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How do tree competition and stand dynamics lead to spatial patterns in monospecific mangroves?

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Abstract

Information on mangrove stand development is rare because long-term monitoring data is often lacking. Such information is important in order to plan management measures effectively. Novel approaches are required to bridge this gap of knowledge based on existing data sets. This study uses a unique combination of field data analyses with simulation experiments in order to demonstrate how information on mangrove dynamics can be extracted if data are sparse. The paper provides a baseline characterization of stand development in a monospecific pioneer mangrove stand of *Kandelia obovata*. Point pattern analyses revealed that in the young stage, self-thinning has started but has not yet lead to a regularity of spatial tree distribution in the entire stand, and trees located in smaller clumps hinder each other in growth but do not lead to a significant size class differentiation. However, after ca. 2 decades the self-thinning and the size class differentiation start to become more visible. A mutual inhibition of growth was observed within 2 m circular distance (r) in the young stage and within 3 m distance after two decades of stand development as confirmed by the negative values of mark correlation function. As a stand grows older the spatial pattern of individuals become more regular from a clustered pattern. In order to understand and predict the future stand development, simulation experiments were carried out by means of the individual-based model KiWi.

1 Introduction

Mangroves dominate the inter-tidal zone of the tropical and subtropical coasts, and play a major role in the food webs and nutrient cycles, also in the adjacent marine ecosystems (Alongi et al., 2000; Machiwa and Hallberg, 2002; Mumby et al., 2004; Kristensen et al., 2008). Although the ecological and economic significance (Rönnbäck, 1999) of mangroves is highly acknowledged, the ecological processes driving their dynamics are still poorly understood (Kathiresan and Bingham, 2001; Comley and McGuinness, 2005; Khan et al., 2007; Berger et al., 2008; Cannicci et al., 2008; Krauss et al., 2008) because of the absence of long-term monitoring data. While numerous studies address the effect of abiotic conditions (Cintron et al., 1978; Ball, 1988; Clarke and Allaway, 1993) and disturbances (Piou et al., 2006) on forest dynamics, the importance of biotic interactions and their impact on the temporal, vertical and horizontal patterns of mangrove forests is still under-represented in scientific investigations (Berger and Hildenbrandt, 2000, 2003).

The spatial patterns and population structure of mangroves, however, constitute important aspects in ecosystem functions (Osunkoya and Greese, 1997; Krause et al., 2001; Ellison, 2002; Sherman et al., 2003). They are fingerprints of important key factors, such as local competition for photosynthetic light in the canopy (Clarke and Allaway, 1993; Khan et al., 2004), microtopography (Dahdouh-Guebas et al., 2007; Di Nitto et al., 2008), vegetation composition (Jayatissa et al., 2002; Kairo et al., 2002), sediment chemistry (Thiobodeau and Nickerson, 1986; Clarke and Allaway, 1993; McKee, 1995; Alongi et al., 2004), tidal elevation (Clarke and Myerscough, 1993), salinity (Clarke and Allaway, 1993; Krauss et al., 2008), dispersal patterns (Rabinowitz, 1978; Clarke and Myerscough, 1991; Clarke, 1993), or the competitive ability of species (Clarke and Myerscough, 1993; Berger and Hildenbrandt, 2000, 2003; Canham et al., 2004).

There are differences in structural patterns (e.g. tree size, species composition, soil plant interaction, etc.) between terrestrial (Manabe et al., 2000; Hegland et al., 2001; Souza and Martins, 2004; Wilson et al., 2004; Kubota, 2006; Salas et al., 2006) and mangrove (Osunkoya and Greese, 1997; Krause et al., 2001; Kairo et al., 2002; Dahdouh-Guebas and Koedam, 2006) forest systems. Structural patterns in mangrove forests depend on the distance to the sea or proximate water channel (e.g. Osunkoya and Greese, 1997; Kairo et al., 2002), elevation (Castaneda-Moya et al., 2006) or even latitudinal gradients (DeLange and DeLange, 1994). In mangrove forests, the spatial patterns of individuals have been analysed based on the distance from the sea to the forest (Osunkoya and Greese, 1997), on soil resources regulators and the hydroperiod

(Castaneda-Moya et al., 2006) or on the ecosystem level (Krause et al., 2001). However, the relationship between local competition among trees as one of the major driving factors and the resulting size and spatial distribution of individuals remain little explained. This is essential for a general understanding of mangrove forest dynamics. In order to analyze mangrove forest dynamics, it is thus critical to analyse comprehensively both the structural and spatial distribution patterns of individuals and their temporal evolution.

The analysis of the self-thinning process (Shinozaki and Kira, 1961; Yoda et al., 1963; Lonsdale, 1990; Osawa and Allen, 1993; Enquist et al., 1998, 1999) and spatial point process (Stoyan and Stoyan, 1994; Stoyan and Penttinen, 2000; Law et al., 2009) of individual trees based on a time series, for example, provides insights about the density dependent mortality induced by local competition and its effect on the overall size of the surviving plants. In the present study, we aimed at addressing the following research questions, in particular: How individual trees in a monospecific pioneer mangrove stand are spatially distributed in course of stand development? What are the mechanisms of the ecological processes (e.g. tree growth, competition, mortality, biomass, etc.) involved during the stand development? How do tree competition and stand dynamics lead to spatial patterns in monospecific mangroves?

2 Materials and methods

2.1 Experiment setup and study site

In order to investigate on the temporal evolution of structural and spatial patterns of individual trees in the mangrove stand, simulation experiments were performed using the individual-based model KiWi (Berger and Hildenbrandt, 2000), which was originally applied for a neotropical mangrove forest (Piou et al., 2006; Berger et al., 2008; Fontalvo-Herazo et al., 2011). For this purpose, at first field data were collected to parameterize the KiWi model so that the model can mimic the dynamic growth, competition and mortality in the monospecific mangrove stand of *Kandelia obovata* (S., L.) Yong (Table 1). The values of the model parameters were obtained according to procedure of pattern oriented modelling (POM) (Grimm et al., 1996, 2005; Fontalvo-Herazo et al., 2011).

Besides the KiWi, there is another model currently available for the simulation of mangrove dynamics: FORMAN (Chen and Twilley, 1998) to simulate long-term dynamics of mangrove development based on soil nutrient conditions and salinity. The KiWi model serves a useful tool for the studies of vegetation dynamics (Berger and Hildenbrandt, 2003; Fontalvo-Herazo et al., 2011) in mangroves, provided that the model parameters (Table 1) are tuned based on the field data obtained from those particular mangroves (Berger and Hildenbrandt, 2000; Piou et al., 2006; Berger et al., 2008). The advantage of KiWi model is that the parameters are easy to obtain even with limited availability of data. This model is spatially explicit and it describes individual trees by their stem position, stem diameter, stem height and the so-called field of neighbourhood (FON) defining the area within which a tree influences and is influenced by its neighbours. The growth of trees depends on a tree's age, environmental conditions at stem position and neighbourhood competition. The mortality increases with growth reduction. The establishment of new saplings depends on both environmental conditions at the particular location and competition strength at this location exerted by the already established trees (described by the sum of their FONs). A detailed description of the model following the ODD (Overview, Design concepts, Details) protocol for describing the individual-based models (Grimm and Railsback, 2005; Grimm et al., 2006, 2010) is provided in Table 2.

For the purpose of field validation, the modelled results were compared with field datasets, which were collected through two decades of stand development. The study site was located in the mangroves at Manko Wetland (26° 11′ N and 127° 40′ E), Okinawa Island, Japan (Fig. 1). The mangrove *Kandelia obovata* (S., L.) Yong has formed continuous monospecific stands in the Manko Wetland. The species *K. obovata* is considered as a pioneer species in mangrove succession. The stem diameter, height and the x-y co-ordinates of all the trees in a $20 \times 20\,\mathrm{m}^2$ plot in a monospecific *K. obovata* stand were recorded at different time steps of stand development. The mean tree height and density in the monospecific stand (ca. 12 yr old) were recorded as ca. 4 m and 15 450 trees ha^{-1}, respectively. In the study site, the mean minimum, mean maximum and mean annual temperatures were 16.8 °C, 28.8 °C and 23.2 °C, respectively. Rainfall was over 100 mm month^{-1} throughout the year, and the mean annual rainfall was 2086 mm yr^{-1} (Khan et al., 2004). The study plot was assumed to be equiformal (isotropic), i.e. without any effective gradient in terms of tidal inundation within the plot.

2.2 Data analyses

Point pattern analyses were carried out (Stoyan and Stoyan, 1994; Stoyan and Penttinen, 2000) in order to gain a deeper understanding of the ecological drivers behind the spatial patterns. The pair correlation function (PCF) $g(r)$, which is related to Ripley's K function (Ripley, 1979), provides a measure of the density of neighbouring plants and gives a general notion of a "plant's-eye" view (Turkington and Harper, 1979; Mahdi and Law, 1987; Law et al., 2009) of a vegetation assemblage. The PCF was used to detect uniform, clumped or random patterns in tree occurrence where trees are considered as points in a spatial point process (Stoyan and Stoyan, 1994):

$$g(r) = \frac{1}{2\pi r}\frac{\mathrm{d}K(r)}{\mathrm{d}r} \tag{1}$$

where $K(r)$ is the Ripley's K function (Ripley, 1979), and r is the particular search radius. Provided that $P(r)$ is the probability of detecting points at locations x and y within a distance r, and λ is the intensity of the point process (Stoyan and Stoyan, 1994):

$$P(r) = \lambda^2 \cdot g(r)\mathrm{d}x \cdot \mathrm{d}y \tag{2}$$

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trees are completely randomly distributed (uniform Poisson process), then $p(r) = \lambda^2$ and $g(r) = 1$. Values $g(r) < 1$ suggest that the trees are more regularly distributed. Values greater than 1 suggest a clustering.

In order to detect the dynamics of intraspecific competition over stand development, a mark correlation function (MCF) $k_{mm}(r)$ using dbh as marks (Stoyan and Stoyan, 1994; Getzin et al., 2008; Law et al., 2009) was used. The MCF provides the distance-dependent size correlation of trees and it detects whether competition affects tree growth. The MCF quantifies the similarity and dissimilarity between dbh marks of two neighbouring trees occurring at a distance r by the function $f(m1, m2) = m1 \times m2$, where $m1$ and $m2$ are dbh values of the two trees. The term $k_{mm}(r)$ is defined as the normalized mean value of $f(m1, m2)$ for all marks at distance r. Marks are considered independent, positively or negatively correlated at distance r if $k_{mm}(r) = 1$, $k_{mm}(r) > 1$ or $k_{mm}(r) < 1$, respectively. A positive mark correlation suggests a "mutual stimulation", i.e. facilitation and a negative mark correlation suggests a "mutual inhibition".

Self-thinning refers to the time-trajectory of mean phytomass w and density ρ of any specific population over time, and when density dependent mortality is occurring (Yoda et al., 1963; Enquist et al., 1998, 1999). The time trajectory of w approaches a line of constant slope with respect to ρ along with the progress of growth and mortality. The relationship between w and ρ is given as

$$w = c\rho^{-\alpha}. \quad (3)$$

In the linearized form

$$\ln w = \ln c - \alpha \ln \rho \quad (4)$$

where α specifies the slope of the self-thinning line, and $\ln c$ the intercept with the vertical axis. The value of the intercept depends on the species and units of measurement (Yoda et al., 1963; Enquist et al., 1998, 1999; Silvertown and Charlesworth, 2001; Berger and Hildenbrandt, 2003). Based on different initial densities and the relationships of w at different stand ages to the corresponding ρ in the whole plot, the time trajectory (Ogawa, 2001, 2005; Ogawa and Hagihara, 2003) of $w$and ρ was approximated as:

$$w = K\rho^{-a}(1-\rho/\rho_0)^b \tag{5}$$

where K and a represent c and α, respectively in Eq. (3), ρ_0 specifies the initial density and b is a constant.

The individual tree weight was approximated using the allometric relationships which were established for the same stand as reported in a previous study (Khan et al., 2005). All data analyses were performed using R-Software version 2.15.2 (R Development Core Team, 2011) and the point pattern analysis (pair correlation and mark correlation), in particular, was performed using the “Spatstat” package of R (Baddeley and Turner, 2005).

2.3 Sensitivity analysis

Sensitivity analysis was performed using the extended Fourier Amplitude Sensitivity Test (eFAST), a variance-based global sensitivity method (Cukier et al., 1978; Saltelli et al., 1999, 2000) for tracing the contribution of model parameters and of the corresponding processes in individual tree size. The eFAST is model-independent and is applicable irrespective of the degree of linearity or additivity of the model. The method quantifies the contribution of the individual input parameters to the variance of the output variables. It reveals both parameter main effects on the model output and the sum of the effects due to its higher-order interactions with other parameters (Saltelli et al., 2000; Saloranta and Andersen, 2007). At first, the model parameters were obtained (Table 1) according to procedure of pattern oriented modeling (POM) (Grimm et al., 1996; Grimm et al., 2005; Fontalvo-Herazo et al., 2011). Then following the specific sampling procedure of the SimLab software package (SimLab, 2011), different parameter sets were calculated with a −10 % to +10 % ranges in each parameter described in Table 1 (except $F_{\max}$, which is constant for all the simulations). Next, the parameter sets were used for multiple simulation runs (65 × 10 parameters = 650 simulations) and the model output (mean tree weight at time step 20) in each simulation was recorded. Finally, the input parameter sets (total 650) and the corresponding model output were used to perform the eFAST sensitivity analysis (Fig. 2) using the "Sensitivity" package (Pujol et al., 2012) in R (R Development Core Team, 2011).

3 Results

3.1 Stand structure

Using the field data, the coefficient of variation (CV %) of tree diameter and height was plotted against the cumulative sample area (Fig. 3). It was observed that the CV of both height and diameter increases with increasing cumulative sample area, but after 200 m^2 area the CV is not influenced by the increasing sample area. This suggests the existence of little horizontal heterogeneity of tree size in the *Kandelia obovata* stand.

3.2 Modelling stand dynamics

The eFAST sensitivity analysis (Fig. 2) suggested that of the model parameters (Table 1) used in the simulation experiments, b is the most influential followed by the mortality parameter $\Delta \mathrm{dbh}_{\mathrm{crit}}$ and the growth parameter G. The parameter b specifies the field of neighbourhood (FON) intensity (Table 2) depending on dbh, and G influences the annual dbh increment. This reveals that in KiWi the tree size (through FON intensity) and growth rate influence the competition strength in individual trees, the probability of death of an individual tree depends of its growth performance.

In the simulation experiments with an initialization (Scenario 1, Table 2) of forest area by trees located identically to the original tree positions, original tree dbh and 12 yr as starting age, it was evident that the time trajectory of mean tree weight w and density ρ (Fig. 4) in the *Kandelia obovata* stand follows the self-thinning line in course of stand development. The simulated values of dynamic mean tree weight showed strong similarity to that of field data suggesting the robustness of the KiWi model for predicting the dynamics in stand development of the mangrove *K. obovata*. Likewise, the relationships of pair correlation function $g(r)$ to distance r at different stand ages using the simulated and field datasets showed strong similarities (Fig. 5). In the young stage (12 yr old), the $g(r)$ values shows large values (>"1") for search radii smaller than 50 cm, verifying the clumping of trees in short distances (Fig. 5). The curve dropping below "1" for distances between 50 cm and 150 cm shows that trees tend to occur slightly regularly within these distances irrespective of age and dbh. However, $g(r)$ specifies overall spatial randomness in tree locations for larger distances. After the stand age reaches 20 yr (Fig. 5), the $g(r)$ shows changes from clumping to slight regularity for search radii smaller than 50 cm and this trend continues up to a distance of 2 m. As stand growth proceeds, the $g(r)$ values for search radii of < 2 m indicated that the spatial pattern of trees changes from clumped to more uniform distribution (Fig. 5).

In the young stage (12 yr old), the mark correlation function $k_{\mathrm{mm}}(r)$ confirmed the existence of intraspecific competition in the stand (Fig. 6) as indicated by the curve dropping below "1" (negative mark correlation) for distances up to 2 m. This suggests that neighbouring trees within 2 m distance are dissimilar in size (dbh) confirming a growth inhibition among the neighbours, and large trees (similar in size) maintain a distance among themselves. This inhibition distance reached up to 3 m after two decades of stand development (Fig. 6). The size distribution of mortality of trees confirmed that the smaller sized trees are more prone to die (Fig. 7) triggering the regularity of spatial pattern over stand development. The phenomenon of clumping in short distances (Fig. 5) in young stage (observed data) and the spatial randomness in larger distances (observed and simulated data) is in agreement with the dynamics of tree size distribution indicating the high proportion of mortality in smaller trees. The mortality process in relation to stand density further clarified by the simulation experiments with an initialization (Scenario 2, Table 2) of forest area by trees located on random initial tree positions, an initial height of 1.37 m and a stem dbh of 2.5 ± 0.25 cm, 1 yr as starting age and varying stand densities. It was confirmed that the higher the initial stand density, the higher the rate of mortality and the quicker the stand reaches the so-called self-thinning line (Fig. 8).

4 Discussion

This study focused on a comprehensive analysis of the early stage of stand development processes in the monospecific *Kandelia obovata* mangrove forest. Simulation experiments, starting with the present configuration of the study sites, provided a forecast of the stand development to be expected in the future. The combined analysis of empirical and simulated data was useful for both finding the baseline for stand development and producing a time series being usually not available for mangrove forests, because of the absence of longterm monitoring data.

Although the modelled results of this study was validated based on a 400 m^2 plot, which seems to be a small sample plot for a vegetation study, it was observed (Fig. 3) that after 200 m^2 cumulative area, the coefficient of variation (CV %) of tree diameter and height is not influenced by the increasing cumulative sample area, indicating the existence of less horizontal heterogeneity of tree size in the stand for a sample area larger than 200 m^2. Thus, the sample plot would be considered as a suitable representative of the model based on changes of the CV of tree diameter and height in relation to the cumulative sample area (Thompson, 1992).

For simulation experiments, the KiWi model was chosen as a suitable tool for our research question. The model uses a simple but well-established growth equation (Shugart, 1984), which was originally developed for the first generation of forest simulation models. This growth equation is not as flexible as of Asaeda and Kalibbala (2009), which describe relevant processes (e.g. photosynthesis and respiration) in detail. However, the main advantage of Shugart's function is that the parameterization is possible with the little data available for our study site as most of the mangroves. It is for this reason that most of the mangrove forest simulators use this growth function (Berger et al., 2008 and citations within). Another advantage of the KiWi model is the spatially-explicit description of the trees. This provides the consideration of forest inventory data by means of point pattern statistics being suitable to reveal essential ecological mechanisms and key factors beyond forest dynamics. Non-spatial mangrove models, such as the one introduced by Asaeda and Kalibbala (2009) are very suitable for describing stand parameters on higher hierarchical levels of the ecosystem (e.g. yield) but are not appropriate for the analysis, description and prediction of dynamic spatial patterns we are focusing on in the frame of this study. The parameters used for the experiments were tuned based on field experience, as well as results of previous reports (Khan et al., 2004, 2005, 2007, 2009) on the same study sites, where the simulated results were validated with real field data, for instance, stand biomass production (Khan et al., 2009).

The mean tree weight (Fig. 4) and frequency distribution of dbh (Fig. 7) in simulated trees (Initialization: Scenario 1, Table 2) corresponded well to the observed datasets. This is a sign of validity of simulated results with observed data (see also Khan et al., 2009). The data points as time series of two decades reveal that density dependent mortality already occurs and the self-thinning process has started. As shown in Fig. 8, the tree growth rate in independent populations having a low stand density is high, even if the populations are of the same age. If the tree growth is limited by resource availability, individuals are forced to compensate for their size, which in turn results in the mortality of some individuals. This effect is popularly known as the competition-density (C–D) effect in non-self-thinning population (Shinozaki and Kira, 1956; Silvertown and Doust, 1993; Xue and Hagihara, 2002, 2008). In the time trajectory, the slope a (i.e. α in the self-thinning line) values in the curves (Fig. 4, dashed line) were estimated as -1.299, which is not as steep as the so-called self-thinning slope -1.5 (i.e. $-3/2$). This is, however, very close to -1.333 (i.e. $-4/3$) as suggested by some investigators (e.g. Lonsdale, 1990; Osawa and Allen, 1993; Enquist et al., 1998, 1999). In agreement with Zeide (1985), Weller (1987), or Berger and Hildenbrandt (2003), however, no particular slope value is claimed. The pattern of density dependent mortality (Fig. 7) suggests a higher mortality of smaller trees in older stands due to intra-specific competition

(Xue et al., 1999; Ogawa and Hagihara, 2003) is supported by the earlier findings that *K. obovata* is intolerant to shade (Khan et al., 2004), and the trees strongly compete for light as is true for other heliophytes (Tüffers et al., 1999; Ball et al., 1988). In the case of a closed canopy stand when larger trees obstruct light to smaller ones, the smaller trees are thinned out because of the shade of larger ones resulting in low photosynthetic production in the former, which still have a normal respiration cost (Weiner and Whigham, 1988; Suwa et al., 2006).

The point pattern analysis of the spatial distribution of trees provides new insights into the study of mangrove stand development, which had not been carried out up to now. The pair correlation function (Fig. 5) gives precise information of a differentiation below the smallest diagonal distance of the smallest observation quadrat, providing the estimation with continuously increasing distances (r). For this reason, it was possible to identify the scale of clumping < 50 cm in young stage (12 yr old), and a more regular distribution of the trees in distances between 50 and 150 cm in the early stages of growth (Fig. 6). The cause for the clumping process can be manifold, ranging from heterogeneities in seed availability due to stochasticity in seed dispersal, to heterogeneities in micro-environmental conditions influencing the growth and survival of the plants (Clarke and Allaway, 1993; Frelich et al., 1993; Osunkoya and Greese, 1997; Yamada and Suzuki, 1997; Dahdouh-Guebas et al., 2007; Krauss et al., 2008). The regularity among the individuals, as indicated by the dropping of $g(r)$ values below “1” along with the increasing stand ages, reflects the intraspecific competition in the monospecific stand. When a short search radius is concerned, after the stand grows older the disappearance of clumping and the change of the spatial pattern of trees to more regularity indicates the existence of intraspecific competition resulting in a density dependent mortality. The intraspecific competition and the density dependent mortality would cause the spatial pattern of individuals to become more regular over stand development. The negative spatial association between trees of different sizes (mutual of inhibition of growth), as indicated by the negative values of $k_{mm}(r)$ within 2 m distance during the early stage and within 3 m distance after two decades of stand development, is an indication that small trees are associated with large neighbouring trees if competition would suppress growth (Law et al., 2009). The overall spatial randomness in tree locations for larger distances (> 2 m in young stage and > 3 m after two decades) might be related to a smaller tree crown in the *K. obovata* as a light-loving species (Khan et al., 2004; Suwa et al., 2006) and dwarf mangrove type (Lee, 1989), and the trees are not large enough to pose any shading threat to neighbours at large distances.

In conclusion, this study is based on a combination of empirical and simulated data describing the early stage of mangrove stand development. Simulation experiments used the current constellation of the empirical plots as the initial configuration providing a forecast of future stand development. The experiments were carried out by means of the mangrove forest simulator KiWi, being the first individual-based model parameterized to South-east Asian mangroves. This study provides insights on spatial patterns of individual trees along with the stand dynamics: in young stage smaller clumps have been detected and self-thinning has started but has not yet lead to a regularity of spatial tree distribution in the entire stand; trees located in smaller clumps hinder each other in growth but do not lead to a significant size class differentiation; after ca. 2 decades the self-thinning and the size class differentiation start to become visible; as stand grows older the spatial pattern of individuals become more regular from a clustered pattern; the mutual of inhibition of growth and the resultant mortality of smaller size class would cause the change of the spatial pattern. Although this study represents a constrained species specific model (every important point that is specific for this model as compared to a more generic mangrove) towards understanding the dynamics of spatial distribution of individual trees along with stand development, we hope that it will stimulate further research in this direction.

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Table 1. Parameters used for the simulations of the mangrove *Kandelia obovata* obtained according to procedure of pattern oriented modelling (POM) (Grimm et al., 1996, 2005; Fontalvo-Herazo et al., 2011) and field data.

Parameters	Description	Value
a	Scaling factor for FON	14.55
b	Scaling factor for FON	0.914
F_{max}	Maximum value of the FON	1
F_{min}	Minimum value of the FON	0.075
G	Growth constant	83.85
D_{max}	Maximum dbh (cm)	20
H_{max}	Maximum height (cm)	600
b_2	Constant in height to dbh relationship	46.3
b_3	Constant in height to dbh relationship	1.158
$\Delta\text{dbh}_{\text{crit}}$	Mortality threshold	0.191
φ	Resource sharing capacity	1.5

Note: FON-field of neighbourhood (Berger and Hildenbrandt, 2000).

Table 2. Model description following the ODD protocol (Grimm and Railsback, 2005; Grimm et al., 2006, 2010).

Overview	
Purpose of the model	The purpose of this study was to analyze the temporal evolution of the spatial distribution pattern of trees and stand development in the monospecific mangrove *K. obovata*, where the trees compete with their neighbours for spatially limited resources such as space and light.
State variables and scales	Individual trees are described primarily by their stem position, stem diameter (dbh), and age. Other descriptors such as stem height or the dimension of the field-of-neighbourhood (FON), used to describe local neighbourhood competition among trees, are derived from the dbh as shown in the growth function (see below). Species-dependent tree growth is calculated annually. The spatial dimension and shape of the forest stand are variable. Plot sizes of the simulation area of 100 m × 100 m were used for this study.
Process overview and scheduling	The following processes occur each year: establishment of new saplings, growth of existing trees, and tree mortality. The stem diameter of all trees are updated synchronously and the derived parameters such as tree height and FON radius are re-calculated.
Design concepts	
Emergence	Population dynamics emerges from the life processes modified by tree-to-tree competition, e.g. oscillation dynamics of tree densities and basal areas, or variations in the spatial distributions of trees ranging from clumped, to random to regular, among others.
Interactions	Interactions Trees compete for all spatially distributed resources (not explicitly specified) via their FONs.
Sensing	Trees “sense” the distance, size and explicit location of their neighbours by their overlapping FONs.
Stochasticity	Saplings establish randomly, depending on local conditions. There is a random mortality in addition to the density dependent mortality, which is completely deterministic.
Observations	The model provides yearly tracking of all state variables and derived parameters for all trees.
Details	
Initialization	*Scenario* 1: the forest area to be colonized by trees located identically to the real plot keeping the original tree positions, original tree dbh and 12 yr as starting age. *Scenario* 2: stand development based on random tree positions, an initial height of 1.37 m and a stem dbh of 2.5 ± 0.25 cm, 1 yr as starting stand age and varying initial stand densities (ca. 5000, 10 000, 15 000 and 20 000 at 12 yr stand age).
Input	Yearly recruitment rates define the establishment of new saplings. Abiotic factors such as topography, inundation height, inundation frequency, pore water salinity and nutrient availability can be addressed explicitly by user-supplied maps corresponding to the simulated forest stand; but for the purpose of this study they were considered to be optimal for the whole forest.
Submodels	
Description of a single tree	A tree is described by its x-y position, dbh, and FON. The latter describes the area within which a tree influences its neighbours and is influenced by its neighbours. The radius R of the FON increases with dbh: $R = a\ .\ (\mathrm{dbh}/2)^b$, where a and b are species specific scaling factors (Table 2). The intensity of FON $(r) = e^{c(r-(\mathrm{dbh}/2))}$.
Recruitment and establishment	Seedling growth is not explicitly modelled due to the lack of field data. Seedling growth and mortality, however, are implicitly included in the sapling recruitment rates. Saplings can establish if tree density and the resulting intra-specific competition are below a certain threshold at the potential, randomly chosen location. This threshold mimics a given shade tolerance of the species.
Tree growth	The model uses a JABOWA-type growth function, where the annual stem increment is a function of dbh and stem height H: $\frac{\Delta \mathrm{dbh}}{\Delta t} = \left[\frac{G \cdot \mathrm{dbh} \cdot \{1-\mathrm{dbh} \cdot H/(\mathrm{dbh}_{\max} \cdot H_{\max})\}}{274+3b_2 \cdot \mathrm{dbh}-4b_3\mathrm{dbh}^2}\right] \cdot (1-\varphi \cdot C_{\mathrm{FON}})$ with $H = 137 + 3b_2 \cdot \mathrm{dbh} - 4b_3\mathrm{dbh}^2$. This function is parameterized for optimal growth conditions. The growth multiplier $(1-\varphi.C_{\mathrm{FON}})$ corrects the stem increment depending on tree neighbourhood competition, where φ represents the resource sharing capacity. The growth multiplier stands one for no neighbouring trees.
Competition	The intensity of the FONs of all neighbouring trees on the FON of a focal tree is taken as a measure of the competition strength the focal tree suffers. This value is related to the area of the FON of the focal tree, assuming that the influence of larger trees on smaller ones is stronger than vice versa.
Mortality	The model considers mortality due to a prolonged period of growth depression. Since there is no field data available on that process, the model describes it phenomenologically. A tree dies if its mean stem increment over a specified time range (here 5 yr) is less than half of the average increment under optimal conditions. This occurs when the stem diameter approaches its maximum, or results from salinity stress, nutrient limitation, or competition among neighbouring trees. This procedure assures that a tree has a chance to recover when conditions improve, e.g. when a neighbouring tree dies.

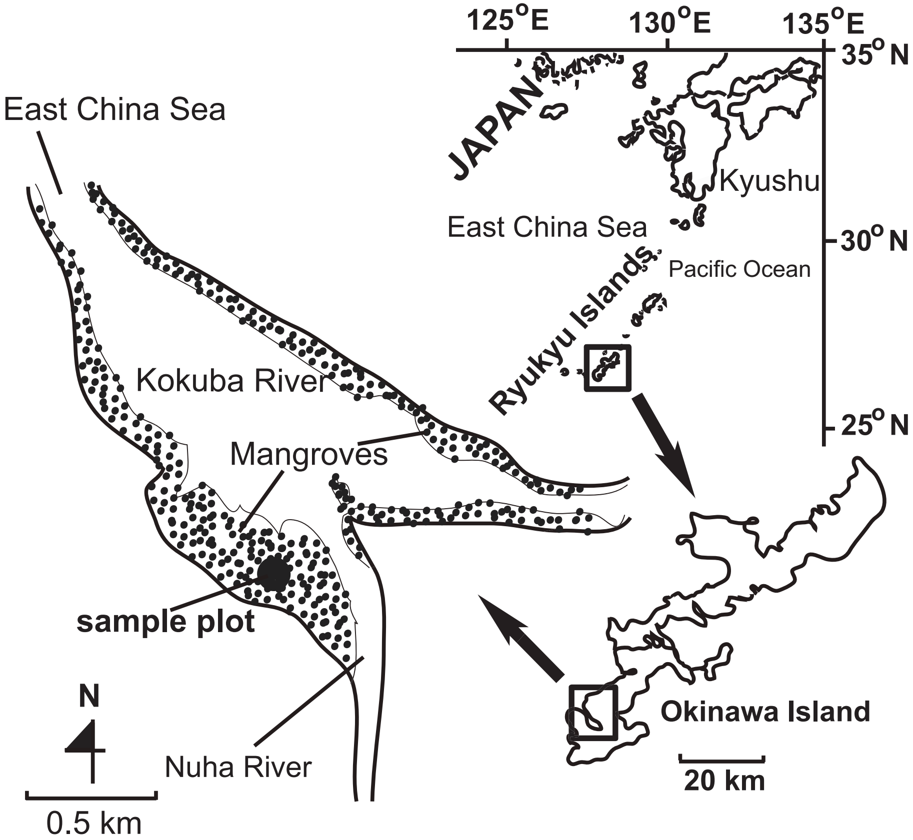

Fig. 1. Location of the study site in the Manko Mangroves, Okinawa, Japan.

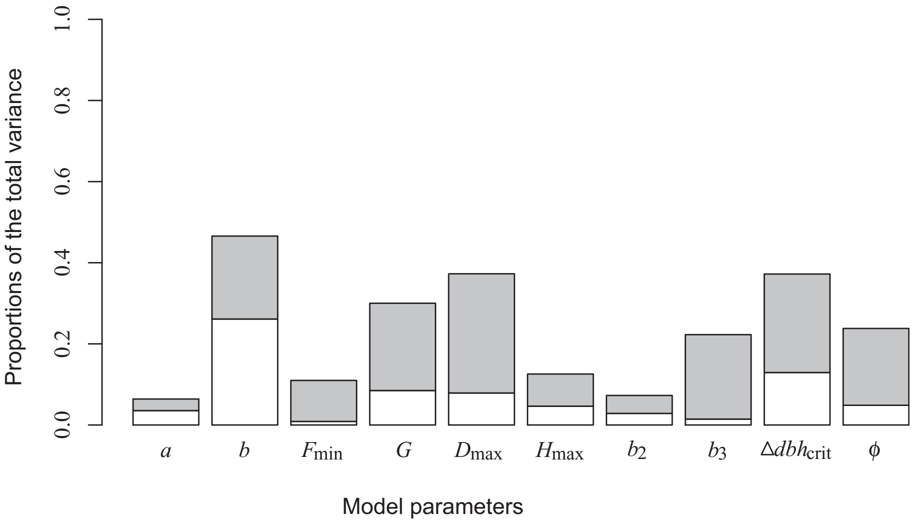

Fig. 2. Proportions of the total variance explained by model parameters (Table 1) with regard to the model output (mean tree weight at stand age 20 yr) analysed by the extended Fourier amplitude sensitivity test (eFAST) method. The white area (main effect) denotes the portion of total variance explained by the particular parameter alone and the gray area (interactions) similarly the part explained by all parameter interactions where the particular parameter is included.

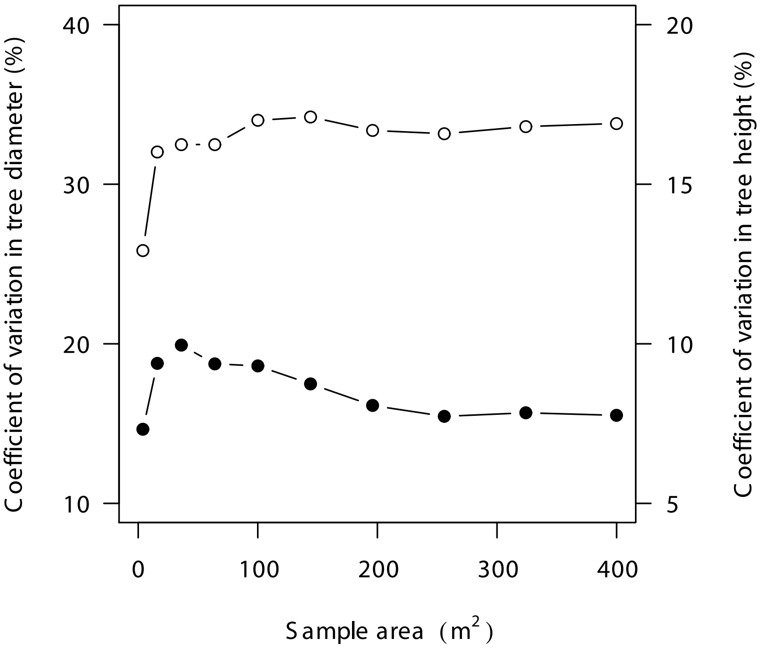

Fig. 3. Relationships of coefficient of variation of tree diameter and height to cumulative sample area in the *Kandelia obovata* sample plot (∘ diameter, • height).

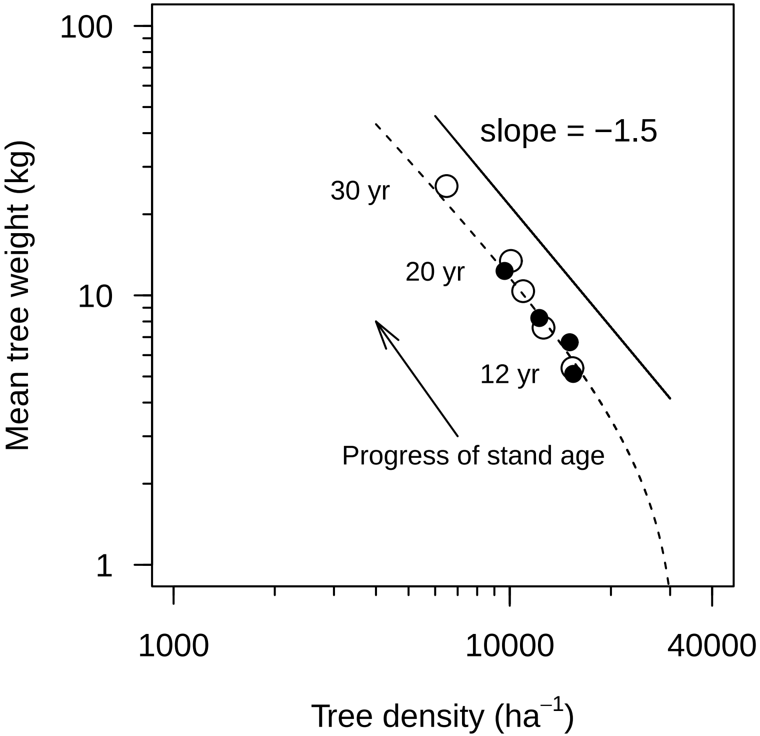

Fig. 4. Time trajectory of mean tree weight (kg) in *Kandelia obovata* in relation to stand development (• observed, ∘ simulated). The curve represents the Eq. (5) fitted ($R^2 = 0.967$) on the observed data set, where the coefficients are $K = 2.202 \times 10^6$, $a = 1.299$, $\rho_0 = 3.164 \times 10^4$ and $b = 0.503$. The straight line indicates the so-called self-thinning line.

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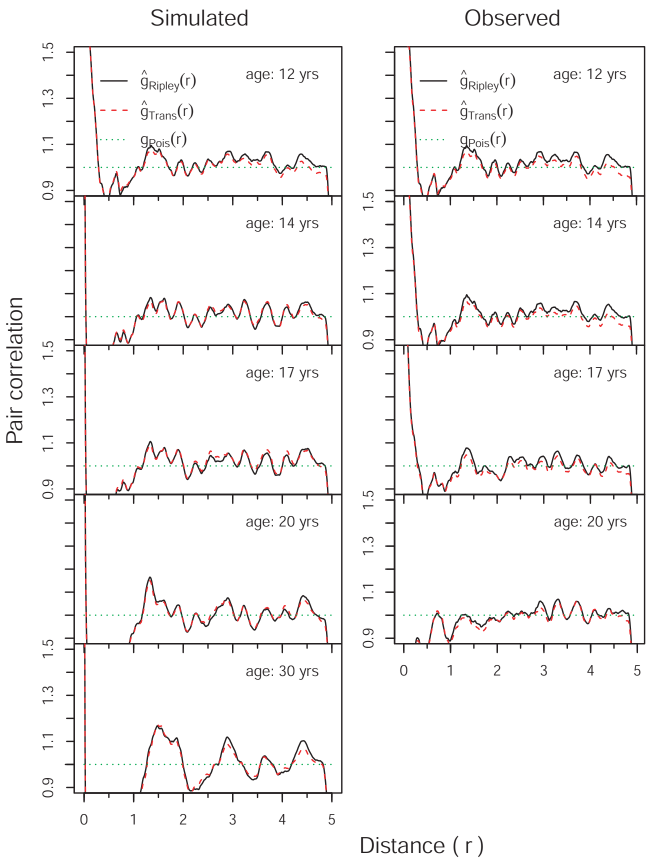

Fig. 5. Relationships of pair correlation function $g(r)$ to distance r at different stand age in the *Kandelia obovata* stand initiated with existing density and based on tree positions obtained from field data. The solid lines indicate isotropic-corrected estimate of $g(r)$, the dashed lines indicate translation-corrected estimate of $g(r)$ and the dotted lines indicate Poisson's expectation.

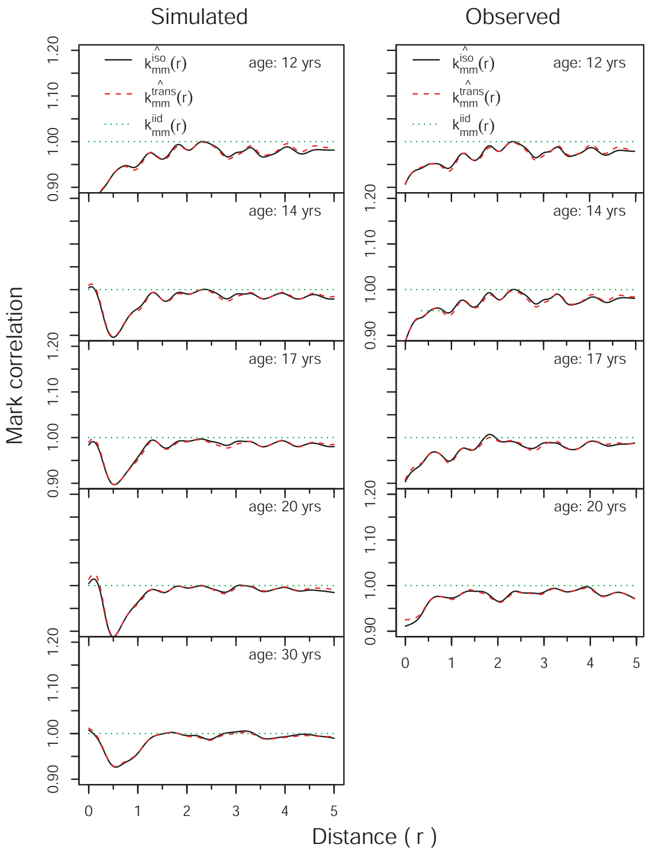

Fig. 6. Relationships of mark correlation function $k_{mm}(r)$ to distance r at different stand age in the *Kandelia obovata* stand initiated with existing density and based on tree positions obtained from field data. The solid lines indicate isotropic-corrected estimate of $k_{mm}(r)$, the dashed lines indicate translation-corrected estimate of $k_{mm}(r)$ and the dotted lines indicate Poisson's expectation.

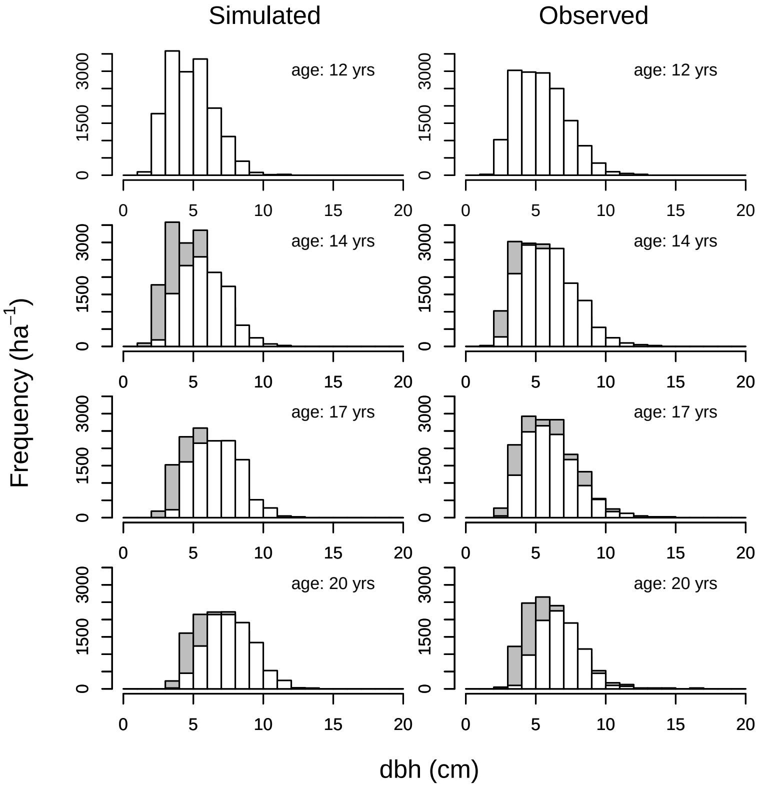

Fig. 7. Frequency distribution of tree dbh along with the mortality distribution in relation to stand development. Shaded bars indicate dead trees (with respect to previous census) and white bars indicate live trees.

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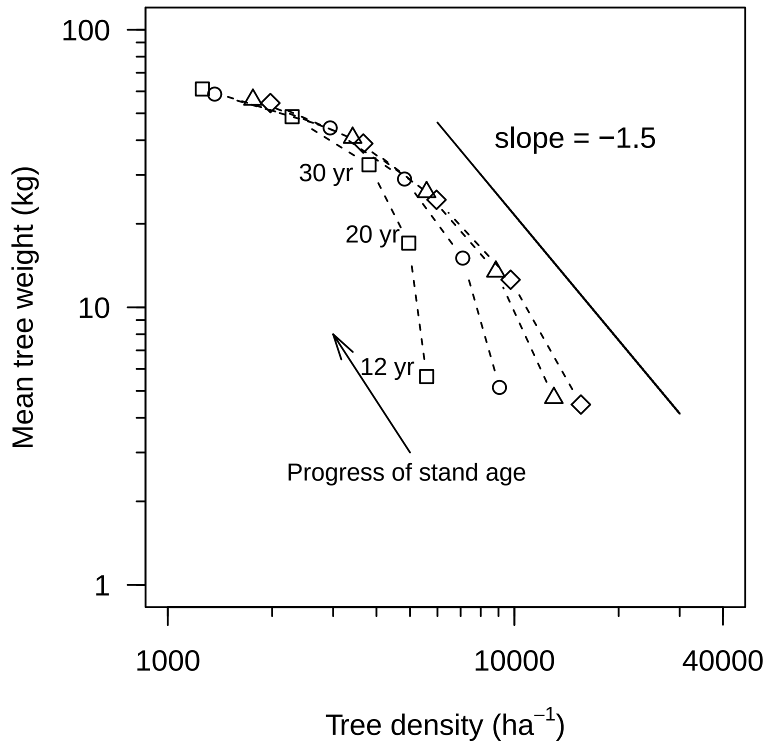

Fig. 8. Relationships of mean tree weight (kg) to tree density (ha^{-1}) in relation to stand development. The arrow indicates the progress of time during stand development based on different initial densities (☐ 5000, ○ 10 000, Δ 15 000, ◊ 20 000 trees ha^{-1}). The straight line indicates the so-called self-thinning line.