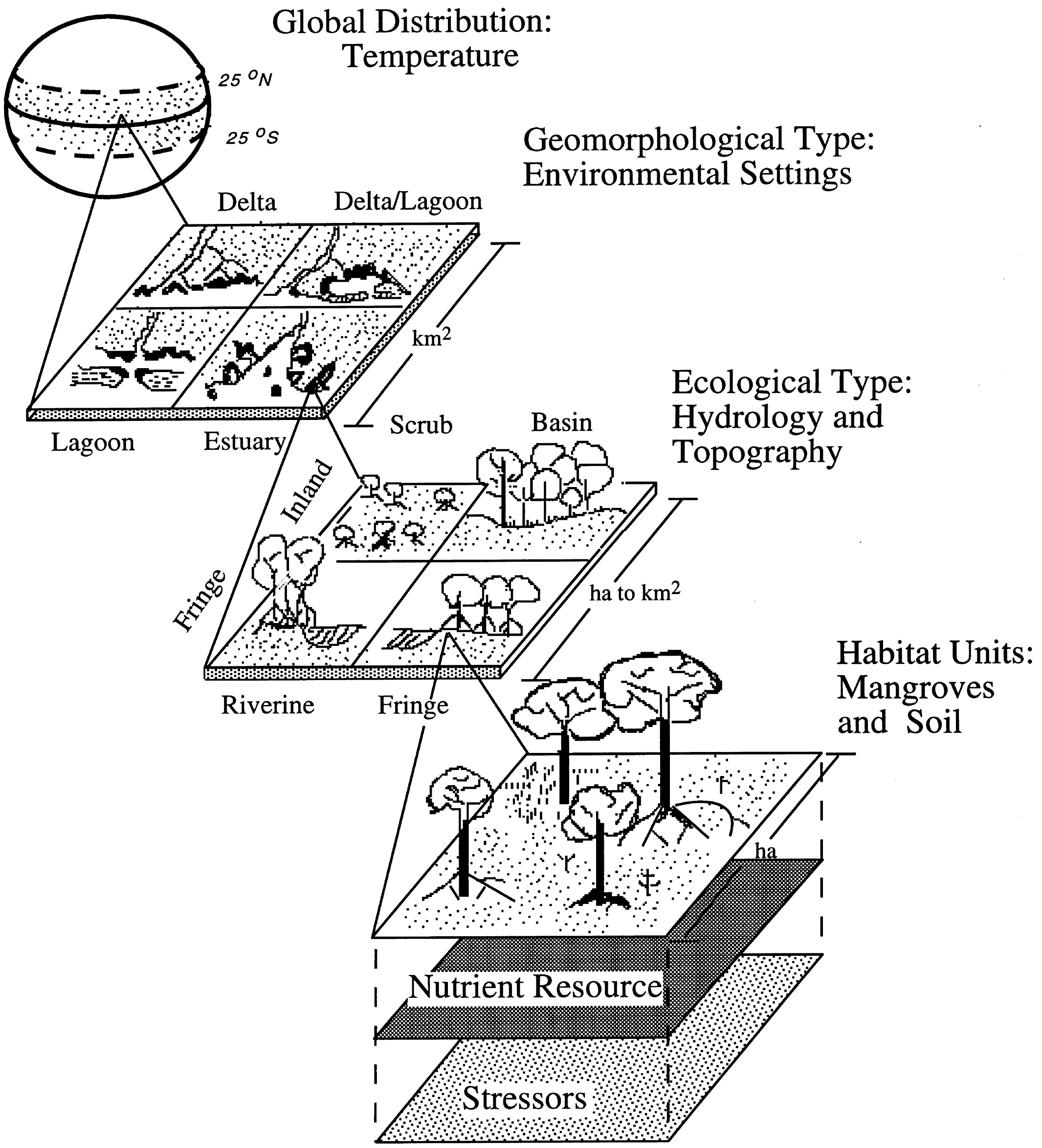


Fig. 1 Hierarchical classification system to describe patterns of mangrove structure and function based on global, geomorphological (regional) and ecological (local) factors that control the concentration of nutrients resources and stressor in soil along gradients from fringe to more inland locations from shore (modified from Twilley, 1997).

can be found in a variety of life zones (e.g. humidity provinces, Blasco, 1984) that depend on regional climate and oceanographic processes. These boundary conditions establish the constraints that control the finer grain processes (referred to as ecological processes) that explain the variety of habitats within any one type of environmental setting.

Lower scale factors such as microtopography and tidal hydrology (Fig. 1) can influence the zonation of mangroves from shoreline to more inland locations forming ecological types of mangrove wetlands (Watson, 1928; Walsh, 1974; Chapman, 1976). For example, Lugo and Snedaker (1974) identified ecological types of mangroves based on topographic location and patterns of inundation at local scales (riverine, fringe, basin and dwarf, Fig. 1). A combination of ecological types of mangroves can occur within any one of the geomorphic settings described above depending on the distribution of soil resources and abiotic stressors (Fig. 1). Thus an ecogeomorphic typology of mangrove wetlands includes processes occurring at a hierarchy of spatial scales that can be used to classify mangrove wetlands. Our hypothesis based on this classification scheme is that a gradient in the geophysical processes of a coastal region together with local ecological factors will determine the diverse patterns of energy flow and biogeochemistry of mangrove wetlands (Twilley, 1995, 1997).

We propose that these hierarchical levels of mangrove ecological types should all be considered in mangrove rehabilitation projects to capture the combined effects of

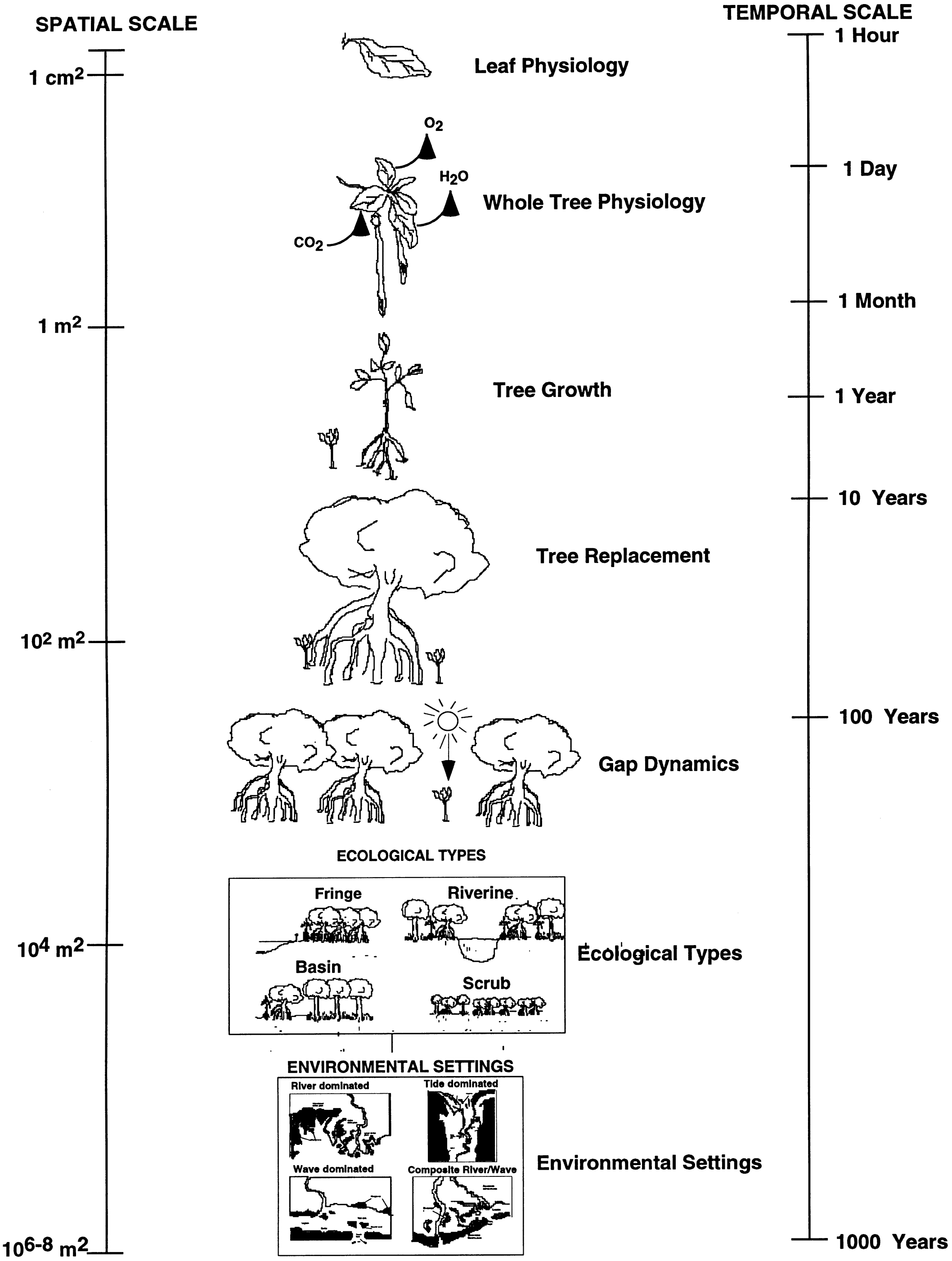


Fig. 2 Temporal and spatial hierarchical organization of dynamic processes in mangrove ecosystems. (Modified from Naveh and Leitherman, 1994).

geophysical, geomorphic and ecological processes that control the mosaic distribution of mangrove wetlands (e.g., nutrient cycling, sedimentation, tidal inundation, species distribution). These ecological types could be considered, within a landscape analysis, as basic landscape units equivalent to an ecotype ecological classification (Naveh and Lieberman, 1994). Direct attempts to manipulate and control mangrove structure and function within the relatively short time periods (i.e., 100 yr) of rehabilitation projects require approaches that integrate these scales of processes (Brown and Lugo, 1994). In this manner, proposed changes at the physiological (e.g., leaf physiology) to landscape levels (e.g., environmental setting) during rehabilitation projects are linked to time scales depending on the ecogeomorphic hierarchical level (Fig. 2). The ecogeomorphic approach proposes that meaningful interactions occur in both directions along a continuum of spatial scales that collectively determine the trajectory of mangrove restoration. This classification system can account for the site-specific criteria that need to be considered to accomplish realistic goals of rehabilitation projects.

Disturbance theory can also help to direct and propose fundamental questions in restoration ecology (Sousa, 1984; Pickett *et al.*, 1989; Pickett, 1994). Structural changes are reflected as a spatial-temporal mosaic of patches at different successional states (Moloney and Levin, 1996), which are influenced by life history characteristics of individual species and community composition (van der Valk, 1981). This spatial pattern of disturbance has in general been ignored and emphasis generally placed on understanding only the effects of changes in the frequency and intensity of disturbance (Risser, 1987; Moloney and Levin, 1996). Natural disturbances are patchy in time and space and range from the removal of individual trees to devastation of many square kilometers (Smith *et al.*, 1994). Disturbances can have very different effects at different points along resource gradients and hierarchical levels (Gosz, 1992), which result in a shifting mosaic of successional states. Disturbances have a larger effect only under particular resource conditions, and occur with a characteristic frequency and intensity in different regions of a landscape potentially establishing a dynamic equilibrium (Smith and Huston, 1989). Thus many systems are in fact highly dependent or contingent on disturbance, and its spatial and temporal distribution should not be considered as extraneous or exceptional events (Pickett and White, 1985; Ehrenfeld and Toth, 1997). Indeed, restoration of natural disturbance regimes must be a part of rehabilitation efforts (Palmer *et al.*, 1997).

A model of the structure and function of a natural system is needed to distinguish between non-disturbed and disturbed states. In mangrove wetlands, natural disturbances can play a major role in controlling the structure and function of these forested ecosystems. Since mangroves are considered naturally stressed ecosystems (Lugo *et al.*, 1981) the effects of climatic influences, such as hurricanes, lightning, frequency of frost or excessive evaporation, can influence mangrove distribution along environmental gradients. Hurricanes in particular can greatly influence mangrove structure and function at the landscape level in tropical regions of the world (Lugo, 1980; Smith *et al.*, 1994; Tilman, 1996). Lugo (1980) argued that mangrove wetlands can usually reach maturity (described as maximum biomass) in 20–30 yr, a period that coincides with the frequency of hurricanes in some tropical regions. Apparently large-scale disturbances are part of the cyclic events that shape the structural complexity of mangrove forests (Lugo, 1980) and therefore mangroves can be considered as systems with multiple equilibrium states (‘metastable’) (Tilman, 1988; Naveh and Lieberman, 1994).

Trajectories of mangrove wetlands are patterns of change in ecological attributes with time among natural, perturbed and relatively restored conditions (Aronson *et al.*, 1995). The nature of these trajectories will depend on the type of exploitation, the magnitude of the impact relative to natural disturbances, the ecogeomorphic type of mangrove wetland that is impacted, and finally the amount of time since a disturbance (Twilley, 1995, 1997). Trajectories include both the structural and functional attributes of sites relative to reference conditions, and the time required to obtain a restored state or condition. We propose that the trajectories of mangrove wetlands in response to restoration efforts will depend on initial conditions of the original disturbance, site modifications proposed in the rehabilitation project, recruitment of new individuals and the environmental constraints of the ecogeomorphic setting. The effect of environmental constraints suggests that restoration trajectories of mangroves will depend on the level of disturbance and local stress (e.g., Grime, 1977) in a coastal environment. The link in environmental constraints and successional trajectories has been successfully documented for tropical upland forests relative to gradients from harsh (dry) to benign (moist) environments (Ewel, 1987). The trajectories of restored mangrove sites will be determined largely by the regional constraints of the geomorphic setting (wet vs dry climate, presence of river input, tidal amplitude), together with the local ecological factors of the site (nutrient resources and abiotic stressors) (Fig. 1).

Natural disturbances at a smaller spatial scale can also influence mangrove species zonation and succession (Ball, 1980; Lugo, 1980; Smith *et al.*, 1994). Natural tree mortality (caused by wind, erosion, hypersalinity, frost, etc.) initiates a process called gap dynamics (Fig. 2). An adult tree dies and creates a gap in the canopy allowing the growth of mangrove seedlings and saplings due to the sudden availability of light and nutrient resources (e.g., Shugart, 1984; Botkin, 1993). Gap dynamics have been directly related to lightening in mangroves in the new and old world tropics (Smith, 1992; Smith *et al.*, 1994). Although generally small in size (1–300 m^2), gaps represent a functional unit that maintains diversity and determines successional changes in forest ecosystems; they also can shape landscape patterns of vegetation distribution at larger spatial and temporal scales (Shugart, 1984; Lertzman *et al.*, 1996). The recovery rate of a forest from a disturbance depends not only on the particular species that are present, but also in the ages and sizes of the individuals that survive the disturbance (Shugart, 1984; Botkin, 1993). Thus initial conditions of forest structure and rates of sapling recruitment (establishment of seedlings to sapling stage) are important determinants of mangrove development (Chen and Twilley, 1998). Differences in mortality and growth rates in several areas across the landscape in mangrove forests will also have a strong influence on the spatial distribution of mangrove species since competition for resources among mangrove species is expected to affect regeneration dynamics (e.g., McKee, 1993, 1995).

The lack of information on trajectories of mangrove forests at regional or landscape scales limits the utility of projections based on small-scale observations of mangrove forests following a disturbance. Mangrove forests are part of heterogeneous landscapes in coastal environments with a dynamic geomorphology, particularly compared to terrestrial forests. It becomes important to determine how ecological interactions from local, fine scale and short-term perturbations are modified or attenuated by geomorphological and geophysical processes that influence ecosystem attributes at the larger, longer term, coarser scales (Risser, 1987; Meentemeyer and Box, 1987; Meentemeyer, 1989; Swanson *et al.*, 1992; Twilley, 1995). Evaluating the effect of natural and human disturbances at different temporal-spatial scales in mangrove ecosystems requires a methodological approach that allows for the analysis of complex geomorphological and ecological responses to site criteria during rehabilitation (Figs. 1 and 2).

Models of Mangrove Restoration

Currently there are a large variety of approaches to develop ecological models (Sklar *et al.*, 1985; Taylor, 1988; Turner and Gardener, 1990; Dunning *et al.*, 1995; Pacala *et al.*, 1996), but it is ultimately their articulation, accuracy and effectiveness (Costanza and Sklar, 1985) that define the success of their utilization as a management tool. Mechanistic process-based models aim to optimize for realism, and therefore their use and development have increased dramatically during the last 10 yr given their potential spatial and temporal articulation at the landscape level (e.g., Boumans and Sklar, 1990; Costanza *et al.*, 1990; Reyes *et al.*, 1994). Models such as individual-based models, successfully used to simulate forest growth dynamics, have proved useful to understand plant growth as a process affected by spatial features (Botkin *et al.*, 1972). Although past forest individual-based models (e.g., gap models) (e.g., JABOWA, FORET, FORNUT) were spatial in a vertical sense rather than in a horizontal sense (Sklar and Costanza, 1990), and vegetation did not directly influence other components (e.g. soil status), individual-based models can be modified to understand plant succession within a mechanistic approach (e.g., Pearlstine *et al.*, 1985). The powerful aspects of individual-based models (e.g. integration of different levels of ecological processes, direct and relatively simple parameterization) and their intrinsic structure to include both temporal and spatial scales make them a powerful tool to test hypotheses and advance ecological principles for both basic ecological knowledge and the restoration of biological diversity (Urban *et al.*, 1987; Huston *et al.*, 1988; Dunning *et al.*, 1995).

Ecological modelling can evaluate the success of restoration efforts by simulating more realistic endpoints, since the desired goals of rehabilitation projects are time-dependent (i.e., long-term). Reference wetlands can be used as standards to compare impacts and determine the level of severity of human and natural disturbances among regional coastal landscapes (Brinson and Rheinhardt, 1996). These reference sites can be considered as a set of possible states for endpoints in restoration projects (Ehrenfeld and Toth, 1997). Returning to a specified historic condition may not be possible, particularly when past effects in the system were of large magnitude (Pickett *et al.*, 1989). A more sensible goal may be to restore natural disturbance regimes (e.g. hydrology) and other ecological processes that maintain biological elements of interest (e.g. species composition, basal area) (Noss, 1985). Management goals and protocols in rehabilitation programs should be viewed as hypotheses of routes to achieve clearly stated goals. Models are useful in measuring the behaviour of a broad suite of ecosystem attributes and allow the selection of alternative courses of action during the rehabilitation project (Lee and Gosselink, 1988; Mitsch, 1994; Lee, 1993). Development of interactive, spatially explicit models that evaluate simulated results of proposed management alternatives across the landscape are therefore strongly recommended (Meyer and Swank, 1996).

There are few ecological simulation models describing the structural and functional characteristics of mangrove forests (e.g. Lugo *et al.*, 1976). The FORMAN model, based on modifications of the JABOWA and FORET models (Shugart, 1984; Botkin, 1993), was developed to simulate demographic processes of mangroves in a 0.05 ha plot (Fig. 3) (Chen and Twilley, 1998). In general, the FORMAN model represents tree growth of three mangrove species (*Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa*) on an annual basis for individual trees in a forest gap. Attributes of each individual tree including diameter and height are summed for each species in the plot at each time interval of the model. These attributes are used to describe different metrics of forest structure such as dominance (basal area, density, average tree height), size class distribution and biomass. These attributes can be used to track both the demographic (e.g., density and dominance) and some of the functional (e.g., biomass and productivity) responses of mangrove wetlands to distribution of resources and stressors in a given plot. The growth function is influenced by the latitude (temperature and degree days), soil conditions (nutrient resources and salinity) and light availability. Initial conditions of forest structure are established, new recruits are added, and trees grow annually depending on the values of resources and stressors. The two sources of tree mortality in the model depend on age and suppressed growth (Solomon, 1986; Pastor and Post, 1986). Details about model calibration and verification can be found in Chen and Twilley (1998).

The FORMAN model assumes that the growth equation for a mangrove tree is as follows:

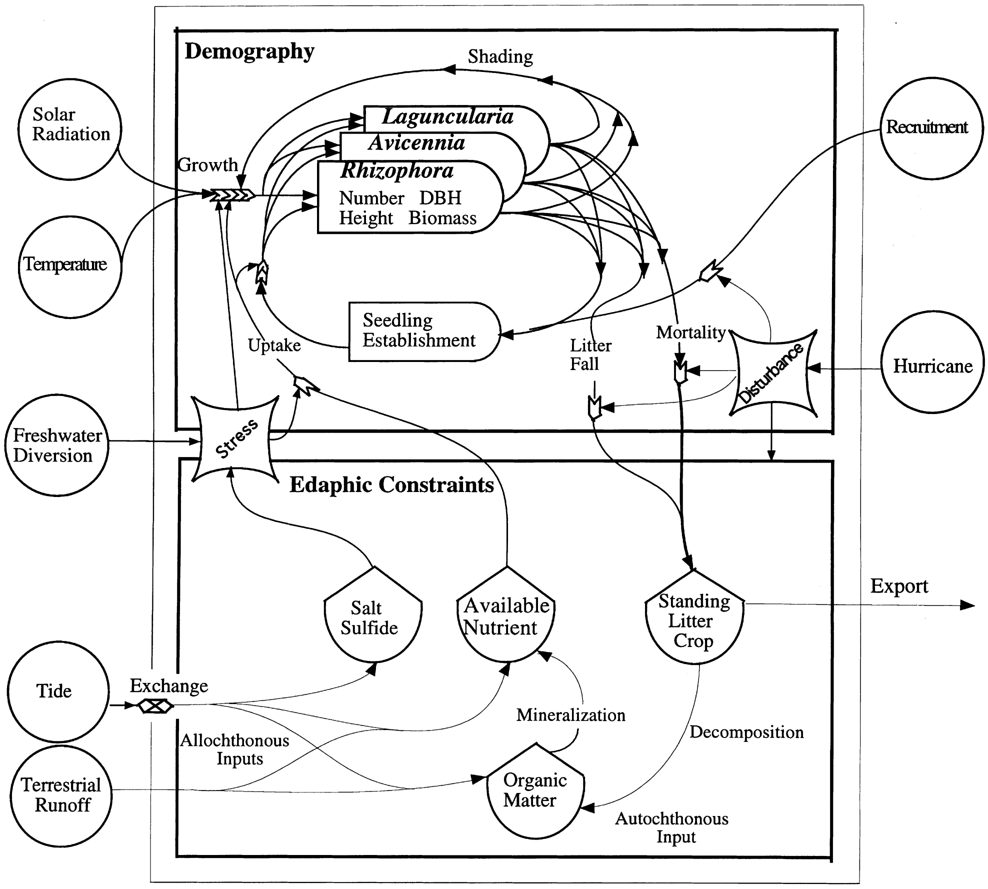


Fig. 3 Conceptual model of mangrove forest development including edaphic constraints and forcing functions (modified from Chen and Twilley 1998).

$$\frac{\mathrm{d}D}{\mathrm{d}t} = \frac{GD(1 - DH/D_{\mathrm{max}}H_{\mathrm{max}})}{(274 + 3b_2D - 4b_3D^2)} \times S(\mathrm{SALT})\ N(\mathrm{NUT}) \times T(\mathrm{DEGD}) \times r(\mathrm{AL}) \qquad (1)$$

in which D is the DBH (diameter at breast height) of the tree (cm), H the tree height (cm), D_{max} and H_{max} the maximum values of diameters and heights for a given tree species. G, b_2 and b_3 the species-specific growth parameters (Chen and Twilley, 1998). The optimal growth is constrained by life history traits however, the realized growth is limited by salt stress [S(SALT)], resource availability including light [r(AL)] and nutrients [N(NUT)] and temperature [T(DEGD)] (Chen and Twilley, 1998). The relative magnitude of these factors among the three mangrove species simulated in FORMAN is based on field and greenhouse studies, although there are several uncertainties in the specific nature of these curves (Chen and Twilley, 1998). The reduction of optimal growth by either light, soil nutrient resources, and/or soil salinity acts independently in the model and evaluated as divergence value of 1.0. The effect of hydroperiod on forest development is included in the rate of seedling establishment for each species (recruitment rate) in the mangrove growth equation.

Mangrove Restoration in a Lagoon-Delta Ecosystem

Mangrove perturbation

The Cienaga Grande de Santa Marta (CGSM) is a lagoon-delta ecosystem and forms the exterior delta of the Magdalena River, which is the largest river in Colombia with an annual average water discharge of 7000 m^3/s (Fig. 4). The region can be classified as Type I setting (river-dominated, arid, with low tidal amplitude), containing fringe, basin and riverine mangroves (Thom, 1982). The system is the largest lagoon-delta ecosystem in the Caribbean area with an extension of 128 000 ha (coastal lagoons, creeks and mangrove swamps). It comprises two main water bodies, the Ciénaga Grande (45 000 ha) and Ciénaga de Pajarales (12 000 ha), as well as several smaller lagoons. The coastal climate zone is arid tropical, with 6–7 dry-months a year (HIMAT, 1987) and a annual deficit of 1031 mm/yr because evapotranspiration (1431 mm/yr) largely exceeds precipitation (400 mm/yr). To the north, the lagoon complex is separated from the Caribbean Sea by a barrier island known as Isla de Salamanca, which has an inlet of approximately 100 m wide and 10 m deep on its eastern end that connects the largest lagoon (Ciénaga Grande) directly to the sea. To the west and south-west the

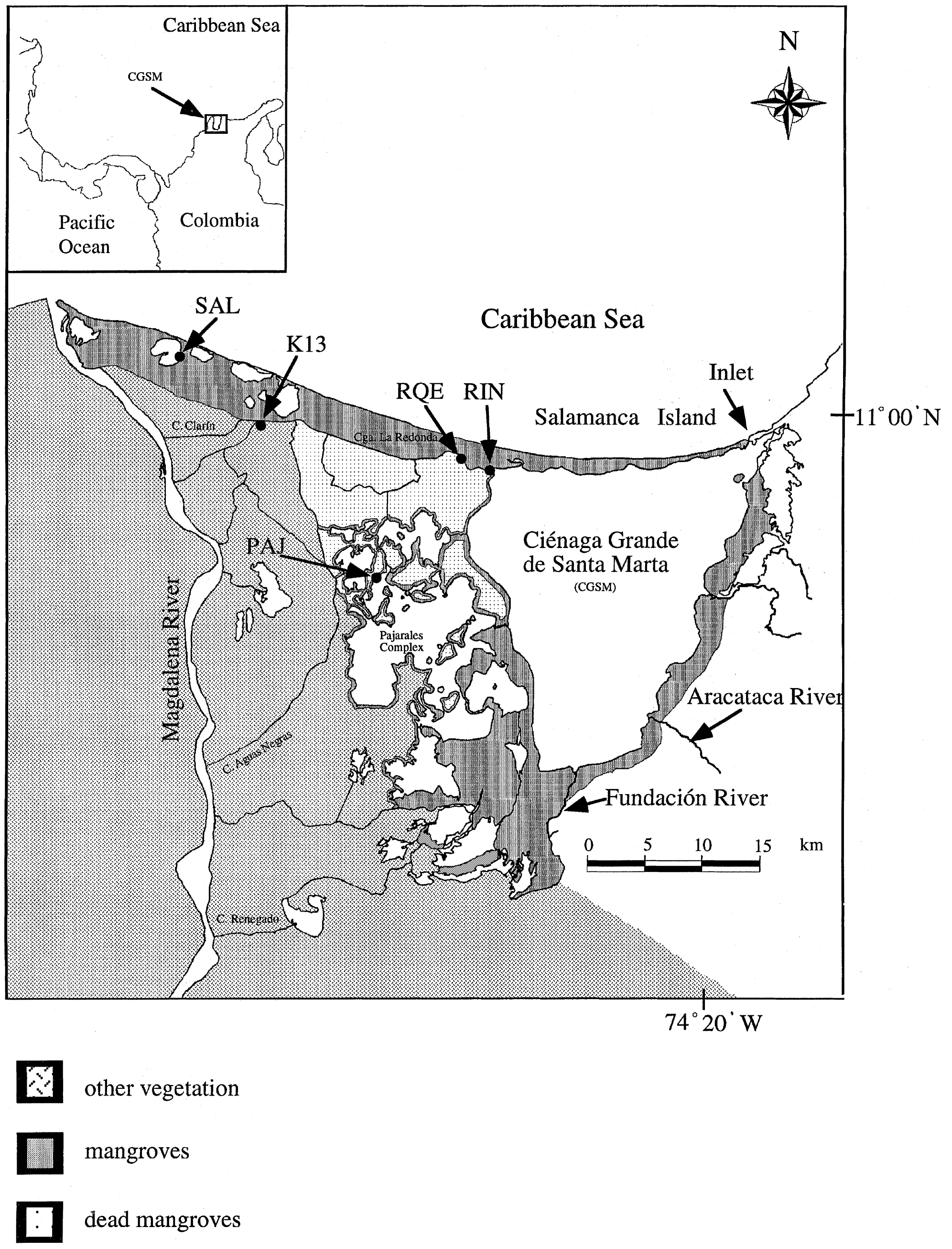


Fig. 4 Map of Cienaga Grande de Santa Marta with location of mangrove sites used to characterize different conditions of forest restoration and the degree of mangrove disturbance following changes in regional hydrology.

lagoon-delta complex is limited by the flood plain of the Magdalena River, through which five main distributaries historically brought freshwater from the river to the complex until the 1970s.

The CGSM has been impacted by the construction of a coastal highway and a road levee along the Magdalena River (Fig. 4). The construction of these two roads has altered the natural flow of marine and freshwaters, respectively; this water diversion resulted in severe environmental damage to this mangrove-lagoon ecosystem. Most of the past alterations in coastal hydrology were due to rediversion of freshwater associated with highway construction, expansion of agriculture (cattle farming and rice), and urban development. Freshwater diversion from the lagoon-delta complex in this arid coastal region has resulted in hypersalinization of mangrove soils (> 100 g/kg for 7 mo a year) leading to a die-off of almost 27 000 ha of mangrove forests in a 36 yr period (Botero, 1990; Cardona and Botero, 1998). Tree mortality rates increased from 174.5 ha/yr during the years of 1956 to 1968, to 984.7 ha/yr from 1968 to 1987 (Gonzalez-Afanador, 1991), and reached 1531 ha/yr from 1987 to 1993. These estuarine regions were surrounded, until around 1960, by approximately 52 000 ha of mangrove wetlands (Fig. 4). In addition to extensive mangrove mortality, several fish kills caused by low oxygen concentrations and eutrophication have occurred during the past 2–4 yr (Mancera and Vidal, 1994). Historically, the CGSM has been a major natural, economic and cultural resource of the Magdalena region of Colombia. Current losses of natural capital due to environmental degradation of the estuary are unknown.

Rehabilitation project

In 1993 a rehabilitation project (Botero, 1994; CORPES-GTZ, 1989) was initiated to reestablish the hydrology in some areas of the CGSM to induce both the recovery of the hydrologic regime and the natural regeneration of mangrove forests. The rehabilitation project consists in opening five of the natural pre-existing distributaries (giving a maximum total capacity freshwater flow of approximately 150 m^3/s) and a partial connection of the lagoon with the sea through a series of box-culverts built under the coastal highway (Fig. 4). So far, three of those culverts have been reopened (providing a maximum water flow of about 24 m^3/s), and freshwater from the river has started to flow through the Canal Clarin (Fig. 4) into the northern part of the lagoon since February 1996. In addition, a monitoring program was initiated to evaluate the success of these rediversions in rehabilitating the forested wetlands along with a mangrove plantation program in localized areas of the estuary. The main hypothesis of this project is that by modifying the hydrological conditions, wetland formation and mangrove forest productivity will increase as soil salinity decreases due to freshwater input. Further, the freshwater diversion along with rehabilitation of mangrove wetlands will restore the water quality and fishery production in this coastal lagoon.

As a consequence of changes in regional hydrology in the CGSM, there are well-defined gradients in mangrove wetland perturbation at the landscape level. This gradient is defined based on high soil salinity and a decrease in forest structure (Fig. 5). Our approach was to define specific sites in the impacted area that represent stages along recovery trajectories, based on both structural and functional attributes of mangrove wetlands obtained in previous studies (Giraldo, 1995). This space-for-time substitution approach (Pickett *et al.*, 1989; Aronson *et al.*, 1995) uses sites with specific vegetation structure and degree of perturbation (soil salinity and inundation regimes) that represent different stages along the restoration trajectory. Hypothetical points along the trajectories of perturbation and/or restoration have been

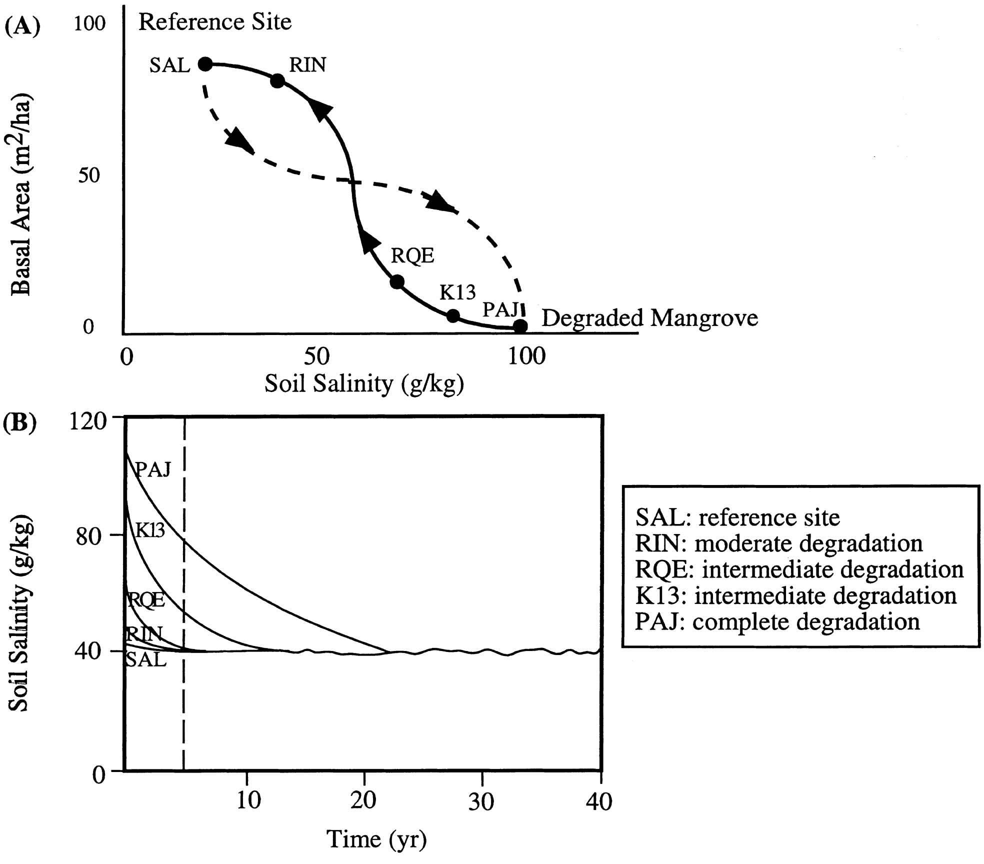


Fig. 5 (A) Hypothetical trajectories of mangrove ecosystem caused by salinity stress, degradation and rehabilitation are expressed as condense and dash line, respectively. (B) Projections of soil salinity in each study site after hydrological changes. Site locations in Cienaga Grande de Santa Marta, Colombia are shown in Fig. 3.

established for specific mangrove sites along a perturbation gradient (Fig. 5A). Two endpoints of the perturbation gradient are represented by an undisturbed reference site (SAL; Isla Salamanca) that include healthy mangroves at the mouth of the Magdalena River (Fig. 4) where freshwater was never diverted (Fig. 5A). This site contains healthy mangrove wetlands with a maximum basal area of 75 m^2/ha and an average soil salinity of 23 g/kg (range: 3–48 g/kg). At the other extreme, the totally perturbed site (PAJ; Cienaga de Pajarales) consists entirely of dead mangrove vegetation; average soil salinity is 99 g/kg with a range from 80 to 130 g/kg (Fig. 5B). This site is not presently planned for any input of freshwater as part of the restoration project.

There are three intermediate sites between the two endpoints of the established perturbation gradient (Fig. 5A). Site RIN (Rinconada) is a moderately degraded area where freshwater was diverted 25 yr ago but which maintains adequate connection with estuarine lagoon waters (Fig. 4). There is limited tree mortality at this site and maximum basal area is 41.8 m^2/ha. Freshwater diversions began in this area in January 1996. Average soil salinity at the onset of hydrological restoration was 38.4 g/kg (range from 23.6 to 52.6 g/kg). At site K13 along Caño Clarin (Fig. 4) environmental conditions are not much different from PAJ, but hydrologic restoration in January 1996 has improved the forest structure from a completely degraded basal area of < 2 m^2/ha (Fig. 5A). Average soil salinity at the onset of hydrological restoration was 104 g/kg (range from 89.5 to 148.4 g/kg) and has reduced to < 90 g/kg. Freshwater was also diverted to site RQE (Caño La Riqueza) 25 yr ago, which represent another intermediate degradation site (Fig. 4). The site is 'intermediately' perturbed and some evidence of forest restoration is also observed (Fig. 5A). Basal area of the forest is < 4.2 m^2/ha and soil salinity at the onset of hydrological restoration was 59 g/kg (range: 52.3 to 99.4 g/kg).

Simulations of mangrove recovery

Simulations of forest regeneration rates and trajectories of forest structure at different temporal and spatial scales as a consequence of hydrologic rehabilitation offer a unique opportunity for understanding and evaluating the mechanisms of forest structure recovery following perturbations. Freshwater rediversions represent changes in the forcing functions of mangrove wetlands (Fig. 3). According to the ecogeomorphology of mangroves, the geophysical processes such as river flow interact with other regional and local scale factors that result in specific patterns in soil conditions (Twilley, 1997). Regional scale hydrologic manipulations test the sensitivity of how the structure and function of coastal wetlands are linked to these geophysical processes. Model simulations are estimates of our quantitative relation of these complex geophysical and ecological interactions at all scales. The response of mangrove wetlands to freshwater diversion and consequent changes in soil salinity must include the complex behaviour of ecosystems to several other non-linear processes. Thus simple correlations and statistical models are not sufficient, but require mechanistic models. Simulations of mangrove wetlands at CGSM during the rehabilitation process will test our knowledge of mangrove development.

The hydrological restoration in CGSM offers a set of conditions at the landscape scale to test hypotheses regarding the mechanisms of mangrove restoration using modelling techniques. To demonstrate the utility of the FORMAN model in forecasting trajectories of mangrove development in areas subjected to human disturbances at a large spatial scale, we performed several preliminary simulations to construct response curves of mangrove structural changes for the CGSM estuary. These curves represent hypotheses about the interactive role of ecological processes (e.g., salinity stress, light and nutrient availability) on forest development at different initial conditions of forest structure.

Response curves of mangrove growth (based on 35 yr simulations of basal area) from ecological simulations provide insights to potential forest recovery under different site conditions (Fig. 6). Site conditions are restricted to soil salinity and nutrient fertility and are the two factors in Eq. (1) that are adjusted in each simulation. We use the 'relative nutrient availability' (RNA) index that describes the amount of nutrient present relative to that required for maximum mangrove growth. The response of tree species to nutrient availability is commonly classified into different types according to forest gap models (Weinstein *et al.*, 1982; Aber and Melillo, 1982; Pastor and Post, 1986) with functions such as the following to constrain growth of plants in response to nutrient availability (Weinstein *et al.*, 1982):

$$N(\mathrm{NUT}) = c_1 + c_2\mathrm{RNA} + c_3\mathrm{RNA}^2, \qquad (2)$$

where $N(\mathrm{NUT})$ is a growth modification factor; c_1, c_2 and c_3 are coefficients; and RNA is relative nutrient availability with a value from 0 to 1.0. Total P (per unit area soil) was used in FORMAN to calculate RNA, because this nutrient explains most of the changes in basal of mangrove forests across a variety of non-hypersaline environments (Chen, 1996; Chen and Twilley, 1998). Basal area of mangrove forests was used as an estimate of production and applied to a Monod model (Bridgham *et al.*, 1995) with total soil P as an index of nutrient availability. Based on values from 10 different mangrove forests in the Caribbean region a half-saturation constant of 29.3 gP/m^2 to a depth of 40 cm (Chen, 1996) was used as an index of the relative P availability (RNA).

Information from the monitoring program indicates that the appropriate axes of the response surfaces are high soil nutrient availability (0.6–0.8 RNA) with extremely high salinities that can reach 80 g/kg (Fig. 6). At such high soil salinities, even with very fertile soil, forest structure is < 5 m^2/ha of basal area. The most significant change in total basal area occurs between salinity of 60 and 70 g/kg at nutrient concentrations (RNA) > 0.5.

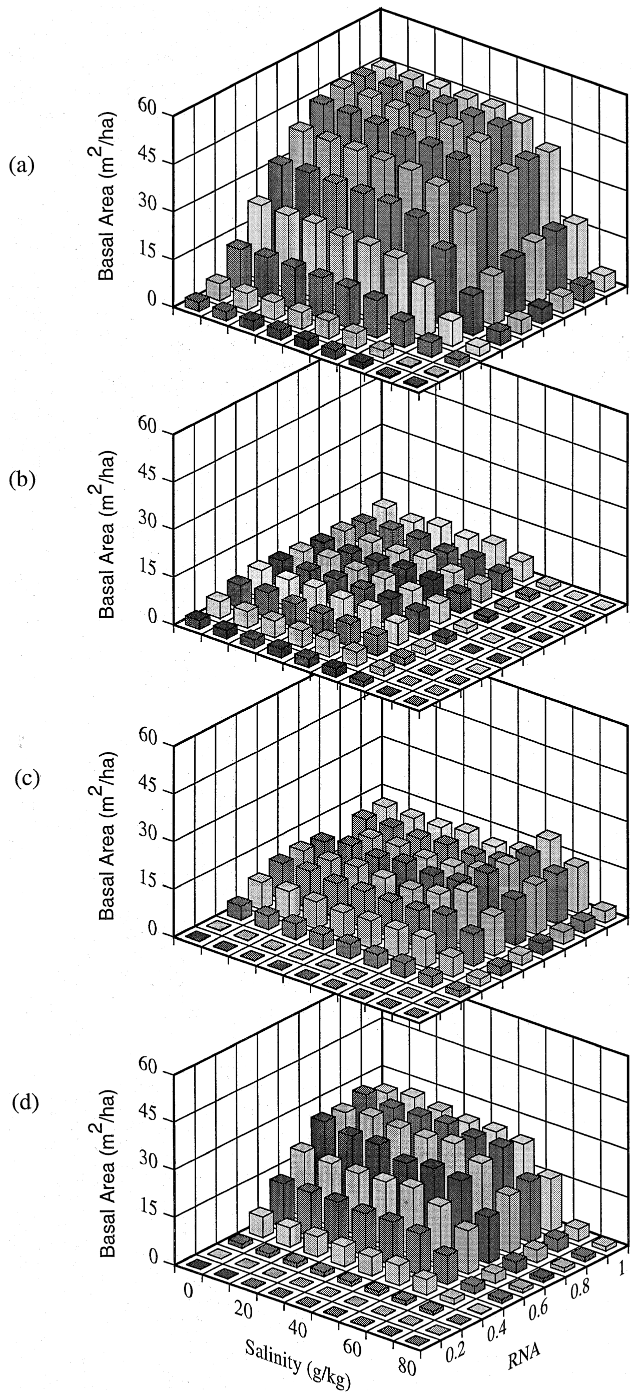


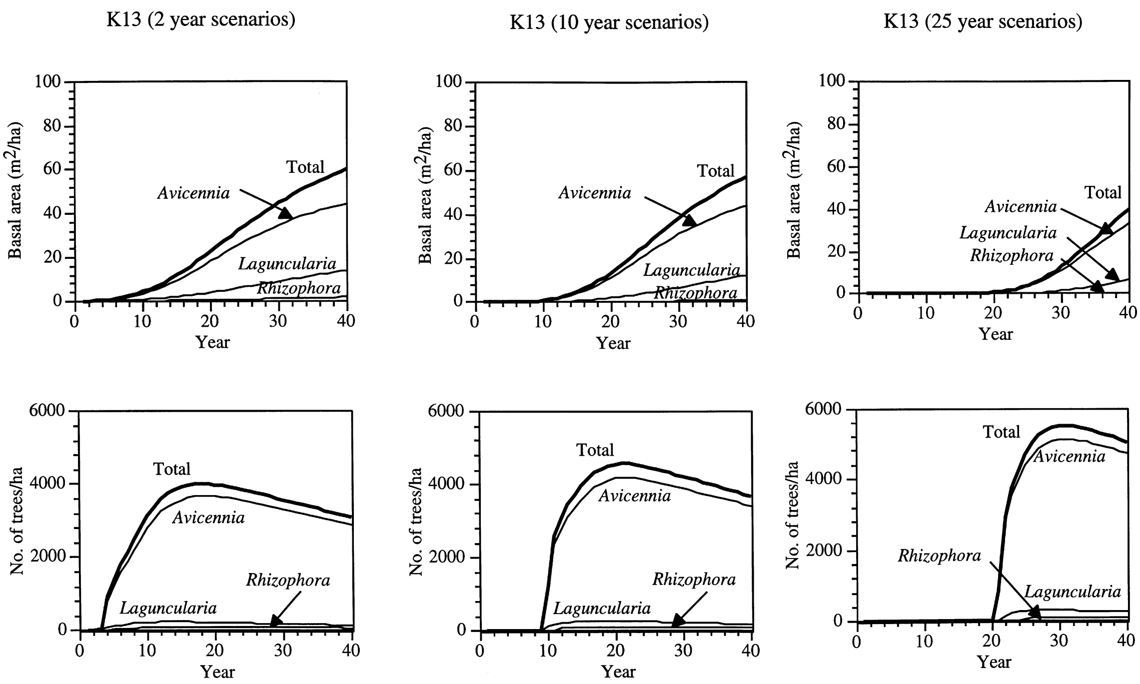
Fig. 6 Response curves of forest basal area (based on 35 yr simulations) by varying the amount of salinity and relative nutrient availability (RNA) in the soil. (A) Total, (B) *Rhizophora mangle*, (C) *Avicennia germinans*, (D) *Laguncularia racemosa*.

Under these site conditions, forests are dominated by *Avicennia* and *Rhizophora* (Fig. 6). When soil salinity is reduced, *Laguncularia* has a high growth potential under fertile soil conditions.

The rate of rehabilitation in CGSM mangroves is considered a function of the decrease in soil water salinity to levels similar to the reference site (SAL) that ranges from 3 to 48 g/kg. Scenarios of wetland rehabilitation can be based on the number of years required to reach an annual soil salinity of 40 g/kg (Fig. 5B). In our preliminary modelling projections, we tested scenarios of 2, 10 and 25 yr estimates to reach this target soil salinity to cover a range of goals in this rehabilitation program. Given the spatial heterogeneity of the sites, these scenarios include gradients in wetland rehabilitation; these time spans capture the degrees of perturbation and expectations of mangrove rehabilitation. Simulations of forest structure were run for 40 yr, which is considered by Brown and Lugo (1994) to be an appropriate time frame to evaluate the success of restoration projects. However, success can be defined at any point along the time scale of the simulations.

Simulations of FORMAN model to project patterns of forest rehabilitation are based on site K13 (Figs. 3 and 4). This site was originally completely degraded, with some initial evidence of rehabilitation. Values of soil fertility and salinity, along with information on forest structure and seedling density from this site, were used for initial conditions in the simulations (Giraldo, 1995; Cardona and Botero, 1998). The simulations assume an RNA of 0.75, and a species-specific recruitment rate of 0.093, 0.008 and 0.004 saplings m^{-2} yr^{-1} for *Avicennia*, *Laguncularia* and *Rhizophora*, respectively. Simulations were run given a linear decrease in salinity from present average of 104 g/kg to 40 g/kg in three different rehabilitation time scenarios (either 2, 10 or 25 yr).

Ecosystem response can be analysed based on total and species-specific basal area, as well as tree density (Fig. 7). Along with estimates of biomass based on the forest structure, the simulation output can be used for both demographic and functional characteristics of the mangrove wetland. Simulations of forest recovery following reductions in soil salinity to 40 g/kg within 2 and 10 yr time frames are similarly based on both basal area and tree density at K13 (Fig. 7). Basal area in both time scenarios is about 60 m^2/ha compared to 80 m^2/ha that occurs in the reference mangrove site at SAL (Figs. 4 and 7). These simulations of forest recovery suggest that both rehabilitation goals (2 and 10 yr time frames to reduce soil salinity to 40 g/kg) would reach about 75% of the density and dominance of reference mangroves in 40 yr. Both forests are $>80\%$ dominated by *Avicennia*, and *Laguncularia* is more prevalent than *Rhizophora* in the remaining structure. Simulations of forest recovery with a 25 yr target for salinity reduction show that basal area recovers to only about 40 m^2/ha after 40 yr, which is only 50% of that of the reference site (Fig. 7). These projections of mangrove recovery suggest that the marginal costs of reducing salinity to target values within 2 yr compared to 10 yr following freshwater diversion may not be effective given the slight increase in forest structure at 40 yr. However, the success of the rehabilitation project has a very different perspective based on the recovery of forest structure compared to the reference site when the salinity reduction target is 10 yr compared to a target time of 25 yr.


K13 (2 year scenarios)

K13 (10 year scenarios)

K13 (25 year scenarios)

Fig. 7 FORMAN model output for development of mangrove vegetation at site K13 with three different scenarios for amount of time to reach a soil salinity of 40 g/kg assuming differential recruitment of saplings for species as follows: *Avicennia* > *Laguncularia* > *Rhizophora*.

The success of this rehabilitation project, by comparing restoration sites to the reference site (SAL), obviously depends on the definition of a recovery period. With a much shorter recovery period used to evaluate the project, say 10 or 20 yr, then differences in the degree of success between 2 and 10 yr target salinities become more apparent (Fig. 7). Simulations of the FORMAN model allow projections of realistic project goals both in perspective to absolute recovery (compared to reference sites) and time scales for that recovery. These goals can then be adjusted given different operational scenarios as a sensitivity analysis of the rehabilitation project.

Operational decisions also include the importance of a mangrove planting program to accompany the freshwater diversion targets in the rehabilitation project. The present simulations use estimated rates of species-specific recruitment based on preliminary information from field studies (Giraldo, 1995). We tested the sensitivity of mangrove forest recovery by increasing the rates of recruitment to 0.093 saplings/m^2 each year for each species, and by planting an additional propagule of *Avicennia* per m^2 after salinity is reduced to < 50 g/kg. After 40 yr of recovery, both the 2 and 10 yr salinity targets produce higher basal area (Fig. 8) under enhanced recruitment than observed under more natural recruitment (Fig. 7). Both scenarios nearly approach the forest structure of the reference site, which is about 80 m^2/ha basal area. One of the key differences between the simulations comparing the effect of recruitment on forest regeneration is the species composition of the forest. Given the fertile soil conditions and available light, when salinity is reduced and propagule availability increases, *Laguncularia* becomes the dominant species in the forest communities within the recovery period simulated (Fig. 8). This is associated with the relative utilization of resources and sensitivity to salinity among the three species programmed in FORMAN (Fig. 3, Chen and Twilley, 1998).

These simulations show how sensitive the success of the CGSM rehabilitation project is to the design and implementation of adequate site criteria and the selection of an appropriate recovery period. The recovery period must be linked to the growth potential of the plant community that is being restored. We have shown that the potential response of mangrove growth to soil salinity and nutrient resources (Fig. 7) provides an idea of the constraints on a proper recovery period to evaluate the CGSM rehabilitation project. By simulating various target salinities, we have estimated different levels of success in mangrove regeneration within the defined recovery period. Also, recovery rates are sensitive to the recruitment of propagules to the mangrove site. Thus the success of this rehabilitation project will depend on the implementation of both the modification in soil salinity linked to the mangrove planting program. There have been projections of salinity reductions in lagoon waters based on engineering designs of canal construction; yet these have not been translated into reductions in soil salinity within mangrove sites. Thus a possible limitation exists in the poor link between simulation results of civil engineers compared to simulations of this ecological model. Coupling these two types

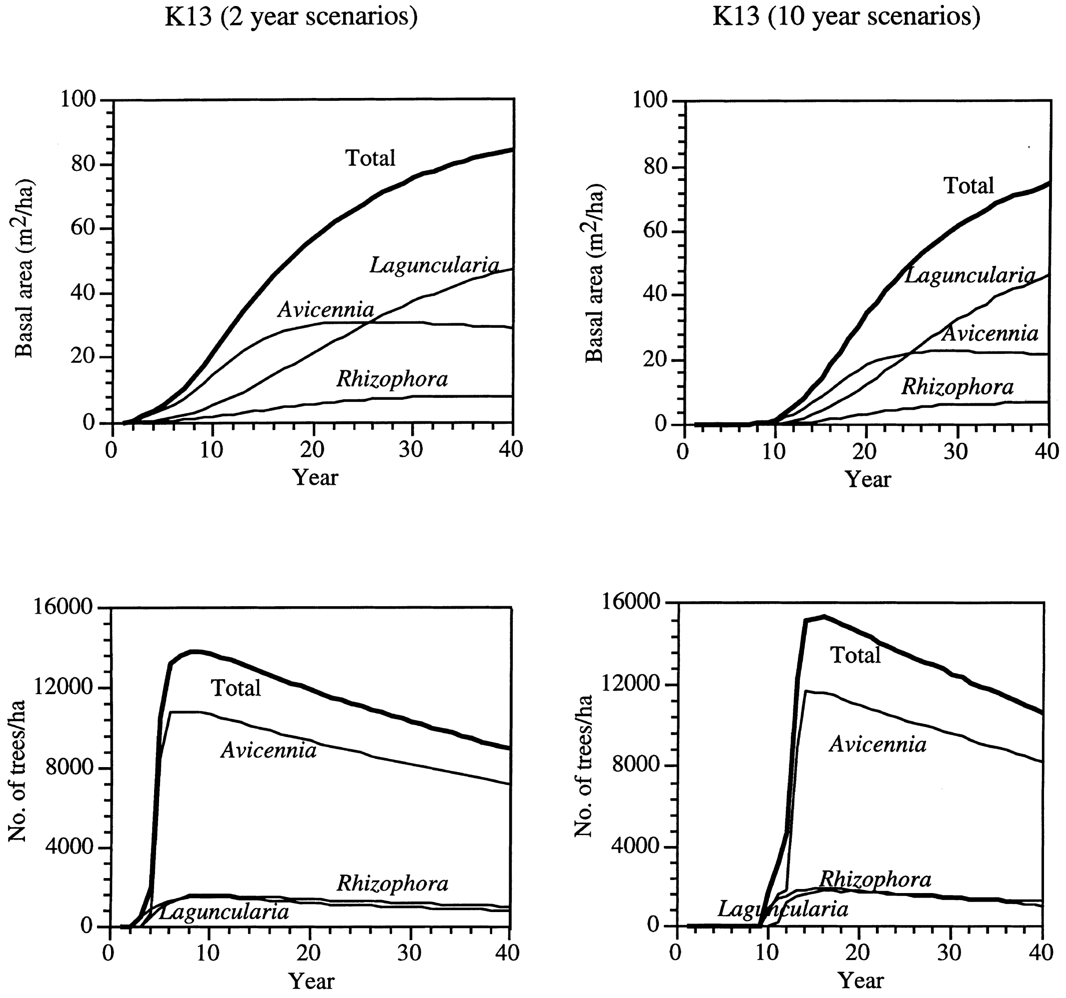


Fig. 8 FORMAN model output for development of mangrove structure at site K13 with a two year scenario for decrease in soil salinity to 40 g/kg. Assuming equal recruitment per species and planting one sapling/m^2 of *Avicennia* once salinity drops to 50 g/kg.

of modelling efforts would promote the design of canals that can more effectively reach target salinities for this rehabilitation project. In addition, maintenance of these canals by dredging will have to be sustained to reach target salinities; and this part of the project will have to be coordinated with mangrove transplanting as changes occur in site conditions. Project implementation, including maintenance of canal operations, monitoring of site conditions and transplanting mangrove propagules, will determine if the mangrove regeneration potentials projected in our simulations will actually be realized. This will require a monitoring program that is coupled to operational phases of the project to assure that the project will be sufficient to remediate the damaged mangrove forests.

Conclusions

Mangrove restoration projects offer unique opportunities to test ecological theories about the response of mangrove trajectories to regional and local scale manipulations relative to scales of disturbance using ecosystem models. The introduction of a modelling component to a restoration program can help forecast the trajectories of success criteria in terms of structure and productivity, hydrology, recruitment, nutrient dynamics and sustainability within a particular domain (e.g., ecophysiology, ecosystem energetics, community organization, landscape patterns). Modelling also can be used in adaptive management to modify or adjust restoration programs or actions, and to provide analysis and guidelines as to the efficiency of different rehabilitation strategies. The identification of important research topics and monitoring criteria to improve the understanding of key ecological processes are also potential products of ecological modelling efforts when linked to restoration projects.

We have demonstrated how a simulation model can be used to project the trajectories of ecosystem attributes during recovery, and therefore contribute to the design and implementation of restoration projects. Ecosystem modelling of restoration projects can also be used to verify key mechanisms controlling ecosystem attributes and provide a synthesis of ecosystem dynamics during the recovery period. However, despite the analytical capabilities of simulation models, it is important to stress that ecological models should be considered as a complement, and not a replacement, of sound experimental and field studies. Only through the design and implementation of field experiments (both 'observational' and manipulative) will we be able to calibrate and verify models to increase their articulation, accuracy and effectiveness as a tool in ecological restoration.

Our modelling strategy highlights the need for interdisciplinary and multidisciplinary approaches in restoration projects to obtain meaningful information for the development of management plans. Ecological questions in mangrove ecosystems are directed at an array of processes occurring at different temporal and spatial scales. This means that several subdisciplines in ecology (e.g., biogeochemistry, landscape ecology, chemical ecology, community ecology, ecophysiology, population and evolutionary ecology) have to be integrated within a conceptual framework to solve problems related to restoration goals. This is not an easy task. Integration of multiple disciplines for the solution of environmental problems at regional scales is a major issue not only in restoration ecology (Allen *et al.*, 1997; Palmer *et al.*, 1997) but in ecology overall (Peters, 1991; Pickett, 1994). Pickett (1994) suggested that integration can be achieved through the identification of particular problems 'at the boundaries between existing specialties'. We believe that these boundaries could be clearly delimited in restoration projects through the use of a modelling approach, which could facilitate the development of a theoretical framework for restoration ecology. Thus, modelling techniques can be used to identify the appropriate spatial and temporal scales of problems associated with mangrove restoration projects that could improve our ability to conserve and manage one of the most valuable forested wetlands in the tropical coastal zone.

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