

Modelling competition with the field-of-neighbourhood
approach

-

from individual interactions to population dynamics of
plants

Dissertation
zur
Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)

dem
Fachbereich Biologie
der Philipps-Universität Marburg

vorgelegt von

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geb. 29.11.1971 in Saalfeld

Leipzig, 01.02.2002

Vom Fachbereich Biologie der Philipps-Universität Marburg als Dissertation
am 22.04.2002 angenommen.

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Tag der mündlichen Prüfung am 30.04.2002

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1. INTRODUCTION

In this thesis, new individual-based modelling approaches are used to analyse intraspecific competition in plant populations. But what, exactly, is ‘competition’, and why is it important to apply new modelling approaches to plant populations? Competition is defined as “*the negative effects that one organism has upon another by consuming, or controlling access to, a resource that is limited in availability*” (Keddy 1989, p. 2). The first part of the definition states that individuals (or populations) *have negative effects upon each other* and these effects should be measurable and testable. The second part indicates the mechanism that causes the negative effects. A variety of experiments have been performed that looked for the division of resources between individuals and furthermore, they have attempted to identify the conditions, e.g. level of resource availability under which competition occurs (e.g. McConnaughay & Bazzaz 1992, Brisson & Reynolds 1994, 1997a, Colasanti & Hunt 1997, Berntson & Wayne 2000). Other definitions specify the negative effects by stating that competition is “*the ability of one individual to inhibit the survival and/ or growth of another individual*” such that this interaction “*reduces the fitness of one or both of them*” (Crawley 1997, p. 239 and 512).

Plants have several characteristics that should be considered in theoretical studies of competition, in particular sedentariness and local interactions: *Sedentariness*: A plant is at the mercy of its local environment and its performance depends on spatial heterogeneity around its stemming point. Population dynamics, which emerges from individual plant performances, is thus affected by spatial heterogeneity over scales from seeds to whole populations. *Local interactions*: Plants interact with other plants only in their neighbourhood. Population dynamics is therefore influenced by the spatial distribution of individuals and as a consequence, models need to specify the location of individuals to properly describe population dynamics.

Competition between individual plants is thus inherently local but to date, theoretical models have either ignored spatial aspects of competition or have, as will be shown in the Chapter 2, disadvantages that restrict their application to specialised fields of plant ecology or to small-scale investigations of cohort-dynamics. Modelling approaches that consider local competition are tessellation models (Kenkel 1990, Okabe *et*

al. 1992, Sletvold & Hestmark 1999) fixed-radius-neighbourhood models (Pacala & Silander 1985, Pacala 1986, 1987), zone-of-influence models (Wyszomirski 1986, Schwinning & Weiner 1998, Wyszomirski *et al.* 1999) and ecological-field models (Wu *et al.* 1985, Walker *et al.* 1989). None of these approaches, however, has been used to study transgenerational population dynamics, including reproduction, establishment, competition between individuals of different age, and mortality.

There is thus a major gap in theoretical studies of plant competition: the intra- and transgenerational consequences of sedentariness and local interactions have not yet been fully explored. This is due mainly to the lack of an appropriate modelling approach. However, a recently developed modelling approach has the potential to fill this gap: the field-of-neighbourhood approach (Berger & Hildenbrandt (2000). This approach attempts to combine advantages and avoid drawbacks of earlier approaches. Compared to the earlier approaches, the field-of-neighbourhood approach evades considering real resources when modelling competition. Instead, a phenomenological description of the outcome of competition is used. Originally, the field-of-neighbourhood approach was developed to model Mangrove forest dynamics (Berger & Hildenbrandt 2000) but not to address theoretical problems. Therefore, one of the two main objectives of this thesis is to use this approach in the domain of earlier theoretical modelling approaches namely the development of size hierarchies in even-aged monocultures and to check if new insights can be gained. The second objective is based on the flexibility of the field-of-neighbourhood approach: reproduction, establishment, and mortality can easily be taken into account (Berger *et al.* 2002) but this has not been done so far. Therefore, I will for the first time use an individual-based, spatially explicit modelling approach to study transgenerational population dynamics. In the following, the topics of these two objectives – size-hierarchies and population dynamics – are introduced in more detail.

The development of size hierarchies in plant populations has attracted the interest of researchers for a long time (e.g. Benjamin 1993, Bonan 1993, Hara & Wyszomirski 1994, Weiner 1995, Weiner *et al.* 1997, Wyszomirski *et al.* 1999, Stoll & Weiner 2000, Weiner *et al.* 2001). Of particular interest were the identification of the patterns, i.e. the proper characterisation and quantification of size structures, and the process leading to the observed patterns, i.e. the mode of competition. As suggested by Weiner (1990), competition between individuals can be asymmetric or symmetric where ‘asymmetric’ refers to the case that a larger individual has a competitive advantage over the smaller individual. He furthermore refined this definition to size-symmetric or size-

asymmetric competition: Symmetric competition is a competitive advantage of a larger individual that is proportional to its size whereas in asymmetric competition the larger individual has an advantage that is over-proportional compared to its size. According to this definition, it was hypothesised that asymmetric competition should lead to greater size-variation than symmetric competition. Much effort has been made to determine the size-distribution of a competing population and moreover, to retrieve the mode of competition from such a distribution (Wyszomirski 1983, Miller & Weiner 1989). Although a consensus about the link between population-level patterns and the process on individual level has not been found, the importance of the interplay between competition and density, spatial distribution and initial conditions has been emphasised (Miller & Weiner 1989, Hara & Wyszomirski 1994, Weiner *et al.* 2001). Therefore, all these factors are included in the model of Chapter 3 where I will use the field-of-neighbourhood approach to gain new insights into the mode of competition of local interactions in plant populations.

Transgenerational population dynamics have hardly been analysed using earlier individual-based approaches such as the zone-of-influence (Wyszomirski 1986) or the ecological-field approach (Wu *et al.* 1985, Walker *et al.* 1989) because they have been designed for short-term small-scale investigations in a cohort (zone-of-influence models) or because it is very difficult to parameterise the model (ecological field models). To my knowledge, no individual-based plant population model exists to date that considers a full population-dynamical cycle, i.e. growth, reproduction and mortality. Hence, consequences of local competition on population dynamics remain unclear.

Obvious effects of local competition on individuals include the reduced growth of individuals and it has been shown that competition leads to size-differences in the participating individuals. If plants can not grow to a certain height they suffer a higher mortality risk than larger plants. It has been reported that mainly individuals of lower size classes experience high mortality (Kenkel *et al.* 1997, Martens *et al.* 1997, Miriti *et al.* 1998). Furthermore, the size of a plant often is proportional to its reproductive output (Thomas & Bazzaz 1993). Consequently, small individuals have less offspring than their larger conspecifics and contribute less to the next generation. Competition can also lead to the production of low-quality seeds that have for instance a lower weight. Such parental effects have been observed by Crone (1997a). Moreover, local competition influences not only growth but may also prevent the establishment of seeds in the vicinity of adult individuals (e.g. Tilman & Wedin 1991b, Foster 1999) and thus delay or prevent population growth.

Hence, local competition can have immediate effects, e.g. growth suppression, but also time-delayed effects, e.g. seed quality. As has been shown in theoretical population ecology, time-delays may lead to fluctuations in population size that are independent of external forces. This means in particular that intraspecific competition has the potential to lead to nonlinear, i.e. oscillatory or chaotic, dynamics, as has been shown theoretically and empirically in animal population ecology (e.g. Ginzburg & Taneyhil 1994, Berryman & Turchin 1997, Saitoh *et al.* 1997, Inchausti & Ginzburg 1998, Berryman 1999, Hansen *et al.* 1999, Stenseth 1999, Dennis *et al.* 2001, Turchin & Hanski 2001).

However, despite the importance of nonlinear dynamics for ecology, the knowledge of this theory has mostly been neglected by plant ecologists. Instead, it has been supposed that plant populations show a stable equilibrium and oscillatory or chaotic behaviour is a seldom exception to the rule (Crawley 1990). The reasons for this were assumed to be the following characteristics of plants: a) physiological plasticity and the ability to reproduce at small size. b) The effects of crowding can be ameliorated by long distance dispersal and c) Recruitment from long-lived seed-banks could also stabilise population dynamics (Rees & Crawley 1989, Crawley 1990). However, some empirical studies have shown, that nonlinear behaviour may occur in plants (Symonides *et al.* 1986, Tilman & Wedin 1991b, Crone 1997a, Buckley *et al.* 2001) and even asked for a re-evaluation of the stable-equilibrium theory (Dodd *et al.* 1995, Stone & Ezrati 1996, Cousens 1995). Therefore, in Chapter 4 I will use a model which is based on the field-of-neighbourhood approach to investigate population dynamical and spatial aspects of competition in a hypothetical population of perennials

The proximate goal of my thesis is to model and understand local competition, but the ultimate goal is to get a better understanding of the development of size hierarchies and of how local competition among individuals determines plant population dynamics. In particular, I will investigate the following questions:

Which individual-based modelling approaches exist to date that explicitly consider local competition?

How do these modelling approaches incorporate local competition, what are their main assumptions and to which problems can they be applied?

How are effects of competition measurable?

Which mode of competition results from a field-of-neighbourhood model?

What kind of population dynamics shows a field-of-neighbourhood model?

Which processes cause this population dynamics?

I will start in Chapter 2 with a review on model approaches that incorporate local competition. Emphasis is given to the individual-based approaches namely the fixed-radius-neighbourhood, the zone-of-influence, ecological-field and field-of-neighbourhood approaches with regard to their main assumptions, drawbacks and typical applications.

2. MODELLING COMPETITION – RECENT INDIVIDUAL-BASED APPROACHES

2.1. ABSTRACT

The common consensus between theoretical and empirical plant ecologists is that plants interact locally and therefore, local processes play an important role in individual performance. Consequently, recent modelling approaches focus on interactions between individual plants but dependent on the given question, different traits and processes have been emphasised. Therefore, individual-based approaches like the fixed-radius-neighbourhood, zone-of-influence, the ecological-field, and the field-of-neighbourhood make different assumptions regarding competition, space and resource use. This chapter attempts to evaluate the different individual-based modelling approaches with regard to local competition and therefore analyses their assumptions, application focus, advantages and shortcomings.

2.2. INTRODUCTION

Recently, plant competition models have increasingly focused on a “plant-centred” view of neighbourhood. This is mainly due to the general consensus between theoretical and empirical ecologists that plants interact locally, that local crowding reduces some measure of plant performance, e.g. growth, survival or fecundity, and that the effect of neighbours weakens with distance (Bergelson 1990, Brisson & Reynolds 1997a, Kadmon 1997, Aguilera & Lauenroth 1993).

But what is meant by a plant’s neighbourhood? It is certainly somehow connected to the position of plants, but spatial extent, shape and character of a neighbourhood are rarely known precisely beforehand. Ecological models have been a powerful tool for analysing different definitions of “neighbourhood” with regard to their outcome on plant performance measures [e.g. Wyszomirski *et al.* 1999, Weiner *et al.* 2001].

Furthermore, model results can be compared to what is known from empirical observations and by this means models generate a deeper understanding of plant interactions. The different assumptions about the shape, extent and character of a plant's neighbourhood have led to the development of several modelling approaches that will be introduced in this chapter.

At present, three major groups of individual-based neighbourhood models exist: grid-based neighbourhood models, tessellation models and distance models (Czárán 1997). All approaches assume that a) individuals are sessile, b) changes in population size result from local events, e.g. dispersal is limited in space, c) the fate of an individual can be followed, and d) interactions occur between neighbouring individuals. Hence, they understand interactions, mortality and reproduction as local events. The main differences in these approaches are the assumptions regarding spatial habitat structure and inclusion of vital characteristics.

The aim of this chapter is to characterise the existing individual-based modelling approaches regarding the inclusion of local neighbour interactions, the definition of a plant's neighbourhood, and the coverage of spatial and temporal scales. Furthermore, these assumptions suggest typical applications for each of these approaches, which will also be introduced.

2.3. GRID-BASED MODELS

Grid-based models have been developed from cellular automaton models (Wolfram 1986) where the central idea is a discretisation of space. The modelled area is typically represented by a regular lattice of cells, which provides the possibility to include spatial heterogeneity or spatially-limited interactions between ecological entities. The definition of an appropriate cell size is one demanding problem in grid-based modelling. Usually, cells should have a reasonable biological scale (Wissel & Jeltsch 1993, Grimm & Jeltsch 1996), e.g. smallest home range size (Wiegand *et al.* 1999a) or crown diameter of one mature tree (Jeltsch *et al.* 1996). The size of a single cell and the total number of cells determine spatial resolution and extend, respectively. Each cell has a location and an ecological state that may change in the course of time. Hereby, biological processes are translated into a set of functions or rules ("state transition rules") which define how the state of a cell changes depending on the current state of the focal cell and its neighbours.

Depending on the competitive neighbourhood interactions, the shape of the cells forms a square or a hexagon. Additionally, the extent of the neighbourhood has to be defined in advance. Two major forms of neighbourhoods have been used in cellular automaton models: the Neumann (4 neighbours in a square-cell grid) and the Moore (8 neighbours in a square-cell grid) neighbourhood. They assume that inhabitants of a particular cell interact only with the 4 or 8 adjacent neighbours, respectively. Grid-based models often extend this restricted neighbourhood definition by allowing interactions at different scales, e.g. one scale for competitive interactions and another scale for seed dispersal. Competitive interactions between neighbouring individuals occurs also via a set of rules or functions.

For local competition, however, grid-based models ignore the spatial dependencies within a cell (Grist 1999). That means, two scales are introduced – a local and a regional scale. In beech forests for instance, trees compete within a cell in a non-spatial way and between cells individual trees do not compete but influence each other via other spatial processes, e.g. wind damage (Rademacher *et al.* 2001). For the development of grid-based models it is therefore necessary to define a scale for local spatial correlation that is based on empirical knowledge.

The main advantages of grid-based models are their easy handling and computability which allows for a coverage of many temporal and spatial scales. Furthermore, all biological processes are easily translated into rules for the change of a cell's state rather than analytically traceable (differential) equations and hence, facilitate the communication between empirical and theoretical scientists and the inclusion of qualitative empirical knowledge.

In ecological modelling, this approach has been applied to a variety of questions, e.g. vegetation dynamics in semi-arid savannahs (Jeltsch *et al.* 1996, Jeltsch *et al.* 1998), problems of habitat fragmentation, metapopulations and extinction (Dytham 1995, Darwen & Green 1996, Bevers & Flather 1999, Caswell & Etter 1999, Valverde & Silvertown 1997, Hiebeler 2000), influence of disturbances such as a special fire-regime on vegetation dynamics (Ratz 1996, Li *et al.* 1997, Bradstock *et al.* 1998, He & Mladenoff 1999), developing vegetation patterns (Dunkerley 1998, Dunkerley 1999, Puigdefabregas *et al.* 1999), grazing and sustainable management (Fuls 1992, Silvertown *et al.* 1992, Dunkerley 1997, Weber *et al.* 1998, Wiegand *et al.* 1999b).

However, for ecological problems, which require the incorporation of individuals, grid-based models are often not the adequate approach. The rigid cell size restricts grid-based models to applications where individuals

are of comparable size and a detailed knowledge about neighbourhood interactions is available. A possible solution to overcome the problem of fixed cell sizes is to model variable cell sizes (e.g. Tischendorf 1997) though this would also destroy the main advantage of this approach – the simplicity in rules and implementation.

The spatial discretisation itself can distort the representation of biotic interactions and sometimes harden obtaining quantitative predictions concerning real empirical data.

2.4. TESSELLATION MODELS

Tessellation models explicitly consider the neighbourhood configuration of individual plants. Herein, the space is subdivided between plants with regard to their position and the position of their neighbours using a special function, e.g. Voronoi-, Dirichelet- or Thiessen-tessellation (Kenkel 1990, Okabe *et al.* 1992, Czárán 1997). Thus, depending on the neighbourhood situation, to every individual a particular portion of the space is available.

The simplest possible tessellation is the Dirichelet-tessellation or the Voronoi-diagram. Herein, all points, which are closer to the plant i than to all other plants, are assigned to plant i . Connecting the perpendicular bisectors of adjacent plants results in the smallest convex polygon of plant i (Fig. 2.1). This polygon is called the Voronoi- or Thiessen-polygon of plant i .

Since a tessellation is primarily a static structure, the dynamic process leading to the further tessellation of space has to be defined. The simplest process leading to a division of space is the simultaneous isotropic growth process. Herein, a set of plants distributed in space starts growing at the same time with the same growth rate. The growth process stops when two or more such “inflating” plants adjoin. Therefore, plants grow until they filled the Voronoi-polygon associated with their stem-points and finally, the space is tessellated (Fig. 2.1).

Tessellation models inherently assume the following: 1) neighbours are those individuals which have polygon sections in common. Although the neighbour definition of tessellation models is biologically plausible because extension and shape of a Voronoi-diagram depends on local density and the geometry of a plant’s neighbourhood, individuals having no contact in terms of a tessellation cannot influence each other. Accordingly longer-distance competition effects, e.g. in the second-order neighbourhood, are not permitted.

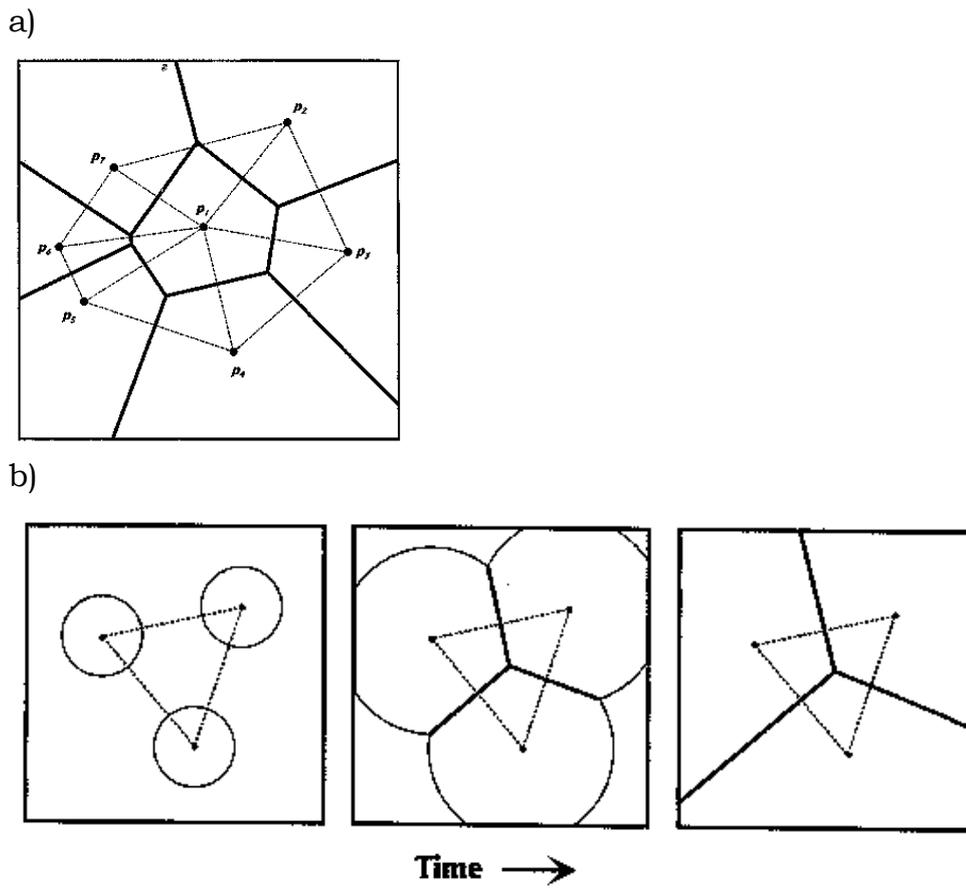


Fig. 2.1. Exemplary illustration of a Dirichlet tessellation (a) and of simultaneous isotropic (b) growth leading to the subdivision of space (after Czárán 1997).

2) If resources are distributed homogeneously in space the area of the Voronoi-polygon might be a good descriptor for the amount of resources and individual performance (Firbank & Watkinson 1987). Since most environments are heterogeneous and resource distribution is far from uniform this might set the sharpest limit for the application of tessellation models.

3) Space use is exclusive and 4) exhaustive. That means that any part of space belongs to and is utilised by only one plant. Exhaustive space use can be a realistic assumption when density is large enough but may be violated when applied to plant competition in unsaturated habitats. Accordingly, exclusive space use is also questionable in many cases, for instance many herbs have entangled root systems.

These assumptions together with a rather complicated methodology and a need for high computational effort set sharp limits to the application of tessellation models. Moreover, to my knowledge there exists no tessellation model that considers both birth and death processes. Hence,

the failure to model full population dynamics restricts the application of existing tessellation models to growth and death processes in even-aged stands. Therefore, Voronoi-polygons have mainly been used for the analysis of empirical studies, e.g. prediction of plant performances (Mithen *et al.* 1984, Aguilera & Lauenroth 1993, Sletvold & Hestmark 1999).

2.5. DISTANCE MODELS

The third group of modelling approaches - distance models – consists of four subgroups: fixed-radius models, zone-of-influence models, ecological field models and field-of-neighbourhood models. These models meet more or less the criteria for individual-based models of plant populations as demanded by Stoll & Weiner (2000), namely that every individual should have an explicit spatial position, it should have a basal extension where no other individual can occur and a zone of influence for interactions with other plants. Furthermore, number, size and distance to neighbours should be taken into account. In particular, these models represent individuals by an explicit spatial position and a circular zone where they gather resources and interact with other individuals. An important advantage in distance models is that they overcome the problem of scale because plants can grow over many scales and their interaction scale changes accordingly.

Additionally, making predictions concerning the influence of specific factors such as density, spatial pattern and size distribution, these models are testable in a way most general ecological models have not been (Weiner 1995, Czárán 1997, Weiner *et al.* 2001).

Beside varying complexity in implementation, the difference between the distance-model approaches is mainly the way they handle competition:

Fixed radius models consider competition in a rather abstract way, in ecological-field models competition is described mechanistically, in zone-of-influence models semi-mechanistically and in field-of-neighbourhood models phenomenologically. That means, one group of models concentrates on mechanisms of competition, i.e. resource dynamics and uptake, and investigates the emerging effects and the other group describes the general effects of competition on population level.

A detailed description of the distance-model approaches, their assumptions and drawbacks are the subjects of the following sub-chapters.

2.5.1 FIXED-RADIUS NEIGHBOURHOOD MODELS

The most simple way to model a “plant-centred” neighbourhood is to define a fixed circular area around each plant that is equivalent to the neighbourhood. Each individual has a circle of a fixed radius around its stem-point and all other individuals occurring within this circle are defined as neighbours. These neighbours affect the survival probability and the expected fecundity of a focal individual. The dependence of plant growth, fecundity and survival from neighbours are called the performance, survival, and fecundity predictor functions, respectively (Pacala & Silander 1985, Pacala 1986, 1987).

In the model of Silander & Pacala (1990), submodels (predictor functions) predict the fate of individuals at successive life stages from seedling to adult given the local density about each seedling. Local density is defined as the number of individuals that occur within a circle of radius r from the focal individual. The different predictor functions, e.g. fecundity or survivorship predictor, might be defined by circles of different radii and can be calibrated from field data. The construction of the fecundity predictor for example starts with setting neighbourhood radii to some initial values. Then, the number of neighbours are counted for each neighbourhood (n) and regressed against focal plant size with an appropriate functional form. Silander & Pacala used a hyperbolic function for the fecundity predictor which is in a 2-species case given by:

$$w_i = M_i / (1 + c_{ii}n_i + c_{ij}n_j)$$

where w_i is the biomass of a species i -plant, M_i is the biomass of species- i plant without neighbours, n_i and n_j are the number of neighbours of both species in the neighbourhood, and c_{ii} and c_{ij} are interference coefficient for intra- and interspecific interactions, respectively. Afterwards, the series of fits for different neighbourhood radii is evaluated with, e.g. a maximum likelihood method, which yields the “best” neighbourhood radii. Biomass predictors are converted to fecundity submodels by regressing seed set versus biomass. The same procedure is applied for the survivorship submodel. The dispersal submodel is derived from fits to plots of seedling number versus distance to mother plants and the function is calibrated from maps of seedlings that recruit from isolated differently-sized mother plants.

Given an initial seedling population size and spatial distribution, the population dynamics results from an application of the submodels, e.g. seedlings survive to adult size and reproduction with a probability that

depends on local neighbourhood conditions as predicted by the survivorship submodel. Accordingly, the number of seeds per individual is derived from the fecundity submodel.

Although the FRN approach is spatially-explicit and incorporates local competition, some modellers have subsequently neglected these important characteristics and applied a mean field approach for the sake of solvability (Pacala & Silander 1985). However, this simplification allows in fact for an analytical solution but averages local effects over the whole study plot.

From a historical perspective, the FRN approach was the first extension of models to include local spatial effects in a simple way and has been widely used on forestry (Dhote 1994, Biging & Dobbertin 1995). Therefore, FRN models stand between classical analytical models and advanced neighbourhood models: Compared to classical models they have the advantage that their parameters are easier obtained in field investigations than those aggregated measure, e.g. population growth rate, used in analytical models. Furthermore, the simple incorporation of spatial effects still allows analytical solutions and applicability to real-world data.

However, neighbour effects are considered in a strict sense: if another plant falls in the neighbourhood radius, the focal plant experiences the full effect of its neighbour (Czárán 1997). That means no other characteristic of a neighbour counts than its presence. But the actual effect of a neighbour may also depend on its distance and angular position or more importantly on its state, e.g. life stage or age (Bergelson 1990, Howard & Goldberg 2001) and some empirical studies have already shown that only the number of neighbours in a fixed radius is not a good predictor for plant performance (Sletvold & Hestmark 1999). Although extensions, i.e. consideration of age or life stage, are possible within the FRN approach, this would increase the number of relevant i -states and the dimensionality of the predictor functions and therefore, such a model would lose its analytical tractability. Furthermore, the consideration of more than 3 species is still tractable for specific cases but such a system or a higher-dimensional system becomes at least impractical and in most cases impossible to treat analytically.

2.5.2 ZONE-OF-INFLUENCE MODELS

Similar to fixed-radius neighbourhood models, individuals in the zone-of-influence (ZOI) approach have also an explicit spatial position and a circular zone that determines the distance up to which a given individual

interacts with other individuals. Furthermore, the ZOI represents the area from which individuals obtain resources, or change their environment. The ZOI is proportional to the size of a plant and hence, expands with the growth of an individual. Accordingly, the ZOI determines the neighbourhood of an individual: neighbours are those individuals that overlap in their ZOI and neighbours influence each others growth, reproduction or survival.

Conceptually, the growth of individuals depends on the amount of resources in the ZOI-area. If a plant grows isolated it always performs its maximum growth. The idea behind ZOI-models is that plants overlapping in their ZOI pre-empt resources which are in turn no longer available to the competitor. Hence, the more resources an individual obtains during competition the greater is its size or biomass increment. In general, overlap in the ZOI area decreases any measure of plant performance. Hence, a large relative overlap area decreases relative performance, i.e. the value of affected vital parameters relative to that without interactions, e.g. lowers a plant's growth or increases its mortality or leads to less offspring (Fig. 2.2).

A relative performance function (Fig. 2.2c) can either be fitted to experimental data or chosen from an analytical form. For the effect of more than one neighbour, a collision rule has to be defined which specifies how multiple overlaps affect performance. If the neighbours are assumed to act at the same time on a focal individual and the effect of one neighbour is independent of the presence of others, the collision rule is simultaneous and the joint effect is the product of individual effects.

If the interactions are assumed to act pairwise, i.e. at different times, then the collision rule is sequential. Herein, after each pairwise interaction the fate of the competitors have to be determined. Depending on the rules, both competitors may survive (contest competition) with the larger individual taking all or most of the resources (asymmetric competition) or both individuals share the resources more or less evenly and may die when the shares are insufficient for survival (scramble and symmetric competition) (Czárán 1997, Weiner *et al.* 2001).

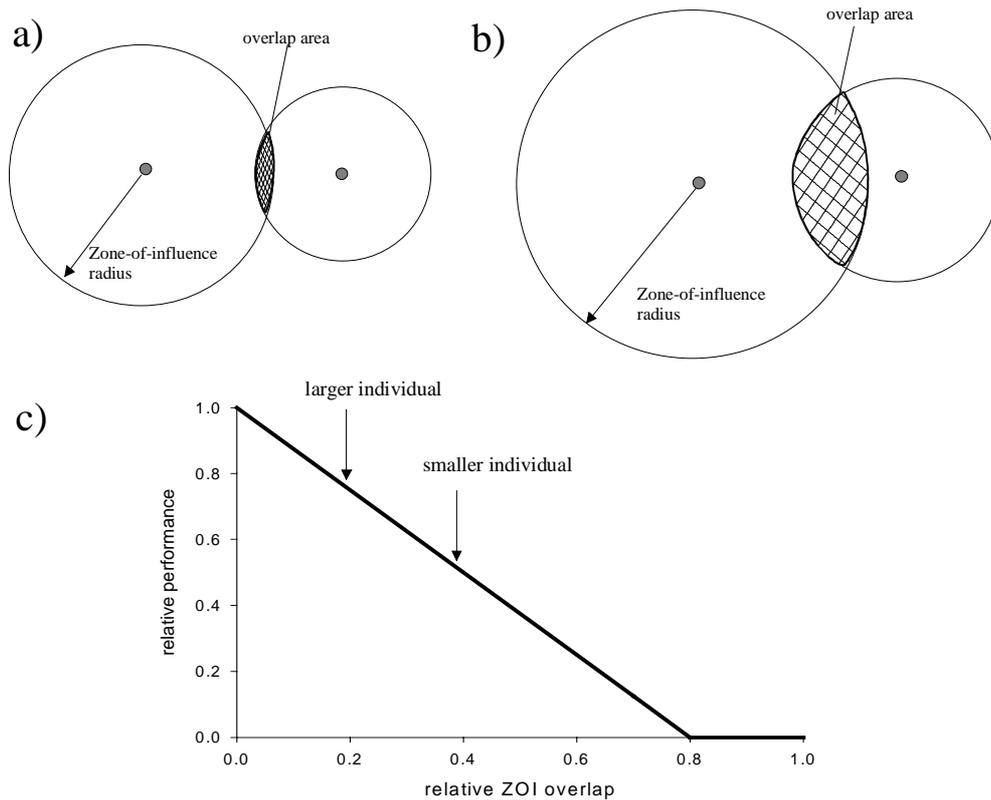


Fig. 2.2. Schematic illustration of the zone-of-influence approach. All individuals have an explicit position and a circular zone of influence (a). Should the ZOI of two or more plants overlap, they are assumed to be neighbours and neighbours compete for resources in the overlap area. Depending on the relative overlap the performance of an individual will be decreased according to a pre-defined function (c). Here, the smaller individual has a larger relative overlap than the larger individual and therefore, the smaller individual's performance will be lower. The initially larger individual (a) has an advantage due to a smaller relative ZOI overlap and will therefore grow larger in the course of time (b) than the smaller individual whose performance is lowered from the beginning.

The ZOI approach is very appealing because it is conceptually simple, semi-mechanistic and includes some essential aspects of spatial competition. Furthermore, as Stoll & Weiner (2000b) pointed out the definition of neighbourhood falls out of the assumptions of the model because in contrast to fixed-radius models (e.g. Pacala & Silander 1985) plants define their neighbourhood by themselves.

ZOI models have been applied to an age-structured model of a multi-species community (Czárán & Bartha 1989) but most applications focus on modelling size hierarchies in plant monocultures and understanding the effects of symmetric vs. asymmetric competition mode on size distributions (Wyszomirski 1983, Hara & Wyszomirski 1994, Schwinning & Weiner 1998, Wyszomirski *et al.* 1999, Weiner *et al.* 2001).

Weiner *et al.* (2001) investigated the effect of spatial pattern, density and competitive asymmetry on size structure dynamics using a ZOI model. The growth form of isolated individuals is given by:

$$\frac{dB}{dt} = r \left(A - \frac{B^2}{B_{\max}^{4/3}} \right) = r \left(cB^{2/3} - \frac{B^2}{B_{\max}^{4/3}} \right)$$

where B and B_{\max} are actual and maximum biomass, respectively, t is time, r is initial growth rate. Hence, the authors assume that plants grow as circles and can be expanded to a three-dimensional ellipsoid with biomass B , as $A = cB^{2/3}$. Overlap in ZOIs indicates competition for resources in overlap areas and the resulting growth is determined from the effective area, A_e , i.e. the total area, A , minus the part of the ZOI-area lost to neighbours:

$$\frac{dB}{dt} = r \left(A_e - \frac{B^2}{B_{\max}^{4/3}} \right)$$

The calculation of the effective area depends on the rules for resource partitioning which reflects the degree of size-asymmetry in competition. When for instance the larger individual obtains all resources in the overlap area, competition is completely size-asymmetric.

Although the ZOI approach is very appealing for its plausibility it has several drawbacks: The mode of competition has to be specified by the modeller, e.g. how resources in the overlap area are divided among competitors. Therefore, the mode of competition does not emerge from the interaction between individuals but is an example of what Railsback (2001) refers to as “imposed behaviour”. The assumption of imposed behaviour largely restricts the insights that could be obtained from an individual-based model.

Furthermore, ZOI models do not differentiate between the influence of neighbours far or close from the focal plant, e.g. for a completely overlapped plant it is irrelevant in which part of its large neighbour it stands. This fact, however, may be of great importance for seedling germination and establishment.

2.5.3 ECOLOGICAL FIELD MODELS

The idea of ecological field (EF) models is that sedentary individuals not only depend but also locally modify their environment. Hence, EF models

consider the spatial distribution of critical environmental factors such as water, nutrients and light as a function of the spatial distribution of individuals (Wu *et al.* 1985, Czárán & Bartha 1992, Czárán 1997).

Individuals influence each other by altering the level of available resources, changing micro-climatic conditions or the concentration of allelopathic chemicals. Hence, interactions are considered mechanistically and the population dynamics consequences are “emergent” in this sense.

In this model approach, an individual changes its initially homogeneous environment around its rooting point in the form of explicit distribution functions for, e.g. soil water availability, light interception or nutrient concentration (Fig. 2.3). These distributions are defined as the ecological field of an individual (Wu *et al.* 1985). The fields of more individuals are assumed to superimpose but how superimposition works depends on the nature of the ecological factor. Superimposition of, e.g. light distribution functions, could simply be represented by a simple multiplicative function whereas nutrient concentration fields should be considered in a more complicated combination (Walker *et al.* 1989).

The germination, establishment or survival of seeds or adult plants depends on local values of the ecological fields. The dependence of population dynamical parameters should be estimated from empirical investigations and afterwards specified with analytical functions. Herewith, the short-term dynamics of a small community is predictable. The prediction then bases on the ecological interference potential surface that specifies the spatial distribution of the survival probability. Survival probability in turn results from the competitive effects of neighbouring individuals.

Li *et al.* (2000) applied the EF approach to investigate self-thinning in plant populations. The authors tried to show that ecological interactions among individuals that result from spatial effects at the microscopic level, i.e. availability of neighbourhood resources, lead to self-thinning at the population level. In their model, individuals interact through their zones of influence by altering the resource level in the neighbourhood. Such interactions are described via the intensity of an ecological field that has two parameters: the origin field intensity, I_0 , and its influence domain, D . The idea is that a plant alters the availability of resources in the neighbourhood and an influence-field arises only when resources are scarce. That means, the influence-field, I_0 , is zero when resources are abundant. When resources are limited, the influence-field $I_0 > 0$ and an individual has a sub-optimal growth rate and exerts the greatest impact on neighbourhood resources.

The influence domain, D , is defined as the distance up to which a plant could influence resource availability. Furthermore, the field intensity diminishes with distance from the plant's origin:

$$I(r) = I_0 \exp\left(-\frac{r^2}{2D^2}\right)$$

Interaction comes into play when the interaction domains of two individuals overlap. In the model, interaction intensity of individual j located at distance r_{ij} from individual i is calculated:

$$\Pi_{ij}(r_{ij}) = \frac{\kappa_{ij} \exp\left[-\frac{r_{ij}^2}{2(D_i^2 + D_j^2)}\right]}{\left[\frac{I_{0i}(D_i^2 + D_j^2)}{2I_{0j}D_j^2}\right] - \kappa_{ij} \exp\left[-\frac{r_{ij}^2}{2(D_i^2 + D_j^2)}\right]}$$

with κ_{ij} the interaction effect, I_{0i}, I_{0j} maximum influence intensities and D_i, D_j the influence domains.

The main assumption behind the EF approach is that individual and population processes can be explained by very basic processes such resource dynamics and resource use. This is quite reductionistic and moreover, requires an enormous effort to parameterise the model.

The application of the EF-approach has been limited because of several facts: 1) calculating the field potential of a community of many individuals is a time-consuming process (even with fast computers) and therefore the spatial scale and the number of individuals considered is very limited; 2) the extension of the EF-approach to long-term dynamics would only be possible by introducing many new parameters, which should be measured or estimated in empirical investigations.

Although it is possible to investigate the dynamics of a small population on a limited spatial scale, long-term predictions are not sensible with this approach since the outcome of small-scale simulations is expected to show a high sensitivity on spatial stochasticity (Czárán 1997). Hence, the application focus of EF models are small-scale, short-term tactic model of field cases with practical motivations, e.g. the determination of optimal sowing patterns for cultivated plants where the ecological field distributions are known (Walker *et al.* 1989, Li *et al.* 2000).

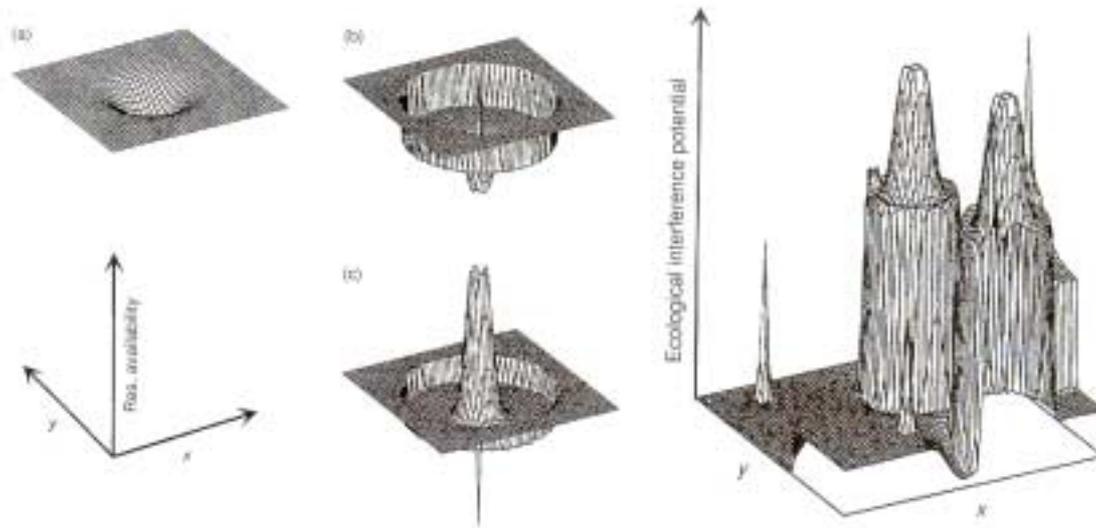


Fig. 2.3. Hypothetical examples for a) soil availability, b) light interception and c) soil nutrient concentration fields around a solitary tree and ecological interference field in a fraction of a mixed life-form plant community (after Wu *et al.* 1985).

2.5.4 FIELD-OF-NEIGHBOURHOOD MODELS

In a new modelling approach, the field-of-neighbourhood (FON) approach, Berger & Hildenbrandt (2000) try to combine advantages of zone-of-influence and ecological-field models.

Similar to the above-mentioned approaches, each individual has a circular zone around its explicit spatial position (or stem point) that defines its neighbourhood. Within this zone a field is defined that quantifies the strength of influence of the focal individual on its potential neighbours. In contrast to ecological field models, this field is rather abstract and no synonym for light, water or nutrient usage. No assumptions are made about the kind of resource in competitive interactions or its division among individuals. The field of neighbourhood is, in fact, a phenomenological description of the influence an individual has on growth, reproduction or survival of neighbours. Therefore, the FON approach phenomenologically considers individual local interactions without specifying the nature of these interactions.

The definition of the field shape is rather arbitrary but Berger and Hildenbrandt (2000) assumed the thinning of roots or crowns with distance from the stem point and chose therefore an exponentially

decreasing field (Fig. 2.4). Herein, the field reaches a maximum value in the central or basal area of the FON. The basal area could be interpreted as stem, tuft or tussock and therefore, the influence on neighbours was assumed to be maximal in this area and no seedlings could establish. From the basal area to the border of the FON the field decreases exponentially and it is thus assumed that the influence on a neighbour decreases the more distant this neighbour is located.

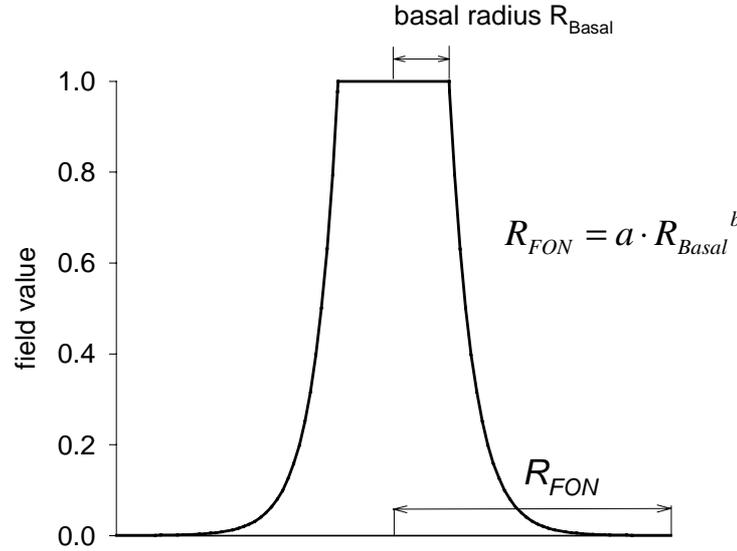


Fig. 2.4. Schematic illustration of the representation of a plant individual in the field-of-neighbourhood (FON) approach. All individuals have a basal extension, R_{Basal} , where no other plant can exist (basal area) and a zone of influence, R_{FON} , where interactions with other individuals take place. Moreover, the zone of influence is superimposed by a field that describes the strength of influence on potential neighbours. In contrast to zone-of-influence models, the zone of influence is not homogeneous but decreases exponentially from the basal area to the border of the zone of influence.

If the FONs of two individuals overlap they influence each other negatively in growth, survival or reproduction. In the FON approach the field area value F_A indicates how strongly the neighbour decreases the focal plant's performance (Fig. 2.5).

F_A is calculated by summarising the field values in the overlap-zones of all neighbours and afterwards scaled to the size of the focal plant:

$$F_A^k = \frac{1}{A} \sum_{n \neq k} \int_{A'} FON_n(x, y) da$$

where A is the FON-area of the k -th plant, n the population size, A' the overlap area (see Berger & Hildenbrandt 2000 for detailed description

of the algorithm for calculating F_A) and $FON_n(x,y)$ the value of the field-of-neighbourhood of a neighbour plant at the point (x,y) . Should the FON of more than two individuals overlap it is assumed that their FON superimpose independently and therefore, all pairwise influences are summarised. Thus, F_A is a relative measure and characterises the competitive pressure experienced by the focal individual and includes number, size and distance of neighbours. Therefore, F_A is easily incorporated in processes such as growth or reproduction.

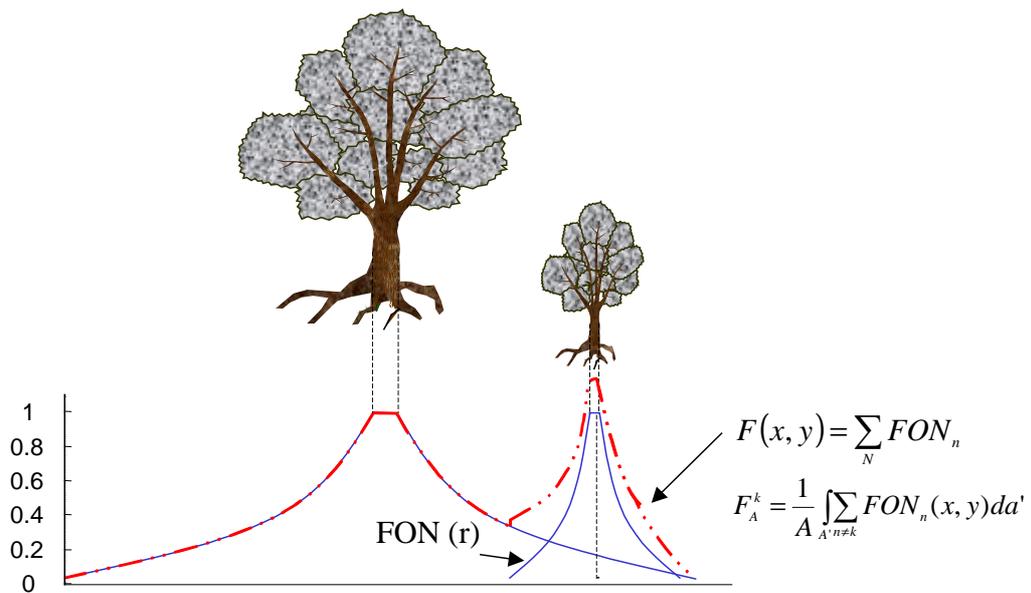


Fig. 2.5. Two individuals of different sizes, i.e. different basal radii (R_{Basal}), overlap in their fields-of-neighbourhood (FON). The field value of the FON at every point is given by $F(x, y)$. The integrated field value F_A calculates the influence of neighbours on a focal individual (after Berger & Hildenbrandt 2000)

Berger & Hildenbrandt (2000) developed a model for the dynamics of Mangrove forests. The model is roughly structured in two descriptive levels: the biotic level describes tree growth, mortality and establishment based on the FON of each plant and the second level describes the abiotic factors, e.g. salinity, nutrients or water, that potentially affect demographic processes. The model covers all population dynamical processes: Growth of an individual plant is a sigmoidal function under optimum conditions. Competition between neighbours influences growth, mortality and establishment. Local competition is derived from the F_A -value at a given location $F(x,y)$ (Fig. 2.5).

Growth, for instance, is calculated as the increase in diameter, dbh , during time-interval t :

$$\frac{\Delta dbh}{\Delta t} = [EGF] \cdot S(U) \cdot C(F_A)$$

where EGF is the empirically derived growth function, $S(U)$ is the salt stress factor and $C(F_A)$ includes tree-to-tree competition and is calculated via:

$$C(F_A) = \begin{cases} 1 - 2F_A & \text{for } F_A \leq 0.5 \\ 0 & \text{for } F_A > 0.5 \end{cases}$$

Therefore, individuals stop growing when the competitive pressure as quantified by F_A exceeds a certain threshold value, e.g. 0.5. Furthermore, in their model seedlings establish whenever the field values $F(x, y)$ at their position reach only under-critical values. The parameters specifying the shape of the FON were hypothesised.

Furthermore, the FON approach has been successfully applied to self-thinning (Berger & Hildenbrandt 2000, 2001, Berger *et al.* 2002).

2.6. SUMMARY AND DISCUSSION

The introduced modelling approaches have been developed with different intentions and scopes of application. A short characterisation of the model approaches, their basic assumptions and the scales they typically cover is given in Table 2.1.

For the investigation of competition, grid-based models are the best solution when competitive interactions occur mainly over one scale, and the interactions between cells are at least qualitatively known. A grid-based model can easily cover large areas and therefore, an important application has been the modelling of community dynamics with the special scope of management and prognosis (e.g. Weber *et al.* 1998, Wissel 2000). However, competition between individuals is not the focus but should be known beforehand.

Fixed-radius-neighbourhood models could predict the fate of a simple population in an abstract way, i.e. where not much detail is taken into account. The advantage of such a model is its analytical solvability but at the expense of biological realism.

In contrast, a zone-of-influence model is the approach of choice when an investigation focuses on details of individual interactions. Various ZOI-models have been developed for the investigation of size-

hierarchies and their dynamics (e.g. Wyszomirski *et al.* 1999, Weiner *et al.* 2001a). However, the predefinition of rules for competitive interactions is an example of imposed behaviour and thereby, probably restrict the insights gained in a particular study.

Ecological field models consider competition mechanistically. Although this allows a direct evaluation of empirical measurements of resource uptake, this procedure also entails complicated modelling details (Walker *et al.* 1989, Li *et al.* 2000c). For instance, the distribution of a resource in the soil and its dynamics should be described in specific functions that were empirically estimated.

Finally, the field of neighbourhood approach intends to overcome the greatest problems of the ZOI and EF models and by having more biological realism than the ZOI approach and being more general than the EF approach. Therefore, it would be very interesting to apply the FON approach to both questions which the earlier approaches attempted to answer namely the development of size hierarchies and to questions that exceed the application scope of earlier approaches, e.g. model full population dynamics.

	<i>grid-based models</i>	<i>tessellation models</i>	<i>distance models</i>			
			FRN	ZOI	EF	FON
Space	discrete	continuous	continuous	continuous	continuous	continuous
Neighbourhood definition	adjacent cells	common intersection of tessellation	number of individuals in fixed-radius	overlap in zone of influence	overlap in influence domain of ecological field	overlap in zone-of-influence of the field-of-neighbour-hood
scale of interactions	adjacent cells	first-order neighbours	variable	variable	variable	variable
Competition	pre-defined rules	occupation of space	abstract, occurrence of neighbours	division of resources	pre-emptying resources	phenomeno-logical, no resources
state variable	state of cell	polygon area	biomass	individual size (ZOI radius)	size-increment	individual size (basal radius)
Typical time-scale	arbitrary	cohort growth	arbitrary	cohort growth	single generation	arbitrary
Typical spatial scale	arbitrary	small	arbitrary	small	small	arbitrary
Computational effort	low	medium	low, analytical solvable	medium	high	medium
Typical applications	population and community dynamics	cohort growth	dynamics of populations and small communities	cohort growth	small communities	dynamics of populations and small communities

Table 2.1. A short characterisation for grid-based, tessellation, fixed-radius-neighbourhood (FRN), zone-of-influence (ZOI), ecological field (EF) and field-of-neighbourhood (FON) models.

3. ASYMMETRIC COMPETITION AS A NATURAL OUTCOME OF NEIGHBOUR INTERACTIONS AMONG PLANTS: RESULTS FROM THE FIELD-OF-NEIGHBOURHOOD APPROACH

3.1. ABSTRACT

Numerous attempts have been made to infer the mode of competition from size or biomass distributions of plant cohorts. However, since the relationship between mode of competition and size distributions may be obscured by a variety of factors such as spatial configuration, density or resource level, empirical investigations often produce ambiguous results. Likewise, the findings of theoretical analyses of asymmetric competition are equivocal. In this paper, we analyse the mode of competition in an individual-based model which is based on the new field-of-neighbourhood approach. In this approach, plants have a zone of influence that determines the distance up to which neighbours are influenced. Additionally, a superimposed field within the zone of influence defines phenomenologically the strength of influence on neighbouring plants. We investigated competition at both individual and population level and characterised the influence of density and of the shape of the field-of-neighbourhood. After finding asymmetric competition emerging in all scenarios, we argue that asymmetric competition is a natural consequence of local competition among neighbouring plants. The failure to find asymmetric competition is thus not necessarily an indicator for symmetric competition.

3.2. INTRODUCTION

Asymmetric competition among individuals is defined as competition in which larger individuals have a disproportionate advantage (relative to their size) over smaller individuals. This asymmetry leads to the growth suppression of smaller individuals (Weiner 1990, Stoll & Weiner 2000), and increasing relative size differences between competitors. By contrast, symmetric competition refers to cases where resources are shared equally or proportionally to the size of the competing individuals. Knowing the mode of competition in which plants are involved (i.e. symmetric or asymmetric) is important since it has a major impact on population and community dynamics (Lomnicki 1980, Pacala & Weiner 1991, Schwinning & Fox 1995, Yastrebov 1996). For example, it is known from theoretical models of animal populations that symmetric (scramble) and asymmetric (contest) competition leads to completely different types of population dynamics (e.g. Uchmanski 2000).

However, the mode of competition among plants is still uncertain. Empirical investigations are difficult because they require knowledge of how plants acquire resources, how these resources are used for growth, survival and reproduction, and how the uptake of resources affects the performance of neighbours (Berntson & Wayne 2000). Moreover, empirical investigations have been hampered by the difficulty of simultaneously measuring the effects of competition for more than one resource. Therefore, numerous attempts have been made to infer the mode of competition from patterns at the population level, i.e. size or weight distributions of cohorts of certain species (Wyszomirski 1983, Uchmanski 1985, Hara & Wyszomirski 1994, Schwinning & Fox 1995, Wyszomirski *et al.* 1999, Stoll & Weiner 2000). It was hoped, for example, that positively skewed size distributions would indicate a size hierarchy in which a few large individuals suppress many small individuals, i.e. asymmetric competition.

Unfortunately, however, there are many factors which may obscure the relationship between the mode of competition and patterns in size distributions, e.g. spatial configuration, density, abiotic heterogeneity, overall resource level, and overall strength of competition. Consequently, despite the numerous empirical findings regarding the existence of size-hierarchies, the underlying mechanisms remain unclear. Furthermore, theoretical analyses are still equivocal (Bonan 1991, Hara & Wyszomirski 1994, Weiner *et al.* 2001).

Theoretically, the relationship between mode of competition and population level pattern has to be addressed with individual-based models

because competition in plants is necessarily local (Houston *et al.* 1988, DeAngelis & Gross 1992). In a recent review, Stoll & Weiner (2000) listed the key elements of realistic individual-based plant population models: each model plant should have an explicit location, a basal extension where no other plant can exist and a zone of influence in which interactions with neighbour plants occur. Furthermore, the number, size and location of neighbours should be taken into account in the description of competition among neighbours. Until recently, only two modelling approaches existed which contained most of these key elements: zone-of-influence (ZOI) (Wyszomirski 1986) and ecological field (EF) models (Wu *et al.* 1985, Walker *et al.* 1989; cf. also a similar approach used by Adler (1996). EF models have not yet been widely used, and never to analyse the mode of competition. In contrast, ZOI models have been used to model the emergence of size-hierarchies in plant cohorts (e.g. Wyszomirski 1983, Wyszomirski 1986, Wyszomirski 1992, Firbank & Watkinson 1987, Bonan 1993; Bonan 1991, Hara & Wyszomirski 1994, Yastrebov 1996, Wyszomirski *et al.* 1999, Weiner *et al.* 2001). However, in these studies the mode of competition had to be specified by the modeller, e.g. whether resources in overlapping areas of ZOIs are shared equally, proportionally to the size of the competitors, or monopolised by the largest competitor (Weiner *et al.* 2001). But the modeller's decision on how to share resources is an example of what Railsback (2001) refers to as "imposed behaviour": the mode of competition does not emerge from the properties of the individuals but is imposed by the modeller. Assuming "imposed behaviour" largely restricts the insights that can be gained from an individual-based model (Railsback 2001). Given the limitations of the ZOI approach, Schwinning & Weiner (1998) conclude that it should be developed and that: "Alternative individually based, spatially explicit models are also needed, since the zone-of-influence approach is only one of several possible ways to model competition for space." (p. 451).

Here, we use a recently developed approach of individual-based modelling, the "field-of-neighbourhood" (FON) approach, to analyse the mode of competition among plants. Although the FON approach was originally developed to model spatio-temporal dynamics of mangrove forests (Berger & Hildenbrandt 2000), it also proved suitable for theoretical studies, e.g. for gaining new insights into self-thinning among plants (Berger *et al.* 2002) and reproducing empirical findings on self-thinning in mangroves (Berger & Hildenbrandt, *unpublished manuscript*). The advantage of the FON approach for analysing the mode of competition is that this mode was not at all in the focus of attention when the approach was developed. Instead, in FON models the influence on

neighbour plants is described phenomenologically and the mode of competition emerges from neighbour interactions. Therefore in the following we analyse the mode of competition in simulation experiments with two plants and with populations at different densities. We show that in the FON approach, asymmetric competition is a natural consequence of neighbour interactions. Based on this result, we will argue that in real plants, too, competition among plants ought naturally to be asymmetric.

3.3. MODEL AND METHODS

3.3.1 FON APPROACH

In the field-of-neighbourhood approach (Berger & Hildenbrandt 2000), individuals have a circular zone of influence (ZOI) whose radius determines the distance up to which the individual interacts with neighbouring individuals. Within the zone of influence, a scalar field is defined which quantifies the strength of influence on potential neighbours (Fig. 3.1). This field of neighbourhood (FON) describes for every point within the ZOI the influence on neighbours.

As soon as the FONs of two or more individuals overlap, competition occurs. To quantify competition, the FON of the neighbour plant within the overlapping area is integrated. The resulting value F thus quantifies the influence of the neighbour on the focal plant. If, for example, the overlap is small, this influence may – depending on the shape of the field (Fig. 3.1) – be small as well. If more neighbours interact with the focal plant, it is assumed that their FONs superimpose independently, i.e. all neighbour fields are summed up in the overlapping areas. The resulting value F is divided by the area A of the ZOI of the focal plant k , which yields:

$$(1) \quad F_A^k = \frac{1}{A} \sum_{n \neq k} \int_{A'} FON_n(x, y) da$$

An efficient algorithm for calculating F_A for each individual of a plant population is described in detail in Berger and Hildenbrandt (2000). F_A is used to calculate a competition factor C

$$(2) \quad C = \begin{cases} 1-2F_A & \text{for } F_A \leq 0.5 \\ 0 & \text{for } F_A > 0.5 \end{cases}$$

which determines how much the growth of the focal individual is reduced due to competition. If there is no interaction with neighbours, F_A is zero and, in turn, $C=1$, i.e. the individual grows at its maximum current growth rate. The more neighbours a plant has, and the closer and larger these neighbours are, the more the growth of the focal plant will be reduced or even completely suppressed. This whole approach describes local competition among individuals by its effects and not by its mechanisms (e.g. resource partitioning) and is thus phenomenological in the same way as, for example, Lotka-Volterra competition models at the population level (Berger *et al.* 2002).

For the shape of the field of neighbourhood, we assume a basal area where the field has the value 1. This means in particular that no recruitment can occur in this area. In real plants, the basal area may, for example, refer to stems in trees, tussocks in grasses, or simply zones of complete resource monopolisation of the focal plant. The basal radius, R_{Basal} , is the basic state variable in the FON approach and represents the individual's size. It may – if the model using the FON approach is designed for real species – be used to calculate individual biomass (for example, for mangrove trees, Berger & Hildenbrandt 2000). We assume that the size of an individual, i.e. its basal radius R_{Basal} , determines the radius of its zone of influence, R_{FON} :

$$(3) \quad R_{FON} = a \cdot R_{Basal}^b$$

For the scaling parameters a and b we here choose $a = 10.0$ and $b = 0.9$ and 0.6 (Fig. 3.1). Note that since R_{Basal} is smaller than one (metre), larger values of b correspond to smaller radii of the zone of influence, R_{FON} .

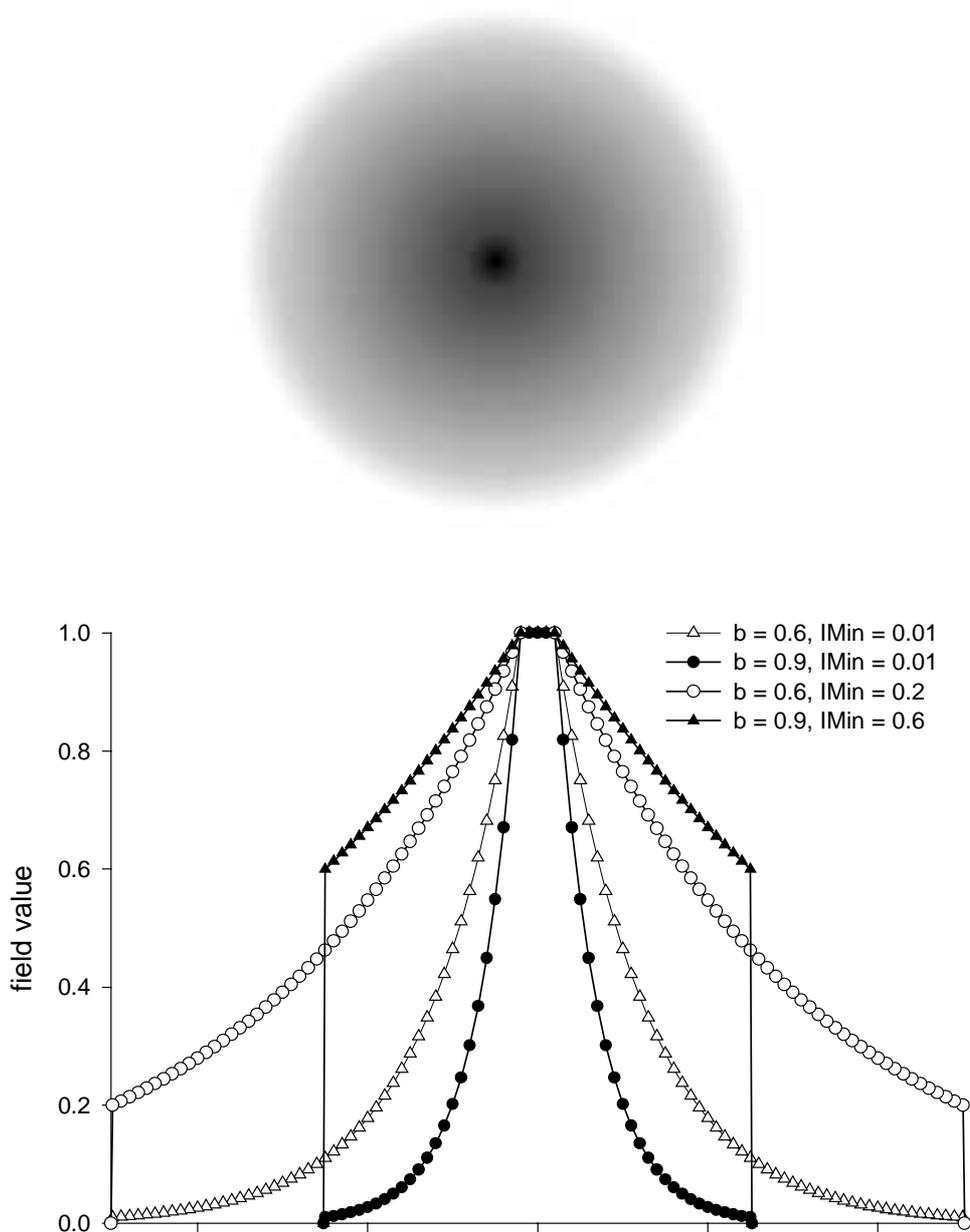


Fig. 3.1. Diagram of the different fields-of-neighbourhood used in our experiments. The differences in field extension and minimum values are shown for the same basal radius. Extended fields result from large b -values in the basal to FON-radius relation whereas compressed fields are typical for smaller b -values. Depending on the field minimum value, the fields-of-neighbourhood either decrease rapidly to a low I_{Min} value or gradually to a higher I_{Min} .

From the basal area to the border of the FON, we assume an exponential decrease in the field of neighbourhood leading to a smaller influence on neighbours in the border ranges of the field:

$$I(r) = \exp\left[-\frac{|\ln(I_{Min})|}{R_{FON} - R_{Basal}}(r - R_{Basal})\right]$$

where r is the distance from the centre of the field and I_{Min} the minimum field value at the border of the FON.

For the size-dependent, potential growth GR rate of the individuals, i.e. of the basal radius R_{Basal} , we assume a quadratic function:

$$GR = \left(\frac{4}{R_{max}} * R_{Basal} - \frac{4}{R_{max}^2} * R_{Basal}^2\right) * MGR$$

where MGR is the maximum growth and R_{max} the maximum basal radius. This growth model would yield a logistic growth curve for isolated individuals. The real growth rate ΔR_{Basal} takes into account the interaction with the neighbours, i.e. the competition factor C :

$$\Delta R_{Basal} = GR \cdot C$$

3.3.2 SIMULATION EXPERIMENTS

We varied the field of neighbourhood with respect to its range, i.e. radius, and its strength at the border of the FON. The radius is determined by parameter b (Eq. 3). We will in the following refer to the field with $b=0.9$ as the ‘compressed’ field and $b=0.6$ as the ‘extended’ field (Fig. 3.1). The strength of the field at the border of the FON is determined by I_{Min} . We used $I_{Min}= 0.01, 0.2$ and 0.6 . Note that I_{Min} determines whether the onset of competition between neighbouring individuals, i.e. when the FONs start to overlap, is gradual (small I_{Min}) or abrupt (large I_{Min}). The reference parameters used in Berger and Hildenbrandt (2000) and Berger et al. (2002) were $b=0.5$ and $I_{Min}= 0.01$.

For all six scenarios (parameter combinations) of b and I_{Min} we performed experiments with two interacting individuals and with populations of 200 individuals. The two individuals were placed at a distance such that the zones of influence start to overlap at the 3rd time-step. For $b=0.9$ this meant that the distance between the centres of the plants was 0.7 while for $b=0.6$ it was 2.3 (all spatial dimensions are give in m). Except for initial size ($R_{Basal} = 0.015$ and $R_{Basal} = 0.02$) the model parameters were identical for both individuals: $MGR = 0.02$ and $R_{Max} = 0.3$. Growth was followed for 20 time-steps. To assign biomasses to the plants,

we assumed the relationship $B = (\pi R_{\text{Basal}}^2)^{3/2}$ between biomass B and basal radius.

In the population study, 200 individuals were randomly distributed over the sample area. The population density was varied from 0.125, 0.25, 0.5, 1 and 2 plants/m². To avoid changing sample sizes, we varied area size to change density. Individual variability was introduced in the maximum growth MGR (normal distribution with $\bar{x} = 0.02$; $\sigma = 0.005$) and initial basal radius ($\bar{x} = 0.015$, $\sigma = 0.01$). The maximum basal radius was equal for all individuals ($R_{\text{Max}} = 0.3$). To avoid edge effects, we used a toroidal sample area, i.e. periodic boundary conditions.

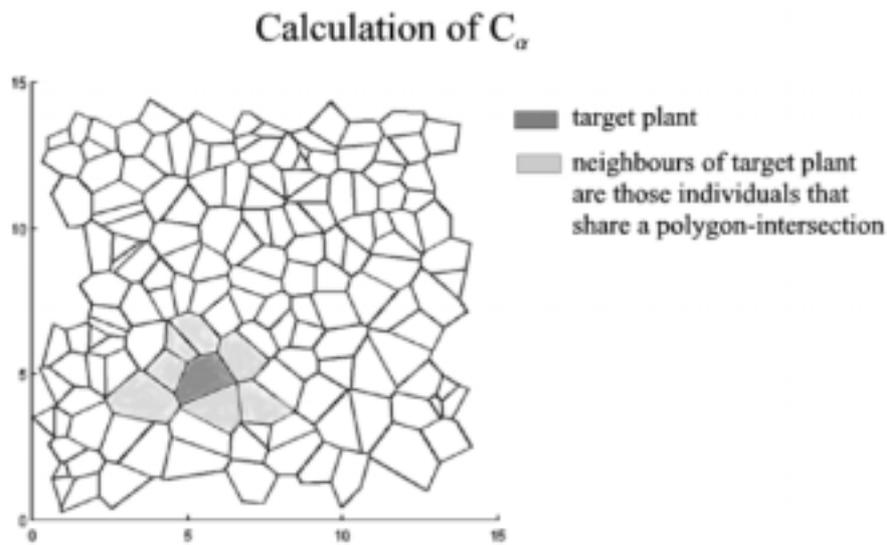


Fig. 3.2. Representation of individual plants in Voronoi-diagrams. The perpendicular bisections of plants are connected and yield individual Voronoi-polygons. We use the area of this polygon to predict the biomass of individual plants. Neighbouring individuals are herein defined as individuals that share at least one polygon intersection.

We analysed asymmetric competition at the population level by calculating a recently developed indicator of asymmetric competition, C_α (Wyszomirski *in prep.*). The advantage of this indicators is that it takes into account the spatial configuration of the individuals. The well-known effect that conventional measures of asymmetric competition (e.g. skewness) may be biased by spatial effects (Wyszomirski 1986, Miller & Weiner 1989, Bonan 1991) is thus reduced.

To calculate C_α , the degree of competitive asymmetry, three steps are required. First, for all plants their Voronoi-polygon is calculated (Fig. 3.2). Individuals at the border, and individuals which have a border individual

as neighbour, are ignored. Then, a linear regression is performed between the log-transformed biomasses and Voronoi-areas of the plants:

$$\log(\text{biomass}) = a \log(\text{Voronoi-area}) + b.$$

This regression largely reflects differences in biomass caused by the spatial arrangements of the plants. Consequently, the residuals, i.e. the differences between predicted (regression) and observed (simulation) biomass, contain information about differences in biomass which are due to asymmetric competition. Therefore, in the third step, for each plant its neighbours' residuals are summarised and correlated with the residual of the target plant. This final correlation yields the indicator of asymmetric competition, C_α .

The rationale behind the indicator C_α is that if a target plant has a greater biomass than predicted by the regression, and its neighbours have lower biomasses than predicted, the residual of the target plant will be positive and the sum of the neighbour residuals will be negative. Hence, a correlation between these residuals will result in a negative value. Asymmetric competition leads to such situations. Therefore, negative values of C_α are indicative of asymmetric competition. Positive values may arise only in very exceptional situations (Wyszomirski *in prep.*), not encountered in the present study.

3.4. RESULTS

3.4.1 POPULATION EXPERIMENTS

The population average of F_A (Eq.1) is an indicator of overall competition strength at the population level. Parameter b (Eq. 3) determines the extension of the field of neighbourhood and, in turn, determines how soon competition starts because the FONs start to overlap. Thus, although competition is initially higher for extended fields (Fig. 3.3a), these differences cease over time. At the end of the growth period studied, average competition strength is determined more by I_{Min} than by b . Note that for individuals differences of F_A larger than 0.5 are irrelevant because for $F_A > 0.5$ growth is completely suppressed (Eq.2).

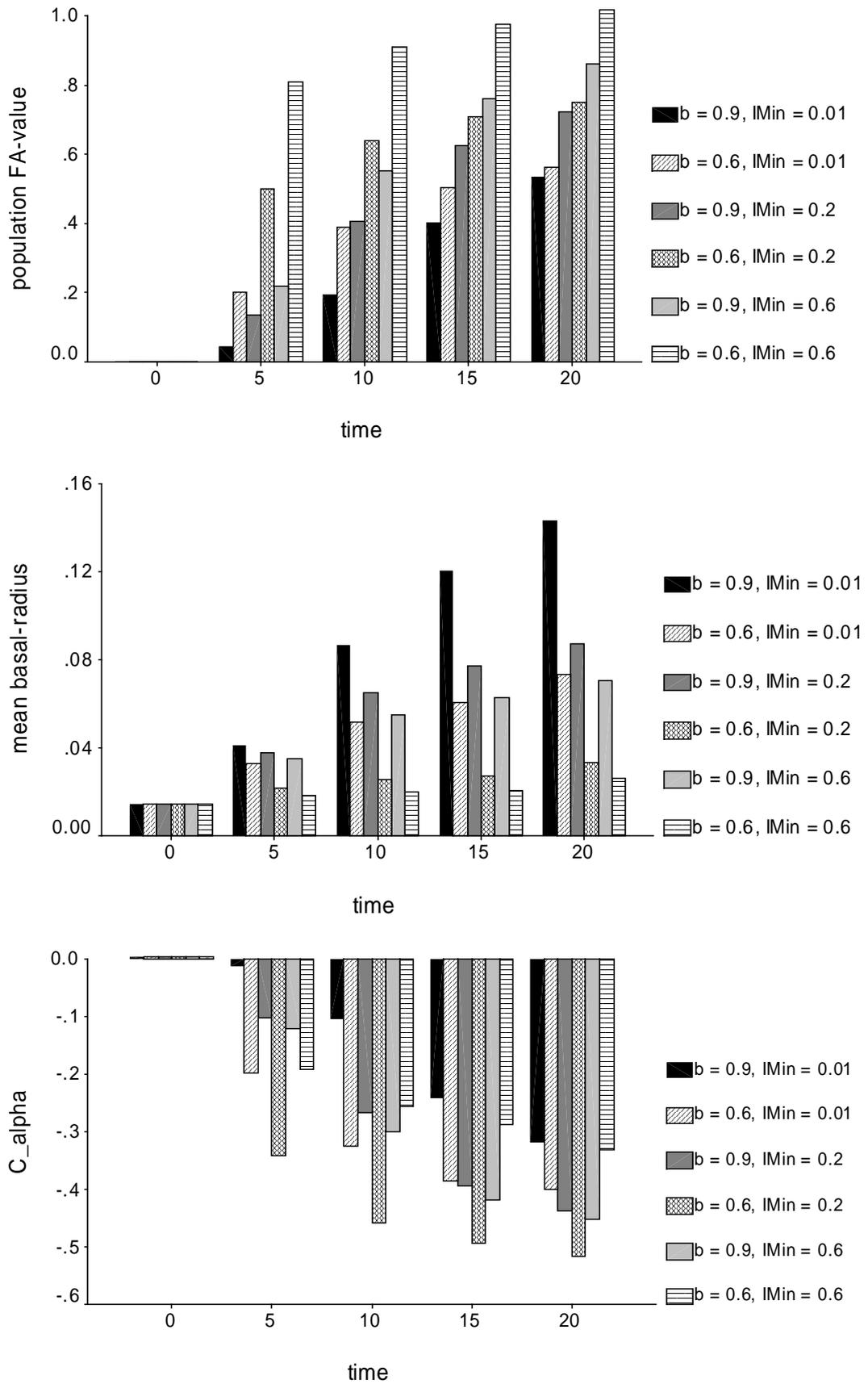


Fig. 3.3. At medium density (0.5 plants/ m²) the temporal development of a) F_A -values, b) basal radius, and c) C_α are shown for all scenarios.

Populations with compressed fields and low values of I_{Min} reached the largest average basal radius (Fig. 3.3b). On the other hand, in populations with extended fields and high I_{Min} , individual growth was already almost completely suppressed in early time-steps. Individuals with extended fields of neighbourhood were generally smaller than their counterparts with the same I_{Min} and compressed fields (Fig. 3.3b).

Asymmetric competition as quantified by C_{α} was detected in all scenarios (Fig. 3.3c). C_{α} increases with increasing I_{Min} and reaches a maximum for $I_{\text{Min}}=0.2$ in extended fields ($b=0.6$) (Fig. 3.3c). Larger I_{Min} values ($I_{\text{Min}}=0.6$) did not lead to a higher degree of asymmetric competition because individuals stopped growing at early time-steps and therefore developed only slight differences in their sizes. For the same I_{Min} , asymmetry was generally higher in extended fields than in compressed fields (except for $I_{\text{Min}}=0.6$).

With increasing density, the average size decreased (Fig. 3.4), but for all densities individuals grew larger when their field of neighbourhood had a border value of $I_{\text{Min}} = 0.01$ and for the same value of I_{Min} individuals were larger when their field was compressed.

Density changed the degree of asymmetric competition (Fig. 3.4). In all scenarios with extended fields, competitive asymmetry reached a maximum at a certain density and decreased thereafter whereas in scenarios with compressed fields competitive asymmetry monotonically increased with density. The density at which maximum competitive asymmetry was observed for extended fields shifted from 0.5 plants/m² for $I_{\text{Min}}=0.01$ to 0.25 plants/m² for $I_{\text{Min}}=0.2$ and 0.6. The highest competitive asymmetry was found for $I_{\text{Min}}=0.2$ at density 0.25 plants/m² for extended fields and at 2 plants/m² for compressed fields.

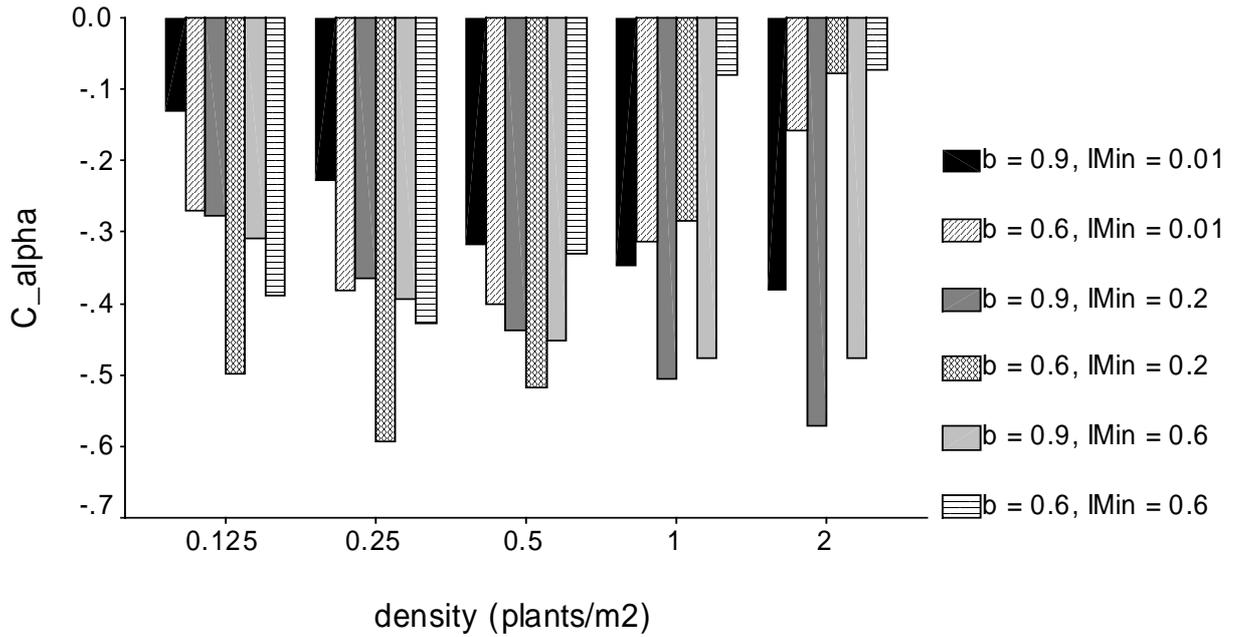


Fig. 3.4. Changing density affects the outcome of competitive interaction as characterised by C_α . While competitive asymmetry reaches a maximum at a particular density in extended fields (striped bars), competitive asymmetry monotonically increases in compressed fields (single-coloured bars).

3.4.2 EXPERIMENTS WITH TWO INDIVIDUALS

Differences in F_A -values between the two individuals rose as I_{Min} values increased (Fig. 3.5, upper row) and were larger for compressed fields. Note that F_A quantifies the influence of the neighbour plant on the focal plant. Consequently, a large F_A means that the growth of the focal plant is strongly suppressed; if $F_A > 0.5$, the focal plant even stops growing altogether (Fig. 3.5, second row). Thus, for $I_{\text{Min}}=0.6$ and $b=0.9$, the individual with a slight initial advantage in size (individual 2) almost completely suppresses individual 1, whereas for $I_{\text{Min}}=0.01$, only weak growth suppression and, in turn, asymmetric competition occurs (Fig. 3.5, lower two rows). However, competition is still not symmetric for $I_{\text{Min}}=0.01$: the difference between the relative growth rates of the two plants, $D = |S_1 - S_2|$, with $S = (GR - \Delta R_{\text{Basal}}) / GR = (1 - C)$, would be zero if both plants were symmetrically suppressed to the same degree, but at the 20th time-step is 0.079 for $b=0.9$ and 0.076 for $b=0.6$.

To understand how asymmetric competition emerges from slight differences in initial size, in Fig. 3.5 not only F_A but also the area A of the zone of influence and $F = F_A \cdot A$ are shown for $I_{\text{Min}}=0.2$ and $b=0.6$. F is the integral over the FON of the neighbour in the overlapping zone (Eq. 1). Due to the almost symmetric configuration of the two individuals (Fig.

3.5), F is almost identical for both individuals for a long time. However, the area A by which F is scaled differs right from the beginning and leads to differences in F_A . Increasing differences in F_A , however, magnify differences in the individuals' size and, in turn, of the areas of their zones of influence. Asymmetric competition thus reinforces itself due to the area scaling of the FON approach.

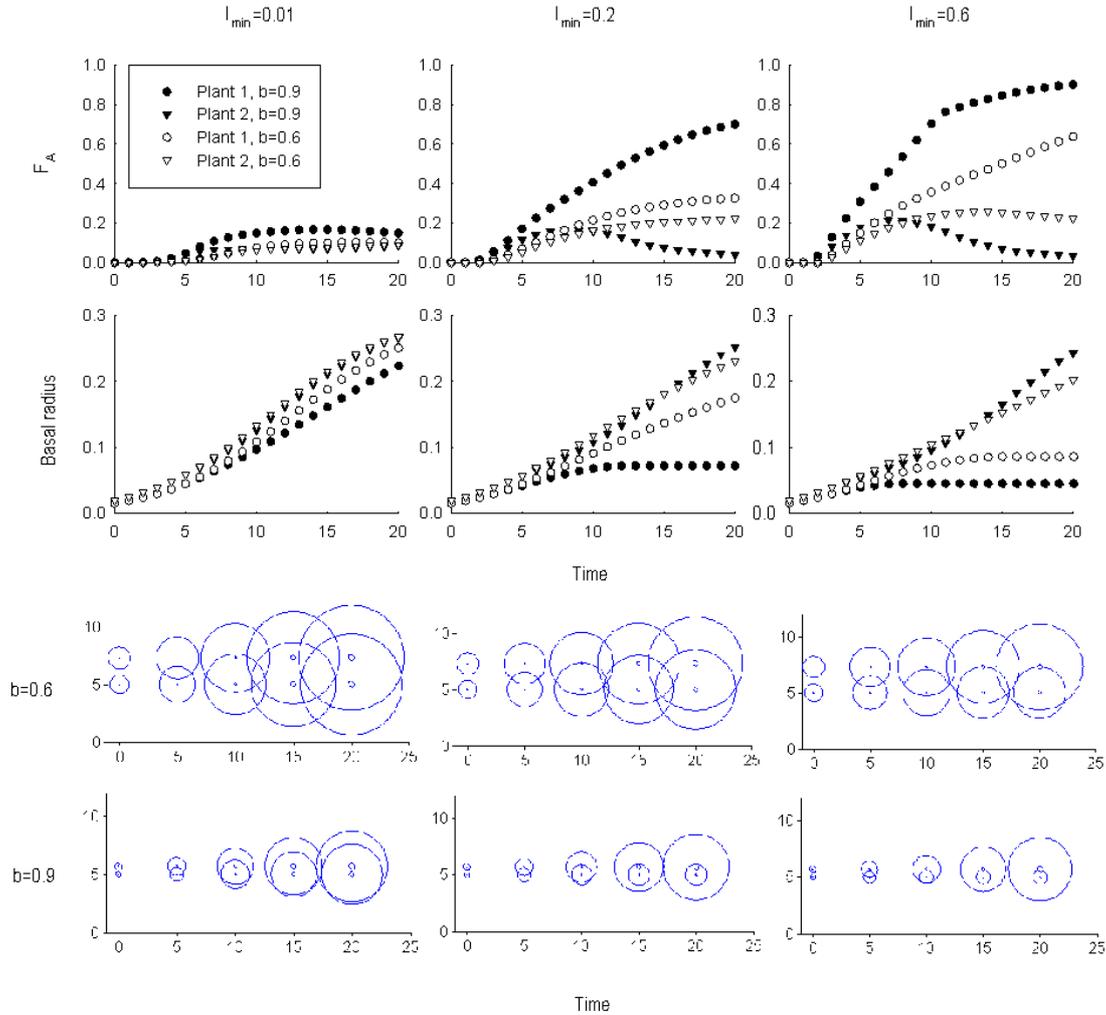


Fig. 3.5. In the 2-individual study, we tested the outcome of different field shapes on individual performance. Here, the F_A -values characterise the intensity of competition between both individuals. Higher I_{min} values lead to greater differences in performance. When using extended fields (empty symbols) the onset of competition is delayed compared to extended fields (filled symbols).

3.5. DISCUSSION

We used the new field-of-neighbourhood (FON) modelling approach to investigate the mode of competition of hypothetical plants. Two parameters of the FON approach which determine the shape of the FON

were varied such that extended, gradually decreasing fields could be compared to compressed and abruptly decreasing fields.

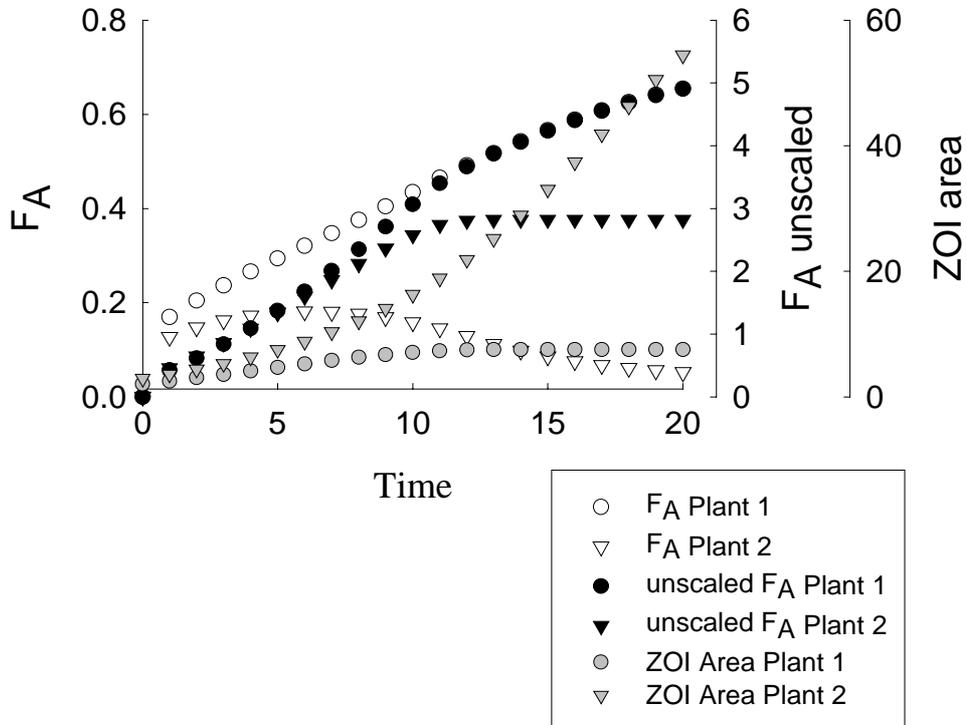


Fig. 3.6. FA, F (un-scaled), and A for the two-individual study $I_{min}=0.2$ and $b=0.6$.

In the population simulations, asymmetry was found in all scenarios, albeit to different degrees. Generally, higher I_{Min} values cause a stronger onset of competition as soon as plants interact and therefore lead to higher competitive asymmetry. However, this trend was not observed for the highest value of I_{Min} ($=0.6$). This is an effect of very strong overall competition which is described by Wyszomirski *et al.* (1999): asymmetric competition has two components, competition and asymmetry. For strong overall competition, growth is reduced so much that size differences hardly emerge and therefore competitive asymmetry is hard to detect.

The same effect is responsible for the effect of density on competitive asymmetry in the case of extended fields. Beyond a certain density the individuals interact with so many neighbours (because the field is extended and the plants are close to each other) that overall competition intensifies to the point where no further increase of competitive asymmetry with density can be observed.

The effects of the shape of the FON and of density on competitive asymmetry are thus easy to understand at the population level. However, to understand the mechanisms underlying asymmetric competition, the local interactions between pairs of individual had to be studied. The simulation experiments with two individuals which were of slightly different size at the beginning revealed that in the FON approach asymmetry, i.e. the suppression of the smaller individual, is not necessarily driven by asymmetric resource use in the overlapping zone which is affected by both plants. In contrast, the integral over the neighbours' FON in the overlapping zone is almost identical for both plants. Asymmetry comes into play by the scaling of the neighbours' effect by the area of the ZOI of the focal plant (Fig. 3.6).

This scaling was introduced for three reasons: (1) To turn F , which has the unit of m^2 , into a dimensionless quantity, F_A ; (2) The calculation of F_A is easy (Berger & Hildenbrandt 2000) because only pairwise interactions have to be quantified. The influence of more than two neighbours is independent of each other; (3) Consider a situation where the ZOI of a small plant is completely overlapped by the periphery of the ZOI of a larger plant. Without scaling, only the integrals over the FON in the overlapping zone, F , would be considered. However, on the one hand the F -value which describes the influence of the small plant on the large plant would be rather high, because F is the integral over the entire FON of the smaller plant. On the other hand, the F -value describing the influence of the larger plant on the smaller one would be rather small, because only the periphery of the larger plants' FON overlaps the smaller plant. As a result, without scaling the mutual effects of the plants on each others growth would be described with the wrong sign: the smaller plant would strongly reduce the growth of the larger one, but the larger one would only slightly affect the smaller one. This would be absurd because the larger plant is only affected by competition in a small part of its zone of influence, whereas the small plant 'feels' the larger one on its entire ZOI. There thus has to be a scaling by the area of the ZOIs of the plants involved.

Asymmetric competition emerges from this scaling by the positive feedback demonstrated in Fig. 3.6: even if F_A is virtually the same for both plants, a larger ZOI means that growth will be less reduced and thus, in the next time step, the size difference increases, and so on. Thus, in the FON approach, asymmetric competition results not from rules imposed on for instance resource partitioning, but mainly from the very simple fact that in plant-plant interactions, for larger individuals the proportion of the ZOI unaffected by the neighbour interaction is larger (a point also made by

Schwinning and Weiner, 1998, Fig. 3.6). Hence, a larger plant does not 'feel' much of the influence of a smaller neighbour and its growth is mainly independent of the interaction. Additionally, size differences may be reinforced because growth is non-linear, which may contribute to the positive feedback between size differences and increase in size differences.

To summarise the results of our study: within the FON approach, asymmetric competition appears to be a natural outcome of local competition among individuals. Consequently, the failure to detect competitive asymmetry at the population level is not necessarily an indicator of symmetric competition at the individual level, but of mechanisms which conceal or prevent the asymmetric competition from unfurling. An important concealing mechanism is spatial configuration, which however can be controlled by using appropriate indicators of competitive asymmetry such as C_α . Moreover, the asymmetry of competition is not markedly expressed if competition is so strong that growth is strongly reduced and therefore the positive feedback described above only weak.

What do these theoretical results tell us about plant competition in the real world? Of course, a modelling study cannot 'prove' the prevalence of asymmetric competition in real plants, but it can provide a logical argument that has the potential to guide future empirical studies. The argument is: if the FON approach and its assumptions are considered realistic, then the consequences of this approach - i.e. that asymmetric competition is a natural outcome of local competition - must be accepted. In this context, the formal details of the FON approach are less important than the underlying idea: plants have a zone of influence in which they influence potential neighbours. We would like to emphasise that the FON approach is not - as the ZOI approach - based on the mechanistic notion of resource use within the zones-of-influence, but is purely phenomenological: the field-of-neighbourhood describes the influence on potential neighbours. If the zones of two plants overlap, they interact, which means that they mutually reduce each others growth. A larger plant is assumed to be less affected by the interaction with its smaller neighbour because a larger proportion of its ZOI is unaffected by neighbour interactions. On this 'free' part of the ZOI, the plant can still acquire resources undisturbed by any interaction. Since the particular form of the FON, which we varied by varying the border value I_{Min} , to some degree reflects the architecture of the plant and of its interaction with neighbour plants, our results also seem to be robust to changes in this architecture.

4. COMPLEX DYNAMICS IN PLANT POPULATIONS

4.1. ABSTRACT

Despite the general interest in nonlinear dynamics in animal populations, plant ecologists have mostly underestimated the importance of complex dynamics. The governing thought was that plant populations are supposed to show a stable equilibrium and this was attributed to fundamental differences compared to animals such as the physiological plasticity and therefore plants achieve reproductive stage at low size. Furthermore, plants could avoid crowding effects by long-distance dispersal and additionally, long-lived seed-banks lead to population turnover with a time-lag. These facts were assumed to stabilise a plant population. However, some empirical and modelling studies have shown that the enigma of stable equilibrium dynamics should be re-thought.

We, therefore, have developed a model using the field-of-neighbourhood approach to investigate the population dynamics of perennials. The field-of-neighbourhood approach assigns a circular zone-of-influence to each plant and additionally superimposes a field on this zone to characterise the strength of influence on potential neighbours. Hence, this approach incorporates competition in a phenomenological manner and thus, avoids the formulation of exact resource-use functions. Furthermore, establishment and reproduction as key processes for population dynamics are easily derived from the competitive situation. We clearly found cyclic population dynamics in this population and hypothesised that periods of recruitment and senescence alternate during one cycle. These periods are characterised by distinctive age-structures and spatial patterns in the population.

Moreover, we tested our hypothesis by changing the modes of reproduction and mortality: In the different scenarios, individuals died and seedlings established according to the competitive situation in their neighbourhood. Population dynamics showed cycles in almost all mortality-scenarios but they disappeared when the thresholds for establishment were low.

Consequently, we argue that non-linear dynamics could have major implications for community dynamics.

4.2. INTRODUCTION

The study of nonlinear dynamics has blossomed in the last decades. Especially in the animal ecology literature one finds wide-spread evidence for nonlinear behaviour of population sizes (e.g. Berryman 1999, Bjornstad 2000, Johnson 2000, Hansen *et al.* 1999, Stenseth 1999, Turchin & Batzli 2001, Krebs 1996). A variety of theoretical studies has attempted to identify patterns in time-series data and the processes leading to fluctuating population densities (Sherratt *et al.* 2000, Dennis *et al.* 2001).

For plant populations, however, it has been supposed that cyclical or chaotic behaviour is unlikely to be found and the existence of a stable equilibrium has been the dominant notion in plant ecology (Crawley 1990). Very few publications discussed the role of nonlinear behaviour in plant populations and mainly, this topic seems to be of minor importance to most plant ecologists (Cousens 1995, Stone & Ezrati 1996). Changes in population size have often been attributed to other mechanisms such as disturbances, variability of environmental factors and pathogens (Wiegand *et al.* 1998, Eriksson & Eriksson 2000). Furthermore, it has been assumed that the stability of plant populations comes from several fundamental differences compared to animals: Plants show extreme physiological plasticity and can reproduce at very small size. The effects of crowding can be ameliorated by long distance dispersal and additionally, recruitment from long-lived seed-banks could also stabilise population dynamics (Rees & Crawley 1989, Crawley 1990).

Evidence for nonlinear behaviour of plant populations is also rare but this does not necessarily mean that plant populations are inherently stable. Even in a long-term study in a Park Grass experiment where the plots probably are the best candidates for stable equilibrium population dynamics, Dodd *et al.* (1995) suggested 'that the existence of outbreaks in a significant number of species calls for a re-evaluation of the concept of stable plant communities' (p. 285). Other empirical examples of nonlinear behaviour in plant populations can be found in Symonides *et al.* (1986), Thrall *et al.* (1989), Silvertown (1991), Tilman & Wedin (1991b), Crone & Taylor (1996). A very impressive field study was conducted by Symonides *et al.* (1986) who provide an example of the application of cycles and potential chaos to a population of annual plants. They found a 2-year

cycle in the field that showed extreme density variations from 1-2 individuals/ m² to 55-65 individuals/ m².

However, as argued by Crone & Taylor (1996) it is generally difficult to interpret the results of studies that found stable equilibrium dynamics because extremely few authors have studied population dynamics over several generations. Furthermore, whether complex dynamic is a general phenomenon or such empirical studies only rare exceptions to stable population dynamics remains still unclear because these examples have not been incorporated into models. In their study, Crone & Taylor (1996) monitored population dynamics in a replicated experimental population of a greenhouse weed, *Cardamine pensylvatica*. They tested for density dependence and fitted the data to both nonlagged and lagged time-discrete density-dependent functions. In contrast to prevailing notion of equilibrium dynamics, a strong cyclical population dynamics was found that could not be accounted to changing environmental conditions. The data support the hypothesis of density-dependent population regulation that acts at various temporal scales but the authors strongly recommend the inclusion of a delay in density dependence. The delay was mainly attributed to the effect of maternal provisioning and the thereby altered offspring quality (see also Crone 1997a).

Furthermore, few modelling studies exist that searched for the conditions of nonlinear behaviour in plant populations: Silander & Pacala (1990) attempted to determine the conditions for oscillatory and chaotic behaviour in annual plant populations. Such behaviour was found to be more likely when annuals have low seed dormancy, high germination success, a minimum plant size threshold for reproduction, or high soil fertility. They demonstrated with their model a range of dynamic behaviour from a stable equilibrium to damped and stable oscillations and apparent chaos. Furthermore, these authors argued that seed dormancy leading to a time-lag actually stabilises a plant population which would otherwise tend to oscillations.

In general, some other models investigating nonlinear behaviour in plant populations did not contain space as an explicit feature (e.g. Solbrig *et al.* 1988). Space however, is important because of the localness of competition, the monopolisation of space by established plants, and the general significance of spatial distribution (Crone 1997b).

A natural approach to model plant population dynamics would be a spatially explicit individual based model (Houston *et al.* 1988, Grimm 1999). Realistic individual-based plant population models should contain the following key-elements: each individual has an explicit spatial location, a basal extension where no other plant can exist and a zone of

influence in which interactions with neighbour plants occur (Stoll & Weiner 2000). Furthermore, the number, size and location of neighbours should be taken into account (Stoll & Weiner 2000). Although there exist such model approaches – for instance the zone-of-influence and the ecological-field approach – question concerning population dynamics have not been investigated with these approaches.

We investigated the dynamics of a population of perennials with an individual-based model based on the recently developed field-of-neighbourhood approach (Berger & Hildenbrandt 2000). Individual plants are represented by circular areas around their stemming-points. These circular areas determine the extension of a plant's zones of influence and additionally a field superimposed on the zone of influence defines the intensity of influence on a potential neighbour. In particular, we investigated the following questions: 1) What kind of dynamics shows a model population of perennials which is based on the FON approach: stable equilibrium, oscillatory or chaotic dynamics? 2) Under which circumstances do cyclic patterns occur in the population dynamics? 3) Which mechanisms drive a population to cycle? The processes investigated were reproduction, recruitment, seed dispersal, and mortality.

4.3. MODEL AND METHODS

4.3.1 GENERAL MODEL DESCRIPTION

The model is individual-based and spatially explicit based on the field-of-neighbourhood approach (Berger & Hildenbrandt 2000, see also Chapter 2 this volume).

At the beginning of each model run, an initial number of individuals is distributed over a 50m² study area. The left and right, and the upper and lower edge of this area are linked to each other (periodic boundary conditions), so that the extension of the study area should not affect the results. The results presented below are also largely independent of the initial number, age and spatial distribution of the plants. During each time-step individuals grow, reproduce or die according to the rules listed below. One time-step can correspond from between months and years. For the analysis of population dynamics, the model was run over 1000 time-steps.

4.3.2 INDIVIDUAL CHARACTERISTICS

All individuals are characterised by their spatially-explicit position, size, and age. The size of an individual is represented by its basal extension – the basal radius that can be interpreted as stem, tussock or tuft area. Furthermore, each individual has a zone of influence where it interacts with neighbours. The extension of this zone is determined by a non-linear function of the basal radius:

$$R_{FON} = a \cdot R_{basal}^b,$$

with $a = 10.0$ and $b = 0.9$. In contrast to zone-of-influence models, the field-of-neighbourhood approach superimposes a field on the zone of influence to quantify the strength of competition (see chapters 2 and 3). Herein, the influence of neighbours on a focal individual is described in a phenomenological manner and thereby the definition of competed resources is avoided. This approach also assumes that the influence of more neighbours and their position can be taken into account. For the quantification of the neighbours' influence, the field values in the overlap areas, F_A , of the k^{th} individual are calculated and summarised (see also chapter 2 and 3 this volume):

$$F_A^k = \frac{1}{A} \sum_{n \neq k} \int_{A'} F_{ON}_n(x, y) da$$

where A is the area of the FON of the k^{th} individual and $F_{ON}_n(x, y)$ is the value of the FON of the neighbouring plant n in the overlap areas A' .

4.3.3 GROWTH OF INDIVIDUALS

Individuals grow according to the neighbourhood situation and their actual size. We assume that isolated individuals show a sigmoidal growth, i.e. their growth rate, GR , is quadratically dependent on their size, R_{Basal} :

$$GR = S_{Size} \cdot MGR,$$

with MGR the maximum growth rate and the correction factor for size S_{Size} :

$$S_{Size} = 4 \frac{R_{Basal}}{R_{max}} \left(1 - \frac{R_{Basal}}{R_{max}} \right)$$

with $R_{max}=0.3$ the maximum basal radius, and R_{Basal} the actual basal radius. For instance, if an individual has almost reached its maximum size, R_{max} , the size-increment will be close to zero. For an isolated individual it takes approximately 20 time-steps to reach its maximum size.

The influence of competition on growth is considered by a correction factor for competition, C , which takes into account the negative influence of the neighbouring plants, F_A :

$$C = \begin{cases} 1-2F_A & \text{for } F_A \leq 0.5 \\ 0 & \text{for } F_A > 0.5 \end{cases}$$

The increment of the basal radius, ΔR_{Basal} is consequently given by $\Delta R_{Basal} = GR \cdot C$. Growth may thus be completely suppressed if local competition by neighbouring plants is too high.

4.3.4 REPRODUCTION

Individuals in the model reproduce by dispersing seeds. We assume a minimum size for reproduction: whenever a plant reached 1/3 of its maximum size the particular individual starts to reproduce a constant number of seeds (i.e. five) per time-step.

Seeds are dispersed locally around the mother individual. For the calculation of a seed's location we used a two-dimensional exponential function:

$$p(r) = \exp(-r / \lambda)$$

with $\lambda = 1.5 \cdot R_{Basal}$ the mean of the probability distribution and r the particular dispersal distance.

Whether the seed establishes on its position depends on the neighbourhood situation. Whenever the local field value $F(x, y)$ defined as the sum of all plant's field's at point (x, y)

$$F(x, y) = \sum_{i=1}^n F_i(x, y)$$

falls below a particular threshold, the seed is assumed to germinate and establish. If $F(x, y)$ exceeds this limit the seed is assumed to die because the competitive pressure is too strong for germination and establishment.

4.3.5 MORTALITY

We assumed that plants suffering from high competitive pressure have a higher mortality risk than isolated plants. Additionally, plants that have grown to their maximum size are senescent and thus, mortality increases. Competitive pressure and senescence are combined in an individual's vigour v :

$$v_t = \sqrt{C \cdot S_{Size}} ,$$

where C is the correction factor for competition and S_{Size} the correction factor of size. The vigour-values of the last five time-steps are averaged assuming that a plant memorises the experience of the competition past:

$$\bar{v} = (v_t + v_{t-1} + v_{t-2} + v_{t-3} + v_{t-4}) / 5$$

with v_t the vigour at time t . If the average vigour falls below a particular threshold the individual is assumed to die. The memory approach allows plants to be able to tolerate competitive pressure for some time, but then die. On the other hand, plants may recover from competition (i.e. forget former competition) if competitive pressure is released due to the death of neighbour plants. A maximum age of 50 time-steps was introduced and hence a plant dies when exceeding this age.

4.3.6 MODEL SCENARIOS

The base model includes mortality and reproduction with the following attributes:

- Reproduction at 1/3 of the maximum size
- Local seed dispersal
- Establishment of seedlings when local field value $F(x, y) \leq 0.0$
- Memory-mortality $\bar{v} \leq 0.5$ with $\bar{v} = (v_t + v_{t-1} + v_{t-2} + v_{t-3} + v_{t-4}) / 5$

The model scenarios deviate from the base model in the processes mortality and reproduction. Mortality was altered between “memory

mortality” referring to a mortality that depended on vigour (see above) and “random mortality” where mortality was purely random and thus, local competition did not influence the probability of dying. In “memory mortality” scenarios different memory functions were implemented, i.e. plants “remembered” the competition of only the one, two or three preceding time-steps, and in which the vigour-threshold value for mortality was changed between 0.6 and 0.4. In the random mortality scenario, a number of individuals as much as 20% of the population died to achieve population sizes similar to those in the base scenario.

Recruitment was changed regarding seed dispersal and seedling establishment. Seeds were dispersed over the whole study period in the “Global seed dispersal” scenario and within a particular dispersal distance in the “Local seed dispersal” scenario. Establishment of seedlings depended on the competition, i.e. overlapping fields-of-influence from established plants, at their particular position. The threshold local field value $F(x, y)$ for successful germination was varied between 0.0, i.e. no other plant must overlap the germination point, and 1.0, i.e. overlaps of fields-of-influence are allowed but no other plant must have its basal area at the germination point.

Furthermore, we varied the extension of the FON by changing parameter b in the FON-basal-relation and thereby switched from compressed fields ($b=0.9$, base model) with a rapidly decreasing field to extended, gradually decreasing fields ($b=0.5$).

4.3.7 MODEL ANALYSIS: TIME SERIES ANALYSIS

Time series were analysed with regard to their cyclic behaviour and its period. Whether a time-series shows cyclic changes was identified with the autocorrelation function (ACF) and the period of such cycles was revealed with spectral analysis.

The ACF is estimated by calculating the correlation coefficient between pairs of population size N_t and $N_{t-\tau}$ separated by lag τ . These correlation coefficients are plotted as a function of τ (Turchin 2001). The ACF of a monotonically damped system is positive at small lags, and then decays exponentially to zero at high lags. Oscillatory ACF can arise either as a result of exogenous periodic forcing, or as a result of endogenous periodic dynamics. A system oscillating in response to an exogenous force will have an ACF that will not decay but continue to cycle indefinitely. Endogenous oscillating forces may let the ACF eventually decay to zero at

high lags and are known as “phase forgetting quasi-cycles” (Nisbet & Gurney 1982).

Spectral analysis identifies the cyclical components of a time-series by decomposing it into underlying sinusoidal (sine and cosine) functions with particular wavelength. This was done by applying a multiple regression where the dependent variable is the observed time series and the independent variables are the sine functions of all possible frequencies:

$$x_t = a_0 + \sum [a_k \cdot \cos(\lambda_k \cdot t) + b_k \cdot \sin(\lambda_k \cdot t)] \quad (\text{for } k = 1 \dots q),$$

where (λ) is the frequency in radians per unit time, i.e. $\lambda = 2\pi \cdot \nu_k$ with $\nu = k/q$.

Time-series of the model data were analysed with Statistica 5.0.

4.3.8 MODEL ANALYSIS: SPATIAL DISTRIBUTION TESTS

The spatial distribution was analysed using Ripley’s L-function (Ripley 1977):

$$\hat{L}(s) = s - \sqrt{K(s)/\pi}$$

with

$$K(s) = A \cdot \sum_i^n \sum_{j \neq i}^n w_{ij} \cdot I_s(i, j) / N^2,$$

Herein, A is the area of the study plot, N the amount of individuals, w_{ij} weighting factor to correct edge effects and

$$I_s = \begin{cases} 1 & \text{for } d(i, j) \leq s \\ 0 & \text{for } d(i, j) > s \end{cases}$$

The procedure therefore counts individuals within a particular distance of the focal individual. The distance is increased step-wise to cover different spatial scales. The null hypothesis is a random pattern which would result in an expected value of $L(s) = 0.0$. Large positive values indicate that plants are overdispersed (i.e. more regular) at scale s and large negative values indicate clumping at a particular scale. However, the absolute $L(s)$ -value is of little use and can hardly be compared between scenarios.

Therefore, we tested for the significance of the results by permutation the null-hypothesis of complete spatial randomness (CSR). For a number of n individuals a random spatial distribution is determined by a Poisson process and for each of these random distributions the Ripley-function is calculated. Furthermore, to detect a significant deviation from the null hypothesis of complete spatial randomness, we calculated a confidence interval with an accuracy of 95%. For calculating the confidence interval of $p\%$ it is necessary to calculate Ripley's K for $p/(100-p)$ random distributions (Bailey & Gatrell 19). For a confidence interval of 95% we need 19 random distributions (Jeltsch *et al.* 1999).

Regularity at scale s is assumed when the $L(s)$ values of random distributions are $L_{model}(s) \leq \min_{random} L(s)$ and accordingly, a distribution is assumed to be clumped when $L_{model}(s) \geq \max_{random} L(s)$.

4.4. RESULTS

4.4.1 POPULATION DYNAMICS OF THE BASE MODEL

In the base model population size cycled between boundary population sizes of 550 and 900 individuals (Fig. 4.1a). Splitting the population into three size classes revealed that the smallest size class contributes most to the oscillations (Fig. 4.1b). Additionally, the fluctuations of the medium and large size class have lower amplitudes and follow the peaks of the lowest size class with a particular lag (Fig. 4.1b).

Time-series analysis revealed a strong periodicity at a period of 43, i.e. population size reaches a peak every 43rd time-step (Fig. 4.2). Furthermore, autocorrelation analysis showed that population sizes are correlated even at high lags (Fig. 4.2). The depleting correlation strength is typical for endogenous periodic forces (Fig. 4.3).

The competitive situation in the population as measured by average F_A -values shows also cyclic changes in the course of time (not shown) but the peaks of F_A -value oscillation are not distinct as the peaks in the population size classes.

Age distribution in the population at a high-peak point ($t = 480$) is characterised by the dominance of young individuals. At a low-peak point ($t = 510$) the distribution is much flatter and has a thicker tail indicating the larger occurrence of medium ages and high ages (Fig. 4.4).

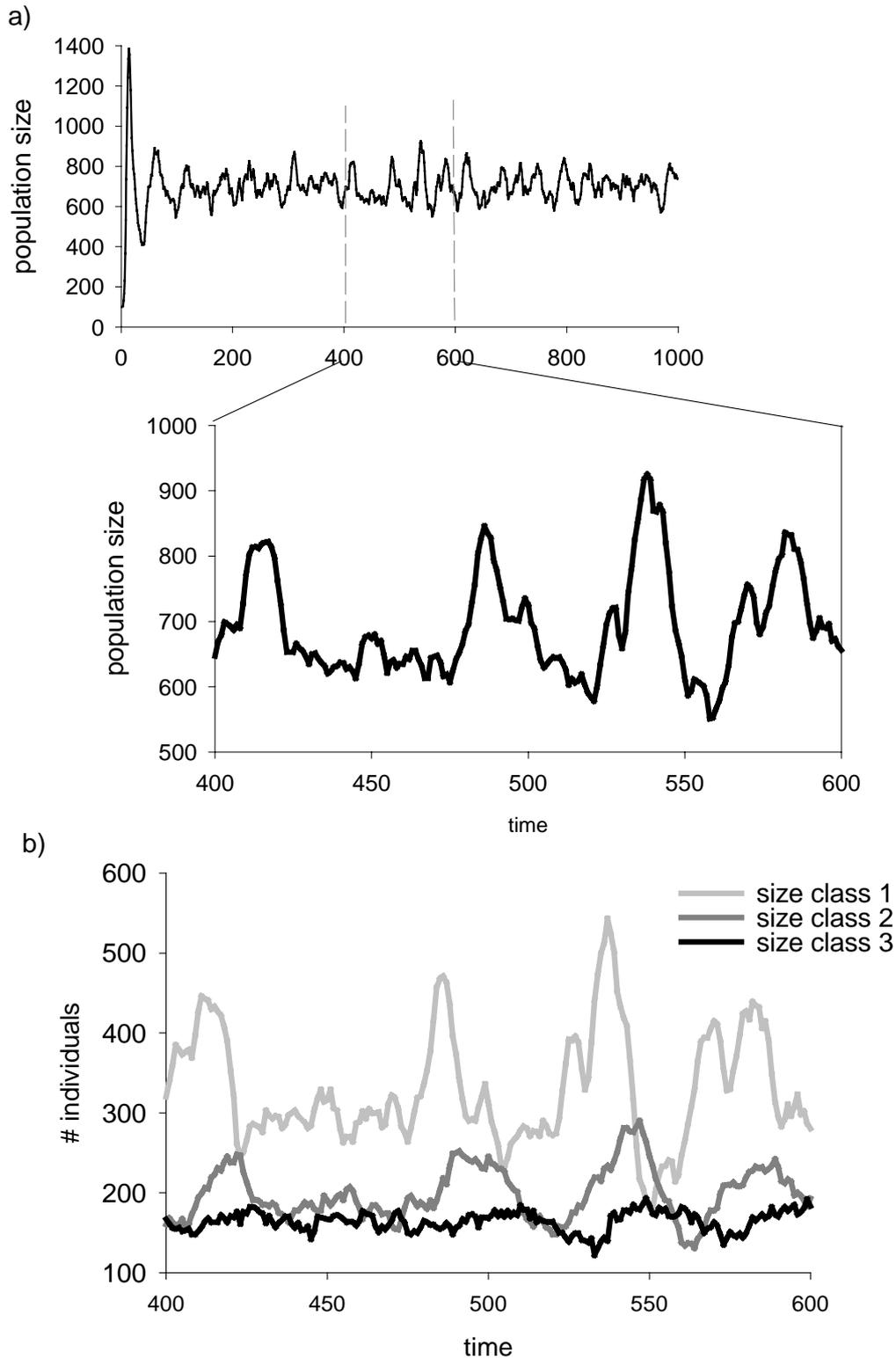


Fig. 4.1. population dynamics of a single species population. The different curves refer to size classes 1-3 where size class 1 contains these individuals that have a size smaller than $1/3$ of the maximum size, size class 2 individuals have a size between $1/3$ and $2/3$ of the maximum size and size class 3 individuals are larger than $2/3$ of the maximum size.

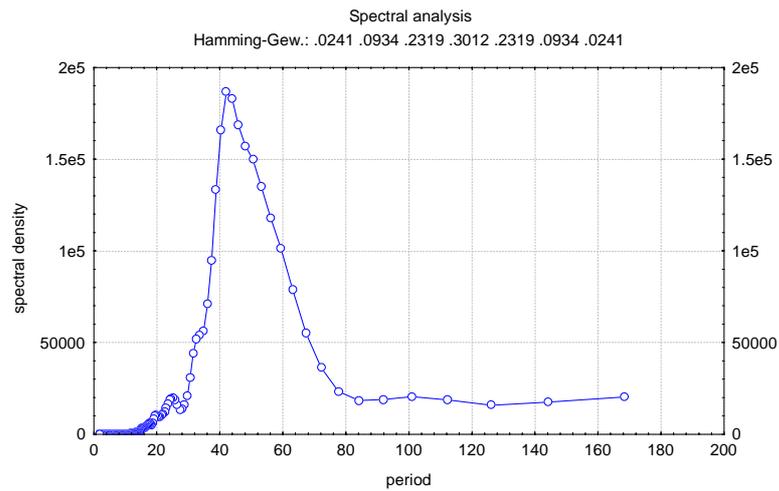
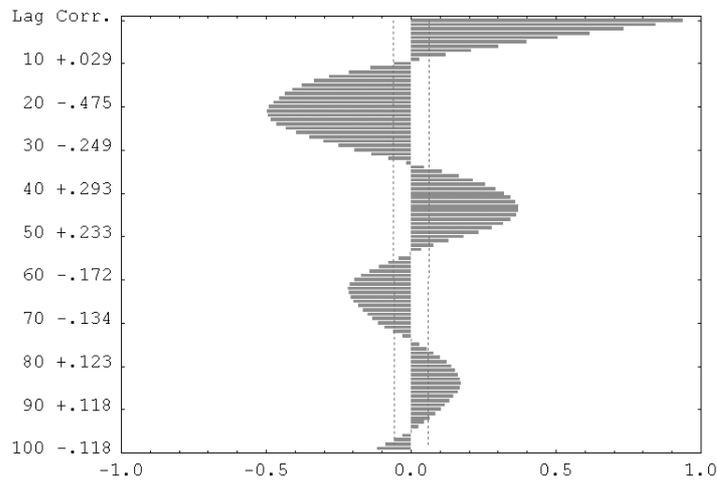


Fig. 4.2. Spectral analysis of population oscillation. There is a clear peak in spectral density at period 43 indicating a population oscillating with period of 43 time-steps.

a)



b)

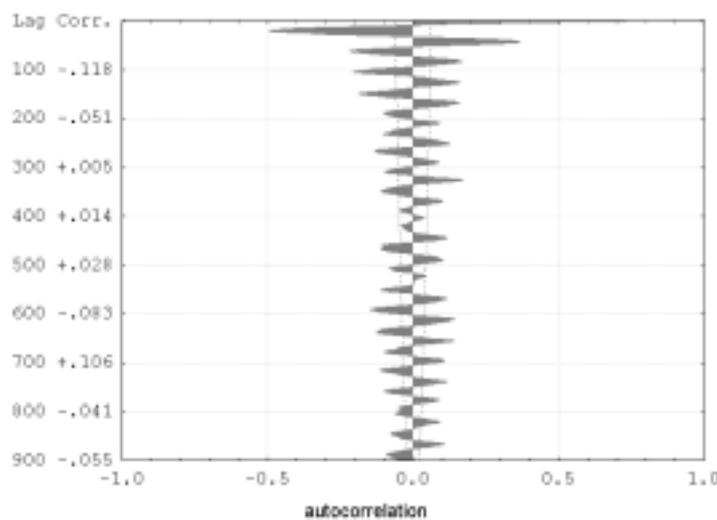


Fig. 4.3. Autocorrelation functions over a) 100 and b) 900 lags for the base model. Even at high lags, the autocorrelation function is significantly different from white noise (dashed line).

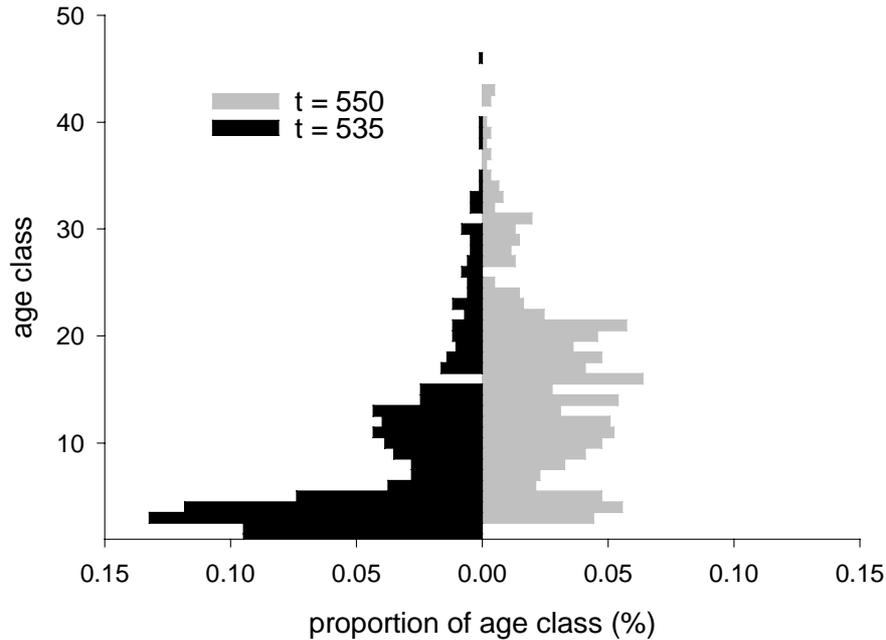


Fig. 4.4. Age distribution in the population at time-step $t = 480$ and $t = 510$. The time-steps refer to a high population size at $t = 480$ and a low population size at $t = 510$. The age distribution shows that at high density young individuals prevail whereas at low population size the distribution is more flattened indicating a higher proportion of larger individuals.

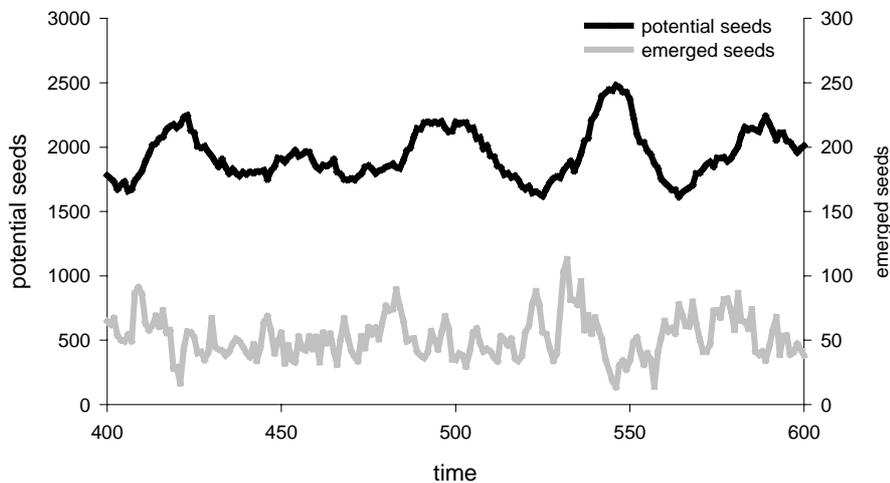


Fig. 4.5. Potential and emerged seeds in the course of time. Potential seed number refers to the overall number of produced seeds whereas emerged seeds are only those that could germinate at their particular position.

Seed production is correlated with the population size and, therefore, shows also cyclic changes (Fig. 4.5). However, only a small proportion of the seeds produced establish successfully: between 10 and 100 individuals seeds established from between 1500 and 2500 produced seeds. Hence, seed availability never restricted population growth.

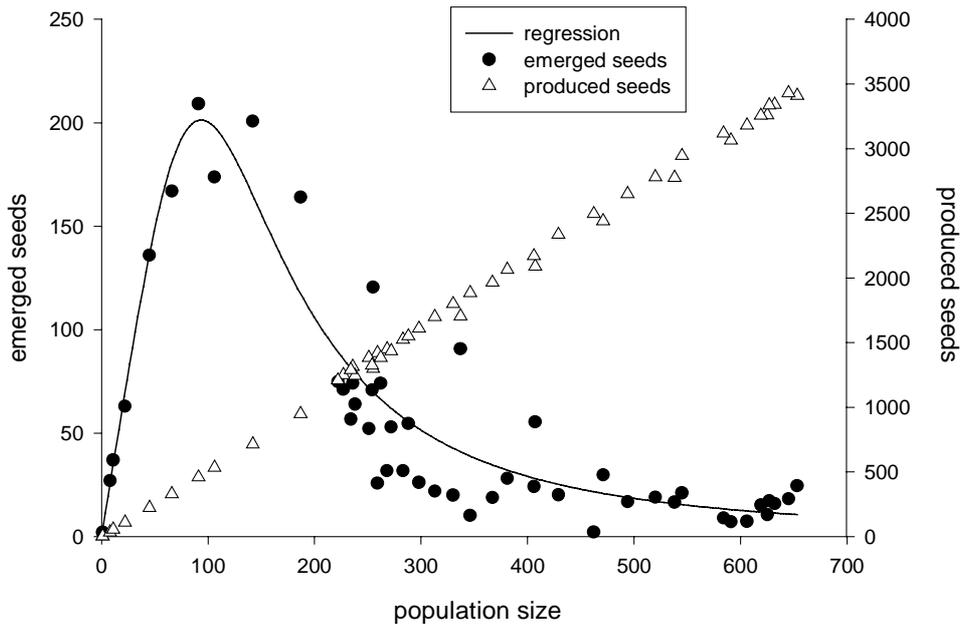


Fig. 4.6. The density dependence of seed emergence. We found a clear dependence between the number of emerged seeds and the corresponding population size. Data were fitted to the density-dependent function of Maynard Smith & Slatkin (1973) ($R^2 = 0.86$, $\lambda = 3.18$, $\alpha = 5.6 \cdot 10^{-8}$, $\beta = 3.4$).

The number seeds that emerged was clearly related to population size (Fig. 4.6): at low population sizes only few seeds emerged because too few mother plants disperse seeds. However, at a population size of approximately 100 individuals a maximum number of emerged seeds (ca. 200) is achieved. Exceeding this population size leads to a decrease in emerging seeds. Please note, that the number of produced seeds increases linearly with population size and thus, a seed limitation is not supposed. We fitted the density-dependent function of Maynard Smith & Slatkin (1973) to the data:

$$N_{emerged\ seeds} = \frac{\lambda \cdot N}{1 + \alpha \cdot N^\beta},$$

where N refers to the population size, $N_{emerged\ seeds}$ is the number of emerged seeds, λ is fertility, α and β parameters of population regulation. In general, β characterises the type of density-dependence: $\beta = 1$ indicates exact compensation, $\beta < 1$ undercompensation and $\beta > 1$ overcompensation. These compensation types correspond to different population dynamics: undercompensation results in a population that

approaches their equilibrium population size with damped oscillations. An exactly compensating population needs only one step to approach equilibrium and overcompensating populations overshoot equilibrium, then strongly regulate and consequently fall below equilibrium. Hence, overcompensation may lead to the appearance of cycles. A β -value of 3.4 was found which indicates that the population is overcompensating.

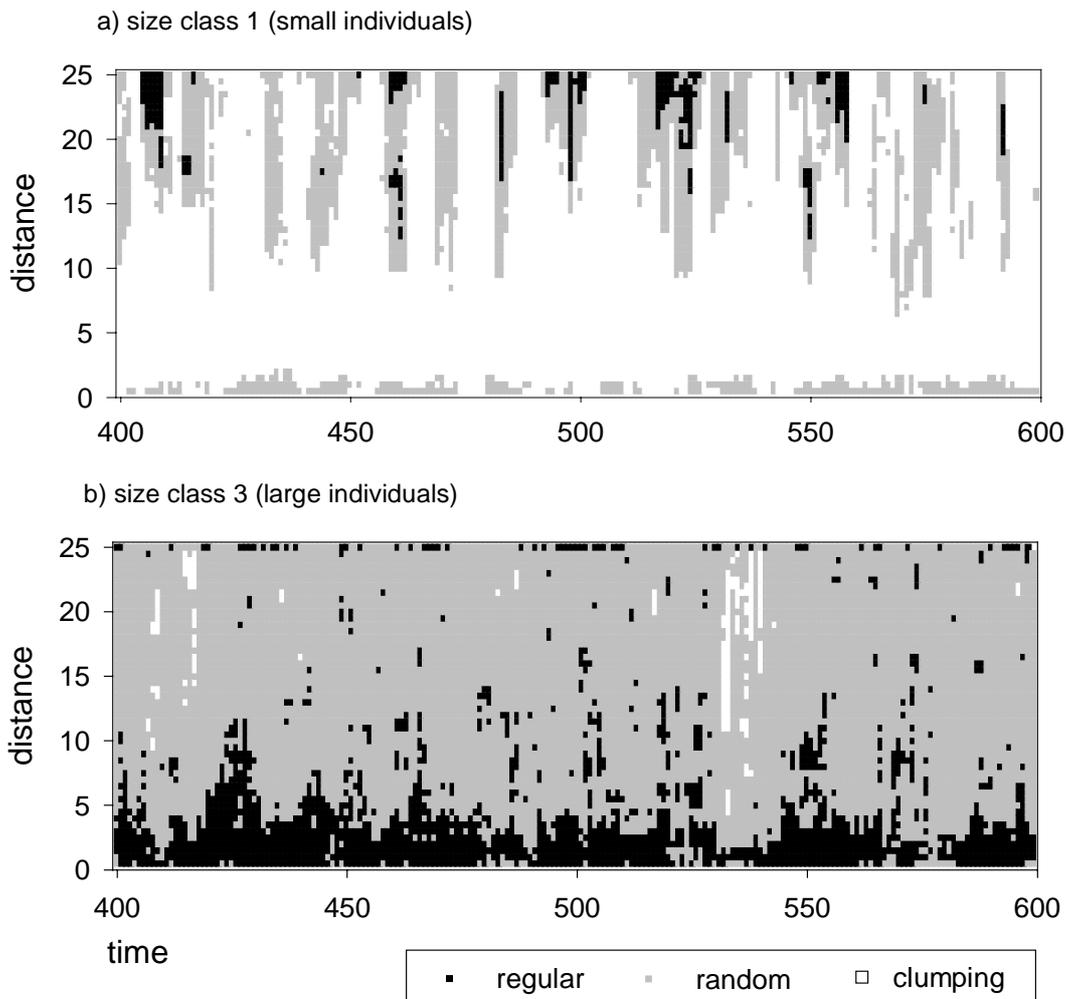


Fig. 4.7. Ripley's K in a) size class 1 (small individuals) and b) size class 3 (large individuals) for time-steps 400 to 600 and distances up to 25 m.

4.4.2 SPATIAL PATTERN AND TIME SERIES ANALYSIS

Spatial pattern was analysed both for the smallest (individuals $< 1/3$ maximum size) and for the largest (individuals $> 2/3$ maximum size) size class. In the largest size class, the pattern is regular at lower scales, i.e. to a distance up to approximately 4-5m (Fig. 4.7a). At larger scales the

pattern is predominately a random distribution. In the smallest size class, spatial distribution shows mostly clumps (Fig. 4.7b).

4.4.3 MORTALITY SCENARIOS

Population size in the mortality-changing scenarios varied between approximately 600 and 900 individuals except in the scenario where individuals died only when older than 50. In the latter, the population contained 1700 – 3000 individuals (Fig. A 1).

Cycles occurred in almost all scenarios (Table 4.1). Only in the very unrealistic scenario of random mortality no cycles were detectable (Fig. A 3). However, population size cycled with different periods, which was determined by spectral analysis. Cycle periods increased when the threshold decreased to 0.4 and periods decreased when the threshold increased to 0.6 compared to the base model's threshold of 0.5 (Table 4.1b-c).

Table 4.1. Occurrence of cyclic population dynamics when varying the mode of mortality

Mortality mode	b = 0.9		b = 0.5	
	Cycles	Period	Cycles	Period
a) Memory-mortality				
$\bar{v} = (v_{t-4} + v_{t-3} + v_{t-2} + v_{t-1} + v_t)/5$	+	42	+	40
$\bar{v} \leq 0.5$ or age > 50				
b) Memory-mortality				
$\bar{v} = (v_{t-4} + v_{t-3} + v_{t-2} + v_{t-1} + v_t)/5$	+	58	+	58
$\bar{v} \leq 0.4$ or age > 50				
c) Memory-mortality				
$\bar{v} = (v_{t-4} + v_{t-3} + v_{t-2} + v_{t-1} + v_t)/5$	+	31	+	33
$\bar{v} \leq 0.5$ or age > 50				
d) Memory-mortality				
$\bar{v} = (v_{t-1} + v_t)/2$	+	40	+	38
$\bar{v} \leq 0.5$ or age > 50				
e) Memory-mortality				
$v_t \leq 0.5$ or age > 50	+	38	+	45
f) No memory				
age > 50	+	55	+	55
g) Random mortality				
age > 50	-	-	-	-

Varying the memory of an individual with regard to past competitive pressure subtly altered the period of the population cycles (Table 4.1d-e).

The most pronounced cycles were found when the individuals had no memory at all but died when reaching an age of 50 (Table 4.1g).

The variation of parameter b of the FON-basal-radius relation had no effect on the appearance of cycles and only slightly changed cycle periods (Tab. 1) but population size was lower compared to scenarios of $b = 0.9$ and varied between 100 and 170 individuals.

4.4.4 RECRUITMENT SCENARIOS

Changing the dispersal pattern to global dispersal, i.e. seeds from one individual could potentially disperse over the whole study plot, changed neither the mean population size nor the cycle period (Table 4.2b, Fig. A 2b). Accordingly, omitting the reproductive size-threshold had neither effect on the existence of cycles nor on their period (Table 4.2f, Fig. A 5f and Fig. A 6f Appendix) but mean population size increased to 1400.

Table 4.2. Occurrence of cyclic population dynamics when varying the mode of reproduction

Reproductive mode	$b = 0.9$		$b = 0.5$	
	Cycles	Period	Cycles	Period
a) Local dispersal				
Establishment $F(x, y) \leq 0.0$	+	42	+	43
b) global dispersal				
Establishment $F(x, y) \leq 0.0$	+	45	+	43
c) Local dispersal				
Establishment $F(x, y) \leq 0.05$	+	41	+	-
d) Local dispersal				
Establishment $F(x, y) \leq 0.1$	-	-	-	-
f) Local dispersal				
Establishment $F(x, y) \leq 0.2$	-	-	-	-
g) Local dispersal				
Establishment $F(x, y) \leq 0.0$				
no size-threshold	+	40	+	40

However, establishment criteria did profoundly affect population cycling: although a threshold of the local field value $F(x, y) \leq 0.05$ still led to cycles, higher thresholds led merely to damped oscillations or complete disappearance of cycles (Fig. A 5c-d and Fig. A 6c-d appendix). Larger $F(x, y)$ thresholds led to higher population sizes. While at threshold $F(x, y) = 0.0$ population size fluctuated between 600 and 900 individuals, with increasing threshold values for $F(x, y)$ population size increased accordingly; for $F(x, y) \leq 0.05$ population size cycled between 1000 and

1500, for $F(x, y) \leq 0.1$ population size varied between 1500 and 2000 and for $F(x, y) < 1.0$ population size was around 15000.

Changing the FON-basal-radius relation to extended fields-of-neighbourhood ($b = 0.5$) had in these scenarios also no effect on the appearance of cycles nor on their period. However, population size was considerably lower than for $b = 0.9$ but showed the same effect of increasing population size when the establishment criterion $F(x, y)$ was lowered.

4.5. DISCUSSION

The occurrence of cycles in plant populations has been doubted and plant populations have rather been supposed to show a stable equilibrium. Contrary to animal ecology literature, in theoretical plant ecology few investigations have focused on non-linear dynamics (but see Silander & Pacala 1990, Cousens 1995, Stone & Ezrati 1996) and those few investigations were mostly did not take into account spatial effects.

We developed an individual-based model with the field of neighbourhood approach (Berger & Hildenbrandt 2000) which assumes that individual plants have a zone-of-influence in which an individual interacts with its neighbours and that the strength of influence changes with distance from the stemming-point. These assumptions meet the conditions of realistic individual-based models as demanded by Stoll & Weiner (2000b).

For the base model describing hypothetical perennials population size was found to cycle between particular boundaries. These cycles were in addition characterised by the kind of individuals involved and the corresponding spatial pattern. We hypothesised that recruitment is restricted due to the limited availability of free sites for the establishment of seedlings. Consequently, we expected a reproductive and a senescent period during one cycle in the population. During the reproductive period, the population is growing and consists mostly of young and small individuals whereas a senescent population contains mainly few large individuals. In accordance with this hypothesis we found different age-structures in the population at peak and trough points. Spatial pattern analysis indicated that large individuals are evenly distributed and small individuals show a random spatial pattern and these patterns are relatively independent from cycle troughs and peaks (Fig. 4.7).

In order to gain detailed insight into which process – recruitment or mortality – was responsible for the cycles, both processes were varied:

first, mortality was changed between memory and random mortality. Memory mortality refers to cases in which individuals remember the competitive pressure of the past. A step-wise reduction in the memory-length had no effect on the occurrence of cycles. Furthermore, the variation of the threshold-value for mortality inversely influenced the period of the cycles, i.e. a lower threshold led to longer periods and vice versa. However, if mortality is random and thus independent of local competition strength, no cycles emerged.

As a second step, we changed reproduction with regard to seed dispersal and establishment of seedlings. Irrespective of whether seeds were dispersed locally around the mother plant or globally over the whole study plot, the population cycled. Moreover, discarding the size-threshold for reproduction had also no influence on the occurrence of cycles which contrasts former expectations (Rees & Crawley 1989, Thrall *et al.* 1989, Rees 1991).

However, changing the establishment rules resulted in the most profound changes in population dynamics. Seedlings established at a given location whenever the local field value fell below a particular threshold. In the most restrictive scenario, seedlings could only establish when no other field-of-neighbourhood overlapped their location. In further scenarios, this restriction was loosened such that seeds could establish in border areas of a FON and finally, seeds could establish everywhere except in the basal area of an already established plant. Although the population dynamics of these scenarios still show cyclic behaviour, the autocorrelation functions diminished after approximately 50 lags below significance which was indicative of a damped oscillation.

The existence of a seed bank was not assumed, but seeds were always abundant such that a shortage of seeds could not be held responsible for the cycles in the population. This assumption could be interpreted as low seed dormancy which would according to Silander & Pacala (1990) lead to cycles. However, seeds in our model germinated only successfully when “safe sites” were available. Safe sites are locations where the competitive pressure is low, i.e. no other plant extends its field-of-influence to the seed’s position. In agreement with theoretical and empirical expectations (e.g. Eccles *et al.* 1999, Mast & Veblen 1999), we found a clumping of seedlings and small plants. Limited seed-dispersal distances led to an augmented occurrence of small individuals around their mother plant. However, large plants were predominately distributed in a regular pattern. Consequently, between seedling and adult plant stage the majority of individuals dies. The cause of mortality is local competition: at seedling stage, individuals are small and their fields of

neighbourhood hardly overlap. Growth increases basal and FON radii and accordingly augments overlap areas. This leads to the depression of growth and vigour which results in a higher mortality risk. Plants suffering too much competition over too long time die. Such self-thinning is well documented from empirical observations (Guo & Rundel 1998, Kenkel *et al.* 1997, Mast & Veblen 1999, Puigdefabregas *et al.* 1999) but models mainly concentrate on even-aged stands.

Interestingly, details of our modelling approach were of minor importance for the existence of cycles. We changed the extension of individual fields-of-neighbourhood by varying the relation between basal and FON-radius which results either in compressed, rapidly decreasing fields or in extended, gradually decreasing fields. Although the population size was in general lower for extended fields, cycles appeared with approximately the same period and disappeared in the same scenarios as for compressed fields.

We conclude from our results that populations of perennial plants may show complex, non-linear dynamics, i.e. cycles, if established plants virtually prevent the establishment of seedlings within their zones of influences. Empirically, so far only one such case has been reported by Tilman & Wedin (1991) where a population of perennials was found to cycle. These perennials accumulated litter and thereby prevented establishment of young plants. Such a litter-layer caused a time-lag in the turn-over. Theoretically, the same mechanism of cycles due to monopolisation of space by adults has been described for models of sessile marine organisms, e.g. corals (Roughgarden *et al.* 1985, Roughgarden & Iwasa 1986).

Our theoretical findings suggest that monopolisation of space by established plants may be a destabilising mechanism of plant population dynamics. This could also have implications for community dynamics, for example for the coexistence of similar species in diverse communities such as tropical forests. One reason for the high diversity of both coral reefs and tropical forests might be that in both ecological systems monopolisation of space is important. Further empirical studies and meta-analyses could possibly detect pattern in the relationship between establishment and temporal and spatial pattern of the plants populations and communities. Further understanding could be gained by a theoretical analysis of a model of annual plants based on the FON approach. Moreover, in the model presented here the strict threshold for establishment could be released by assuming seedling banks, i.e. cohorts of seedlings which are able to survive, without growing, longer periods of time within the zone of influence of established plants.

5. DISCUSSION

The understanding of competition between individuals is a central issue in plant ecology because interactions between individuals structure populations and consequently communities (e.g. Crawley 1997). In plants, competition is inherently local and therefore, the modelling of local competition and its effects on intra- and intergenerational population dynamics was the focus of my thesis.

As a first step towards a better understanding of local competition, an appropriate modelling approach has been searched. In a recent review, Stoll & Weiner (2000) proposed a list for realistic individual-based models, e.g. that each plant should have an explicit spatial position, a basal extension and a zone where interaction with neighbours occurs. Several modelling approaches exist at time that more or less meet these criteria: fixed-radius neighbourhood models (e.g. Pacala & Silander 1985), zone-of-influence models (e.g. Wyszomirski *et al.* 1999), ecological field models (e.g. Walker *et al.* 1989) and field-of-neighbourhood models (Berger & Hildenbrandt 2000). The basic assumption all these models have in common is that the number of neighbours influences the performance of a focal plant individual. Their differences consist in the degree of detail they include and how they understand competition: In fixed radius models, only the number of neighbours in a fixed-radius zone around a focal plant is of interest for the focal plant's performance. Although zones of different radii can be defined for the influence of neighbours on different processes, e.g. growth or reproduction, interactions are rather abstractly estimated from fits to empirical data.

Zone-of-influence models include additionally size and distance to neighbours for the determination of growth. Furthermore, the zone-of-influence is variable and increases in diameter during growth. In general, the zone-of-influence is the area where the individual gathers resources and hence, competition is included in a semi-mechanistic manner: Overlapping zones-of-influence indicate competition for resources and hence, affect performance of participating individuals.

In ecological field models number, size and distance to neighbours is taken into account. Competition is considered mechanistically as common demand for various resources. For each resource, an individual has a

particular spatial up-take function and the combinations of these functions for all individuals leads either to deficits or surplus for the particular resource. Consequently, deficits lead to suppressed growth.

Finally, field-of-neighbourhood models try to fill the gap between the realism though high parameter demands of ecological-field-models and the rather abstract view of competition in zone-of-influence models. Competition is considered in a phenomenological manner where not the mechanism but the effect of competition between individuals is important. Hence, this approach is phenomenological as the Lotka-Volterra approach is but at the level of individuals (Berger *et al.* 2002). The idea to calculate the abstract negative influence of neighbours on a focal individual allows the inclusion of competitive effects on all processes, e.g. growth, reproduction and mortality. Hence, this approach potentially extends the applications of the other modelling approaches to intergenerational population dynamics but beforehand this approach must show that it covers also the domain of earlier approaches.

Therefore, one objective of this study was the test of the field-of-neighbourhood approach in the development of size hierarchies in plant populations. The model investigates the mode of competition emerging from the FON approach in an even-aged monoculture of hypothetical plants. The FON-shape is characterised by the value of the parameter b from the relation between basal- and FON-radius. It determines whether a plant has an extended, gradually decreasing (small b) or a compressed, abruptly decreasing FON. Furthermore, the field value at the border of the FON, I_{Min} , defines how strong competition onsets. Both parameters were varied and the effects characterised in terms of competition mode. The resulting mode of competition was calculated with a new measure, C_a (Wyszomirski *in prep.*). It was hypothesised that compressed fields would lead to asymmetric competition whereas extended fields would lead to symmetric competition.

However, the results in general showed that irrespective of the b and I_{Min} -values the individuals within the population were competing asymmetrically. Higher degrees of competitive asymmetry resulted from higher I_{Min} -values. However, at highest values for I_{Min} and high density, growth is reduced so much that asymmetry is hard to detect. Furthermore, in studies with two individuals only it was shown that asymmetry is a logical consequence of plant interactions via zones-of-influence. This argument has already been mentioned by Schwinning & Weiner (1998) but a detailed test of this hypothesis was still to be done.

It was, therefore, argued that plant competition via zones-of-influence is necessarily asymmetric. Difficulties of earlier studies to detect

asymmetry at population level (e.g. Bonan 1991, Hara & Wyszomirski 1994, Wyszomirski *et al.* 1999, Weiner *et al.* 2001) should therefore not necessarily be ascribed to symmetric competition among individuals, but to spatial or density effects.

A further topic of my study was the investigation of intergenerational consequences of local competition. As none of the earlier approaches covered a full population-dynamical cycle, i.e. growth, mortality, reproduction and establishment, the basic FON model was extended to include these processes. Population size in this model oscillated around a mean population size with a period of approximately 40 time-steps. These oscillations resulted from an endogenous process as concluded from the autocorrelation analysis. It was hypothesised that one cycle consists of two periods: a reproductive and a senescent period. Both are characterised by a specific age-pyramid and spatial distribution. In the reproductive period, small, young individuals prevail in the population; the age-pyramid is consequently left-biased and the spatial pattern clumped or random. In contrast, in the senescent period large, older individuals form the majority of the population. These individuals are distributed in a regular spatial pattern. Hence, the negative feedback is as follows: Starting with a low population size, most individuals feel only weakly the presence of others and therefore grow to a large size. During each time-step they reproduce and the majority of seedlings can establish because enough free sites are available. These processes continue until most of the space is occupied and establishing becomes impossible. Although plants still grow slowly the dominant process at this point is mortality. But mortality affects mostly those individuals that stand closely and suffer from strong competition. Consequently, population size decreases to the lower limit from where individuals have the largest possible distance from each other, i.e. regularly distributed. From this lower limit the population starts to rebuild because free space is abundant.

Although nonlinear behaviour has long intrigued animal ecologists, the occurrence of cyclic or chaotic population dynamics has mostly been ignored by plant ecologists. Instead, plant populations were not supposed to show oscillatory or chaotic behaviour but to run into a stable equilibrium (Rees & Crawley 1989, Crawley 1990, 1997). However, some empirical observations revealed cyclic population dynamics also in plants (Symonides *et al.* 1986) and other authors called for a re-evaluation of the stable-equilibrium concept in plant communities (Dodd *et al.* 1995). Only few modelling studies have tested for nonlinear behaviour in plant species

(e.g. annuals: Thrall *et al.* 1989) and none of them investigated the population dynamics of perennials.

To test for the specific influence of mortality and reproductive parameters, modified model scenarios were analysed. With regard to the occurrence of cycles in the population dynamics, mortality modes were of minor importance compared to reproductive modes. Although changing the threshold values in vigour needed to survive altered the period of the cycles, only the unrealistic scenario of random mortality led to the disappearance of cycles. In contrast, reproductive scenarios profoundly affected population cycling: loosening the rigid establishment rule changed the mode of population dynamics to damped oscillations.

Hence, it was concluded that plant populations may show complex, non-linear behaviour, if the establishment of seedlings is prevented by the presence of already established plants and a therefore, high competitive pressure. Evidence of cycles from similar establishment restrictions comes from Tilman & Wedin (1991) who found oscillatory behaviour in *Agrostis scabra*. This perennial accumulates litter which prevented subsequent growth or establishment of seedlings in a time-delayed manner. A similar mechanisms of monopolising space has been described for models of sessile marine organisms (Roughgarden *et al.* 1985, Roughgarden & Iwasa 1986).

Such a monopolisation of space could also have implications for community dynamics. Therefore, further studies should investigate the consequences of non-linear population dynamics in a single species population for coexistence of species and the consequences of space-monopolisation for community dynamics.

In general, the idea of this study was to apply a new approach of local plant competition – the field-of-neighbourhood approach – and to check if this approach leads to new insights into plant population dynamics. It has been claimed that the FON-approach has the potential to become a new standard for individual-based models of sessile species (Berger *et al.* 2002). The results of this thesis largely corroborate this claim. It was shown that the FON-approach is even more powerful than the zone-of-influence models for the investigation of size-hierarchies. Furthermore, a logical argument was provided for explaining the difficulties of finding a link between mode of competition and a particular size-structure.

More importantly, the FON-approach expands the range of application of former approaches: population dynamical questions can easily be addressed. It is therefore concluded that the FON-approach is in fact an important enhancement of model approaches because it is both

realistic and phenomenological and applies consequently for models of real species and also for theoretical questions.

The next step in investigating competition should be the extension of the FON model to multi-species communities. The results for a one-species population have shown that intrinsic processes can lead to nonlinear dynamics. In a multi-species community such a behaviour could also alter interactions between species and therefore affect species coexistence. To this end, however, the run-time behaviour of the approach has to be improved, otherwise too few species, or too small areas could be simulated. The current run-time limitation of the FON-approach is a limitation of all individual-based plant models which include local competition: the computation time for checking which plants are neighbours, i.e. interact via competition, increases exponentially with the size of the population. However, advanced algorithms exist which will overcome this problem (Hildenbrandt *in prep.*).

The overall conclusion of my thesis is that the explicit, and effective, description of local competition in plant population models leads to new and important insights. These insights are certainly important for theoretical plant population ecology, but even more for explaining diversity patterns in, for example, tropical forests and coral reefs. Recent theories explaining diversity patterns, for example the neutral model of Hubbell (2001), are highly aggregated and rely on assumptions which are not fully understood. For example, Hubbell (2001) assumed that all tree species in a forest are competitively equivalent, i.e. are identical with regard to the outcome of local competition. This assumption has been criticized because it seems unrealistic (e.g. Yu *et al.* 1998). However, a spatially explicit individual-based community model which is based on the FON-approach could easily test if Hubbell's assumption is supported by a mechanistic model.

Thus, the main result of this thesis is – besides of the results regarding the mode of competition and nonlinear population dynamics in plants – that modelling plant population and community dynamics with an appropriate approach, e.g. the FON-approach, has the potential to lead to fundamental and new insights. An individual-based ecology seems indeed, as has been predicted by Huston *et al.* (1988), to emerge which is likely to contribute to a more unifying theory, or at least notion, of ecological systems. This thesis is one step towards such a notion, and many more steps have to come. However, what I tried to show here, is that these steps are easy to make, once a carefully designed and tested modelling approach has been chosen.

6. SUMMARY

6.1. SUMMARY

This study investigates theoretically local competition within plant population and seeks to characterise the effects of local competition on population size-structure and population dynamics. The study consists of three main parts:

1. As a first step, an appropriate modelling approach has been searched and therefore, existing approaches that incorporate individual, local interactions were reviewed namely the tessellation approach, ecological field, and zone of influence. These approaches focus on different details of competition, and therefore describe different processes in a more or less mechanistic manner. The recently developed field of neighbourhood approach departs from a mechanistic view and describes local competition in a phenomenological manner. Hence, this approach attempts to be applicable to a variety of problems and was therefore chosen for analyses of local competition in this thesis.

2. Size distributions are often studied in order to infer the mode of competition, i.e. symmetric or asymmetric, but the results remain still ambiguous. Hence, a field-of-neighbourhood model was developed for the analysis of the mode of competition that emerges from such an approach. Herein, plants have a zone-of-influence where they interact with other plants. Furthermore, a field is superimposed on this zone that defines the strength of interaction. Competition was investigated at the individual and population level and the effects of density and field-of-neighbourhood shape were characterised. Asymmetric competition emerged in all scenarios and it was therefore argued that asymmetric competition is a natural consequence of local competition. This finding could resolve much of the argument about symmetric versus asymmetric competition.

3. To model plant population dynamics, the processes of plant reproduction and mortality were added to the basic field-of-neighbourhood model. Population dynamics of this model was clearly cyclic and herewith contrasts to former expectations of plant ecology. The occurrence of cycles was robust to changes in model parameters and assumption. By varying

the model assumptions, The processes leading to cycles were identified. One precondition is that competition is local: a model scenario with random mortality did not produce cycles. The second and most profound mechanism leading to cycles was monopolisation of space by established plants. The conditions for successful establishment of seedlings were of great importance. As soon as seedlings could also establish in slightly competitive environments the cycles disappeared.

In total, the focus on local competition and the usage of a new, more appropriate modelling approach led to new insights into the mode of local competition, into cohort dynamics leading to size hierarchies, and into non-linear dynamics in plant populations.

6.2. ZUSAMMENFASSUNG

Die lokale Konkurrenz innerhalb von Pflanzenpopulationen wurde in der vorliegenden Arbeit auf theoretischer Ebene untersucht. Hauptziel waren die Charakterisierung der Effekte lokaler Konkurrenz auf die Ausbildung von Größenhierarchien in einer Population und die Auswirkungen der Konkurrenz auf die Populationsdynamik.

Die Arbeit besteht aus drei Teilen:

1. Zur Auswahl eines adäquaten Modellansatzes wurde eine Übersicht zu den derzeit existierenden Ansätzen erstellt, die lokale, individuelle Interaktionen beinhalten. Im einzelnen sind das der Tessellation-Ansatz, der Ansatz der ökologischen Felder und der Ansatz der Einflusszonen. Diese Ansätze konzentrieren sich auf verschiedene Details der Konkurrenz und beschreiben sie auf mehr oder weniger mechanistische Weise. Der kürzlich entwickelte Ansatz der Nachbarschaftsfelder weicht von den genannten Modellansätzen ab, da er Konkurrenz nicht mechanistisch sondern phänomenologisch beschreibt. Daher ist dieser Ansatz potentiell auf eine Vielzahl ökologischer Fragestellungen anwendbar und wurde deshalb in der vorliegenden Studie zur Untersuchung lokaler Konkurrenz gewählt.

2. Größenverteilungen von Pflanzenpopulation wurden in der Vergangenheit oft untersucht, um Rückschlüsse auf den Modus der Konkurrenz (symmetrisch oder asymmetrisch) zu ziehen. Die Ergebnisse dieser Untersuchungen waren jedoch nicht eindeutig interpretierbar.

Daher wurde ein Modell mit dem Ansatz der Nachbarschaftsfelder entwickelt, um auf den daraus resultierenden Konkurrenzmodus zu

schliessen. In diesem Modell besitzen Pflanzen eine Einflusszone, in der sie mit anderen Pflanzen interagieren. Zusätzlich ist dieser Einflusszone ein Feld überlagert, das die Interaktionsstärke definiert.

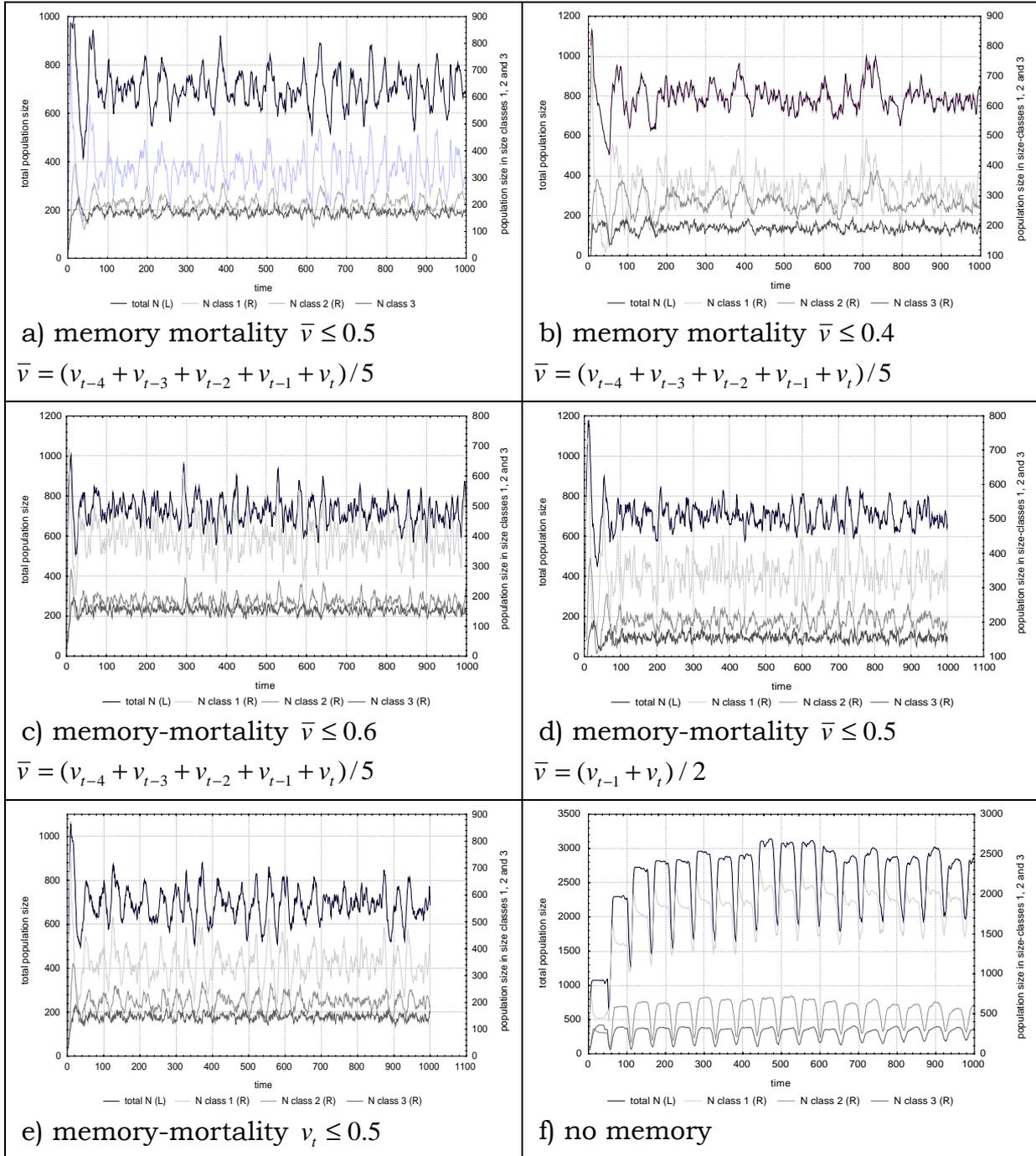
Die Konkurrenz wurde auf individueller und Populationsebene untersucht und die Einflüsse von Dichte und Form des Nachbarschaftsfeldes charakterisiert. Asymmetrische Konkurrenz resultierte in allen Szenarios und deshalb wurde argumentiert, dass asymmetrische Konkurrenz eine natürliche Konsequenz lokaler Konkurrenz ist. Dieses Ergebnis könnte viele Argumente der Diskussion über symmetrische und asymmetrische Konkurrenz auflösen.

3. Zur Modellierung der Populationsdynamik bei Pflanzen wurde das Basismodell um die Prozesse Reproduktion und Mortalität erweitert. Die Populationsgröße im Modell zeigte zyklische Schwankungen, die den Erwartungen einer stabilen Gleichgewichtsdynamik in der Pflanzenökologie widersprechen. Die Zyklen waren robust gegenüber Änderungen in den Modellparametern und -annahmen. Durch diese Änderungen konnten ebenfalls die Prozesse identifiziert werden, die zu den Zyklen führten: Eine Voraussetzung ist, dass Konkurrenz lokal ist - ein Modellszenario mit zufälliger Mortalität zeigte keine zyklischen Schwankungen. Der zweite und entscheidende Mechanismus für zyklische Populationsdynamik ist die Monopolisierung des Raumes durch etablierte Pflanzen. Die Zyklen verschwanden, sobald sich Keimlinge nicht nur in konkurrenzfreien sondern auch in gering-kompetitiven Umgebungen etablieren konnten.

Mit dieser Arbeit konnte gezeigt werden, dass die Fokussierung auf lokale Konkurrenz und die Verwendung eines neuen Modellansatzes zu neuen Erkenntnissen über die Ausbildung der Größenhierarchien in Kohorten und über nichtlineare Dynamik in Pflanzenpopulationen führt.

7. APPENDIX A

7.1.1 SIMULATED TIME-SERIES OF MORTALITY MODES



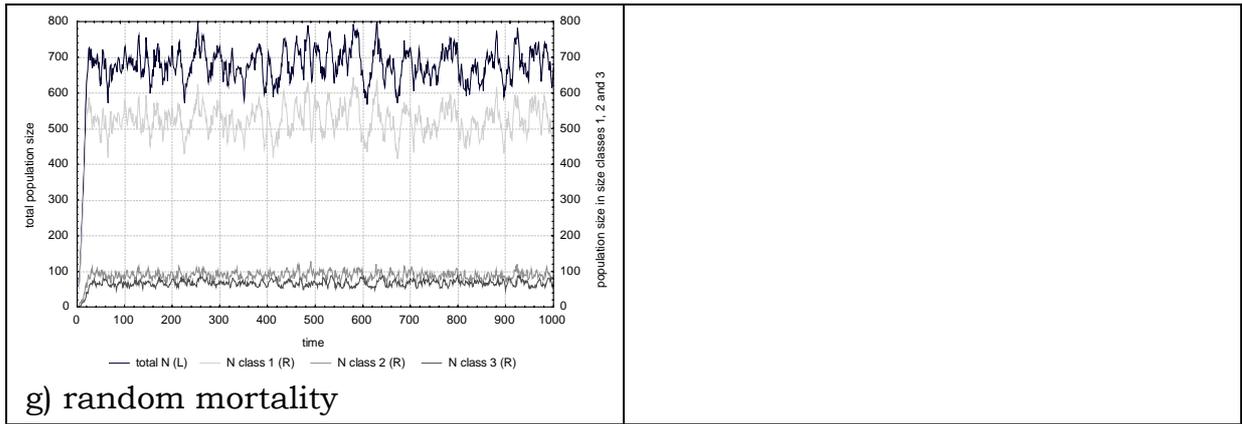
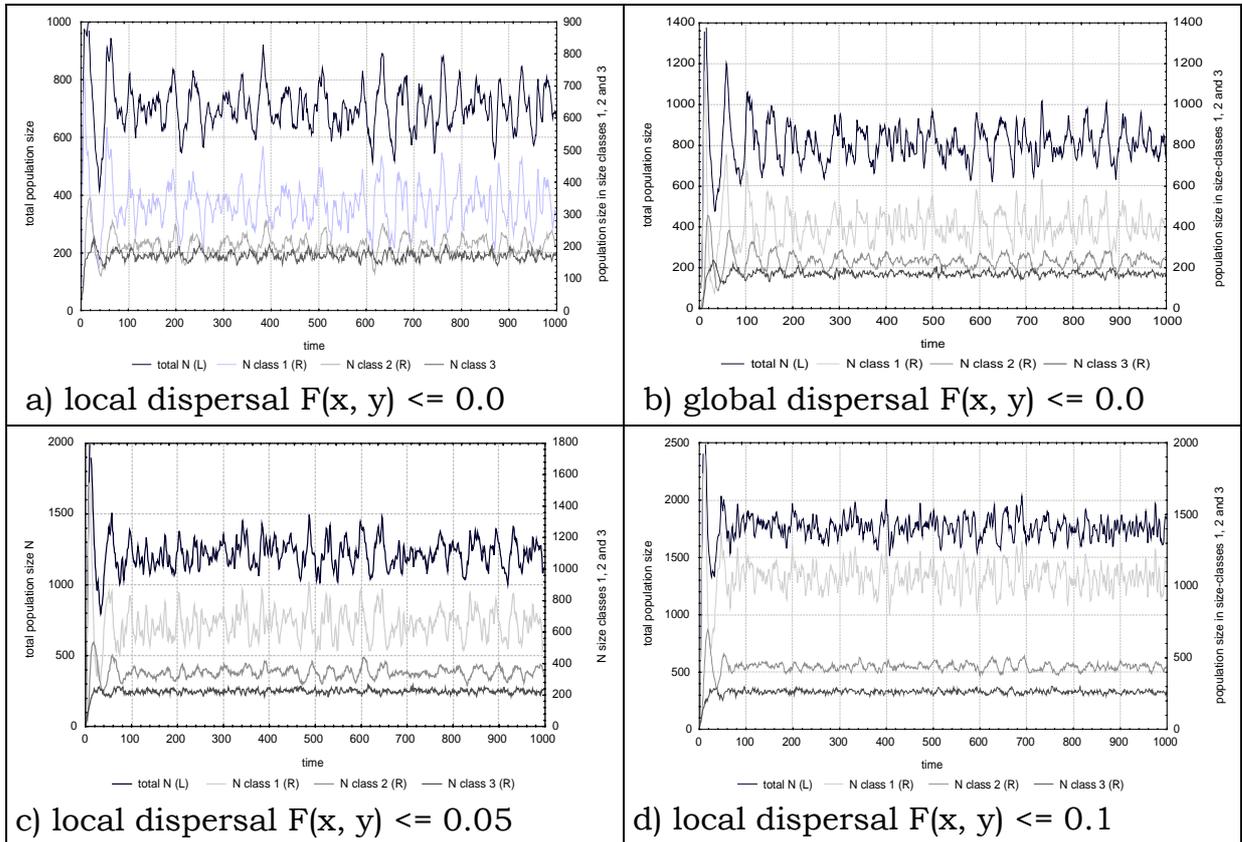


Fig. A 1. Time-series in the mortality-changing scenarios

7.1.2 SIMULATED TIME-SERIES OF REPRODUCTIVE MODES



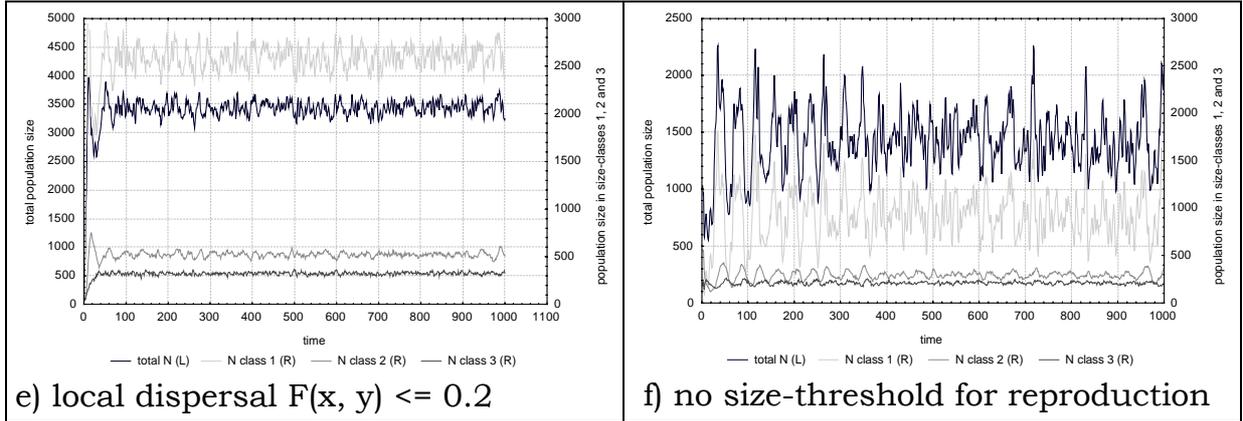
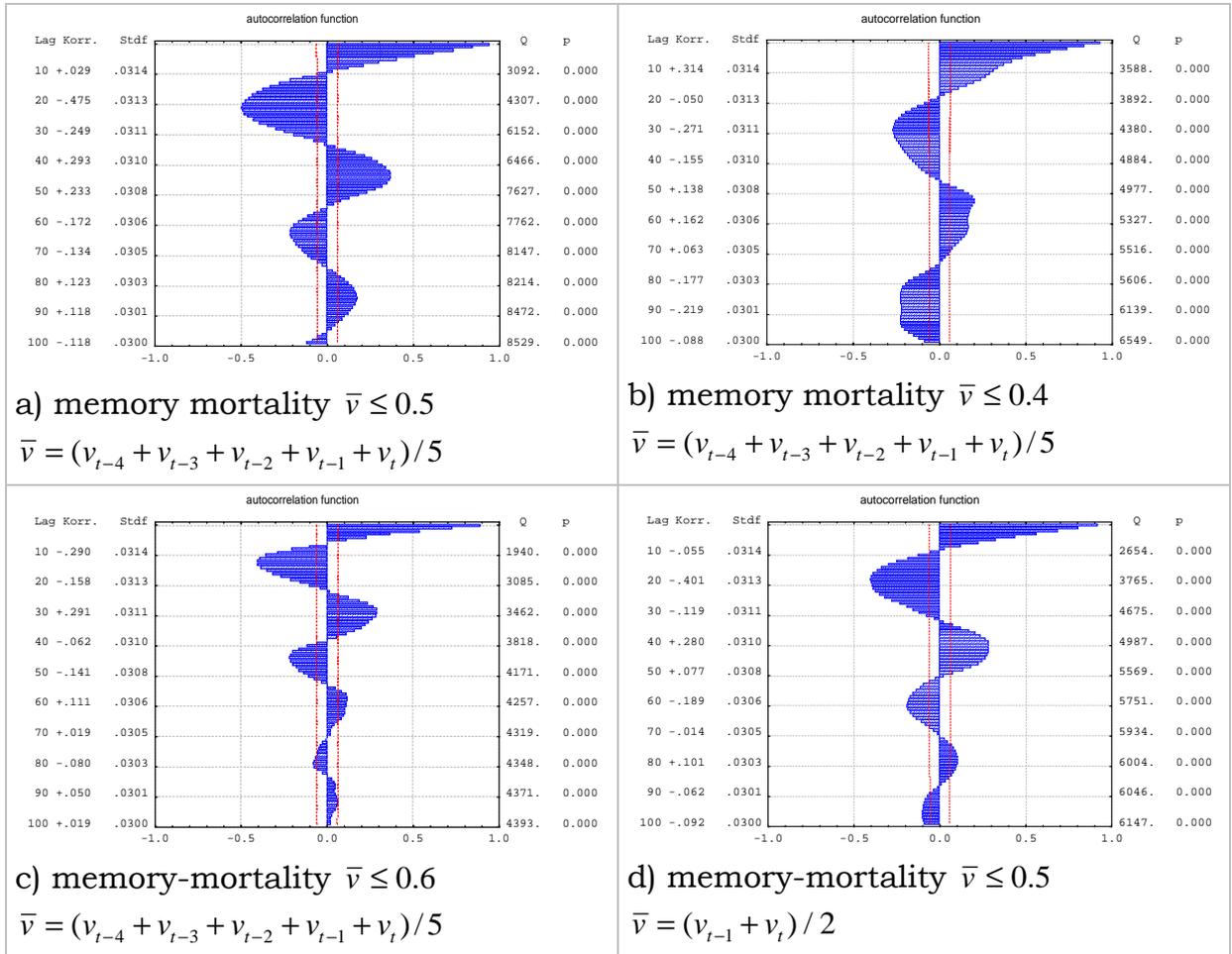


Fig. A 2 Time series of scenarios with different reproductive modes

7.1.3 ACF OVER 100 LAGS - MORTALITY MODES



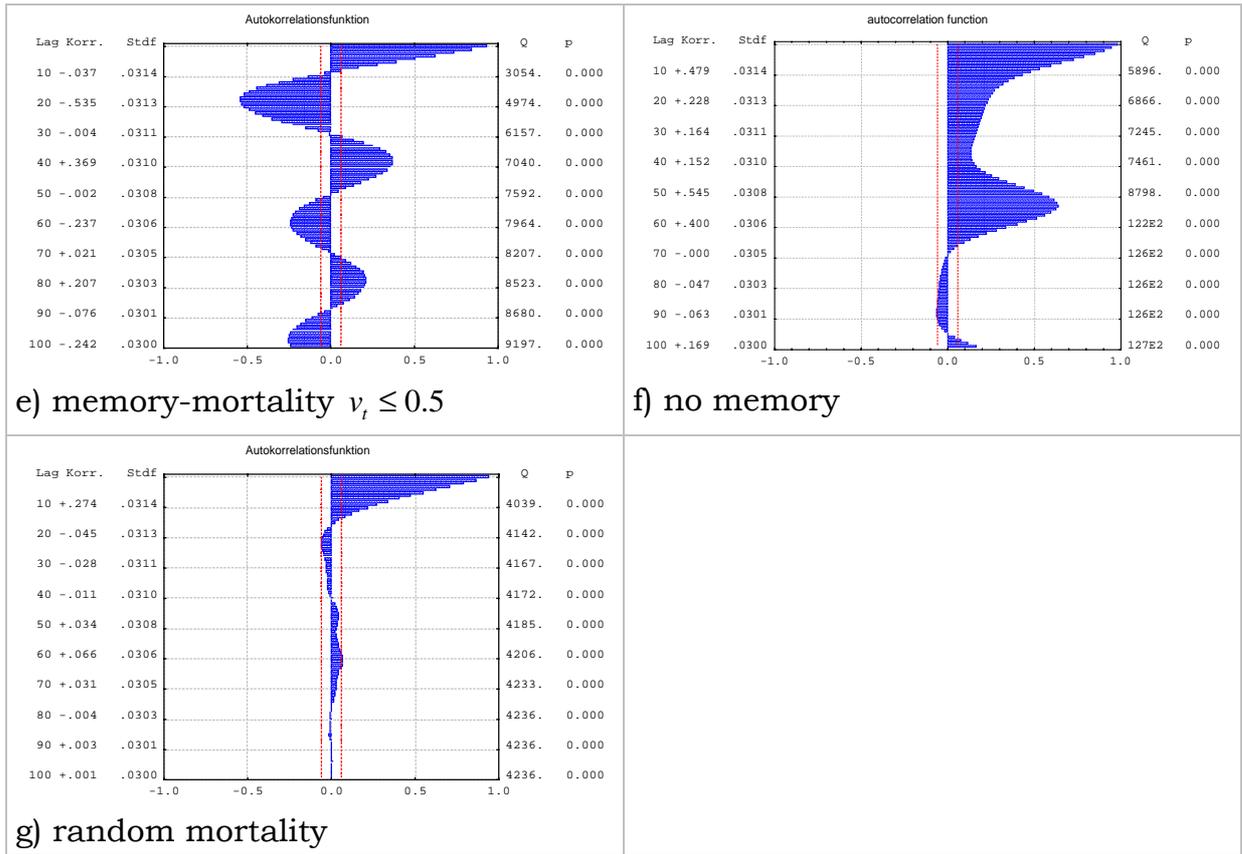
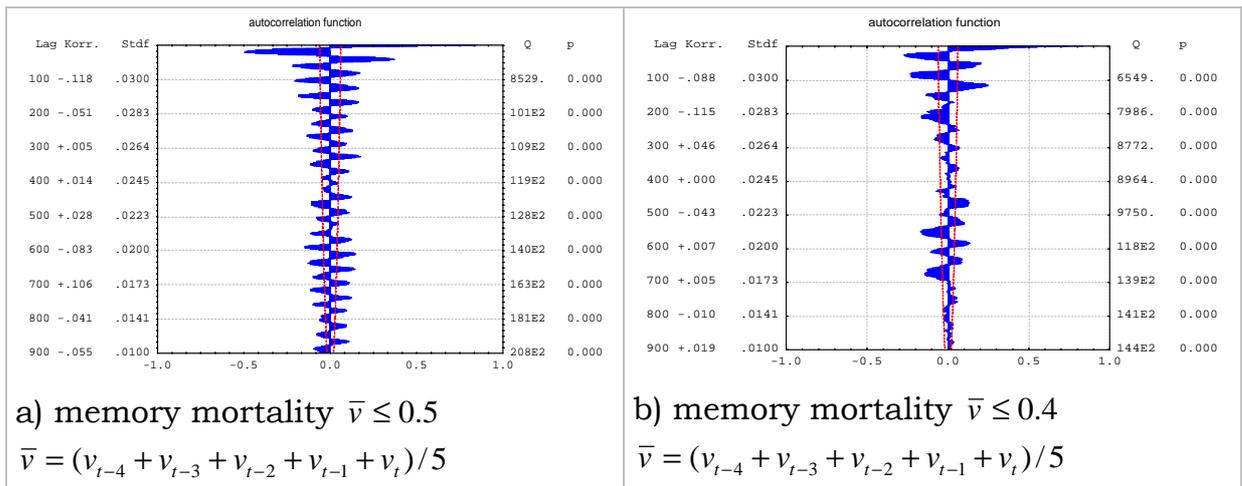


Fig. A 3 Autocorrelation functions over 100 time-lags in the scenarios with different mortality modes

7.1.4 ACF OVER 900 LAGS - MORTALITY MODES



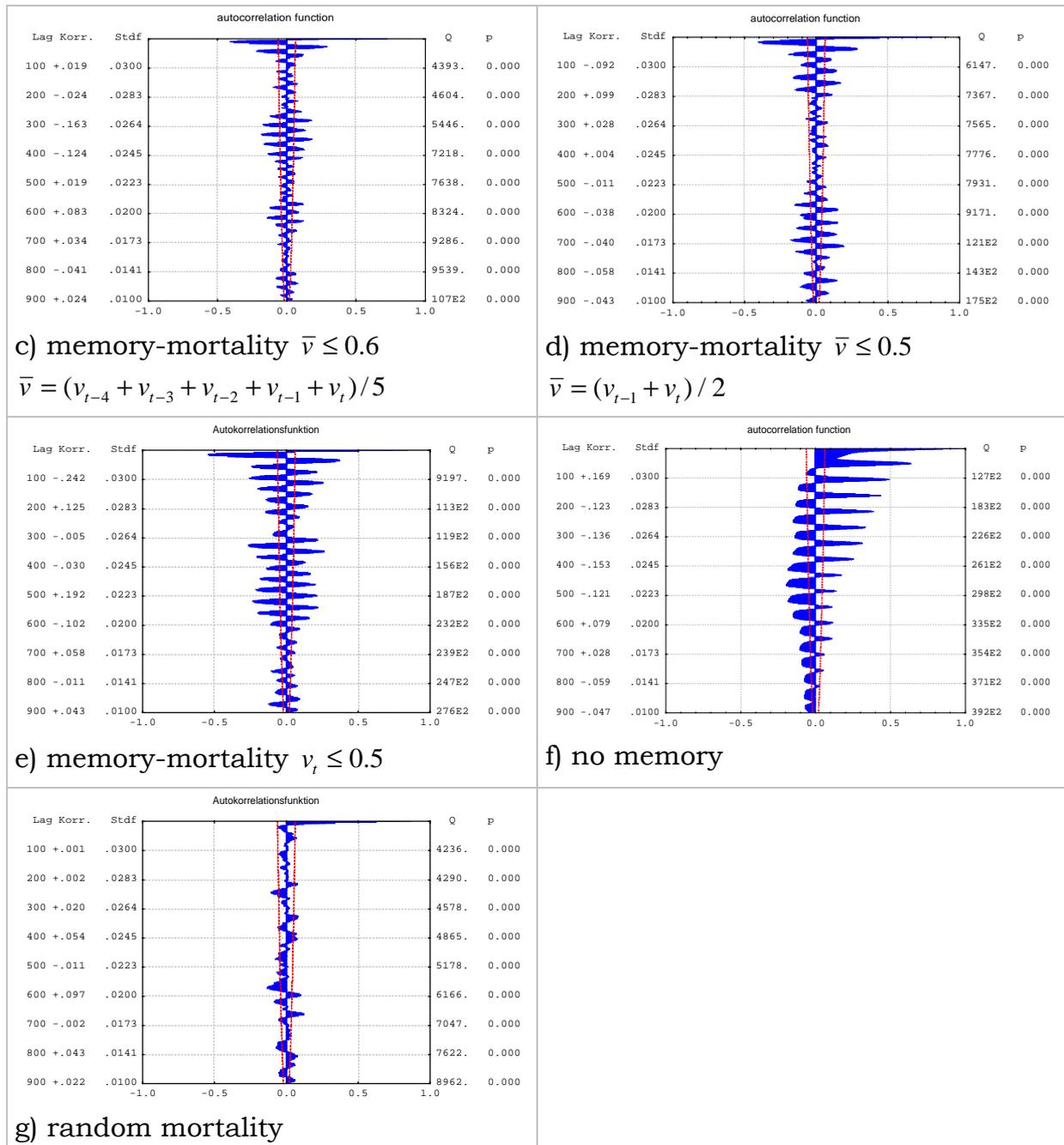


Fig. A 4 Autocorrelation function for 900 lags of mortality-changing scenarios

7.1.5 ACF OVER 100 LAGS - REPRODUCTIVE MODES

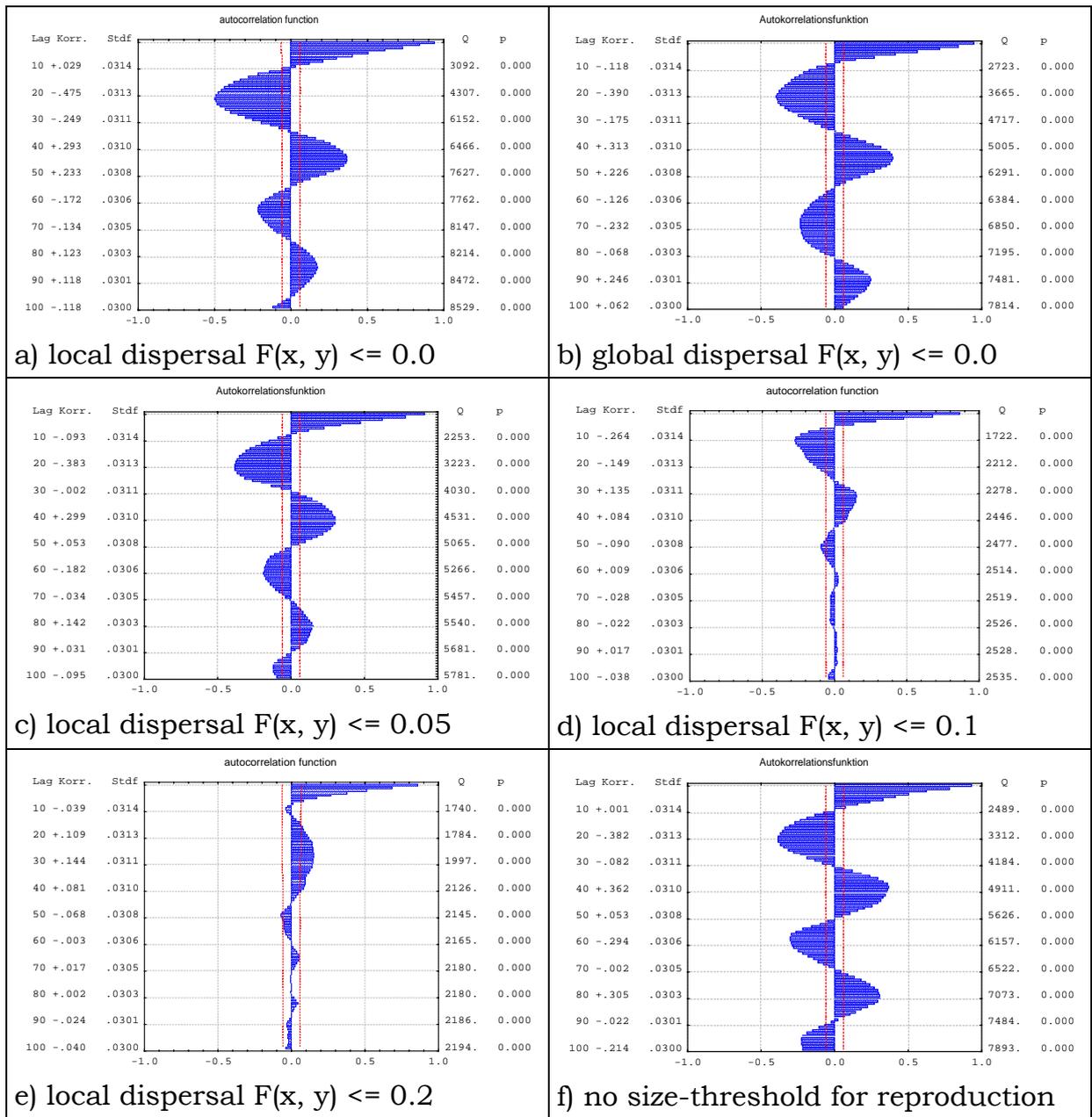


Fig. A 5 Autocorrelation function (100 lags) for scenarios with altered reproductive modes

7.1.6 ACF OVER 900 LAGS - REPRODUCTIVE MODES

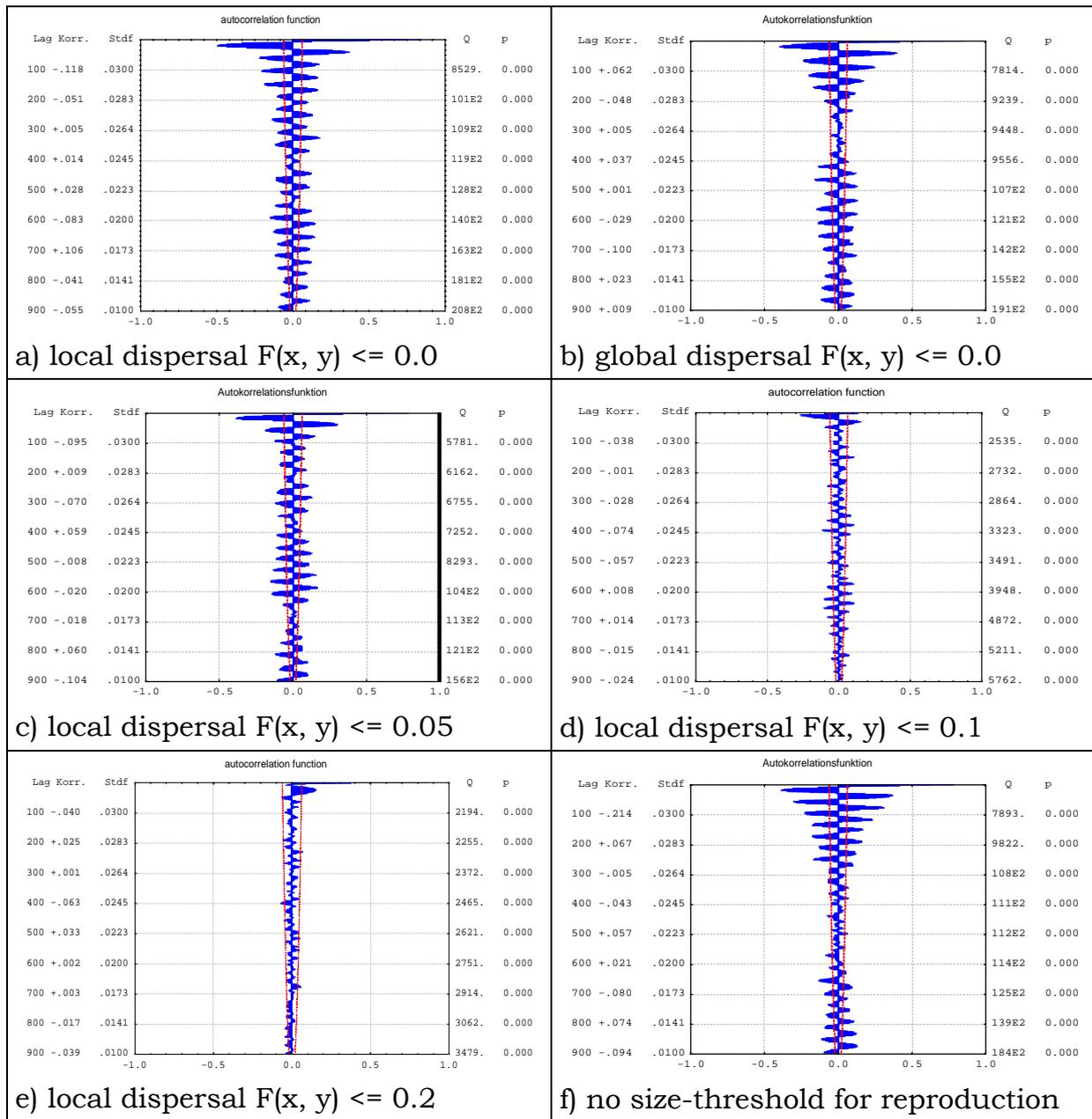


Fig. A 6

8. APPENDIX B: MEASURING COMPETITION BETWEEN NEIGHBOURS

8.1. HOW TO QUANTIFY NEIGHBOURHOOD COMPETITION?

The structures that we can identify in plant populations result from biotic and abiotic forces to which the individuals of a population have been exposed in the past. Size¹, age and genetic structure and spatial distribution are affected by the interactions that have taken place in the past. As a first step it is necessary to describe and measure the differences in plant performance, e.g. size inequality. Therefore, I will describe the most common quantities that are used to describe size-inequality in plant populations. In general, these measures can be subdivided into two sub-groups: first, conventional measures of size-distribution, e.g. mean, variance, skewness and second, measures that include spatial configuration, e.g. partial correlation and C_{α} . Size-distribution measures characterise the shape of a frequency-distribution of sizes in a population. Hence, the average size and standard deviation, variance or coefficient of variation were first used to describe important characteristics of a distribution. If, however, this distribution deviates from a Gauss-curve, these measures get biased. Therefore, skewness and kurtosis as third or fourth-order measures or the Gini-coefficient have been used to describe the shape of the size distribution. These measures describe whether large or small individuals prevail in a population by quantifying magnitude and sign of the deviation from a bell-shaped distribution.

However, all these size-distribution measures ignore the spatial distribution of individuals. Recently, measures have been developed that explicitly consider the local nature of competition (Wyszomirski *in prep.*). These measures correlate size of neighbours with the size of a focal plant. The simplest possible way is to calculate the Pearson correlation coefficient between size of neighbours and focal individual. Advanced

¹ Herein, size generally indicates any measure of a plant that can be related to size, i.e. height, diameter, biomass, or area.

measures, e.g. partial correlation and C_{α} , include space by calculating the deviation from an expected size that is determined by the individual available space.

8.1.1 STANDARD STATISTICAL MEASURES: MEAN, VARIANCE, SKEWNESS AND KURTOSIS

The simplest way to characterise size distributions are mean, variance, skewness and kurtosis. The mean is simply the average plant size and variance describes the variability in size (calculated as the average of the squared residuals). Skewness indicates whether a distribution has a long tail to the left (skewness < 0), to the right (skewness > 0) or whether the distribution is bell-shaped (skewness = 0). Skewness is calculated on the basis of the cubes of the residuals. Kurtosis measures the degree to which the distribution is more pointy (leptokurtic) or more flat-topped (platykurtic) than a normal distribution. Kurtosis is based on the fourth power of the residuals, with negative values indicating platykurtosis and positive values showing leptokurtosis. Normal distributions have kurtosis=0. The calculation of these measures is described in, e.g. Zar (1998).

8.1.2 COEFFICIENT OF VARIATION

Size inequality is often calculated with the coefficient of variation (CV). For plants of mean size x , with a standard deviation of s , CV is given by:

$$CV = (s/x).$$

The CV scales the standard deviation to the mean and thereby, indicates relative fluctuations. Therefore, the CV is independent of the units in which mean and standard deviation are expressed.

8.1.3 LORENZ CURVE, GINI-COEFFICIENT, AND LORENZ CURVE ASYMMETRY COEFFICIENT

The Gini-coefficient is a measure of inequality that bases on the Lorenz-curve (Lorenz 1905, Gini 1912, Weiner & Solbrig 1984). The Lorenz-curve is a plot of the cumulative proportion of individuals that are ranked by size versus the cumulative proportion of the total size. When all individuals are of the same size, the Lorenz-curve is a straight line (line of

equality) otherwise, the Lorenz-curve falls below the line of equality. The Gini-coefficient quantifies the deviation of a population's Lorenz-curve from the equality line by calculating the area which is enclosed by both lines (Fig. B.1). Values of the Gini-coefficient range from 0 – in a population where all individuals are equally-sized – to 1 in the abstract case of an infinite population where all but one individual are infinitely small sized (size = 0).

If a population consists of n individuals and x_i is the size of plant i , all individuals are sorted to $x_1' \leq x_2' \dots x_n'$ and the Lorenz-curve is the polygon from the points $(h/n, L_h/L_n)$ with $h = 0, 1, \dots, n$, $L_0 = 0$ and $L_h = \sum_{i=1}^h x_i'$ (Damgaard & Weiner 2000). For unordered population data the Gini-coefficient is calculated as follows:

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2 n^2 \mu}$$

where n is the total number of individuals, μ is average plant size, and x_i and x_j being the biomass of individual i and j , respectively.

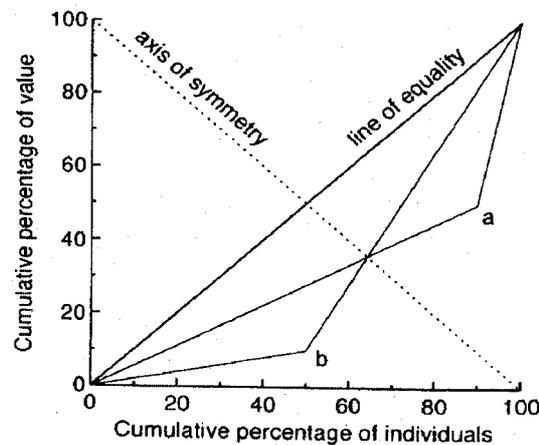


Fig. B.1. In the Lorenz-curve individuals are sorted by size and then, their cumulative proportion is plotted versus their cumulative proportion of size. The line of equality results when all individuals in a population have the same size. For characterising whether small or large individuals prevail in the population the Lorenz-curve asymmetry coefficient (LAC) is calculated. A population where small individuals prevail (population b), LAC-values are below one and accordingly, $LAC > 1$ when the population (a) consists of mainly large individuals (after Damgaard & Weiner 2000).

The Lorenz curve asymmetry coefficient (LAC) seeks the point where the Lorenz-curve is parallel to the equality line, i.e. where the deviation of the

Lorenz-curve has a slope = 1. Hence, when the Lorenz curve is parallel to the symmetry axis above the line of equality, the LAC is larger than one indicating the prevalence of large plants in a population. Accordingly, populations with many small plants result in LAC-values smaller than 1. The LAC is calculated by seeking the point $(F(\mu), L(\mu))$. Here $LAC = F(\mu) + L(\mu)$ with

$$F(\mu) = \frac{m + \delta}{n}, \quad L(\mu) = \frac{L_m + \delta x'_{m-1}}{L_n} \quad \text{and} \quad \delta = \frac{\mu - x'_m}{x'_{m-1} - x'_m},$$

where m is the number of plants with a size less than μ .

8.1.4 CORRELATION BETWEEN NEIGHBOURS

Correlation between neighbours' biomasses has been used to characterise competition (Wyszomirski *in prep.*). It is one of the newer measures that do not focus on size-distribution but on local competitive effects. Herein, the size of neighbours as indicated by their sum or mean size, is supposed to be responsible for the size of a focal plant. Negative correlation coefficients indicate asymmetric competition. Positive correlations may occur when spatial arrangement is irregular and plants grow under symmetric competition because here large individuals tend to have large neighbours (Wyszomirski 2001a).

As tested in a simple simulation model using regular spatial arrangements of individuals, correlation between neighbours almost perfectly reflected competitive asymmetry (Wyszomirski 2001b). This measure has the important advantage that it does not depend on initial variation like size distribution measures. Therefore, in comparison to size distribution measures correlation between neighbours does not over- or underestimate competitive asymmetry. A refinement of this analysis is to take the distance between neighbours additionally into account (Oosthuizen *et al.* 1996, Sletvold & Hestmark 1999).

8.1.5 PARTIAL CORRELATION BETWEEN NEIGHBOURS

In irregular arrangements, simple correlation between neighbours may result in positive values because, e.g. a large individuals standing in relative large distance to a neighbour will have a large neighbour. Therefore, simple correlation may obscure effects which are biologically

important and it is an improvement to use two other measures namely partial and semi-partial correlation.

Partial correlation is defined by:

$$r_{fa \cdot n} = \frac{r_{fa} - r_{fn} \cdot r_{na}}{\sqrt{(1 - r_{fn}^2)(1 - r_{na}^2)}},$$

where r_{fn} is the simple correlation between biomass of focal plant and number of neighbours, r_{fa} is the correlation between biomass of focal individual and average biomass of neighbours and r_{na} is the correlation between number of neighbours and their average biomass (Zar 1998). Hence, partial correlation measures the relationship between the biomass of an individual and its neighbours biomasses after removing the dependence of each variable on the number of neighbours (Wyszomirski 2001a).

8.1.6 CORRELATION BETWEEN RESIDUALS

Another measure that takes spatial configuration into account is C_α (Wyszomirski in prep.). C_α calculates the mass-excess or -deficit and compares it to the mass expected from available space, i.e. it is assumed that available area and biomass are correlated. Therefore, the available area is calculated first by defining the Voronoi-polygon around each individual, then follows the determination of the expected biomass that is afterwards compared with the real achieved biomass.

More precisely, C_α results when the following procedure is applied to morel or empirical data:

The first step is the calculation of the individual Voronoi-polygons. Thereto, the perpendiculars bisectors of adjacent plants are connected resulting in the smallest convex polygon around each individual (for algorithm see Okabe *et al.* 1992). The polygon-shape determines which individuals are closest to a focal plant because these plants have polygon intersections in common and are therefore defined as neighbours (Fig. B.2). The polygon-area is supposed to be an indicator of the individual's biomass.

In the second step, a regression between Voronoi-polygon area and biomass of each plant is calculated. The magnitude of the correlation coefficient determines the variation in biomass explained by spatial effects. Herein lies an inherent assumption namely that individuals with sparse available area, i.e. neighbours are very close, should not grow large

due to strong competition. In contrast, individuals having only remote neighbours should grow large because they do not experience competition until they filled up the available space.

The deviation of individual biomass values from the regression line are assumed to be due to variations in local competition. Thus, in the third step the residuals of the regression are calculated.

Furthermore, the neighbours' residuals are summarised for each individual and afterwards, correlated to the residual of the target plant. The magnitude of this correlation coefficient indicates the mode of competition: if the correlation is highly negative, competition is assumed to be asymmetric. In this case, the biomass of a target plant is well above the regression line, i.e. its biomass is greater than expected whereas the biomasses of its neighbours are below the regression line and therefore, smaller than expected. This leads to a negative correlation between a target plant's biomass and the biomass of its neighbours.

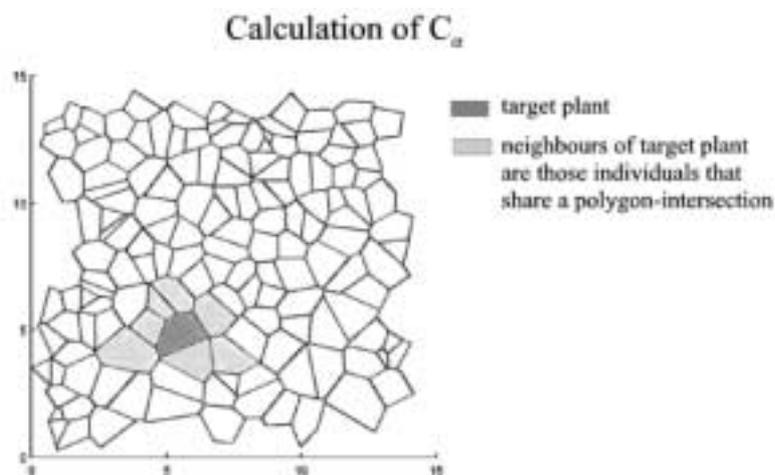


Fig. B.2. The calculation of C_{α} (after Wyszomirski, unpublished manuscript) – a new measure for quantifying the mode of competition (see text for details).

This measure was first applied to empirical data of a greenhouse experiment and afterwards to data of simulations (Wyszomirski *et al.* in prep, Chap. 3). These studies are quite promising regarding the robustness of C_α to initial variability and its ability to detect competitive asymmetry. However, future studies are needed that apply C_α to data from simulations and empirical studies to fully explore the characteristics of this measure.

8.2. CONCLUDING COMPARISON OF THE MEASURES OF NEIGHBOUR COMPETITION

Although many studies and much effort have been undertaken, an unequivocal link between competitive asymmetry and patterns of variability and skewness of size distributions has not been found yet. The origin of this search was the consideration that asymmetric competition increases skewness or variation or inequality of size-distributions with increasing density while this was not supposed to occur when competition is symmetric. Wyszomirski (2001b) attributes this failure to the fact that competition is highly local and therefore, irregularity in spatial arrangement may have many effects on skewness and variation (Firbank & Watkinson 1987, Bonan 1991, Miller & Weiner 1989, Hara & Wyszomirski 1994).

Two of the most severe drawbacks of size-distribution measures are: First, the relationship between skewness (or any measure of variation) and population density need not be monotonic because competitive asymmetry can have two effects: competitive asymmetry increases size variation because of asymmetry but could also limit variability by slowing growth that plants hardly grow at all and do not develop size variation (Wyszomirski *et al.* 1999). Second, size distribution measures are sensitive to the type and amount of initial variation which may obscure competitive asymmetry (Wyszomirski 2001b). Moreover, they lack a clear reference value and are therefore difficult to interpret (Wyszomirski 2001b), e.g. variation and skewness changed during growth also for non-competing individuals (Turner & Rabinowitz 1983). To conclude, size distribution measures ignore the fact that competition is local and thus are sensitive to other sources of growth variation.

Measures that account for local variation in competitive conditions have recently been developed and first tests for their ability to detect asymmetric competition are quite promising. They explicitly measure the effects of neighbours on a focal individual by somehow correlating their sizes. The simplest possible measure is the correlation between sum or mean of neighbours' sizes and the size of a focal individual. In contrast to size-distribution measures, the correlation between neighbours in a regularly distributed population almost perfectly reflected the degree of competitive asymmetry as tested in a simulation model (Wyszomirski 2001b).

Accordingly, partial correlation and C_α showed in their first tests that they also reflected competitive asymmetry in a population where

individuals were distributed in an irregular spatial pattern (Wyszomirski in prep.). However, additional tests with more empirical data and other simulation approaches are needed to find the strengths, shortcomings, and limitations of these measures.

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Erklärung

Ich versichere, dass ich meine Dissertation “Modelling competition with the field-of-neighbourhood approach – from individual interactions to population dynamics of plants” selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Leipzig, 01.02.2002

ACKNOWLEDGEMENTS

Volker Grimm hat alle Höhen und Tiefen dieser Arbeit begleitet. Ich danke ihm für aufmunternde Worte („Du machst das schon ..“), konstruktive Kritik („Da musst du noch mal bei ..“) und tatkräftige Hilfe.

Prof. Wissel danke ich für die Freiheit der Themenwahl, vielseitige Unterstützung, kritische Durchsicht des ersten Entwurfs dieser Arbeit und ständige Diskussionsbereitschaft.

Prof. Brandl danke ich für die kurzfristige und unkomplizierte Übernahme der Arbeit sowie für kritische Kommentare zum Manuskript.

Uta Berger und Hanno Hildenbrandt entwickelten den field-of-neighbourhood Ansatz und stellten ihn mir zusammen mit einem Algorithmus zur Verfügung, wofür ich ihnen danken möchte.

Tomek Wyszomirski half enorm bei der Entwicklung der Ideen für Asymmetrie in der Konkurrenz. Ich danke ihm für hilfreiche Diskussionen, Schaffen von Klarheit, berechtigte Einwände und das Maß C_α .

Meinen Freunden und Kollegen in der ÖSA – besonders Dirk Eisinger, Jürgen Groeneveld, Stephanie Schadt, Björn Reineking, Hans Thulke - möchte ich für viele Sachen danken: Hilfe beim Programmieren, weitreichende Diskussionen, aufbauende Worte, Kekse.

Danken möchte ich auch meinen FreundInnen in Leipzig und Jena für das Leben neben der Diss, besonders Steffen Hahn, Susanne und Lilly Gerth, Silke Pätzoldt, Claudia Herold, Hubertus Böhm und der Bigband.

Ganz besonders danken möchte ich Steffen Hahn für das Ertragen gehäufte Missstimmungen, Trost und Zuspruch in schwierigen Phasen der Arbeit und die erforderliche Zufuhr von Sauerstoff.