

Review

Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review

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Abstract

Mangrove ecosystems are considered vulnerable to climate change as coastal development limits the ecosystem services and adaptations important to their survival. Although they appear rather simple in terms of species diversity, their ecology is complex due to interacting geophysical forces of tides, surface runoff, river and groundwater discharge, waves, and constituents of sediment, nutrients and saltwater. These interactions limit developing a comprehensive framework for science-based sustainable management practices. A suite of models have been developed independently by various academic and government institutions worldwide to understand the dynamics of mangrove ecosystems and to provide ecological forecasting capabilities under different management scenarios and natural disturbance regimes. The models have progressed from statistical tables representing growth and yield to more sophisticated models describing various system components and processes. Among these models are three individual-based models (IBMs) (FORMAN, KIWI, and MANGRO). A comparison of models' designs reveal differences in the details of process description, particularly, regarding neighbor competition among trees. Each model has thus its specific range of applications. Whereas FORMAN and KIWI are most suitable to address mangrove forest dynamics of stands, MANGRO focuses on landscape dynamics on larger spatial scale. A comparison of the models and a comparison of the models with empirical knowledge further reveal the general needs for further field and validation studies to advance our ecological understanding and management of mangrove wetlands.

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1. Introduction

Mangrove forests grow in coastal settings of (sub)tropical climates characterized by freshwater runoff, multiple substrate conditions, prolonged hydroperiod, salinity, anoxic conditions, and accumulation of toxic substances (Lugo, 1980; Ball, 1996). Species composition is strongly influenced by these coastal settings because they are linked to differences in mangrove tree species' capability to become established and grow. According to Thom (1967), mangroves should be viewed as woody vegetation in the intertidal zone that migrates up and down slope from the sea in relation to eustatic natural and human-induced changes in sea level. In their final remarks, Lugo and Snedaker (1974) conclude that "mangrove ecosystems are self-maintaining coastal landscape units that are responsive to long-term geomorphological processes and to continuous interactions with contiguous ecosystems in the regional mosaic". However, when coastal landscapes become fragmented by human transformations of regional and coastal settings, mangroves are less self-maintaining as coastal processes are modified.

Along with coastal processes of geomorphological settings, natural disturbances (e.g., hurricanes) shape the structural complexity of mangrove forests including maximum stand height and tree morphology (Lugo, 1980, 2000; Doyle et al., 1995; Doyle and Girod, 1997; Duke, 2001). The impact of such events may be responsible for multiple equilibrium states that are observed more often than single equilibrium states in mature stands (Lugo, 1997; Duke, 2001). This might be one reason why succession and species composition along hydroperiod and regulator gradients continue to be two of the major research priorities in mangroves (e.g., Lugo and Snedaker, 1974; Ellison et al., 2000; Sherman et al., 2000; Dahdouh-Guebas and Koedam, 2002; Ellison, 2002; Rivera-Monroy et al., 2004; Berger et al., 2006; Castaneda-Moya et al., 2006; Piou et al., in press).

One approach to document forest dynamics employs remote sensing imagery. There are numerous studies that describe temporal changes in spatial extension of mangrove ecosystems (Calzadilla Pérez et al., 2002; Lucas et al., 2002; Cohen and Lara, 2003; Fromard et al., 2004; Hernández-Cornejo et al., 2005; Dahdouh-Guebas and Koedam, 2008) such as shifts in species composition (Dahdouh-Guebas et al., 2000b, 2004, 2005a,b; Kovacs et al., 2001; Wang et al., 2004), changes in mangrove cover before and after natural hazards (Smith et al., 1994; Krauss et al., 2005; Ramachandran et al., 2005), and dynamics of mangrove forest types (Dahdouh-Guebas and Koedam, 2002; Krauss et al., 2005; Simard et al., 2006). Remote sensing approaches document changes in vegetation cover, however they are limited in providing descriptions of ecological processes causing these changes.

Model simulations have been useful in synthesizing current knowledge about mangrove forest dynamics (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000). The modeling approach is suitable for simultaneously evaluating the effects of environmental changes and disturbances on ecological processes such as tree recruitment, establishment, growth, productivity, and mortality. Such estimates on the sustainability of mangrove resources may contribute to evaluating impacts of mangrove degradation to socio-economic systems (Alongi, 2002; Balmford et al., 2002; Macintosh et al., 2002; Rivera-Monroy et al., 2004; Davis et al., 2005). Consequently, simulation models have been proposed as tools for developing management plans for mangrove protection, rehabilitation and restoration (Twilley, 1997; Doyle et al., 2003; Field, 1998, 1999; Duke et al., 2005; Twilley and Rivera-Monroy, 2005). Such utility in resource management requires that model structure captures the mechanisms that explain forest dynamics, such as (a) controlling role of stressors, (b) plant–plant and plant–soil interactions, as well as (c) impacts of

natural and anthropogenic disturbances at different temporal and spatial scales (Ellison, 2002; Clarke, 2004).

The first pioneers in mangrove simulation models were Lugo et al. (1976) who used a process-based model to simulate the effects of upland run-off and tidal flushing on the biomass production of an over-washed mangrove wetland. Burns and Ogden (1985) used a Leslie-Matrix model to predict the development of an *Avicennia marina* monoculture assuming an exponential population growth. Clarke (1995) used a Lefkovich matrix for predicting the recovery of an *Avicennia germinans* population following disturbances differing in strength. There are also a few static trophic models estimating matter and energy flow in mangrove ecosystems (e.g. Ray et al., 2000; Vega-Cendejas and Arreguin-Sanchez, 2001; Wolff, 2006). Currently there are only three spatially explicit individual-based simulation models (IBMs) describing Neotropical mangrove forests: FORMAN, KIWI, and MANGRO (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000).

In this paper, we describe these IBMs and discuss their design and specific features. We first explain the essential processes that are assumed to control and regulate mangrove forest dynamics. Based on this assessment, we then compile a list of eight key functional relationships necessary for understanding mangrove forest dynamics. This list will serve as an overview to compare and contrast the purposes and applications of each particular model. Finally, we discuss the application perspectives of IBMs within the field of mangrove ecology, and propose future research directions to continue developing models as research and management tools. The models reviewed focus primarily on the Neotropics, restricting discussion of mangrove forest dynamics to that region.

2. Driving forces of mangrove structure and dynamics

2.1. Linkages between environmental conditions and species performance

According to hierarchy theory (Hölker and Breckling, 2002), processes at a particular organization level can be explained by constraints at higher levels along with mechanisms at lower levels of organization (Pickett et al., 1989). Thus, it is essential to evaluate the climatic and landform characteristics of coastal regions which result in local and often gradual environmental gradients, that represent top-down constraints of mangrove forest development (Fig. 1, Thom, 1984; Woodroffe, 1992; Twilley, 1995; Duke et al., 1998; Twilley et al., 1999b). At the same time, tree performance, growth response, and interactions among trees affect bottom-up patterns of forest development (Smith, 1992).

A conceptual model has been developed that integrates both of these levels of regional environmental constraints and local biotic interactions on the structure and function of mangrove forests (Twilley and Rivera-Monroy, 2005; Fig. 2). According to this model, three types of factors – regulators, resources, and hydroperiod – control mangrove structure and function (Huston, 1994). ‘Regulators’ are defined as non-resource variables including salinity, sulfide, pH, and redox potential. Resource variables, on the other hand, include nutrients, light or space that are consumed by trees for growth (and thus determine levels of competition). Hydroperiod, the duration, frequency and depth of inundation, is another critical factor controlling mangrove productivity (Wolanski, 1992). According to this model, the interactions among the three factors form a “constraint envelope” which defines the primary productivity of the system. This model links the top-down regional drivers

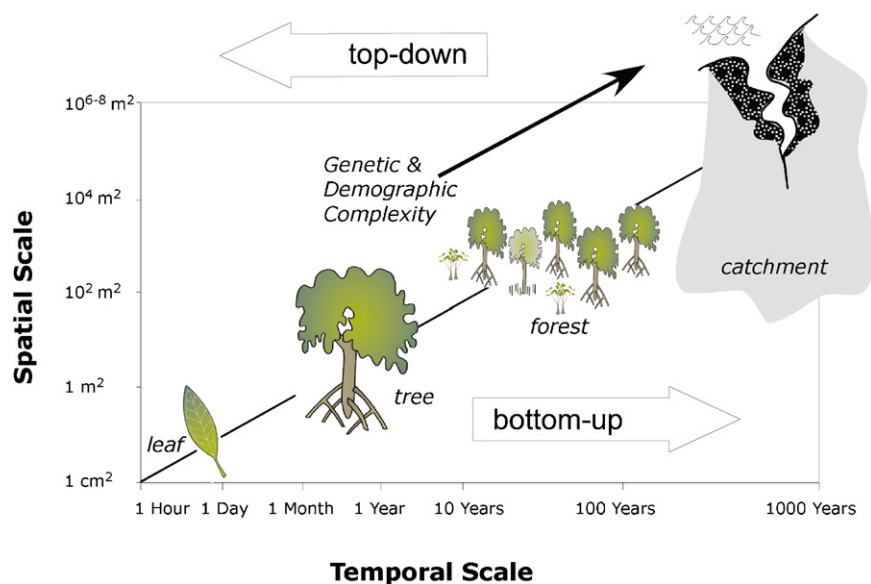


Fig. 1. Temporal and spatial hierarchical organization of key ecosystem components in mangrove forests including leaves, trees, forests and watershed regions. Processes at higher scales include combinations of different species and age classes, with differences in physiology and growth of leaves and trees. These processes affect forest turnover and replacement, depending on landscape scale influences of salinity, elevation, tidal inundation, climate, and geomorphic setting.

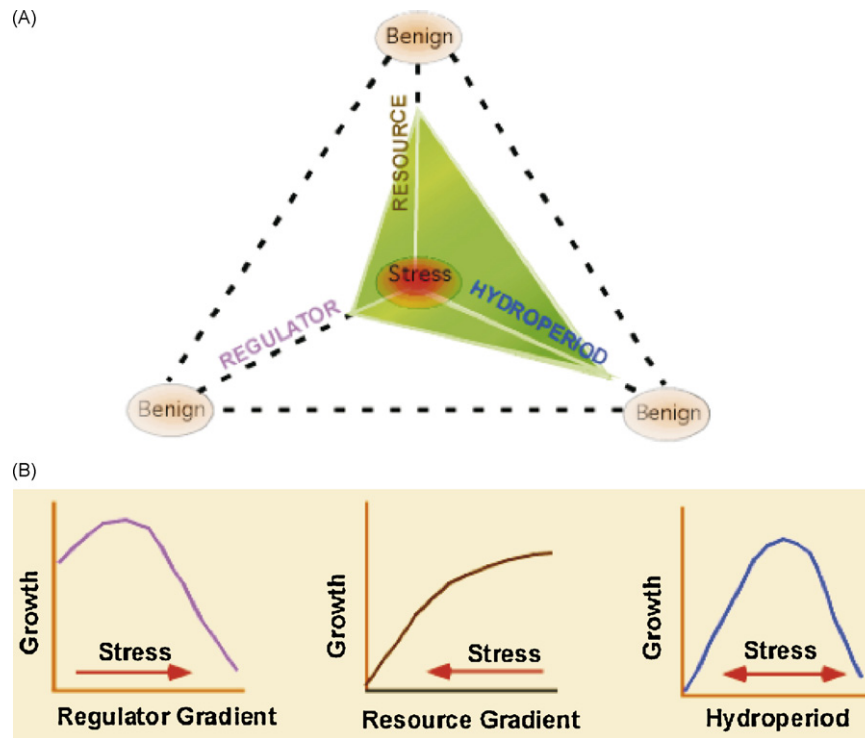


Fig. 2. Factorial interaction of three factors controlling productivity of mangrove forests including regulators, resources, and hydroperiod. (A) Production envelope associated with levels of each factor interaction to demonstrate responding levels of net primary productivity. (B) Definition of stress associated with how gradients in each factor control growth of wetland vegetation (from Twilley and Rivera-Monroy, 2005).

with the bottom-up processes through the responses of individual trees to environmental settings.

In order to analyze a particular forest succession trajectory, it is critical to evaluate ecological processes in more detail. For example, mangrove species adapted to capture photosynthetically active radiation more effectively will have a competitive advantage to colonize available, but shaded, space. In Neotropical mangrove tree species, shade tolerance during seedling and sapling stage decreases from *Rhizophora mangle* and *A. germinans* to *Laguncularia racemosa* (Ball, 1980; Roth, 1992). Yet species-specific irradiance-related tolerances currently have not been evaluated in the field neither in gaps nor under closed canopy.

Nutrients are another key resource that can define growth and spatial distribution patterns in mangrove forests (Kristensen et al., 2008). Neotropical mangrove forests can immobilize nitrogen (N) as a result of high N demand by bacteria decomposing leaf litter (Rivera-Monroy et al., 1995; Rivera-Monroy and Twilley, 1996). This suggests that plant growth might be critically N-limited, depending on the magnitudes of N fixation rates. However, essential nutrients are not necessarily uniformly distributed, and soil fertility can switch from conditions of N- to P-limitation across narrow topographic gradients (Feller and McKee, 1999; Feller et al., 2003a,b). In situ fertilization experiments have shown that nutrient enrichment reduces the efficiency of within-stand and within-tree nutrient conservation mechanisms, which influences species-specific growth rate ratios and, therefore, competition among trees (Lovelock and Feller, 2003).

Salt-tolerance varies among mangrove species (Scholander et al., 1962; Ball, 1998, 2002; Krauss et al., 2008) establishing soil pore water salinity as one of the most critical regulators influencing the structure of mangrove forests (Cintrón et al., 1978; Ball, 1980, 2002; Castaneda-Moya et al., 2006). Studies show that neotropical *R. mangle* and *L. racemosa* have narrower salt-tolerances than *A. germinans* because of their limited ability to balance water and salt uptake. This might be a reason why, *A. germinans* is generally dominant in areas where evaporation exceeds precipitation and soil salinities are $>120 \text{ g kg}^{-1}$ (e.g., Cintrón et al., 1978; Castaneda-Moya et al., 2006). Despite numerous reports on species-specific response of propagules to salinity (see e.g., McKee, 1993; Lopez-Hoffman et al., 2007) there is still insufficient knowledge supporting a general mathematical description of this mechanism for propagule establishment up to mature trees along salinity gradients.

Flooded mangrove soils have reducing conditions depending on frequency and duration of standing water and the presence of sulfide. Greenhouse experiments have shown differential tolerance of mangrove seedlings to flooding demonstrating that the interaction between salinity and hydroperiod controls seedling establishment and growth (e.g., Cardona-Olarte et al., 2006). Elevations in mangroves respond to hydroperiod and sediment input, along with feedback effects of mangrove trees that effectively raise the rhizosphere to depths with greater oxygen content. Also, adult trees of *A. germinans* and *R. mangle* are both capable of oxidizing sulfide around the rhizosphere by transporting oxygen through roots (McKee et al., 1988). These

mechanisms might explain why adult mangrove plants can grow in soils with high concentrations of sulfide (Matthijs et al., 1999), indicating the large spatial variability of this stressor among and within sites (Rivera-Monroy et al., 2004). Yet, mathematical formulations of how mangroves respond to hydroperiod, particularly mixed with other soil conditions, are poorly understood in mangrove ecology.

Although there are some uncertainties about specific mechanisms linking light, nutrients, salinity, and flooding with tree performance, it is widely recognized that these are essential factors driving mangrove forest dynamics. Thus, simulation models should describe the essential life processes of trees linked to resource, regulator and hydroperiod gradients, and test their relative importance in controlling mangrove forest dynamics (task 1).

2.2. The role of canopy disturbances and gap size on mangrove dynamics

Canopy disturbances at different spatial scales have a strong influence on mangrove forest structure and function, including tree fall, lightning, frost or excessive drought (Lugo, 1980, 2000; Tilman, 1988; Smith, 1992; Smith et al., 1994; Doyle et al., 1995; Fromard et al., 1998; Twilley et al., 1999b; Baldwin et al., 2001; Duke, 2001; Kairo et al., 2002). Specific effects of disturbances depend on their frequency and intensity along resource gradients and hierarchical levels (e.g., hurricanes, deforestation, selective wood cutting) (Gosz, 1992; Roth, 1992; Davis et al., 2005; Ward et al., 2006; Piou et al., 2006; Dahdouh-Guebas et al., 2000a; Glaser, 2003; Walters, 2005; Walters et al., 2008). Although it is desirable to empirically test hypotheses on disturbance regimes, large-scale (>1 km²) field experiments are often impracticable due to ethical, temporal or spatial constraints. Based on these limitations, there are two further tasks that mangrove models should perform: *test the impact of changes in disturbance regimes on mangrove forest dynamics (task 2)*, and *compile so-called “traffic light lists” which evaluate different management scenarios according to their potential ecological, economic, or social outcome of mangrove sustainability (task 3)*.

Disturbances result in resource heterogeneity within a gap, and can be seen as “moving windows of opportunity” for seedling establishment. Several studies document gradients of irradiance and light fleck frequency through gaps; mangrove tree establishment corresponds to these gradients and thus indicates the importance of gaps for forest regeneration (Whelan, 2005; Ward et al., 2006). In contrast, there is little information on changes in nutrient availability or sulfide concentration in such gaps, which possibly could affect recolonization. Therefore, comparative field studies addressing this topic are needed in addition to simulation experiments *comparing empirical against simulated recovery patterns to test the plausibility of different hypotheses explaining the role of resource gradients in mangrove gaps (task 4)*.

The seasonal input of propagules is significant to the recovery rate of a forest from a disturbance, and this recruitment depends on (a) the reproductive phenology of

the mature trees, along with the local hydrology (Sherman and Fahey, 2001), and (b) the selective mortality of propagules and seedlings (Lewis, 1982; Cintrón, 1990). Forest recovery also depends on age and size of the individuals that survive disturbances (Shugart, 1984; Botkin, 1993a) such as tree species with re-sprouting capabilities (e.g., *A. germinans* or *L. racemosa*, Baldwin et al., 2001). Survivors will influence light regime, microclimate and soil chemistry and may release propagules immediately within the disturbed area. Therefore, pre-disturbance conditions of previous forest structure and recruitment rates are determinants of mangrove development following a disturbance (Doyle and Girod, 1997; Chen and Twilley, 1998; Berger et al., 2006; Ross et al., 2006; Ward et al., 2006; Piou et al., 2006; Bosire et al., 2008). Thus, mangrove simulation models should: *synthesize the species-specific and age-specific regeneration potential of individual trees after disturbances and their importance for forest recovery (task 5)*.

One of the current debates in forest and community ecology is the role of gaps in explaining tree diversity and secondary succession trajectories in temporal, tropical and subtropical forests (Doyle, 1981; Pacala et al., 1993; Denslow et al., 1998; Moorcroft et al., 2001; Felton et al., 2006; Khurana and Singh, 2006; Perry and Enright, 2006). Niche partitioning assumes that competition among individuals for resources determines the diversity of trees regenerating in gaps (Brokaw and Busing, 2000). An opposing view assumes that species composition lacks any specific pattern and is unpredictable, suggesting that no specific successional sequence occurs within gaps following disturbances. Currently, there is not enough information to determine whether niche partitioning or the size of the species pool is more important for the regeneration of canopy gaps in mangrove habitats. Although gap dynamics is recognized as one of the most critical processes regulating mangrove forest structure and productivity, there are only few empirical studies evaluating their impact at different temporal and spatial scales (Sherman et al., 2000; Duke, 2001; Whelan, 2005; Ward et al., 2006). Simulation experiments can focus on dispersal effects and establishment of mangrove trees, and thus contribute *to understanding the roles and relative contribution of inter-specific competition and “chance” in structuring mangrove forests following gap formation (task 6)*.

Numerous studies in terrestrial forests have shown that the interplay of gap locations, gap frequency, and the successional stage of forest patches at time of gap creation frequently result in a de-synchronization of the successional states of neighboring forest patches and lead to spatial–temporal mosaics of vegetation structure (i.e., the mosaic cycle theory Mueller-Dombois, 1991; Remmert, 1991). Although spatial patterns in mangrove forests have long been recognized, specific gap dynamic studies are lacking in mangrove ecology (but see Dahdouh-Guebas et al., 2000b). One possible explanation is that physical factors like salinity and nutrient cycling have traditionally been considered as sufficiently effective to account for all of the observed structural patterns. To capture the processes associated with gap dynamics, we propose that models should *test the synchronization and de-synchronization effect of canopy disturbances on mosaic cycles of successional*

forest stages on a landscape level to develop a general understanding of mangrove forest dynamics (task 7).

Now that we have derived these seven key tasks for modeling mangrove, we use these tasks to summarize the specific structure and objectives of published mangrove forest model simulations, as well as their utility in ecological forecasting and natural resources management.

3. From specific data to abstractions: modeling approaches for describing mangrove forest dynamics at different spatial scales

Individual-based models became widely accepted in ecology during the 1990s and are recognized as suitable tools for simulating the variability of individual plants or animals and its influence on complex life systems (DeAngelis and Gross, 1992; Grimm, 1999; DeAngelis and Mooij, 2005). These models integrate different hierarchical levels of ecological processes, and they can be directly and relatively simply parameterized. They have an intrinsic ability to include both temporal and spatial scales. All these features make them powerful “virtual laboratories”, which help testing hypotheses about specific behaviors and traits of individuals, 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; Liu and Ashton, 1995; Twilley et al., 1999b). In this section, we describe the three available IBMs focusing on mangrove forest dynamics following the ODD protocol developed to facilitate the comparison and understand model structure and output (ODD = Overview, Design concepts, Detail as described in Grimm et al., 2005, 2006; Grimm and Railsback, 2005).

3.1. Purposes of the models

All three models, FORMAN, KIWI, and MANGRO were developed to understand long-term dynamics of mangrove forests under different environmental and management settings. They are parameterized for the neotropical mangrove species, *R. mangle*, *A. germinans*, and *L. racemosa* (Doyle and Girod, 1997; Chen and Twilley, 1998; Doyle, 1998; Doyle et al., 2003; Berger and Hildenbrandt, 2000), although model applications focus on different (sub)tropical regions. For example, FORMAN was applied to various forests in different coastal locations in Florida (Chen and Twilley, 1998) and Colombia (Twilley et al., 1999b). The KIWI model was applied to mangrove forests in North Brazil (e.g., Berger et al., 2006) and Belize (Piou et al., in press; Piou, 2007). Only recently, this model was parameterized for *Rhizophora apiculata*, a mangrove species occurring in the Indo-West-Pacific region (Fontalvo et al., in preparation). Embedded in the landscape scale vegetation model SELVA, the MANGRO model has the most specific regional focus: the Everglades in south Florida, USA. The specific purposes of each model application also differ ranging from the assessment of management scenarios, forecast of landscape development, and assessment of theoretical ecological issues (see Table 1).

3.2. State variables and spatial scales

All three models describe a tree by its species and stem diameter, which are used to derive other descriptors such as stem height and biomass. The models differ in the spatial description of the trees including stem position, leaf area, and crown dimension (see also Table 1). The FORMAN model is a

Table 1
Differences of the FORMAN, KIWI, and MANGRO models in structure and design

	FORMAN	KIWI	MANGRO
Differences in purpose(s)	Applied to particular sites in Florida, Louisiana, and Colombia	Applied to theoretical issues, and particular sites in Brazil and Belize	Applied to the Everglades (Florida, USA)
Differences in variables	No explicit stem position, leaf area	Stem position, size and shape of FON, no leaf area	Stem position, crown dimension, leaf area
Differences in spatial scales	Forest stand (matrix of gaps 500 m ² each)	Forest stand with variable extension and shape	Landscape as matrix of squared forest stands (default size 1 ha)
Differences in resource description	Nutrients/salinity homogeneous within a gap. Light availability per height class	Nutrients/salinity heterogeneous. Light availability implicitly	Salinity/soil quality homogeneous within stand. Light availability per tree
Differences in design concepts	<i>Interactions of trees</i> : light competition through sum of leaf areas per height class. <i>Sensing of trees</i> : nutrients/salinity within gap, neighbors via total leaf area above, number of degree days	<i>Interactions of trees</i> : competition for all spatial distributed resources phenol-menologically via FON. <i>Sensing of trees</i> : nutrient/salinity at stem position, neighbors in spatially explicit constellation, no temperature sensing	<i>Interactions of trees</i> : competition for growing space and light explicitly. <i>Sensing of trees</i> : flooding/salinity/stand quality at stand unit, neighbors via distance and azimuth
Differences in initialization	Saplings	Saplings	Seedlings
Differences in submodels	No explicit saplings dispersal. <i>Tree growth</i> affected by nutrients, light, and temperature defined growth period. <i>Tree mortality</i> due to age and growth suppression, gap creation by a reduction of total leaf area	Explicit saplings dispersal. <i>Tree growth</i> affected by nutrients, neighbor competition (FON overlap). <i>Tree mortality</i> due growth suppression, gap creation spatially explicit	No explicit seedlings dispersal. <i>Tree growth</i> affected by flooding, crown volume, light. <i>Tree mortality</i> : due to growth suppression, gap creation spatially explicit

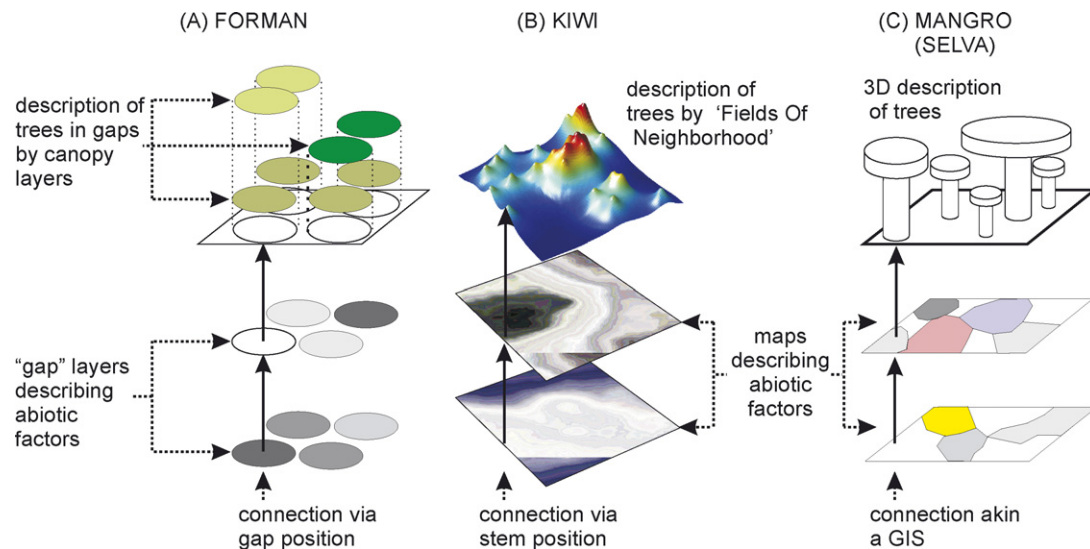


Fig. 3. Vertical and horizontal considerations of the mangrove models. Individual subfigures represent (A) the FORMAN model describing vertical competition for light in even sized gaps. Different layers describe abiotic factors like salinity or nutrient availability. They are connected by the gap position. The factors may vary among but not within the gaps. (B) The KIWI model represents individual trees by “fields-of-neighborhood” describing the intensity of competition exerted by the trees against their neighbors. Map layers representing abiotic factors are connected by the stem positions of the trees. (C) The MANGRO model represents each tree in its 3D architecture including spatial position, stem diameter, stem height, crown dimension, and leaf area. All data layers are connected akin to a Geographical Information System.

gap model with a code based on the JABOWA and FORET models (Botkin et al., 1972; Shugart, 1984, see also Fig. 3A). The forest stand is assumed as a composite of many gaps, which do not interact with each other. The gaps described in FORMAN are equal-sized (500 m^2) corresponding to the area covered by single large, dominant trees in natural forests. The specific location of a tree within a gap is not considered in FORMAN, and light competition is represented by stratified, averaged leaf layers. Also salinity and nutrient availability are assumed to be homogeneous within a gap. The authors generated other models to simulate these parameters (e.g. NUMAN and HYMAN models), yet those models are not directly linked with the simulation of the FORMAN model (Chen and Twilley, 1999; Twilley et al., 1999a).

The KIWI model characterizes each tree by its stem position within a Cartesian coordinate system. Tree competition is spatially explicit: each tree has a size-dependent circular zone around its stem. The overlap of these circular zones defines the competition among neighbor trees (Fig. 3B). In contrast to ‘zone-of-influence’ (ZOI) models, KIWI superimposes a scalar field on the ZOI. This field, or FON (‘field-of-neighborhood’), decreases from the stem to its boundary and represents declining competition strength with increasing distance from the stem. This approach thus links the ZOI approach with so-called Ecological Field (EF) theory (see Berger and Hildenbrandt, 2000; Berger et al., 2002 for further details). The extension and shape of the forest stand are chosen by the experimenter and may thus correspond directly to natural stand conditions. Typical experiments have used stand sizes from 100 to $10,000 \text{ m}^2$. The physical environment like topography, inundation height, inundation frequency, salinity and nutrient availability are mapped explicitly by user-supplied layers corresponding to the simulated stand coordinate system (Fig. 3B).

The MANGRO model represents trees in its three-dimensional architecture (Fig. 3C). Trees are simulated in square plots of side dimensions of no less than dominant tree height or larger. A stand is a composite of many plots; the default stand size is 1 ha. Each tree and stand is spatially defined by latitude and longitude. MANGRO has the flexibility to run as a stand-alone stand simulator like FORMAN and KIWI with user-specified inputs, or in a hierarchically linked mode with the SELVA model which manages landscape level forcing functions and site conditions, such as mean monthly sea level, soil elevation, daily river flow, hurricane recurrence, predicted wind speed and potential for lightning strike. SELVA can also provide disturbance probabilities from the larger landscape unit, which may be user-specified at the regional, continental, or global scale.

3.3. Processes overview and scheduling

All three models use discrete time steps of one simulation year. Within each year the following processes occur: establishment of seedlings/saplings, growth of existing trees, and tree mortality. The stem diameter of all trees is updated synchronously. From this update, the specific derived parameters such as tree height are also re-calculated.

3.4. Design concepts

3.4.1. Emergence

In all three models, population dynamics (e.g., the temporal variation of basal area, a specific vertical height structure, or species dominance) emerges from the life processes (establishment, growth and mortality) of trees modified by competition and abiotic conditions. Due to the explicit description of trees

local constellations, the following characteristic patterns emerge in forests simulated by the KIWI model: clumped to regular spatial distribution of trees, spatial grouping of species, size-class- or fitness-dependent frequency distributions of trees. During MANGRO simulations within the frame of the SELVA-model, landscape change emerges as a process of collective stand responses and habitat redistribution by migration or retreat.

3.4.2. Interaction

In FORMAN, trees interact through vertical competition for light described by the sums of leaf areas as proxies for the transparencies of height classes. This competition for light is dependent on growth potential of each species to nutrient and salinity conditions explicitly described for the plot. In KIWI, trees compete via their field-of-neighborhood for all spatially distributed resources, which are not specified explicitly. In MANGRO, trees compete for growing space and light within and between canopy layers, horizontally and vertically considering the position and shading of neighboring trees, thereby affecting crown geometry, light attenuation, and reception.

3.4.3. Sensing

Tree growth is influenced by the salinity and nutrient availability in the gap (FORMAN), at stem position (KIWI), or at each tree and stand unit (MANGRO model). In FORMAN, trees are “informed” about the presence of neighboring trees by the total leaf area in the canopy above them. In KIWI, the influence of neighbors on a tree is described by overlapping FONs considering the distance, explicit location and size of all neighbors. In MANGRO, neighbor competition is described in terms of the distance among the trees and the azimuth of every neighbor tree. In FORMAN applications to Florida, trees growth is influenced by the species-specific extension of the annual growth period, defined by an annual accrued number of degree days above some threshold temperature. This feature is not implemented in the KIWI model which was exclusively applied to tropical forests without temperature growth limitation so far.

3.4.4. Stochasticity

During the initialization, trees are randomly distributed over the gaps (FORMAN) or within the stand (KIWI, MANGRO) when eligible and unoccupied space is available. Tree mortality by disturbances is also described as a random function.

3.4.5. Observation

All three models provide a yearly tracking of variables on individuals such as stem diameter and stem height, and on stand level such as total basal area, importance values, or complexity indices.

3.5. Initialization

All three models provide variations in initial data depending on selected scenario or data availability. While smallest trees

(assumed to be saplings) have a minimum height of 1.27 m in the FORMAN and KIWI model, MANGRO also describes first year seedlings. The initial number of trees and the species composition can be set corresponding to the requirements of the particular experiment. However, 30 individuals per species per 500 m² are used on average in the FORMAN model. For the KIWI model, a typical initial density is 300 individuals per species per 10,000 m². The default mode of the MANGRO model allows full stand stocking for every square meter of unoccupied space.

3.6. Input

The models use sapling (FORMAN, KIWI) or seedling (MANGRO) recruitment rates per species defining quasi-externally the annual establishment of new trees. Furthermore, abiotic conditions (e.g., salinity, nutrient availability or stand quality, which are parameters characterizing the inundation regime) are given for each gap (FORMAN), tree location (KIWI) or stand (MANGRO) and may be temporally variable. Discrete events modulating tree mortality (natural hazards, tree cut) or an overall disturbance regime can be scheduled at each time step as required by the experiment.

3.7. Submodels

3.7.1. Recruitment and establishment

In FORMAN and KIWI, seedling growth is not explicitly simulated for two reasons: (a) due to lack of field data, and (b) in order to save computational expense. However, factors affecting seedling growth and mortality – such as grazing or sulfides – are implicitly included in sapling recruitment rates. In FORMAN, the annual number of established saplings added to a gap is arbitrary based on empirical evidence of biotic and abiotic factors controlling recruitment. Following establishment, growth is controlled by available light and soil conditions (nutrients and salinity). In KIWI, the potential location of a sapling is chosen randomly, including a range restriction to simulate establishment beneath a parent tree. Yet, trees can only establish if competition of existing trees is below a given species-specific threshold simulating shade-tolerance of the sapling. In the MANGRO model, stands are stocked with new recruits for every square meter of unoccupied space released by the eventual death of standing trees. In addition, the MANGRO model possesses several seedling regeneration submodels that control species recruitment relative to site elevation, tidal flooding, and proximity and composition of neighboring mangrove stands. In all three submodels, the local recruitment rate of each species can be a function of parent tree density and establishment might be modified by environmental conditions such as salinity, sea level, soil elevation, and flooding potential expressed as gap characteristic or depending on tree location in the flooding gradient.

3.7.2. Tree growth

All three models use the JABOWA-type growth function and a yearly time step. Stem increment is a function of stem

diameter in breast height (dbh), tree height, and the maximum values of dbh and height for a given tree species. This function and its parameterization are defined for optimal growth conditions. To simulate sub-optimal conditions and stress, growth multiplier functions correct the stem increment depending on salinity conditions and available nutrients (total soil P). The FORMAN model also uses correction functions for the light availability and temperature-defined length of the annual growth period. In the KIWI model, a multiplier function considering a neighbor effect is introduced. The intensity of a neighbor's field-of-neighborhood (FON) exerted on the FON of the focal tree is taken as measure for this multiplier. Unlike FORMAN and KIWI, MANGRO contains no nutrient functions, but models site fertility implicitly as a function of maximum potential tree height. Annual stem diameter increase depends on species growth potential for a given tree diameter reduced by derived crown volume, light availability, and light quality. Flooding and salinity further modify stem growth. Crowns grow as a function of crown space and pre-eminence as to which tree fills space first for a given crown height and class. Crown structure is modeled as a three-dimensional process of crown height, width, and depth in relation to sun angle and shading by neighboring trees.

3.7.3. Mortality

All current individual-based mangrove models describe sapling mortality explicitly. The FORMAN and the KIWI model consider the factors that limit seedling establishment (predation, stress, hydroperiod) by sapling recruitment rates. For trees, there is a similar source of mortality in all three models: the probability of tree mortality risk increases after a prolonged period of growth suppression resulting from the compound effect of salinity stress, nutrient limitation, and/or neighborhood competition. In the FORMAN model, mortality is triggered if the annual stem increment is below a specified threshold in two subsequent years. In the KIWI model, a tree dies if the mean stem increment over a user-supplied time range (typically 5 years) is less than half of the average increment under optimal conditions. Such a growth suppression is more frequently met when the environmental conditions constantly deteriorate and when a tree stem diameter approaches the species-specific maximum. Whereas KIWI uses these conditions for an indirect description of tree mortality depending on tree age, an explicit function is used in the FORMAN model. Here, a tree dies with a certain probability which increases with age (as in Botkin, 1993b). However, by considering growth suppression within a time window of several years, a tree has a chance to 'convalesce' when conditions after a shorter stress period ameliorate, that is, salinity decreases, more nutrients become available, or when a neighbor trees die. Also, all three models consider tree death due to stochastic events. In FORMAN and KIWI probabilities (e.g., that a hurricane appears in a particular year and affects a certain percentage of trees) are controlled by the experimenter. For the MANGRO model, the separate HURASIM model reconstructs wind fields from historic storm data for each land unit managed by SELVA and relates specific storm data to each distributed MANGRO

model which describes species-specific tree mortality functions for given wind speeds (Doyle and Girod, 1997). Mortality due to cutting of trees or lightning strikes can be implemented similarly in the three models. This might lead to a decrease of leaf area in the particular height class of a gap (FORMAN model), to the creation of circular gaps according to a gap size distribution (MANGRO model), or to canopy gaps of various sizes and shapes (KIWI model).

3.7.4. Evaluation

The robustness of all three models has been tested by classical sensitivity analyses (Doyle and Girod, 1997; Chen and Twilley, 1998; Piou, 2007). For testing the suitability of the models for simulating particular mangrove stands, model results have been regularly tested against field patterns. Total basal area simulated for the Shark river estuary by the FORMAN model was within $\pm 10\%$ of that observed in the field (Chen and Twilley, 1998). Doyle and Girod (1997) shows similar results regarding forest structure of south Florida mangrove ecosystems. Berger et al. (2004) demonstrates that the KIWI model produces both mixed size classes (with a size class dominance in less disturbed stands), and a u-shaped stem diameter size class distribution of the dead trees corresponding to empirical time series (Monserud and Sterba, 1999) and other modeling studies (Keane et al., 2001). Piou (2007) developed an information criterion based on the Akaike's Information Criterion, the so-called Pattern-Oriented-Information-Criterion (POMIC). This technique was applied to evaluate how well different KIWI parameterizations reproduce zonation patterns of Belizean mangroves by "visual debugging" methods (Piou, 2007). The latter method was also applied to the vertical canopy structure during secondary succession (Berger et al., 2006) to tune the KIWI model for a mangrove forest in North Brazil.

3.7.5. Availability

The KIWI model is available on demand via the corresponding author. The online appendix of this paper gives an overview about model's output.

4. Contribution of individual-based modeling to understanding mangrove forest dynamics: advances and challenges

Given the generality, objectives and applications of the FORMAN, KIWI, and MANGRO models, they have contributed to the synthesis of available quantitative and qualitative knowledge of mangrove forests. All three models describe the essential life processes of trees (establishment, growth, and mortality) depending on resources (light, nutrients), regulators (salinity), and competition (task 1). Model simulations demonstrate how environmental constraints in a given geomorphological setting influence forest dynamics. For example, using FORMAN simulation experiments, Chen and Twilley (1998) showed that resource competition for nutrient availability from marine to mesohaline environments might explain a reduction in *A. germinans* and *L. racemosa* basal areas as observed in the Shark river estuary following impacts by

Hurricane Donna in 1960. The same study illustrated that the relative rates of recruitment of *A. germinans*, *L. racemosa*, and *R. mangle* over time was also significant to explain spatial patterns in forest dynamics. Simulation experiments with KIWI showed that a temporal decrease in nutrient availability in combination with species-specific differences in nutrient-uptake efficiency between *L. racemosa* and *A. germinans* (Lovelock and Feller, 2003) were likely to explain the gradual replacement of the pioneer species (*L. racemosa*) in the canopy as observed on northern Brazil after the abandonment of rice cultivation fields (Berger et al., 2006). These findings compare with studies in tropical wet forests where gaps with high nutrient pools significantly affected more the growth rates of high-light demanding species than those of shade-tolerant species.

In addition to demonstrating the role of nutrient concentrations in forest growth, simulation experiments also indicate the significant effects of tree-to-tree competition on forest structure. For example, KIWI simulations support the hypothesis that the slope of the so-called self-thinning-line is not fixed but confined in two directions, i.e., the strength of neighbor competition defines the upper limit whereas morphological constraints such as the stem diameter versus crown diameter relationship determines the lower limit (Berger et al., 2002, 2006). Furthermore it appears that the self-thinning line is linked to a homogenization process in the plot forcing the symmetry of the stem diameter distribution (Berger and Hildenbrandt, 2003). In general, KIWI applications frequently address theoretical issues in vegetation ecology such as asymmetric competition among plants, or the age-related declines in forest production (e.g., Bauer et al., 2004; Berger et al., 2004).

All three mangrove models have been used to test the impact of natural and human-induced disturbances on forest dynamics (task 2). Twilley et al. (1999b) used the FORMAN model to simulate the impact of different restoration regimes on the recovery of mangroves in the Ciénaga Grande de Santa Marta, Colombia (CGSM) in specific site conditions and at decadal time scales. The authors predicted forest recovery in terms of basal area and species composition depending on different scenarios of freshwater inflow, natural recruitment, and planting regimes. Berger et al. (2006) simulated the secondary succession of mangroves after clear-cutting and rice cultivation under brackish water conditions in the Bragança peninsula, North Brazil. Simulations suggested that a combination of disturbance history, nutrient and/or salinity heterogeneity determines species growth potential, but biogenic changes in abiotic conditions, tree competition, and dispersal actually defines the succession trajectory. This study showed that these factors could create multiple outcomes in terms of species composition, even in forests with only a few species under optimal growth conditions. Doyle and Girod (1997) applied hindcast simulations of the MANGRO model linked with a hurricane simulation model, HURASIM, to evaluate the effect of hurricane history on the landscape composition and structure of mangroves in the Florida Everglades. They identified the occurrence of major storms every 30 years as the most

important factor controlling mangrove structure and dynamics in south Florida. Based on forecast simulations with more intense storm events expected under projected climate change, the authors predicted a further alteration in the landscape structure and composition during the next century.

In principle, all revised IBMs provide a framework for evaluating management scenarios according to their potential ecological, economic, or social outcome of mangrove sustainability (task 3). MANGRO simulations of future sea-level rise from climate change suggest that tidal inundation increases across the Everglades landscape and enhances mangrove encroachment and expansion onto the low-lying Everglades slope (Doyle et al., 2003). The MANGRO model also considers management options such as hydrologic restoration of freshwater flow in the Everglades which may help to stall the rate of mangrove expansion into former freshwater habitats under rising sea levels and future climate change. Twilley et al. (1999b) used FORMAN to evaluate potential management scenarios regarding the hydrological regime, which was proposed for the rehabilitation of CGSM. The authors compile a so-called “traffic light list” signifying which scenario is best (“green light”), intermediate (“yellow light”), or worst (“red light”) in terms of basal area recovery and species composition.

A comparison of empirical versus simulated recovery patterns is a suitable strategy to test the plausibility of different hypotheses regarding resource gradients in gaps (task 4). This procedure refers to the strategy of “Pattern-Oriented-Modeling” (Grimm and Railsback, 2005) and is a general advantage of spatially explicit, individual-based models. Berger et al. (2006) use a comparison of temporal changes in canopy structure (height differentiation and species composition) to explain recovery phenomena of mangrove forests. Similarly, Doyle and Girod (1997) compared forest structure of field plots with simulated results to gauge the contribution and role of hurricanes in controlling forest dynamics of south Florida mangrove ecosystems. Finally, Piou (2007) tested the importance of intertidal gradients for the establishment and growth processes of Caribbean mangroves in an attempt to reproduce the recovery of Belizean sites destroyed by hurricane Hattie in 1961.

5. Recommendations, future research directions, and conclusions

Despite the successful model applications described above, there still exist several model limitations and underutilized model resources that restrict the use of these tools to advance our understanding of mangrove forest dynamics. For example, all three mangrove forest simulators have been used to evaluate the relative role of niche partitioning and “chance” in structuring mangrove forests (task 6), but to a different extent according to their formulation of the recruitment process. Comparing the simulation results of the three different mangrove IBMs under similar scenario and disturbance regimes could evaluate the relative importance of recruitment and specific sapling dispersal mechanisms on regulating forest trajectories over time which have been suggested by empirical

studies (e.g. [Thampanya et al., 2002](#); [Thampanya, 2006](#)). Nevertheless, specific factors determining seedling and sapling survival rates such as predation are not explicitly formulated in model simulations. There is only one IBM, the so-called IBU model, which simulates local movement of individual *Ucides cordatus* crabs ([Piou et al., 2007](#)). This model has been used to analyze recovery patterns of a crab population after fishing in North Brazil. A link of such a model to forest dynamics through microhabitat conditions, leaf litter consumption and seed predation is still an open research question (cf. [Cannicci et al., 2008](#)).

There is no consensus about the detail of physiological mechanisms and competition processes needed for more accurate modeling of forest dynamics ([Busing and Mailly, 2004](#)). Regarding mangrove forests, this question is particularly critical since physiological field studies in mature forests are lacking in comparison to mesocosms and greenhouse studies (e.g., [Cardona-Olarte et al., 2006](#)). Further studies comparing simulations of FORMAN, KIWI, and MANGRO models to determine whether more detailed formulations of the spatial distribution of resources like light and tree dimensions such as crown volume and orientation can significantly improve model accuracy as suggested by [Reynolds and Ford \(2005\)](#).

Field studies on vegetation patch dynamics show that gap size influences forest dynamics (e.g., [Pickett and White, 1985](#)). For example, pioneer species are often excluded when gap size falls below a certain level; these small gaps might restrict regrowth and promote closure from the surrounding canopy ([Baldwin et al., 2001](#)). KIWI and MANGRO address this aspect because gaps of different sizes and shapes appear “naturally” when trees die. In this case, the created gap conditions control dispersal, establishment, survivorship, and growth of new recruits. However, to enhance our understanding of the relative importance of resource gradient partitioning and recruitment limitation in maintaining tree species richness and spatial distribution, further simulation experiments are needed. Such experiments should be linked to integrative (across scales) field experiments on the relationship among gap and patch geometry and on species distribution in mangrove forests. Moreover, there is a need for both comparative and multifactor experiments designed to examine how soil nutrient concentrations and hydroperiod interact with stressors to limit growth of both seedlings and adult trees (e.g., [Thampanya et al., 2002](#); [Cardona-Olarte et al., 2006](#)). In this context, mechanistic submodels could be suitable to support the analysis of field experiments which are often hard to interpret with increasing complexity.

FORMAN and MANGRO have focused on site-specific predictions of forest productivity, and although SELVA–MANGRO ([Doyle and Girod, 1997](#); [Doyle et al., 2003](#)) and FORMAN ([Twilley et al., 1999b](#)) have also simulated regional productivities and responses to global change, model results are limited due to the lack of a description of belowground processes ([Twilley et al., 1992](#)). This limitation includes multi-layer representation of soil water and nutrient availability as well as processes like biomass allocation to roots and root distribution within the soil, which have been neglected in

mangrove research (but see [Komiyama et al., 1987, 2008](#)). Currently, there is only one published mangrove nutrient mechanistic model that simulates profiles of soil carbon, N and P and organic matter (NUMAN; [Chen and Twilley, 1998](#)). We also describe the need to produce a synthesis of the species-specific and age-specific regeneration potential of individual trees after disturbances and their importance for system recovery as grasped by the simulation models (task 5). The MANGRO model partly focuses on this topic by including an adaptive function for effecting tree growth rate and performance based on disturbance ([Doyle and Girod, 1997](#)). Nevertheless, investigations regarding the importance of re-sprouting on the recovery of mangrove systems after mechanical disturbances cannot be carried out by the available IBMs. Current models do not provide the needed flexibility in representation of tree architecture (e.g., sprouting branches and deviations from circular crown shapes), which could be an important process for analyzing system recovery after mechanic disturbances, like hurricanes. Until now, the “virtual trees” do not show “adaptive behavior”. Trees grow faster or slower based on environmental conditions and their local neighborhood, but they are unable to respond in terms of reproduction time, reproduction type, or specific tree morphology (e.g., asymmetry of tree extension, scrub stature, or tree shape). The lack of phenotypic plasticity is a general limitation of plant models ([Grimm and Railsback, 2005](#)).

Since all three models describe landscape vegetation patterns, they are suitable to test the synchronization and de-synchronization effect of canopy disturbances on mosaic cycles of successional forest stages on a landscape level (task 7). This is, however, an open challenge and still on the list of potential applications of the FORMAN, KIWI, and MANGRO models.

We further suggest to replicate field and mesocosm experiments across latitudinal gradients (see, e.g., [Cardona-Olarte et al., 2006](#)), or within a wider geographic range, to determine the relative importance of interacting factors such as climatic settings or specific adaptations of spatially distant populations, on forest dynamics. In this context it is necessary to stress that parameterization of the current mangrove IBMs is based on data collected within a very narrow geographical range. Stem growth data as well as information about tree age and mortality from different regions of the world are essential to test the general applicability of current simulation experiment results (see, e.g., [Menezes et al., 2003](#); [Verheyden et al., 2005](#)). Model applications to mangrove forests in Africa, Asia, or Australia could support research related to coastal protection and sustainable use of coastal wetlands worldwide, but will depend on the acceptance of such models as research tools for developing management recommendations.

The mangrove models discussed in this paper have contributed to the understanding of critical processes in mangrove wetlands by identifying relationships and mechanisms that need further study; particularly those regulating recruitment, productivity and forest structure. Being complex hypothesis formulations, our models are part of the scientific method, and serve as “blue prints” to define research priorities ([Wullschleger et al., 2001](#)). This paper uniquely summarizes

the advances and applications of existing forest simulation models that have been independently designed to understand mangrove forest dynamics and management. Hopefully, this review will spur additional field and modeling research that will enhance and expand model functionality and utility for a better understanding of one of the most productive ecosystems in the world.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.aquabot.2007.12.015](https://doi.org/10.1016/j.aquabot.2007.12.015).

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