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A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees

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Abstract

This paper presents a new approach to spatially explicit modelling that enables the influence of neighbourhood effects on the dynamics of forests and plant communities to be analysed. We refer to this approach as ‘field of neighbourhood’ (FON). It combines the ‘neighbourhood philosophy’ of grid-based models with the description of individual spacing in the ‘zone of influence’ (ZOI) approach. The novel feature of FON is that modelling of local competition between neighbouring trees is based on the notion of a field of neighbourhood exerted by each tree. This field is defined only on the ZOI of a tree and depends on the distance to the stemming point. For the demonstration of FON’s power, a simulation model (KiWi) was implemented that focuses on the dynamic of mangrove forests. The realistic self-thinning behaviour of modelled stands of *Avicennia germinans* and *Rhizophora mangle* confirms the suitability of the FON approach for the description of intra- and inter-specific competition. In KiWi, mortality is modelled in terms of a ‘memory function’, i.e. the yearly stem increment of each tree is stored in its ‘memory’ over a certain time period and determines — as a sign of vitality — tree mortality. The results of KiWi demonstrate that this description is sufficient to keep the maximum age of the trees within a reasonable limit. The model thus manages without a description of individual tree age. This is an important feature considering the fact that a direct relationship between tree age and mortality is questioned and there is no established method as yet for determining the age of mangrove trees. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Ecology is spatial, but theoretical ecology has ignored this dimension for decades, or has taken it into account only in an indirect or highly idealised manner. Only since computers became powerful and inexpensive enough to be generally

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available has space been an explicit issue in theoretical ecology and ecological modelling. Once these computers were available one model type in particular helped to establish the spatially explicit approach in ecology, namely grid-based models in which space is divided into quadratic or other grid cells of the same size (Zeigler, 1977; Wolfram, 1984; Green et al., 1985; Turner, 1987; Hogeweg, 1988; Baker, 1992; Jeltsch, 1992; Silvertown et al., 1992; Wissel, 1992; Jeltsch and Wissel, 1994; Jeltsch et al., 1996, 1997; Berger et al., 1999a; Grimm, 1999; Jeltsch et al., 1999). Cell size is chosen to represent the smallest spatial unit of interest in relation to the problem addressed by the model, e.g. canopies of mature trees, territories, local forest stands, sampling units, etc. Within the cells, spatial effects are ignored; spatial interactions occur only between neighbouring cells.

Although grid-based models have proved to be extremely powerful and have been applied to almost all kinds of ecological systems and to scales ranging from square metres to entire continents, there are still questions and systems for which the grid-based approach is unsuitable. We became aware of these limitations of the grid-based approach when we tried to develop a spatially explicit model of mangrove forests. The development of such a model is one of the tasks of our Brazilian–German project MADAM. The name MADAM stands for ‘Mangrove Dynamics and Management’ and explains the focus of the scientific program (Berger et al., 1999b). The model should allow the dynamic of the mangrove forest to be analysed. Although we had to consider the specific environmental conditions exposed at our study area near Braganca (northern Brazil), we looked for a modelling approach being adequate for the description of mangrove stands in a more general sense.

To our knowledge there is only one spatially explicit mangrove model FORMAN (see Chen and Twilley (1998) for an overview of other, non-spatial mangrove models), a gap model (Chen and Twilley, 1998). FORMAN demonstrates the existence of different successional stages. In a three-species forest consisting of *Avicennia germinans*, *Rhizophora mangle*, and *Lagun-*

ularia racemosa, the abundance of *A. germinans* increases over time. If large-scale disturbances are absent this species will dominate the forest not only at higher salinities, but also under benign conditions, i.e. lower salinities. These results show that FORMAN is a powerful tool for investigating mangrove dynamics, but a number of important questions remain unanswered: the influence of site-specific establishment rates, the role of seedlings dispersal, the influence of small scale heterogeneities of environmental factors on tree growth, and the process of species replacement by competition.

Some of these limitations are common to both gap models and the grid-based approach. The main problem with these vegetation models is that they do not permit the consistent application of an individual-based approach (Huston et al., 1988; DeAngelis and Gross, 1992; Uchmanski and Grimm, 1996; Grimm, 1999) in which individuals of all possible size are considered at their very locations. We, therefore, developed a new approach to the spatial modelling of vegetation dynamics. Our approach, which we will refer to as the field of neighbourhood (FON) approach, combines the advantages of the grid-based and the zone of influence (ZOI) approaches (Czárán, 1998). Although we developed this new approach as a means of modelling mangrove forest dynamics, we believe it can be used to model communities of any sessile organisms, i.e. plant and benthic communities.

The purpose of this paper is to introduce the FON approach. First, we will explain the limitations of the grid-based and other approaches and how these limitations led us to our own approach. We will then introduce the FON approach; a detailed and easily applied algorithm is provided in the Appendix A so that our approach can be easily implemented and tested by others. Then, as an sample application, we will develop the mangrove model KiWi in order to apply FON to some aspects of mangrove dynamics that have not yet been modelled: self-thinning and inter-specific competition leading to different outcomes under different initial conditions. Finally, we will discuss both the potentials of the FON approach to modelling vegetation dynamics and the potential of

FON and KiWi to advance theoretical synthesis within mangrove research.

2. Why a new approach to spatially explicit modelling of mangroves?

The fixed cell size used in grid-based models, e.g. canopy size of mature trees, is not suitable for modelling mangrove forests. Mangrove tree architecture and maximum trunk diameter are highly variable, and depend on several stress factors such as pore water salinity or water logging. A grid-based model of mangrove forests would, therefore, need an adaptive grid size with different sets of model rules for each grid size. Besides the problem of sufficient empirical knowledge being available to formulate all these rules, the resultant number of model rules would be so high that the grid-based approach would lose its key advantage, namely the representation of quantitative and qualitative ecological knowledge by a small number of simple rules that can be easily formulated and implemented.

Furthermore, grid-based models are often particularly successful when they are combined with the strategy of 'pattern-oriented modelling' (Grimm, 1994; Grimm et al., 1996), in which both model construction and validation are focused on distinguishing patterns observable in the system being studied. However, in grid-based forest models with cells representing the canopy size of mature trees, trees would be 'forced' to adopt an artificial, regular distribution. Besides this drawback, a suitable approach to modelling mangroves should focus on explicit description of the small-scale processes that generate patterns on both small and larger scales. To this end, our new approach has to give explicit consideration to the position of each tree within a continuous space.

There are two recent modelling approaches which explicitly consider the exact position of individuals — the 'tessellation' and the 'zone of influence' approach. Since there is no community model based on these approaches, we examined their suitability for multi-species systems. Tessellations are used in single-species plant models to study intraspecific competition for different spa-

tial arrangements of the plants (Czárán, 1998). The performance, e.g. growth, of each individual depends on the area of its Voronoi polygon, which is determined by the number, size, location and, in particular, the proximity of its neighbours. A dynamic tessellation model for an even-aged tree monoculture was developed by Galitsky (1990)). This model enables self-thinning processes in plant communities to be analysed.

Nevertheless, the tessellation approach is difficult to extend to multi-species systems. Although the differences in architecture between the various species could be taken into account by weighted distances (Okabe et al., 1992), the implementation of different growth rates is not straightforward. Furthermore, the tessellation approach usually considers death as the only demographic process, yet establishment would also be necessary for the analysis of mangrove forest dynamics. Moreover, the tessellation approach does not permit the superimposed influence of several trees to be represented at a given location. Yet precisely this 'local density' seems to be decisive for tree growth and for sapling establishment, especially. In summary, the tessellation approach is not suitable for modelling mangrove forests.

The 'zone of influence' (ZOI) approach is based on the notion that each individual exploits resources within a circular zone around its stemming point (Czárán, 1998). Resource competition occurs wherever the zones of influence of individuals overlap. The strength of competition depends on the fraction of zones overlapped (Gates and Westcott, 1978). However, the ZOI of a tree describes only the area used by a tree but does not consider that the influence of a tree, e.g. the intensity of exploitation, will usually vary with the distance from the stem. Hence, as soon as the ZOI of one tree is completely superimposed by the ZOI of another tree, the specific distance between the two trees and their actual sizes become irrelevant, which seems to be rather unrealistic, especially in the case of sapling establishment.

In summary, what we need in order to model mangrove forests is an approach which combines the advantages of the grid-based and the ZOI approach while avoiding their limitations. The strength of grid-based models is the simple but

powerful consideration of local interactions, i.e. neighbourhood effects such as competition; whereas the strength of the ZOI approach is that it enables modelling of individuals of all sizes at their real, exact location (Wyszomirski, 1983; Wyszomirski et al., 1999). The FON approach is designed to combine these advantages. Another important aim of our approach is that it avoids spatial effects at the local scale being ignored, as is the case with grid-based models. In this way, we hope to show how the strategy of ‘pattern oriented modelling’ at the local scale can be applied to the modelling of mangrove forests.

3. The FON approach

Consider a single, isolated tree. If abiotic conditions are benign, the tree will grow at maximum growth rate and achieve a maximum final size. Now consider a second tree. As long as this tree is not too close to the first, both trees will grow at the maximum growth rate. However, if the two trees stand closer to each other than a certain, critical distance, they will disturb each other, resulting in a reduced growth rate for both trees. This is true in general and does not depend on the particular mechanism and level of interaction, e.g. root competition, competition for light in the canopy, or whatever. The extent to which a tree’s growth rate is reduced depends on the ‘strength’ and distance of its neighbour(s).

In order to model this general phenomenon of local competition a tree is firstly characterised by its stem position and a circular ZOI around this position. The radius R of the ZOI depends on the size of the tree. In our demonstration model KiWi (see the following section below) we use the simple relationship:

$$R = a\sqrt{rbh} \quad (\text{m}), \quad A = \pi a^2 rbh \quad (\text{m}^2) \quad (1)$$

where rbh is the half diameter at breast height (dbh), a is a scaling parameter, and A is the area of the ZOI.

The ZOI, however, defines only the neighbourhood of a plant: two plants are, by definition, neighbours whenever their ZOIs overlap. ZOIs do not provide any weighting of the neighbourhood

in terms of tree distances, despite the fact that a remote tree will certainly exert a smaller competition on a focal tree than a tree in the vicinity. To model this distance-dependent intensity of neighbourhood, we introduce a scalar field (the FON) on the ZOI. This field of neighbourhood indicates at any point within the ZOI the strength of competition or the ‘degree’ of neighbourhood that the focal tree would exert at that point. FON corresponds with the competition function used by Adler (1996), and Davie (1999). Its interpretation is not limited to a particular mechanism of competition, such as resource competition; in any case, it is not necessary to know such mechanisms in detail.

In KiWi, we chose the following field it amounts to 1 at the stem, decreases exponentially with increasing distance to a small value F_{\min} at the borderline of the ZOI, and it is 0 outside the ZOI (Fig. 1):

$$\begin{aligned} \text{FON}(r) &= 1; \quad \text{for } 0 \leq r < rbh, \\ \text{FON}(r) &= e^{-c(r - rbh)}, \\ R \text{ from Eq. (1);} \quad &\text{for } rbh \leq r \leq R, \\ \text{FON}(r) &= 0 \quad \text{otherwise.} \end{aligned} \quad (2)$$

Now, the basic assumption of our approach is that the FON’s of all trees superimpose. At a given location (x, y) , the aggregate field strength $F(x, y)$ of all trees is, therefore, given by the sum of their single field intensities. Hence, in the case of N trees $F(x, y)$ is:

$$F(x, y) = \sum_N \text{FON}_n(x, y). \quad (3)$$

The specific, dimensionless value of $F(x, y)$ depends on the local configuration of all neighbouring trees (Fig. 1). It represents the local neighbourhood situation and takes into account the number, the weighted distance and the individual size of the neighbouring trees. A location influenced by some smaller trees can be characterised by the same $F(x, y)$ value as a location influenced by a single, larger tree. A location which is not influenced by any tree has an aggregate field strength $F(x, y)$ of 0.

For the description of the neighbourhood situation of a tree, we assume that a tree ‘perceives’ the aggregate field strength F on its entire ZOI. Consequently, we compute the mean value F_A of the aggregate field strength F produced by all other trees on the tree’s area A (Eq. (1)). For example, F_A for k th of N trees is:

$$F_A^k = \frac{1}{A} \int_A F'(x,y) da = \frac{1}{A} \int_{A_n \neq k} \sum \text{FON}_n(x,y) da$$

$$= \frac{1}{A} \sum_{n \neq k} \int_{A'} \text{FON}_n(x,y) da'. \quad (4)$$

In this case, F' corresponds to the total field F without the contribution of the k th tree (a tree is not its own neighbour). A' is the overlapping area of the FONs of the n th and the k th tree.

Computing F_A as a mean has three advantages: first, it makes sense biologically to scale the influence of all neighbours by the ZOI of the focal tree; second, F_A is a dimensionless variable and third, changing the sequence of integration and summation in Eq. (4) enables a very simple al-

gorithm for calculating F_A to be used, because integrals now have to be taken only over overlapping ZOIs in pairs (see Appendix A for a detailed description of the algorithm for calculating F_A).

F_A supplies the same information for a tree as $F(x, y)$ for a point: the description of the neighbourhood strength depending on the number, size, and proximity of its neighbours. F_A can cause growth depression as well as the deformation of a tree. Because FON is the ‘neighbourhood field’ exerted by a tree and not the tree itself, it cannot be deformed.

4. Using the FON approach: the KiWi model

In this section we present the KiWi model based on the FON approach. KiWi was developed in order to analyse demographic processes of mangrove forests according to abiotic environmental factors, individual tree spacing, and intra- and inter-species competition.

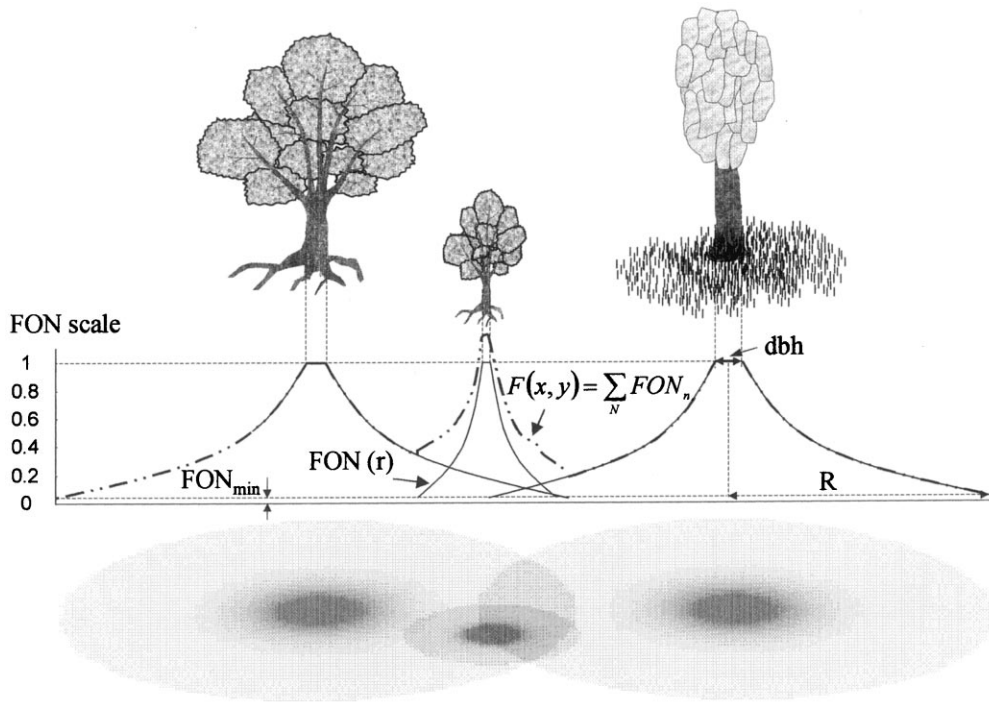


Fig. 1. The principal components of the FON approach describing the competition strength of an individual in its environment (see text for explanations).

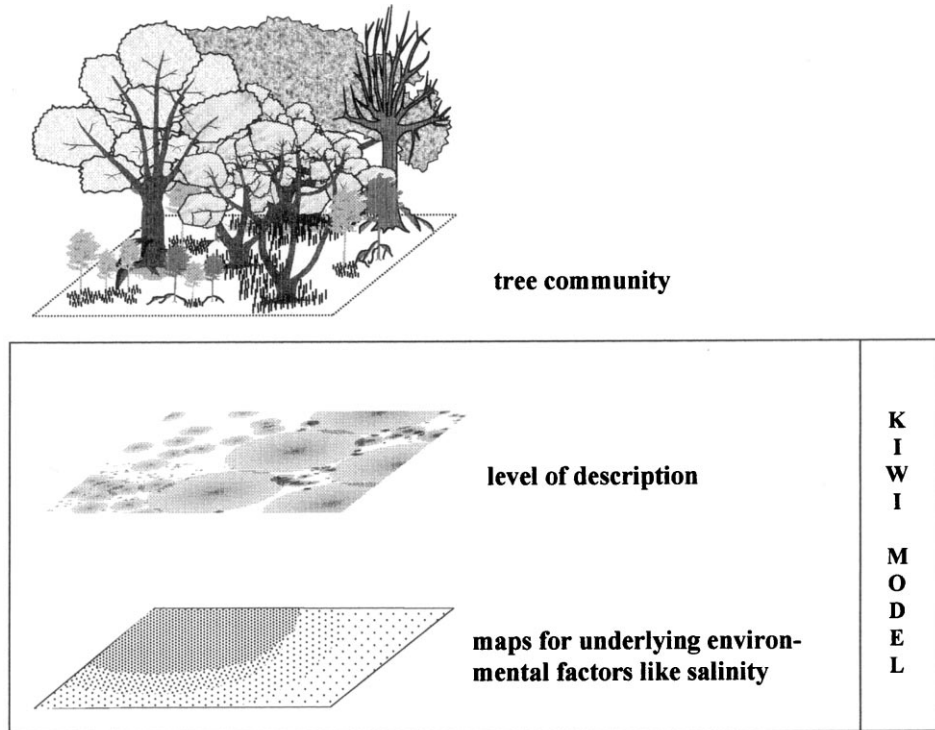


Fig. 2. Architecture of the KiWi model. There are only two levels of description: one for the life history of the trees and one for the abiotic factors.

Fig. 2 shows the basic structure of the model. It requires only one 'biotic' level for describing the trees, because modelling of growth, mortality and sapling establishment is based on a single module, the FON module. The FON approach permits this compact handling of the demographic processes, because all plant-to-plant interactions are expressed in terms of FON. Sapling establishment depends on $F(x, y)$ (see below). Tree competition is influenced by F_A .

The second level of the model describes the abiotic factors influencing the demographic processes. Since the primary focus of this paper is to introduce FON we limited the complexity of the model and considered pore water salinity only. We implemented the spatial distribution of pore water salinity as a bitmap in which the particular colour strength (e.g., a value between 0 and 256) defines salinity at a given position. In this way it is possible to specify a simple, artificial salinity distribution as well as distribution maps based on

field studies. The dynamics of the salinity distribution can be taken into account by specifying different bitmaps at different time steps. Extending KiWi by including other abiotic factors such as nutrients or water level can be done in the same manner as described for salinity. A time step in KiWi corresponds to 1 year. The salinity distribution used for the simulations presented below was homogeneous. The concrete value never exceeded 50‰.

4.1. Setting the FON

We apply Eqs. (1) and (2). The parameters a in Eq. (1) and F_{\min} in Eq. (2) are species-specific (Table 1). In general, there is no simple method for specifying the parameters or the functional relationships in Eqs. (1) and (2). As long as no detailed field studies exist which would deliver information about these relationships one has to work with biologically reasonable ad hoc assump-

tions which are then tested and fine-tuned by comparing model output with patterns in the real system (Grimm, 1994; Grimm et al., 1996).

4.2. Growth

For the description of optimal tree growth we need a sigmoid function to define the growth rate in relation to actual tree size and the upper limit of tree height. The depression of the growth rate under less than optimal conditions (e.g. at higher pore water salinities, or with a strong competition of neighbouring trees) is taken into account by including a multiplier for correcting the ‘optimal’ function. This multiplier should range between 0 (pessimal conditions) and 1 (optimal conditions).

KiWi uses the time-discrete ($\Delta t = 1$ year) form of the growth function for optimal conditions and the correction factor for salt stress already provided and well documented for the FORMAN model (Chen and Twilley, 1998):

$$\frac{\Delta \text{dbh}}{\Delta t} = \left[\frac{G \cdot \text{dbh} \cdot (1 - \text{dbh} \cdot H / \text{dbh}_{\max} \cdot H_{\max})}{274 + 3b_2 \cdot \text{dbh} - 4b_3 \cdot \text{dbh}^2} \right] \cdot S(U) \cdot C(F_A)$$

with

$$H = 137 + b_2 \cdot \text{dbh} - b_3 \cdot \text{dbh}^2 \tag{5}$$

(height of the tree)

and

$$S(U) = \frac{1}{1 + \exp[d(U_i - U)]} \quad (\text{salt stress factor}) \tag{6}$$

H and dbh are indicated here in cm. The species-specific parameters G , dbh_{\max} , H_{\max} , b_2 , b_3 , d and U_i are provided for *Avicennia germinans*, *Rhizophora mangle*, and *Laguncularia racemosa* by Chen and Twilley (1998) (Table 1). The value U specifies the salinity at the stem position of the tree.

The second factor, $C(F_A)$, considers tree-to-tree competition. We assume that growth is impossible if the ‘strength of neighbourhood’ F_A (Eq. (3)) exceeds 0.5. Below this threshold, $C(F_A)$ must be 1 if the tree has no competing neighbours, and must decrease with the ‘stress factor’ F_A . Thus, $C(F_A)$ is given by:

$$C(F_A) = (1 - 2 \cdot F_A) \tag{7}$$

4.3. Mortality

Doubts exist as to any direct relationship between tree mortality and tree age in the case of mangrove trees, because, as in some terrestrial forests, trees which have been exposed to the highest stress may become the oldest trees. Moreover, the age of mangrove trees is generally unknown. In the FORMAN model Chen and Twilley (1998) handle this problem by using different mortality functions. KiWi abandons any

Table 1
Species-specific parameters for *A. germinans* and *R. mangle* used in the KiWi model

Parameters	Description	<i>A. germinans</i>	<i>R. mangle</i>	References
a	Scaling factor in Eq. (1)	10	10	Assumed
F_{\min}	Min. value of the FON (Eq. (2))	0.1	0.1	Assumed
G	Grow constant	162	267	Chen and Twilley (1998)
D_{\max}	Maximum dbh (cm)	140	100	Chen and Twilley (1998)
H_{\max}	Maximum height (cm)	3500	3000	Chen and Twilley (1998)
age_{\max}	Maximum age (year)	300	250	Chen and Twilley (1998)
b_2	Constant in height to dbh relationship	48.04	77.26	Chen and Twilley (1998)
b_3	Constant in height to dbh relationship	0.172	0.396	Chen and Twilley (1998)
d	Constant for salt effect on growth	-0.18	-0.25	Chen and Twilley (1998)
U_I	Salt effect on growth (g kg^{-1})	72.0	58.0	Chen and Twilley (1998)
ε	Additional yearly mortality	1/600	1/500	Assumed

relationship between age and mortality. Instead, we assume that the probability of dying increases after continuous periods of growth depression. In the model growth depression is effected by the two stress factors pore water salinity and competition. For the calculation of growth depression we do not differentiate between these particular causes. We only consider the effect on the yearly increment of the stem diameter, Δdbh . If Δdbh decreases in time the probability that the tree will die increases. However, it is unrealistic to assume that a tree reacts immediately to bad environmental conditions. As is known from field studies a tree can survive with a certain probability even when it does not grow during a certain time period. We thus included a ‘memory effect’ — each tree ‘remembers’ the growth increment Δdbh over a specified time range (5 years in KiWi). A tree dies if the mean over this time range, $\overline{\Delta dbh}$, is less than 1/2 of the average stem diameter increment under optimal conditions, D_{\max}/age_{\max} (Table 1). The use of age_{\max} to define the value ‘1/2’ is optional. Field measurements focusing on the varying mortality of mangrove trees under different stress regimes were able to validate this value. Note that $\overline{\Delta dbh}$ decreases the more the stem diameter approaches its maximum, or the more the environmental conditions, both abiotic and biotic, deteriorate in consecutive years. The tree ‘revives’ if the stress period is followed by better years in which $\overline{\Delta dbh}$ increases. This happens, for example, when pore water salinity decreases or when neighbouring trees die. To consider other sources of tree mortality we use a small, additional yearly mortality ε . Altogether, the mortality submodel assures a moderate maximum age of a single tree.

4.4. Sapling establishment

Saplings are distributed randomly at the beginning of a simulation year. Whether a sapling establishes or not is dependent on the environmental conditions at the sapling’s position. The probability of establishment at a given position is taken to be:

$$P_{\text{Sap}}(x,y) = (1 - 2 \cdot F(x,y)) \quad (8)$$

Biologically, Eq. (8) expresses how the probability of establishment depends on the competition strength of the older trees influencing the sapling. $P_{\text{Sap}}(x,y)$ is analogous to the correction factor $C(F_A)$ (Eq. (7)). The rationale behind this analogy is that, under conditions which prevent tree growth, it should also be impossible that a sapling becomes established. The influence of pore water salinity on sapling establishment is not considered directly. But an established sapling will die in the same year if this factor prevents its growth, i.e. the establishment module is run first, then the growth module.

4.5. Output variables

In order to analyse the output from the model, we use the relationship between dbh and the crown diameter of *R. mangle* trees and the relation between dbh and the biomass of *R. mangle* and *A. germinans* trees, respectively. The biomass calculation has been approximated by Fromard et al. (1998). It is expressed for *A. germinans* as:

$$\text{BIOM} = 1.2 - 1.3 \cdot D + 0.5 \cdot D^2 \quad (R^2 = 0.9) \quad \text{for } 1 < \text{dbh} < 4 \text{ cm} \quad (9)$$

and

$$\text{BIOM} = 63.3 - 17.1 \cdot D + 1.2 \cdot D^2 \quad (R^2 = 0.9) \quad \text{for } 4 \text{ cm} < \text{dbh} \quad (10)$$

and for *R. mangle* as:

$$\text{BIOM} = 8.1 - 5.6 \cdot D + 1.2 \cdot D^2 \quad (R^2 = 0.9) \quad (11)$$

with BIOM as biomass (t ha⁻¹) and $D = \text{dbh}$ (cm).

The calculation of the crown diameter of *R. mangle* (used for Fig. 4) derives from the approximation given by Cintrón and Schaeffer Novelli (1985):

$$r = 0.222 \cdot D^{0.654} \quad (12)$$

with crown diameter r (m) and $D = \text{dbh}$ (cm).

5. Results

5.1. Intra-specific competition

The explicit description of tree spacing by KiWi enables the process of self-thinning caused by competition among individuals to be studied. Our working hypothesis is that self-thinning occurs in natural mangrove forests in a similar way to that in terrestrial forest. We therefore studied self-thinning in order to test the FON approach, i.e. to see whether FON is able to reproduce self-thinning realistically.

We started with randomly distributed sapling cohorts of *A. germinans* and *R. mangle*. The size of the simulated area was 1 ha according to the ecological scale of the empirical studies being under focus. Initial density was 1000, 2000 and 3000 individuals per ha; initial age was 0, and dbh 1.37 cm. After initialisation no new sapling entered the plot. Fig. 3 shows self-thinning trajectories, i.e. how the number of individuals and the averaged biomass change in the course of time as a result of growth and mortality. The lines with a slope of $-3/2$ are the so-called ‘self-thinning lines’ (Begon et al., 1991). Regardless of initial density, all curves approach this line after a certain time period. The slope of $-3/2$ means that biomass increases faster than density decreases. This trend is not unlimited because the trees ‘cannot grow to the sky’. Consequently, the self-thinning section of the trajectories is followed by a section where the loss of individuals is balanced by biomass increase of the remaining trees. The peak at the beginning of the trajectories of *A. germinans* (Fig. 3a) is caused by the different calculation of the biomass for trees with a dbh larger or smaller than 4 cm (Eqs. (9) and (10)). A comparison of Fig. 3a and b shows that the cohorts of *A. germinans* reach the self-thinning line at higher N than those of *R. mangle*.

Fig. 4 illustrates the self-thinning process described above. It presents the model output of an exemplary simulation run of an *R. mangle* cohort initialised at 1000 individuals per ha.

5.2. Inter-specific competition

Simulations were run with the same configura-

tion as for the self-thinning process, except that now both *R. mangle* and *A. germinans* occur in the same plot. If both species enter the habitat at the same time, *R. mangle* dominates the forest at the beginning (Fig. 5a). This is caused by the faster initial growth of this species. However, because *A. germinans* has a longer mean lifetime, dominance is reversed after 200 years.

In Fig. 5b, saplings of *A. germinans* enter the plot 10 years after *R. mangle*. In this scenario, the initial advantage allows *R. mangle* to suppress the growth of *A. germinans* individuals, leading to a markedly smaller overall biomass of *A. germinans*. On the other hand, if *A. germinans* is the first species in the plot and *R. mangle* enters 10 years later, *A. germinans* dominates *R. mangle* all the time (Fig. 5c). Note that in all three scenarios in Fig. 5, the maximum overall biomass that 1 ha can produce is more or less the same (about 90 000 kg ha⁻¹).

6. Discussion

The main objective of this paper is to introduce the FON approach and to demonstrate its suitability for the analysis of tree spacing effects on forest dynamics. The suitability of the FON approach was tested by its implementation in the KiWi model. Here, we will first discuss whether KiWi provides new insights into mangrove forest dynamics, before assessing the potential of the FON approach in general.

6.1. The KiWi model

Compared with FORMAN (Chen and Twilley, 1998) KiWi uses one mortality function only. This ‘memory function’ considers parts of the tree’s life history. Tree mortality is described as depending on this function only and, in turn, on the growth rate of the trees. The model results show that this description is sufficient to keep the maximum age within a reasonable range. Since there are doubts as to any direct relationship between tree age and mortality in the case of mangrove trees, and that the age of a mangrove tree cannot be determined as yet, this feature of KiWi is especially important.

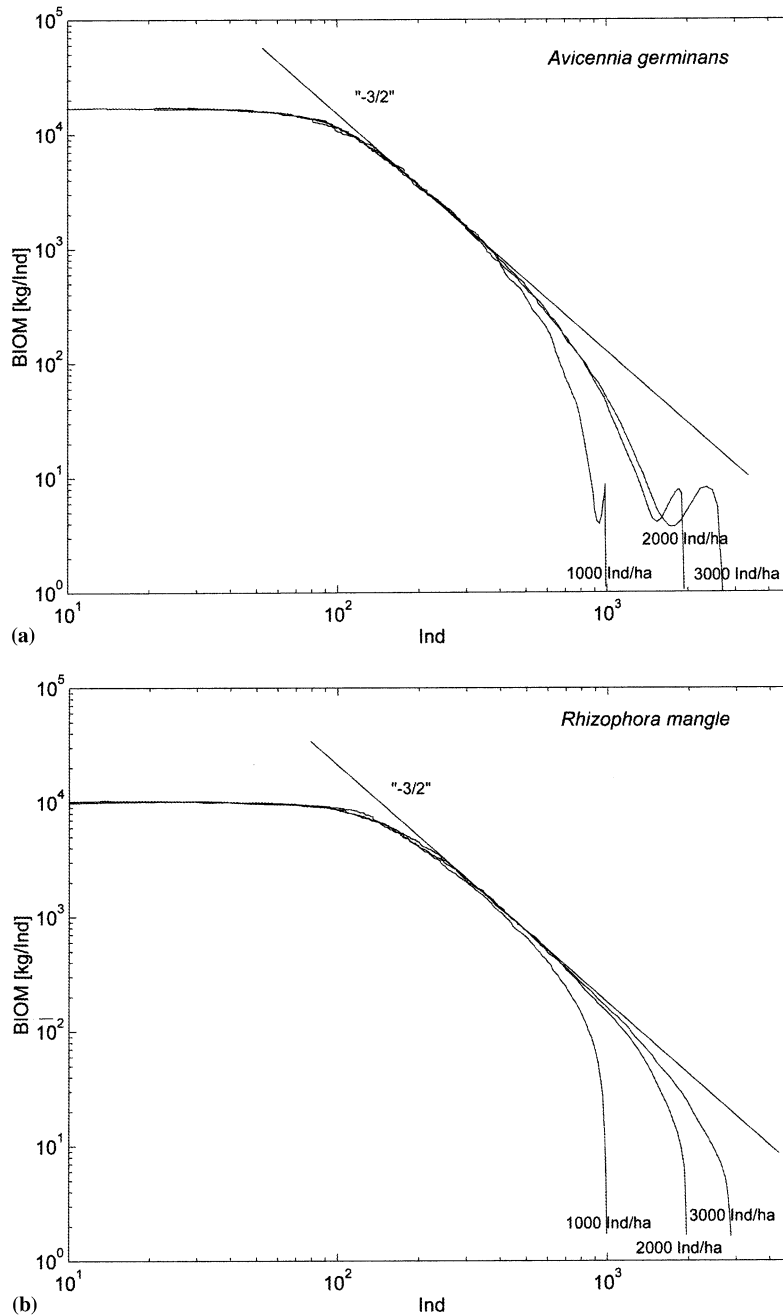


Fig. 3. Self-thinning trajectories of even-aged mangrove cohorts, i.e. development of density and averaged biomass in the course of time. Initial points of the trajectories are labelled with initial densities. (a) *A. germinans*; (b) *R. mangle*.

Another powerful feature of KiWi is its potential to give explicit consideration to tree spacing and, in turn, local competition. The resultant

self-thinning trajectories match theoretical (Begon et al., 1991) and empirical trajectories (Lonsdale and Watkinson, 1982; Cintrón and Schaeffer

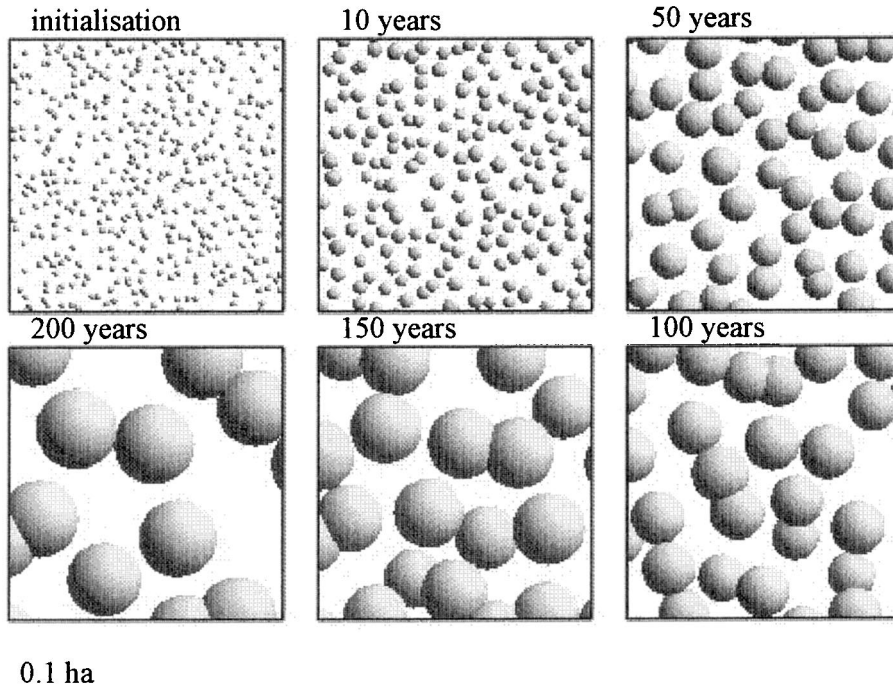


Fig. 4. Exemplary simulation run showing the development of a *R. mangle* cohort with an initial density of 1000 individuals per ha. The panels show the distribution of trees for consecutive time steps. The fate of selected individuals can thus be traced.

Novelli, 1985) astonishingly well. Thus, the self-thinning simulations show that the phenomenological description of local competition by ZOIs and FONs leads to realistic stand dynamics.

The self-thinning trajectories might suggest, erroneously, that the number of individuals is the independent variable and overall biomass the dependent one. Overall biomass increases due to the growth of the trees. Due to the constant and limited space available, an increase in overall biomass directly influences mortality and, in turn, the number of individuals. On the other hand, a high tree density may cause a depression of individual growth rates, which means there is a mutual relationship between biomass and density.

The overall maximum biomass which can be produced per ha is species-independent and limited to about $9 \times 10^5 \text{ kg ha}^{-1}$. This result is confirmed by the results of the two-species system (Fig. 4). The specific values of the maximum overall biomass and of the density associated with it are dependent on the assumed relationship be-

tween FON and dbh, and on the calculation of the biomass as a function of dbh. Hence, they are suitable quantities for calibration and validation of KiWi against field data.

The self-thinning trajectories can also be used for validation. Although the specific slope of “ $-3/2$ ” cannot be expected for uneven-aged or mixed forests, a comparison of simulated forests with structural data for real forests of known age will help to prove the goodness-of-fit of the FON assumptions and to improve our understanding of the colonisation dynamics of existing habitats.

Despite the demonstration character of the simulations focusing on inter-specific competition, the results shown in Fig. 5 are interesting. Depending on the temporal sequence of establishment and on the delay between the date of emergence of the different species, the species dominating the forest may alternate.

The structure of the model is such that extensions can easily be made. Other heterogeneously distributed environmental parameters (e.g. flood

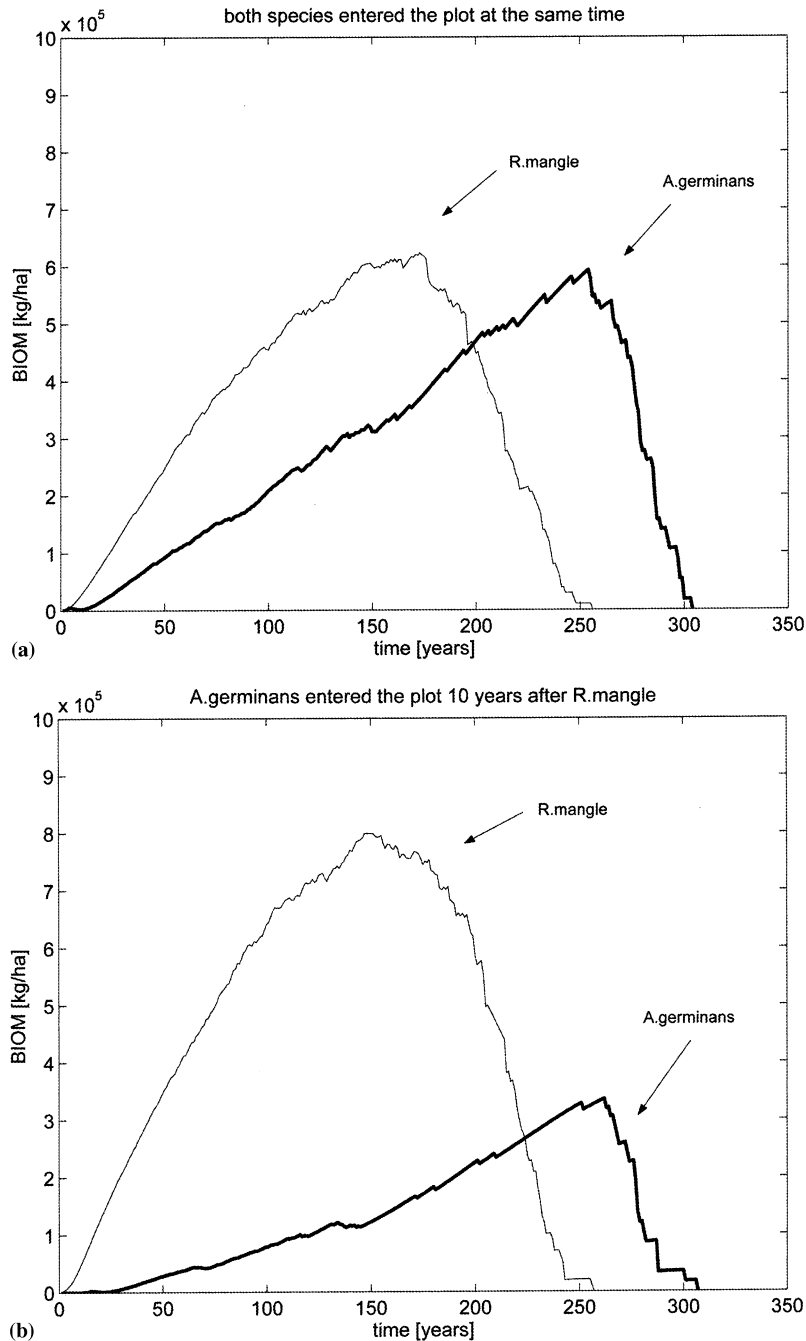


Fig. 5. Plot of overall biomass against time for two competing cohorts of *A. germinans* and *R. mangle*. The runs were performed as in Figs. 3 and 4: the habitat is initialised by a fixed numbers of individuals. After this initialisation, no more individuals enter the plot. (a) Saplings (1000) of both *A. germinans* and *R. mangle* enter the area at the same time. (b) The saplings of *R. mangle* enter the plot 10 years earlier than *A. germinans*. (c) The saplings of *A. germinans* enter the plot 10 years earlier than *R. mangle*.

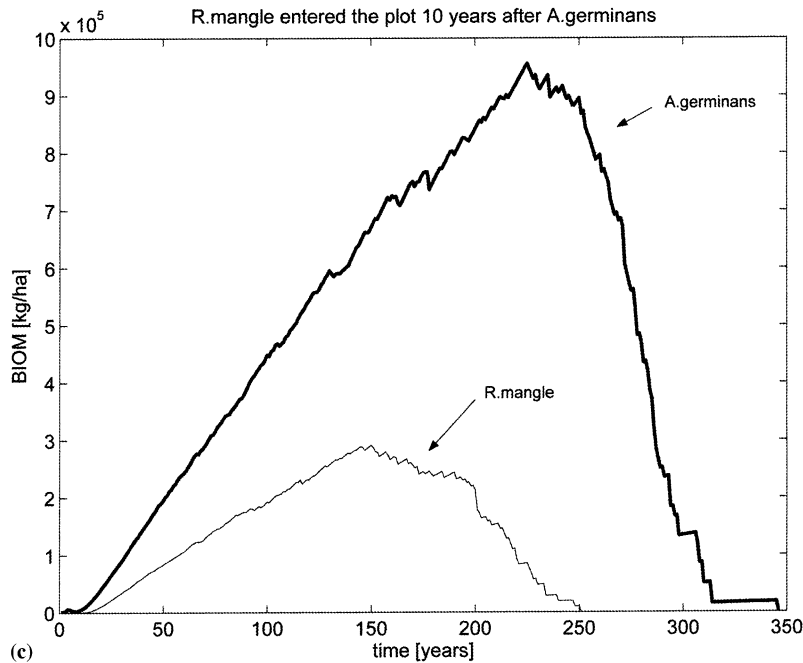


Fig. 5. (Continued)

ing, light and nutrient availability) can be described by additional maps (analogous to the salinity bitmap) and would then enter the growth equation as additional correction factors or logical rules. Likewise, differences in the environmental conditions for saplings, younger trees, or mature trees in different soil horizons can be considered by using further maps.

However, even the results obtained with the most simple version of a mangrove model based on the FON approach, i.e. the KiWi model, are promising and suggest further analyses using this and extended models. The KiWi model seems to be a step in the right direction towards the tool for theoretical synthesis needed by mangrove research.

6.2. The FON approach

FORMAN (Chen and Twilley, 1998), considers competition as well that is related to density of trees—using a mechanistic relationship with light. The FON approach is phenomenological in the same way as the Lotka–Volterra model of compe-

tion, but at the individual and neighbourhood level, not the population level. Competition is described by its results, not by its mechanism. Its consideration is not specifically linked to any resource. Although FON does not differentiate between the specific kinds of neighbourhood competition (e.g. canopy or root competition), the preliminary results of KiWi show that FON is a good metaphor for describing local competition. This may be due to the fact that the FON approach combines the advantages of grid-based and ZOI models, i.e. the emphasis on neighbourhood description with explicit consideration of the continuous space.

The function describing the FON, as well as the minimal field strength at the boundary of the ZOI of a tree, are not derived from field measurements. However, the analysis of aerial photographs could help to derive empirically motivated functions and parameters. Furthermore, the integration of photo imaging, field experiments and simulations would offer new opportunities for tree competition research. This could be especially important with regard to root spacing, considering

the complicated and hence limited options for field experiments in most cases.

Finally, it should be noted that the FON approach is not limited to mangrove forest models. In our opinion, FON provides the basis for a great number of powerful models for explicit analysis of spatial heterogeneity and neighbourhood effects, not only of other forests and plant communities, but also of communities of other sessile organisms, e.g. benthic organisms. We do not view FON as an exclusive alternative to grid-based models, but as a tool for tackling problems which cannot be addressed with grid-based models. Often, a combination of FON at the local scale and grid cells at larger scales might be the most appropriate choice.

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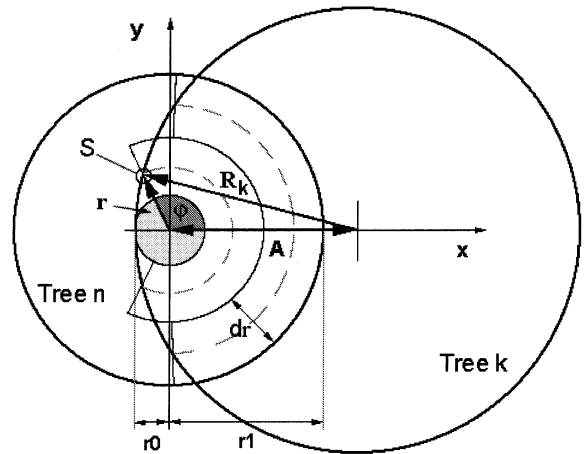
Appendix A. The calculation of F_A

As mentioned in Section 3, interpreting F_A as a mean value tremendously simplifies the calculation of the integrals in:

$$F_A^k = \frac{1}{A_{n \neq k}} \int_{A'} \text{FON}_n(x,y) da'. \tag{A1}$$

But still, depending on the complexity of the local FON, it could be hard to give an exact solution for Eq. (A1). This appendix gives a simple but effective generic algorithm to compute (Eq. (A1)) approximately.

In the given form the algorithm addresses only FONs that are rotationally symmetrically, i.e. the only independent variable is the distance r to the stem position. The idea of this algorithm is to divide the overlapping area of two ZOIs, into pitch circle rings (Graphic A1: dividing the overlapping area of two trees into pitch circle rings).



Hence you have to implement a function like this:

```
// Calculate the integral over the pitch circle
// ring with
// the half central angle phi and the thickness
// (r1 - r0)
double Tree.FON_PCR(double phi, double r0,
double r1)
{
```

```
return  $\int_{-\varphi}^{\varphi} \int_{r0}^{r1} \text{FON}(r) dr d\varphi;$ 
```

```
}
```

Due to the rotational symmetry the φ -integral collapses to the factor 2φ .

Now, if we focus on the k th tree, we have to integrate the FON of the n th tree over the over-

lapping area of the n th with the k th tree. We calculate this in the local system of coordinates of the n th tree with the origin at its stemming point and the x -axis pointing toward the stemming point of the k th tree (Graphic A1).

```
// Calculate the integral over the overlapping area
of two trees.
// treeK is the focused, treeN the neighbour tree.
// treeN.R resp. treeK.R give the radius of the
ZOI/FON.
double FA_kn(tree treeK, tree treeN)
{
    result = 0.0// suppose, they do not overlap
    A = distance between the steaming positions
    if (A > treeN.R + treeK.R)
    return result; // no overlap
    // first we compute the max. diameter of the
overlapping area
    r0 = A - treeK.R // 'left' side of overlap-
ing area
    if ( r0 < 0.0)
    {
        // a whole concentric circle (grayed in Fig.
A1) is overlapped
        r0 = -r0;
        result = treeN.FON_PCR( $\pi$ , 0.0, r0);
        if (r0 > = treeN.R)
        {
            // treeN is completely overlapped by treeK
return result;// return the (exact) result to the
caller
        }
    }
}
r1 = min( treeN.R, A + treeK.R); // 'right' side
of overlapping area
// the (rest of the) overlapping area reaches from
|r0| to r1
// and is now divided into nStrides pitch circle
rings.
// (in Fig. A1 nStrides is only 2)
dr = (r1 - r0)/nStrides; // s. Fig. A1
r = r0 + dr/2; // centre radius of the first PCR,
s. Fig A1
for (i = 0, i < nStrides, + + i)
{
    // we have to calculate the angle  $\varphi$  ( $\square$  in Fig. A1).
// with a little help from Pythagoras the coordi-
nates of the
```

```
// intersection S (s. Fig. A1) are:
x = ( $A^2 + r^2 - \text{treeK.R}^2$ )/(2*A);
y = sqrt( $r^2 - x^2$ );
// and hence  $\varphi$  is given by:
phi = arctan(y/x);
// add the integral over this pitch circle ring
result = result + treeN.FON_PCR( $\varphi$ , r dr/2,
r + dr/2);
r = r + dr; // go to the next pitch circle ring
}
return result; // return the result to the caller
}
```

Next, the summation in Eq. (A1) has to be performed, i.e. the summation of the overlapping FON of all trees:

```
// Calculate FA for all trees.
// N is the total number of trees.
// tree[k].FA holds the result for the kth tree
void CalculateFA( void)
{
    // supposing you have an array [0...N-1] of
trees...
    for (n = 0; n < N; + + n)
        tree[n].FA = 0.0;
    for (k = 0; k < N; + + k)
    {
        for (n = k + 1; n < N; + + n)
        {
            tree[k].FA = tree[k].FA + FA_kn( tree[k],
tree[n]);
            tree[n].FA = tree[n].FA + FA_kn( tree[n],
tree[k]);
        }
    }
    // get rid of the dimension: dividing by the ZOI
tree[k].FA = tree[k].FA/( $\pi*\text{tree[k].R}^2$ );
}
}
```

Although the code presented here has not been optimised at all, performance of this algorithm should not be worse than traversing a huge grid.

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