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Dissertation

A model of the
spatio-temporal population dynamics
of *Acacia raddiana*

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**A model of the
spatio-temporal population dynamics
of *Acacia raddiana***

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Introduction

1.1 General Introduction

The sparse woody vegetation of the Negev desert, Israel is dominated by the genus *Acacia*, mainly *Acacia tortilis* subsp. *raddiana*, *A. tortilis* subsp. *tortilis* and *A. gerrardii* subsp. *negevensis* (Zohary, 1972). These keystone species (Milton and Dean, 1995; Ward and Rohner, 1997) supply food and shelter to many desert animals. They are also used by the local Bedouin people for fuel, fodder and as remedies (Ashkenazi, 1995). Despite the important function these trees have in the Negev ecosystem, there has been little information on the demography of *Acacia* trees. It is not clear to what extent studies from Africa (e.g. Muthana and Arora, 1980; Coughenour and Detling, 1986; Smith and Shackleton, 1987; Kennenni and Van der Maarel, 1990; Kiyiapi, 1994; Miller, 1995; Martin and Moss, 1997) are applicable to Negev populations, because Israel is at the northern edge of the distribution of these trees (Halevy and Orshan, 1972; Ross, 1981). Recently, there have been alarming reports of large-scale mortality, drying and lack of regeneration of the *Acacia* trees in the Negev (Ashkenazi, 1995). Subsequent to these reports, some studies on the population dynamics have been conducted in the Negev (Peled, 1995; Ward and Rohner, 1997; Rohner and Ward, in press). However, information is not complete and misinterpretations of observed mortality patterns are likely. As possible reasons for the decline of the Negev's *Acacias*, the following factors have been discussed:

(i) the semi-parasitic mistletoe *Loranthus acaciae* is suspected to cause drying and mortality of the *Acacia* trees (Ashkenazi, 1995).

(ii) *Acacia* trees suffer extraordinarily high infestation rates by seed beetles (Bruchidae - mostly *Bruchidius arabis* and *Caryedon palaestinus*) (Halevy and Orshan, 1972; Rohner and Ward, in press). For example, Rohner and Ward (in press) found a seed infestation rate of 96% in *A. tortilis* and 98% in *A. raddiana*. Because of the substantially lower germination rates of infested seeds (Halevy, 1974; Lamprey et al., 1974; Coe and Coe, 1987; Rohner and Ward, in press) recruitment might be seriously limited by bruchids.

(iii) The alteration of water availability due to anthropogenic activities, such as aquifer depletion and the construction of roads crossing the ephemeral river beds (wadis) where most trees occur, is another factor that has been suspected to accelerate tree mortality and to prevent recruitment. Roads cross-cutting wadis reduce the amount of water and seeds reaching the lower wadi sections during the rare but important flood events. This factor has been shown to decrease survival and regeneration of *Acacia* trees in the Negev (Ward and Rohner, 1997; Wiegand et al., 1998). However, aquifer depletion proved to be of minor importance for *Acacia* survival, most probably because roots do not reach as deep as the groundwater level, which means these *Acacias* get their water exclusively from surface flows and not from aquifers (BenDavid-Novak and Schick, 1997; Ward and Rohner, 1997).

Due to the obvious need for knowledge on the population dynamics of *Acacia* trees and their interaction with mistletoes and seed beetles in the Negev, we developed a computer simulation model to accompany the ongoing field studies (Peled, 1988; Peled, 1995; Ward and Rohner,

1997; Ward and Rohner, in press). Field studies covering a few years provide only short-term information, while the lifespan of *Acacia* trees is several decades. With a model, it is possible to extrapolate from short-term information to time scales appropriate to the study of long-lived species (Wiegand et al., 1995; Jeltsch et al., 1997; Jeltsch et al., 1997a). In addition, the relative importance of different processes to survival and recruitment can be evaluated by sensitivity analysis (Overton, 1977; Starfield and Bleloch, 1986). This is useful information when planning new field experiments. Priorities for future research should be given to those processes, or parameters, that have a strong influence on *Acacia* survival and recruitment, but are not yet measured or are highly variable in their estimates (Swartzman and Kaluzny, 1987). Simulation experiments can be conducted in order to improve general understanding of the population dynamics and to test the effectiveness of different possible management strategies (Starfield and Bleloch, 1986; Swartzman and Kaluzny, 1987; Bart, 1995; Dunning et al., 1995).

Note: for references see Chapter 2.

1.2 Structure of this thesis

This thesis consists of five major chapters that can be read independently. All chapters are organized like journal publications. This form has been chosen because Chapters 2 and 3 have already been published in *Ecological Modelling* and in a book, Chapter 5 will be published in *Plant Ecology*, and Chapters 4 and 6 have been submitted to *Folia Geobotanica* and *Journal of Vegetation Science*. The idea to publish the single chapters is the reason why this thesis has been written in the first person plural. Coauthors have been partners of discussion and were involved in the final presentation of the results. However, besides the collection of field data, which has been conducted by the ecologist Dr. David Ward of Ben Gurion University of the Negev, Israel, all work has been done independently by the author of this thesis.

From the cumulative form of this dissertation follows that there is some overlap between the single chapters. This involves mainly the description of the model. Therefore, I inserted some notes for those readers who want to read the entire thesis telling them which paragraphs they can skip. Furthermore, I linked the main chapters by transitions which explain the connections between the single chapters and provide the major thread to the thesis. Abstracts of the main chapters are given at the beginning of each chapter.

Chapter 2 is the main part of this thesis, because it gives a comprehensive overview of the simulation model. It explains the landscape-related, spatially-explicit and individual-based approach of the model, gives the biological basis and describes how this basis has been complemented via parameter fitting. A sensitivity analysis is employed in order to evaluate the relative importance of different processes such as seed distribution, germination, and mortality to the survival and recruitment of *Acacia* trees. Furthermore, the increase in large mammalian herbivore densities as a possible management option for the endangered *Acacias* is investigated.

Management aspects are also important in **Chapter 3**. This chapter deals with a specific cause of *Acacia* mortality in the Negev, namely roads bisecting *Acacia* populations. Simulation experiments are conducted investigating the effect of the roads on the long-term population survival and possible management measures are discussed. Readers interested in getting a brief overview of the structure and potentials of the model should choose to read **Chapter 3**, because it gives a short overview of the model. However, there are some differences between the two model versions used in **Chapters 2 and 3** regarding mortality (age dependent vs. not age-

dependent), seed distribution (clumped near seed producing trees and not), and weather (based on field data and not). However, having read **Chapter 3**, it should be easy to find the respective details in the second chapter.

An important reason for developing a spatially-explicit model was to link the model with a Geographical Information System (GIS) containing site-specific data relevant to the population dynamics of the *Acacia* trees. This is very appealing because it would allow me to further develop the model into a tool for the development of management measures for site-specific problems (e.g. caused by roads; cf. Chapter 3). Thus the model could easily be applied to any wadi and could also be used by other people, because site-specific parameterization would be standardized. However, investigations showed that a linkage between model and GIS makes little sense. These investigations are presented and discussed in **Chapter 4**. Furthermore, in **Chapter 4**, an introduction into GIS and methods of remote sensing towards linkage with spatially-explicit simulation models is given. Due to high computational demands, linkage of models and GIS has not been possible until recently. Therefore, this introduction is specifically written for modelers interested in this new approach.

The main idea of the last two chapters is to gain as much information as possible from the field data currently available. **Chapter 5** uses size-frequency distributions of several *Acacia* populations in the Negev to learn about the long-term population dynamics of these trees. Two important prerequisites of this study have been the investigation of the growth pattern including an estimation of a size-age relation, which was previously unknown, and the development of indices characterizing size-frequency distributions. The latter makes it possible to efficiently compare distributions observed in the field with those produced by the model.

In **Chapter 6**, I took full advantage of the spatially-explicit approach of the model, because I studied the spatial pattern of the *Acacia* trees. Using a scale-dependent pattern analysis technique, I investigated for different size classes, if trees are randomly distributed, aggregated, or regularly spaced. A comparison between patterns observed in the field and produced by the model gives insights into the processes causing the patterns.

Finally, at the end of the thesis, an English **Summary and Discussion** and a German **Zusammenfassung** are given.

Analysis of the population dynamics of *Acacia* trees in the Negev desert, Israel with a spatially-explicit computer simulation model¹

2.1 Abstract

Most trees in the Negev desert, Israel, are either *Acacia raddiana*, *A. tortilis* or *A. negevensis*. They provide food and shelter for many desert animals and are a major source of livestock feed and firewood for the native Bedouin people. High mortality and low recruitment of these trees have been reported. To develop sustainable conservation strategies it is necessary to understand the population dynamics of the *Acacia* trees. Therefore, on the basis of demographic data gained by field studies, a spatially-explicit, individual-based computer simulation model of the population dynamics of *A. raddiana* has been developed. We evaluate the relative importance of different processes such as seed production and seed infestation by parasites, germination, mortality, and mistletoe infestation to the survival and recruitment of *Acacia* trees in the Negev. Mortality rates at different life stages, the production of uninfested seeds and the weather regime were most influential. The infection of trees by semi-parasitic mistletoes proved to be of minor importance. The most important result is that an increase in the germination rate of *Acacia* seeds, such as may result from passage through the digestive tract of large mammalian herbivores, is capable of counteracting the detrimental effect of unfavourable climatic conditions. Consequently, we discuss the use of increased large mammalian herbivore densities as a possible management option for enhancing the survival of *Acacia* populations in the Negev.

2.2 Introduction²

In this study, we present SAM (Spatial Acacia Model), a stochastic, spatially-explicit, individual-based simulation model of the population dynamics of *A. raddiana*, the most abundant and widespread tree species in the Negev. We chose a stochastic approach because rare random effects are known to be important for the population dynamics of plants in (semi)arid regions (Wiegand et al., 1995). The distribution of *A. raddiana* is dominated by the landscape. In most areas, these trees do not grow outside wadis (Halevy and Orshan, 1972) and, inside the wadis, the fate of these trees as sedentary organisms depends to a large extent on abiotic local site conditions and interaction with neighbouring trees (compare Wiens, 1976; Czarán and Barthá, 1992). Therefore, and because of our plan to link the model to a GIS (see Chapter 4) we've chosen a spatially-explicit modelling approach. We evaluate the relative importance of different natural processes, such as seedling mortality, seed production and mistletoe infestation, to the survival of *A. raddiana* and discuss which factors constitute major threats to the survival of trees and which key factors would be most suitable for management measures. In this study, we focus on factors inherent to the system and do not consider anthropogenic disturbances such as road

¹ Authors: K. Wiegand, F. Jeltsch & D. Ward. A slightly different version has been accepted in combination with Chapter 1.1 in October 1998 by *Ecological Modelling*

² This Introduction is closely interlinked with Chapter 1.1 which should be read before reading this chapter.

construction (which will be discussed in Chapter 3). This facilitates evaluation of the extent to which natural factors and processes contribute to a possible decline of *A. raddiana* in the Negev.

2.3 Methods

2.3.1 Site description

Simulations in this study are applied to two sections of two different wadis near the Arava valley, both including approximately 200 trees: a 1.5 km long section of Nahal Katzra and a 2 km long part of Nahal Saif (Katzra: 35°08'E, 30°32'N; Saif: 35°10'E, 30°52'N). Both areas are hot in summer (mean maximum temperature in the hottest month = 35°C; Stern et al., 1986) and very dry (mean annual precipitation: Katzra: 38 mm, Saif: 45 mm). Rain falls in winter (October - April), is mostly very localized (Sharon, 1972) and leads on average to less than 2 flood events in the wadi beds per year (Stern et al., 1986). The modelled parts of Nahal Saif and Katzra have a catchment area of 4.7 km² and 26.3 km² respectively. Both wadis are subject to intense field studies since 1994 (Ward and Rohner, 1997).

2.3.2 General model structure

Scales and output variables

First of all, it is necessary to define the spatial and temporal scales of the SAM model. A scale is characterized by both grain and extent (*sensu* Wiens, 1989). The ideal spatial extent would be a population. However, for logistic reasons, we have to restrict the model to just a part of a population comprising initially about 200 trees. The temporal extent has been chosen to be 200 years. This allows us to follow the growth and development of *A. raddiana* over several generations (longevity is about 50 years; Ward and Rohner, 1997). The spatial grain, or resolution, of SAM has been derived from the inherent units of populations, individuals, to be a cell 5m*5m in size. This corresponds to a typical canopy size of a young adult tree (pers. obs.). The temporal grain of one year is defined by the temporal resolution of the data used to determine the parameters of the model (Hyman et al., 1990). Furthermore, it is necessary to choose a reliable index of population viability for the description of the population dynamics and survival. We chose both a selective index, the average number of trees after 200 years, as well as a summarizing index, the long-term growth rate of the population. These two indices will be used simultaneously.

Factors and processes

Fig.2.1 shows the causal structure of the relevant factors and processes. Population dynamics are mainly determined by the establishment of tree seedlings and the growth and mortality of trees. Tree establishment is initially influenced by germination and seedling mortality. On one hand, a prerequisite for germination is the availability of seeds and moisture. Sufficient moisture depends on the occurrence of winter floods which, in turn, depends on the amount of precipitation, and also on the wadi morphology. The other prerequisite for germination, availability of seeds, is determined by seed production, which is a result of the size, moisture status, and degree of infestation by parasites (i.e. mistletoes) of the seed-producing trees. However, only those seeds produced by the tree that are unharmed by seed predators (i.e. bruchid beetles) are available for germination. The amount of seeds available at a specific location is altered by seed dispersal by flood events and large mammalian herbivores. On the

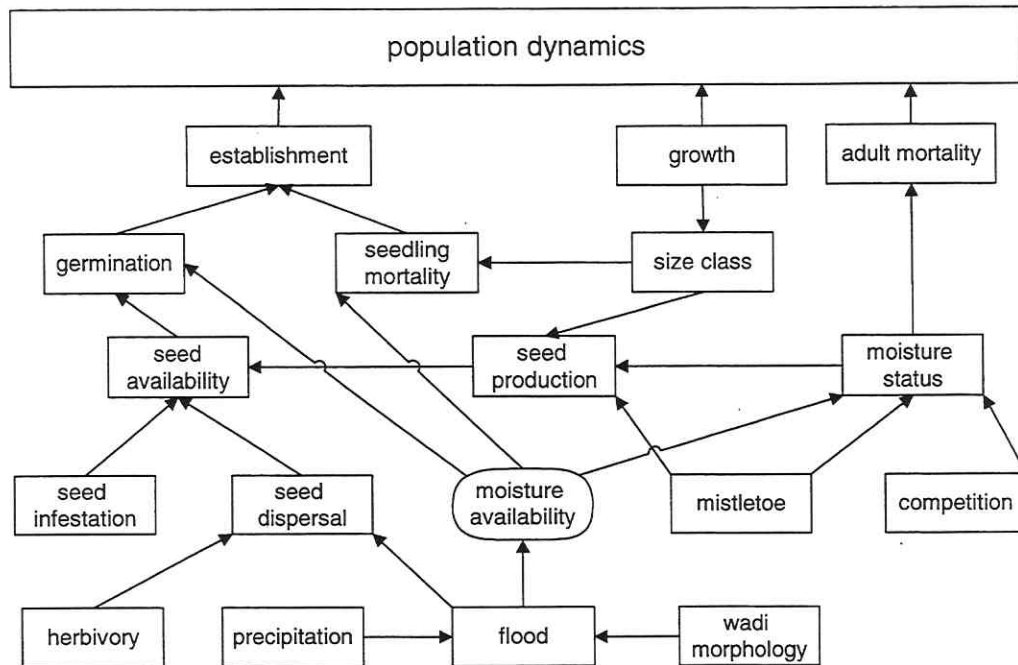


Figure 2.1: Graphical model of the population dynamics of *A. raddiana* in the Negev. Arrows point in the direction of the respective effects.

other hand, tree establishment also depends on seedling mortality, which is higher for smaller seedlings and for those with insufficient water availability. Once a tree has established successfully we assume a constant growth rate, resulting in changes of tree size. Finally, mortality of adult trees depends mainly on tree moisture status. Moisture status may deteriorate from good to poor (just two statuses are considered) if moisture availability is low and the degree of infestation by parasites (i.e. mistletoes) high. Because older trees may have reduced ability to alter root development to reach changing water sources and mistletoe infestation tends to increase (see below), older trees have a higher risk of mortality than young adult trees.

Technical aspects

Grid-based models have been shown to be an appropriate approach for modeling spatial vegetation dynamics in semi-arid systems (Thiéry et al., 1995; Wiegand et al., 1995; Jeltsch et al., 1996). An important advantage of grid-based models is that necessary biological information for modelled processes can be included in the form of rules rather than mathematical equations. This allows for direct consideration of expert knowledge that is not necessarily restricted to data and is particularly useful in more complex systems (Jeltsch et al., 1996). Another advantage is the possibility of linking grid-based models to Geographical Information Systems (GIS, cf. Chapter 4). At linkage, digital landscape data of the GIS enter the simulation model as spatially explicit parameters (Dunning et al., 1995; Liu et al., 1995;

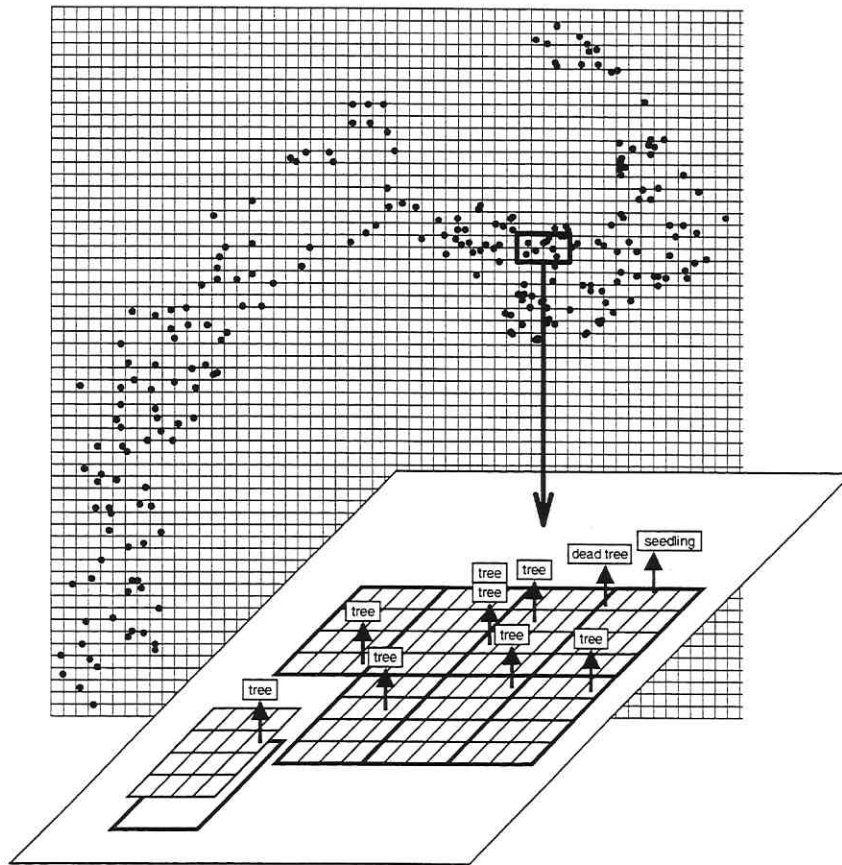


Figure 2.2: Current distribution of *A. raddiana* in Nahal Katzra as seen by the model. Closed symbols: location of *tree_bases*; grid: grid of *super_cells*. The enlargement shows *super_cells* (bold squares) divided into patches of 16 cells (fine squares) and pointers (arrows) to the objects *seedling*, *tree* or *dead_tree* which inherit (their position) from *tree_base*.

Carey, 1996; Mladenoff et al., 1996). However, in grid-based models, the modelled area is usually represented as a regular mosaic of cells (Childress et al., 1996), cell size being determined by typical biological scales (Jeltsch et al., 1996). In our case, typical biological scale has been determined as the canopy size of an adult tree (5m*5m). In the arid Negev, trees may grow within distances of a few meters, but mean nearest-neighbour distance is about 20 m. Furthermore, tree distribution is largely restricted to wadi beds. Thus, a standard grid-based model approach would result in a waste of computer memory capacity (many unoccupied cells outside the wadi) and tremendous simulation times (at each time step an iteration over the entire,

essentially empty grid) (Tischendorf, 1997). Therefore, we introduced an irregular grid by dividing the rectangular, modelled area into a grid of supercells (Fig. 2.2). A supercell represents an area of 20m*20m and serves to administer landscape data (e.g. location: inside or outside the wadi). For each supercell within the wadi, there is a pointer from this supercell to a grid of 4 * 4 cells, each 5m *5m in size. These small cells correspond to cells used in most grid-based models. An additional difference of SAM, the simulation model used in this study, from these models is that in SAM a cell does not directly represent an ecological state, e.g. "no tree", "young tree" or "adult tree" (simplified example taken from Thiery 1995), but is mainly an administrative object. A cell may contain a pointer or a list of pointers to tree objects. Dynamic memory allocation allows us to create these tree objects and to link them to the cell of their location once they are established and to detach this linkage and to remove the object once the tree is dead (Congleton et al., 1997). Both the introduction of a two stage grid and the dynamic representation of the trees minimizes memory requirements. Furthermore, with this approach, we can easily reduce simulation time by administering the tree objects in a linked list. Instead of an iteration of the entire grid, we only follow actual members of the list. For implementation, we chose the object-oriented programming language C++. In C++, user-defined abstract data types, 'classes', can be defined. Each class predefines a group of data ('members') and a set of procedures ('methods' or 'member functions') for manipulating that data. An instance of a class is called an 'object' (for further explanations see Maley and Caswell (1993) and Breymann (1994)). Hence, the class supercell allows for data on landscape features, for a pointer to a grid of 16 cells, and for procedures to manipulate this data, for example, for construction or destruction of 16-cell-grids. Furthermore, each cell provides a pointer to the general base class 'tree_base'. The class tree_base allows for information on (1) location and (2) size of a tree represented by tree_base. Three classes may inherit this information from tree_base: 'seedlings', 'trees' and 'dead_trees'. Additionally, for dead_trees the time since death is recorded, and trees have a procedure for seed production and information on moisture status and cover of mistletoes hosted by tree. This means, that the pointer from a cell to an object of the base class tree_base provides an interface between the landscape and a tree, the choice of class representing this tree depending on the actual trunk circumference (an index of tree age). For empty cells, the pointer is directed to NULL (NULL is a macro equivalent to 0).

Object-oriented individual-based approach

The aim to minimize memory requirements as well as simulation time led us naturally to an object-oriented individual-based representation of *Acacia* trees (more explicitly: an individual-based configuration model *sensu* Caswell and John (1992) or: a 'narrowly defined' individual-based model *sensu* Uchmanski and Grimm (1996)). Judson (1994) compiled a list of situations when individual-based models should be used. In this study, those situations are represented by: (1) individuals have many parameters of interest (location, size, moisture status, mistletoe coverage,...); (2) population size is small (this becomes especially true for simulation experiments leading towards extinction); (3) interactions between individuals are local, and mixing can not be assumed; (4) rare events are important. This provides a strong support for our modelling approach.

2.3.3 The rule set

In SAM, a year is divided into two periods, summer and winter. In each period, different life history events take place (Fig. 2.3). In both periods, we successively employ modules for

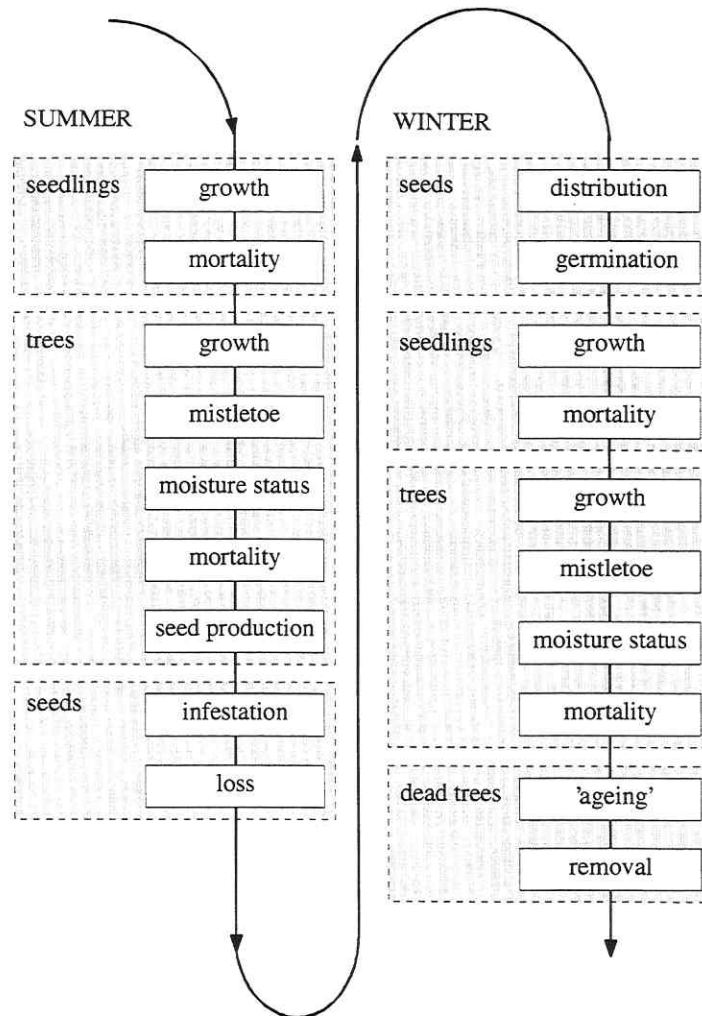


Figure 2.3: Flow chart showing the annual cycle of events simulated in SAM.

growth and mortalities of seedlings, for growth of trees, infestation of trees by mistletoes, deterioration of moisture status of trees and for tree mortality. Additionally, in summer, seeds are produced, suffer infestation and disappear from the wadibed. In winter, seeds are dispersed and germinate, and the 'ageing' and removal of dead trees takes place.

For plants, demographic parameters are determined by life history stage or size of an individual rather than by its age (Harper1977; Coughenour et al., 1990; Schemske et al., 1994). Thus, SAM records trunk circumference, which is representative of *A. raddiana* size, because most other parameters of tree life history (e.g. seed production, canopy size) are scaled allometrically to trunk circumference (Ward and Rohner, 1997).

The rules that follow are based on published and unpublished field studies conducted in Nahal

Katzra, Saif and other wadis throughout the Negev (Ward and Rohner, 1997; Rohner and Ward, in press, D. Ward, unpublished data). Field data have been used to estimate parameters both directly and indirectly (via a parameter fit). Initial location and size of trees are taken from respective wadi and initial mistletoe infestation and moisture status of subadult and adult trees are assigned randomly, based on frequencies observed in the field (e.g. 57% (77%) of adult trees in Nahal Katzra (Saif) are not infested by mistletoes and 92% (86%) have a good moisture status; see also Table 2.1).

Weather

We evaluated rainfall data from weather stations at Hatzeva (close to Saif) and at Nahal Paran (close to Katzra) with respect to the *Acacia* tree biology and distinguished between three classes of years: 'good', 'intermediate' and 'dry' years. The occurrence probabilities have been estimated as 23%, 61%, and 16%, respectively. For Nahal Katzra, the corresponding cutoff points are at 20 mm and 55 mm (Nahal Saif: 20 mm and 60 mm) rain per year. These values are only guidelines for the frequency distribution of dry, average or wet years, because not only the local precipitation in the wadis is important for *Acacia* condition, but also the catchment areas of the wadis. In SAM, weather is determined at the beginning of each simulated year.

Seedling and tree growth

Trunk circumference of seedlings and of trees increases by 0.68 cm per six months (Kiyiapi, 1994), starting at a size of 0 cm. Once trunk circumference exceeds 15 cm or 45 cm the seedling becomes a subadult or an adult tree, respectively. This simple approach will be further developed once we'll have enough field data on the growth regime of Acacias in the Negev.

Seedling mortality

During their first 5 half-years, seedling mortality depends on rainfall. In good years, seedlings undergo a semi-annual mortality of 60% (Rohner and Ward, in press; Ward, unpubl. data). In intermediate and dry years, seedlings are assumed to suffer mortalities of 80% and 100%, respectively. Older seedlings are assumed to follow the semi-annual mortality of 0.87% measured for *A. tortilis* trees with a trunk circumference greater than 8 cm (Ward and Rohner, 1997) irrespective of actual weather.

Mistletoe infestation

SAM models population dynamics of mistletoe in a simple way. Cover of mistletoes hosted by a tree is classified as 0, 1, 2 or 3 quarters of the canopy. A tree becomes infested by a mistletoe and mistletoe cover may increase to 2 or 3 quarters at probability rates fitted to actual abundance of mistletoes living on *A. raddiana* (see section *Parameter fit*). According to this fit, uninfested trees have a semi-annual probability of 0.4% (Nahal Katzra) to catch a mistletoe and infested trees have a probability of 1.5% (both wadis) that their mistletoe cover increases by another quarter.

Moisture status

SAM classifies the moisture status of trees as either good or low. A low moisture status means that a tree has many dry branches. In Nahal Saif 6.8% of subadult and 14.1% of adult *A. raddiana* have a low moisture status. SAM assumes a good moisture status for seedlings, but moisture status of subadult and adult trees may decrease at rates fitted to field data. Every six months, actual risk of moisture status decrease is recorded for each tree showing a good moisture

status. Relative contributions of different factors increasing this risk are balanced in the form of 'risk points'. Each of the following factors adds 'risk points' in the balance:

- (1) Bad long-term weather (i.e. five or more consecutive dry years) results in 1 'risk point'.
- (2) Competition for water with neighbouring trees: One or more subadult trees living within the eight cells that are adjacent to the cell containing the tree under consideration results in 1 'risk point', subadult trees located in the same cell and adult trees in adjacent cells result in 2 'risk points', and adult trees in the same cell account for 3 'risk points'.
- (3) Mistletoe infestation adds 1 'risk point', because mistletoes take water from the trees.
- (4) Other pooled undistinguished factors result in 1 'risk point'.

Hence, each tree has at least one risk point (factor 4). The actual probability for each tree to worsen in moisture status is the sum of 'risk points' divided by the fitted parameter '*worse_moist_scale*' (=500 in Nahal Katzra and =900 in Nahal Saif; see section: *Parameter fit*). We assume that trees in poor moisture conditions cannot recover to a good moisture status. This hypothesis is currently being tested by field measurements.

Mortality

Tree mortality is modelled via a vitality function dependent on actual moisture status *ms* of the tree (*ms*=1: good; *ms*=0: bad):

$$\text{mortality} = 1 - \text{vitality} \quad (1a)$$

with

$$\text{vitality} = \text{basic_vitality} + \text{moist_factor} * ms \quad (1b)$$

The parameters *basic_vitality* (=96.91%) and *moist_factor* (=0.025) are fitted in order to add up to the semi-annual mortality rate of 0.87% (averaged over the wadis), as measured by Ward and Rohner (1997).

Seed production

Seed production of breeding trees in good moisture condition and without mistletoes depends on trunk circumference, *tc*. A regression of data from Nahal Saif gives, for the number of produced seeds *S* per tree:

$$\log S = 3.84 + \log tc * 1.11 \quad (2)$$

SAM uses this regression, but reduces *S* for trees with a poor moisture status by 50% and for trees with a mistletoe cover of *x*% by *x*%. These factors are estimates derived from the idea that a poor moisture status (leading to dead branches) as well as a mistletoe infestation reduces canopy volume available for seed production. Individual trees do not breed every year. For example, in Nahal Katzra only 50% of the subadult trees and 87% of the adult trees breed in a year (see Tables 2.1 and 2.2). Using random numbers, SAM determines for each tree if this tree will be breeding.

Seed infestation

Seed infestation of *A. raddiana* in the Negev desert, mostly by *Bruchidius arabicus* and *Caryedon palaestinus*, is as high as 95% - 98% (Rohner and Ward, in press). In the model, we

used a infestation rate of 96.5% and assumed that infested seeds do not germinate.

Seed loss

Very high seed loss rates (i.e. more than 90%) have recently been reported for African indehiscent *Acacia* trees (Miller, 1994a). *Acacia* seeds may be transported out of wadis by floods (Hauser, 1994) and ungulates (Halevy, 1974; Murray, 1986; Miller, 1996) and many seeds eaten by rodents and ungulates are destroyed (Miller, 1994a). In the model, seed loss rate was fitted to be 93% (see section *Parameter fit*).

Seed distribution (wadi morphology I)

SAM follows the destiny of each seed individually. It is assumed that seed distribution is dominated by flood events and that seeds will be distributed unevenly corresponding to wadi morphology. At present, the SAM model does not describe details of the wadi morphology and seed distribution but rather simulates the essential features of the outcome of the seed distribution process. Numbers given below are *ad hoc* estimates. However, sensitivity analysis demonstrates that the exact values of these parameters have no major effect on overall population survival. Supercells (patches of 16 cells) are categorized as either 'normal' or 'seed-attractive' (representing topographic features). On average, seed numbers in cells belonging to a seed-attractive supercell are five times as high as in normal cells. We assume that current distribution of seedlings reflects the actual morphology and, in particular, seed attractivity. Therefore, initially (year = 0), those supercells are identified to be attractive, that already contain at least one seedling. For example, in Nahal Saif 26 out of 448 supercells are initially seed-attractive. This number remains constant over time, but locations change due to the following rule. In years with germination (i.e. years with good rainfall and therefore extraordinary flood events) each attractive supercell has a probability of 5% of being relocated.

Depending on actual seed production within the wadi, the average number of seeds in normal and in attractive cells is calculated. However, to allow for a clumped seed distribution with few cells containing many seeds and many cells with few seeds, the actual number of seeds within a given cell is drawn from a negative exponential distribution with corresponding mean. More explicitly, we first draw the seed portions from the exponential distributions. The size(s) of the last seed portion(s) is determined by the total number of seeds (=0 if all seeds have been distributed, all remaining seeds if seeds are left). Then, we randomly distribute the seed portions into the cells. This procedure is applied separately for seeds for normal and for attractive cells.

Germination (wadi morphology II)

Germination in arid environments depends primarily on local water availability (Coughenour and Detling, 1986; Kennenni and Van der Maarel, 1990). Thus, we assume two conditions that need to be fulfilled for successful germination. First, germination takes place only in years with good weather (see above). Secondly, germination takes place only in safe sites, i.e. microsites that provide optimal water and shade conditions (Miller, 1994a). SAM depicts the heterogeneous distribution of safe sites within the wadi. There are three classes of grid cells depending on availability of safe sites: (1) 90%, (2) 50% or (3) 10% of cell area offer suitable germination conditions. Thus, a seed within a cell of category (1) has a 90% probability to be at a safe site. All 16 cells belonging to a supercell have the same density of safe sites. Therefore, supercells have two independent properties: seed attraction and safe site density. Classification of supercells is done randomly at the beginning of each simulation (year = 0; frequency (1):(2):(3) = 1:2:1). These numbers are again *ad hoc* estimates. Other distributions of safe sites tested in the model

are described in the section *Simulation experiments*. Finally, in good years, seeds that are at a safe site have a germination probability of 15.6% (Rohner and Ward, in press).

'Ageing' and removal of dead trees

Because of the low decomposition rate, dead trees in the Negev desert remain standing for about 10 years (Ward and Rohner, 1997) before they get washed away by a flood. In the model, this has been implemented by a yearly chance of 10% for dead trees to fall and to be subsequently removed from SAM. Size-dependent scenarios might be investigated in the future. Once a year, time since death of the dead trees is updated.

2.3.4 Parameter fit

Some of the parameters used by SAM are already known from field data (see *The rule set*). For other parameters (i.e. *seed_loss*, probabilities of mistletoe infestation and increment rates, *worse_moist_scale*, *basic_vitality* and *moist_factor*) reasonable values could be derived from a parameter fitting procedure, i.e. a comparison of observed field data (tree size distribution, mortality rate, tree moisture status, mistletoe infestation) with the output of various simulation runs with differing parameter values.

Because only a few years of field observations are available for comparison, we have to make the unverified assumption that, on average, the actual population size of trees remains fairly constant over time. However, general trends and sensitivities of certain factors and processes should be independent of this assumption.

We performed a multiple parameter fit by running the model under different, specifically chosen, parameter sets and comparing model output to these field data. Initially, parameter sets have been educated guesses, while further parameter sets were chosen based on the simulation results of previous parameter sets. We accepted a set of parameters as successfully fitted if after several tree generations (i.e. year 200 of the simulations) the relevant model outputs (average over 1000 simulation runs) did not significantly differ from the actual field data (t-test, $p < 5\%$). We believe there is no point in trying to minimize this deviation any further beyond the accuracy of the field measurements. For comparison of the degree of infestation by mistletoes, we calculated the Kolmogorov-Smirnov test statistic and compared it to the minimal possible deviation of 0. The year 200 was chosen, because this time span assures that the state of the population is sufficiently independent of the initial conditions while still being a time span meaningful to humans.

Tree size distribution deserves a special analysis, because the population dynamics of *A. raddiana* in the Negev are event-driven (Wiegand et al., 1995; Wiegand et al., 1998) with rare recruitment events. Therefore, if we compare two size distributions observed in the field, both taken at the same time but at different places, we will most probably find 2 irregular distributions that are very different from each other, because by chance the recruitment events at these places may have occurred at different times. Hence, for a meaningful comparison between two size distributions, it is necessary to integrate them over a long time interval. In this study, we want to compare model output to field data. Because it is not possible to wait for some 100 years until sufficient data have accumulated, we have to 'replace time by location'. That is, we compare the cumulative size distribution from trees in 75 (0.1 ha) plots throughout the Negev (Ward and Rohner, 1997) to the total cumulative size distribution of 1000 simulation runs in the year 200 (both scaled to 1). For this purpose, we calculated the Kolmogorov-Smirnov test statistic D_{\max} for comparison between cumulative size frequency distributions (size class width: 1 cm in trunk circumference) for trees bigger than 25 cm in trunk circumference. This size restriction is

necessary because field data do not include smaller trees (Ward and Rohner, 1997). The chosen statistics describes the absolute maximum deviation in the cumulative frequency of trees of certain sizes between field data and simulation output for a given parameter set. Because we have a sample size of 1, it is not possible to get statistical information on the goodness of fit. We expect the size distributions of single simulation runs to fluctuate around the average of many field distributions (see section *Results*).

The parameter values as given in the model description or as determined by the parameter fit serve as the standard parameter set (see Table 2.1) for the following simulation experiments.

2.3.5 Sensitivity analysis and simulation experiments

Our aim is to evaluate the relative importance of different processes to the survival of *A. raddiana*. As a major step towards this goal, we conducted a sensitivity analysis of model parameters and assumptions. Initially, we determined the 95% confidence limits of all parameters that have been derived from field data. For the remaining parameters we calculated a range that usually corresponds to an increase and decrease of parameters by 10% (Table 2.1). Exceptions were made due to mathematical constraints (probabilities have to be within [0,1]) and whenever we wanted to test larger deviations intentionally (e.g. trunk circumference increment, because SAM uses data from Kenya which might differ from the growth regime in the Negev). Sensitivity to the distribution of safe sites was determined for two extreme scenarios: (1) a high concentration of safe sites (95%) in one third of cells and (2) an equal distribution of safe sites. For parameters that are expressed as rates, we always used the 'positive' parameter rate as the basis for this calculation, e.g. survival rate, instead of mortality. Hereafter, we call these parameter ranges as well as the 95% confidence interval, 'range'. Furthermore, we calculated 95% confidence limits of model outputs 'number of trees' and 'long-term growth rate' for Nahal Saif and Nahal Katzra. For this purpose we ran 12 simulations each under the standard parameter set, each consisting of 500 runs.

Starting from standard parameter values, we successively increased and decreased each parameter to the maximum and thereafter to the minimum value of the corresponding range. For both Nahal Saif und Nahal Katzra, we ran the model for each parameter set (200 years, 500 simulation runs) and determined the average number of trees in the year 200 and the long-term growth rate of the population ($\text{mean } \ln(\text{trees}(t)/\text{trees}(t-1))$) over all 200 years and 500 runs with 'trees' being all *A. raddiana* individuals that are older than one year. Furthermore, we calculated the elasticity (proportional sensitivity) of each parameter. Similar to matrix models (Caswell, 1989) we defined the elasticity as

$$\text{elasticity} = \frac{\text{trees}(P_{\max}) - \text{trees}(P_{\min})}{\text{trees}(P_{\text{standard}})} * \frac{P_{\text{standard}}}{P_{\max} - P_{\min}} \quad (3)$$

where P is the parameter under consideration, and max and min indicate extremes of the range given in Tables 2.1 and 2.2. Small elasticities indicate that tree survival is insensitive to small changes in this parameter.

Furthermore, to test for impact of initial trunk circumferences and initial tree locations on simulation results we started simulations with random tree sizes drawn from the size distribution given in Ward and Rohner (1997) and random locations within the wadi, both separately and in combination.

In addition to the described sensitivity analysis, we conducted specific simulation

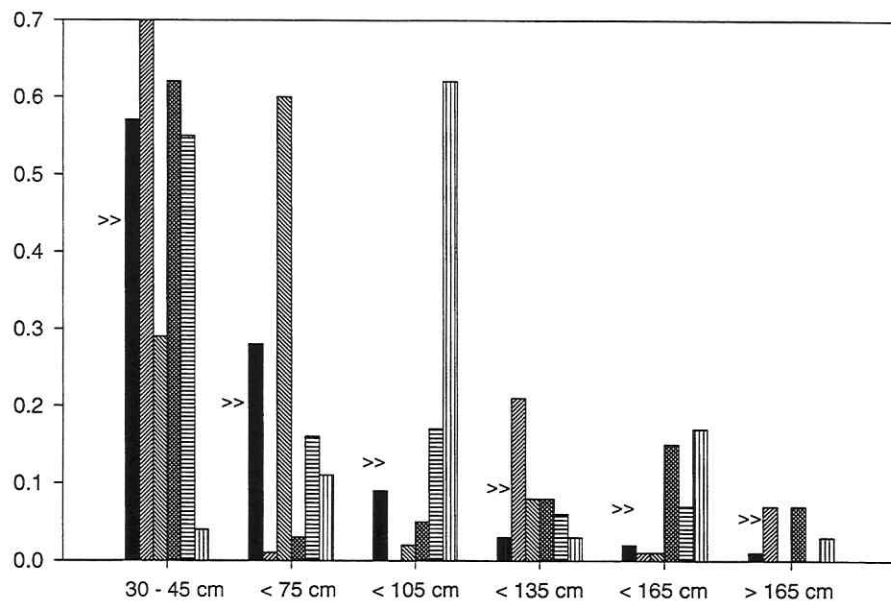


Figure 2.4: Relative size distribution of trees throughout the Negev (field data; black bars) and in the year 200 of five sample (single) simulation runs (hatched bars) for Nahal Katzra under standard parameters. The simulation runs represent the first 5 of the 1000 runs which are used for the (final) fit. >> indicates the average size distribution of the (final) fit.

experiments focusing on two factors that are possible key factors for the decline of the *Acacias* of the Negev, i.e. distribution of high and low rainfall years and germination probabilities of tree seeds. Frequencies of good, i.e. high rainfall, and bad, i.e. low rainfall years were varied over wide ranges, both separately and together, whereas frequency of intermediate years was adjusted accordingly. The germination rate was varied from low to extremely high and was evaluated under 'normal' (i.e. distributions of good and dry years that are based on weather data for Nahal Katzra) and under 'deteriorated' weather conditions (good years were 40% less frequent compared to the actual weather distribution).

2.4 Results

2.4.1 Parameter fit and population dynamics under standard parameter set

The parameter fit has been carried out successfully. Resulting parameters are given in Table 2.1 and a comparison between field data and model results under the fitted parameters can be found in Table 2.2. Per definition, congruence between field data and model results is high. In the following, we discuss the meaning of the results of the parameter fit and interesting aspects of Table 2.2.

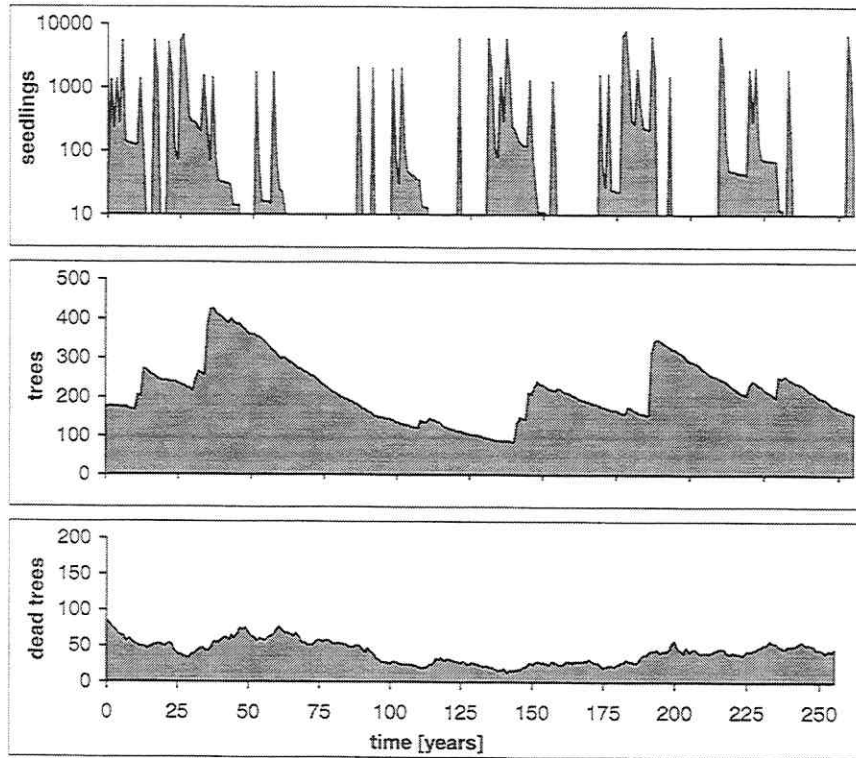


Figure 2.5: Typical time series. The average population growth rate over the shown 256 years is 0.0027.

The parameter fit resulted in a seed loss rate of 93% (Table 2.1), which is similar to that recorded by Miller (1994). The model result of semi-annual vitality rates of 99.41% and 96.91% for trees in good and bad moisture conditions (resulting from Equation 1; Table 2.1) are both close to the overall survival rate of 99.13% measured in the field. On the short time scale, this difference in vitality of trees in good and bad moisture conditions of 2.5% indicates that a bad moisture status does not lead to a sudden, extremely high, mortality risk but to a rather slow dying process. The factor describing the conversion from ‘risk points’ into the probability to deteriorate in moisture status, *worse_moist_scale*, was determined as 500 by the parameter fit. This means that a tree with 5 ‘risk points’ has a probability of 1% to worsen in moisture status within half a year. This low probability of moisture status deterioration reflects the high robustness of trees to low moisture availability. At first sight, it is surprising that the probability of deteriorating in moisture status and therefore suffering a high mortality risk is rather low. However, drying and dying processes of *A. raddiana* take place over many years.

Probability for first infestation by a mistletoe is higher in Nahal Katzra than in Nahal Saif (Tables 2.1 and 2.2) because of higher overall infestation rates in Katzra. However, further increase in mistletoe cover is similar in both wadis. This is due to the fact that the increase is modelled as a net rate. In Nahal Katzra, there is a higher infestation, but also more camels

removing mistletoes (Ward, pers. obs.) than in Nahal Saif.

Under the standard parameter set (Table 2.1), we have a slight population increase in Nahal Katzra (from 187 to 191 trees within the modelled period), while number of trees is slightly decreasing in Nahal Saif (from 172 to 163 trees), because of poorer moisture conditions in the latter site (Table 2.2). The long-term growth rate is close to zero (Table 2.2), as follows from the assumption that, on average, the population size remains fairly constant (see above). As expected, for individual runs of SAM, the size distribution of trees fluctuates around the average distribution observed in the field (Fig. 2.4). A comparison between the size distribution observed throughout the Negev to the average simulated size distribution under the final fit (Fig. 2.4), shows a systematic deviation towards more large trees in the model than in the field. This deviation is also reflected in the Kolmogorov-Smirnov test statistic of 0.15 - 0.17 (Table 2.2). Nevertheless, given that growth is modelled very simple based on field data from Kenya, the congruence between field and model size distributions is very good.

For individual simulation runs, number of seedlings over time has high peaks (Fig. 2.5), due to rare events of high germination. Periods of increased recruitment cause a subsequent increase in the abundance of adult trees (Fig. 2.5). However, long lifespan of the trees leads to less prominent fluctuations than is the case for seedling numbers. The number of dead trees is fairly constant; because trees are long-lived and die stochastically.

2.4.2 Results from the sensitivity analysis

Table 2.1 gives the changes in the number of trees and the long-term growth rate as well as the elasticity that result from a simulation at the maximum and at the minimum value of a certain parameter, as given by the parameter range. For a first classification of the changes in tree number and long-term growth rate, we selected those parameters that give a model output beyond the 95% limits of the standard simulations (indicated bold in Table 2.1). For example, for Nahal Katzra, a (confidence) interval of 173 to 213 trees or a interval of $1 \cdot 10^{-4}$ to $-1.3 \cdot 10^{-3}$ in population growth rate can be explained by stochasticity alone. That means that the effect of parameters that result in a smaller change in tree numbers or population growth is so weak that it cannot be discriminated from natural stochasticity. Simulations show that seedling mortality rates (*dry_year_mort*, *medium_year_mort*, *good_year_mort[1]*, *good_year_mort[2]*), the regression between tree size and number of seeds produced (*seed_equ_intercept*, *seed_equ_slope*) and parameters which determine the difference in mortality for trees under good and poor moisture conditions (*v_basic_vitality*, *v_moist_factor*) are the most important factors for the survival of *A. raddiana* (Table 2.1). Weather (probability distribution of good, medium and dry years), as a trigger for many mortality processes, is very influential as well. Furthermore, germination probability (*germination*), half annual increase in trunk circumference (*growth_per_hyear*) and size at first reproduction (*sub_circum_threshold*), as well as loss of germinable seeds in general (*seed_infest* and *seed_loss*) have a notable effect on tree density and long-term growth rate (Table 2.1). However, in contrast to popular perception (Ashkenazi, 1995), infestation by mistletoes plays a minor role in the population dynamics of *A. raddiana*.

In general, elasticity of the parameters is an indication of their importance to the survival (Table 2.1) of the tree population. Evaluating importance of the parameters according to their elasticities results in a higher rank of seedling mortalities than evaluation according to the change in tree numbers or in average population growth rate. Whereas elasticity is a relative index that is more or less independent of the chosen range do tree numbers and growth rate highly depend on the chosen range. Therefore, changes in tree numbers and growth rate give a lower limit of the influence of seedling mortality on *Acacia* survival, because uncertainties in field

| Parameter | standard value | range | Δ trees $\Delta r * 10^4$ | | elasticity | | Δ trees elasticity | | description of parameter |
|---------------------------------------|----------------|-----------------------|----------------------------------|--------|------------|------|---------------------------|--|--------------------------|
| | | | Katzra | Katzra | Katzra | Saif | Saif | | |
| Weather | | | | | | | | | |
| good | 23 % | 13 - 35 | } 778 | 136 | 12.53 | 696 | 9.74 | | |
| intermediate | 61 % | 70 - 52 | | | | | | | |
| dry | 16 % | 17 - 13 | | | | | | | |
| Seed distribution and germination | | | | | | | | | |
| seed_attr_factor | 5 | 2 - 10 | 14 | 2 | 0.05 | 13 | 0.05 | . times more seeds in attractive cells | |
| seed_attr_change | 5 % | 2 - 10 | 20 | 1 | 0.08 | 9 | 0.03 | . of attractive cells change location | |
| germination | 15.6 % | 8.9 - 23.3* | 248 | 22 | 1.65 | 189 | 1.26 | germination rate | |
| site_safety_value[0] | 10 % | 50 - 5 | } 34 | 9 | 0.70 | 10 | 0.20 | proportion of cell area offering safe sites | |
| site_safety_value[1] | 50 % | 50 - 50 | | | | | | | |
| site_safety_value[2] | 90 % | 50 - 95 | | | | | | | |
| site_safety_frequ[0] | 25 % | 33 | | | | | | frequency of cells with certain | |
| site_safety_frequ[1] | 50 % | 33 | | | | | | site_safety_value | |
| site_safety_frequ[2] | 25 % | 33 | | | | | | | |
| Seedling mortality | | | | | | | | | |
| dry_year_mort | 100 % | 90 - 100 | 37 | 11 | 5.50 | 25 | 0.75 | mortality of small seedlings in dry years | |
| medium_year_mort | 80 % | 82 - 78 | 125 | 29 | 14.50 | 87 | 12.50 | mortality of small seedlings in intermediate years | |
| good_year_mort[0] | 60 % | 64 - 56 | 165 | 37 | 18.50 | 120 | 17.50 | mortality of small seedlings in good years | |
| good_year_mort[1] | 1.74 % | 11.6 - 0 | 272 | 106 | 89.79 | 208 | 93.50 | mortality of older seedlings | |
| Growth | | | | | | | | | |
| growth_per_hyear | 0.684 | 0.616-0.752 | 55 | 9 | 1.7 | 75 | 2.31 | increase in trunk circumference in cm | |
| Seed production, infestation and loss | | | | | | | | | |
| seed_equ_intercept | 3.84 | 3.77 - 3.91 * | } 72 | 2 | 12.12 | 62 | 10.43 | seed production regression | |
| seed_equ_slope | 1.11 | - * | | | | | | | |
| breeding_subadult | 50 % (20 %) | 38 - 62 * (12 -30) | 27 | 3 | 0.35 | 7 | 0.05 | . subadults breed per year | |
| breeding_adult | 87 % | 81 - 93* | 25 | 11 | 1.03 | 26 | 1.07 | . adults breed per year | |
| seed_infest | 96.5 % | 98 - 95* | 163 | 54 | 1.17 | 162 | 1.16 | . seeds are infested by bruchids | |
| seed_loss | 93 % | 91.6 - 94.4∇ | 75 | 24 | 1.15 | 88 | 1.35 | . seeds are lost from wadi bed | |
| sub_circum_thresh | 15 cm | 23 - 8* | 225 | 100 | 1.38 | 170 | 1.04 | minimum size of subadults | |

| | | | | | | | | |
|---|-----------------------|-------------------------------|-------------|----------------|-------|-------------|-------|---|
| adu_circum_thresh | 45 cm | 55 - 34* | 11 | 1 | 0.11 | 6 | 0.06 | minimum size of adults |
| <i>Mistletoe infestation, moisture status and vitality of trees</i> | | | | | | | | |
| init_mistle_sa[0] | 83 % (96 %) | 70 - 92* (92 - 100) | } 7 | 7 | 0.21 | 9 | 0.69 | . subadult trees have initially mistletoe cover of [i] quarters of the canopy |
| init_mistle_sa[1] | 15 % (4 %) | 24 - 8* (8 - 0) | | | | | | |
| init_mistle_sa[2] | 2 % (0 %) | 6 - 0* - | | | | | | |
| init_mistle_sa[3] | 0 % (0 %) | -* - | } 15 | 2 | 0.34 | 12 | 0.27 | . adult trees have initially a mistletoe cover of [i] quarters of the canopy |
| init_mistle_a[0] | 57 % (77 %) | 37 - 75* (51 - 91) | | | | | | |
| init_mistle_a[1] | 17 % (10 %) | 24 - 10* (16 - 4) | | | | | | |
| init_mistle_a[2] | 15 % (4 %) | 22 - 9* (9 - 1) | | | | | | |
| init_mistle_a[3] | 11 % (9 %) | 17 - 6* (16 - 4) | 5 | 3 | 0.15 | 8 | 0.25 | . uninfested trees catch mistletoe |
| mistle_incr_prob[0] | 0.4 % (0.2 %) | 0.36 - 0.44∇ (0.18 - 0.22) | | | | | | |
| mistle_incr_prob[1] | 1.5 % | 1.35 - 1.65∇ | | | | | | |
| mistle_incr_prob[2] | 1.5 % | 1.35 - 1.65∇ | | | | | | |
| good_moist_sa | 97 % (93 %) | 92 - 100* (68 - 99) | 9 | 0 | 0.67 | 4 | 0.07 | initially, . subadults have good moisture status |
| good_moist_a | 92 % (86 %) | 87 - 97* (78 - 92) | 1 | 5 | 0.01 | 26 | 0.13 | initially, . adults have good moisture status |
| worse_moist_scale | 500 (900) | 450 - 550∇ (990 - 810) | 14 | 3 | 0.43 | 6 | 0.18 | conversion factor: risk points -> poor moisture |
| v_basic_vitality | 96.91 % | 87.2 - 100∇ | 1370 | >500 | 63.63 | 1495 | 69.44 | vitality under bad moisture status |
| v_moist_factor | 0.0250.0225 - 0.0275∇ | | 278 | 69 | 8.53 | 193 | 5.92 | conversion factor: good moisture -> low mortality |

Table 2.1: Overview of model parameters for Nahal Katzra and Nahal Saif: standard set of parameters, tested range and results of sensitivity analysis. Parameters for Nahal Saif are given in parenthesis if differing from Nahal Katzra.

range = parameter range, given in the same unit as the respective parameter (see *Methods* for further explanations), Δ *trees* = change in number of trees when running the model under the two extreme parameter values given by the range, Δr = change in long-term population growth rate, *j* = several rows belong together, **bold** numbers indicate that the deviation from simulation output under standard parameter set can not be explained by stochasticity, * = range corresponds to 95% confidence limits of field data, ∇ = parameter value fitted (see *Methods* for further explanations), for shortness, *dots* in the parameter description replace the respective parameter name (e.g. . times more seeds in attractive cells means: 'seed_attr_factor' times more seeds in attractive cells).

| | number of trees | number of seedlings (1 year old) | population growth rate | adult mortality in % | moisture | mistle 0 | 1 | 2 | 3 | D_{max} |
|--------|--------------------|--|---------------------------|----------------------------|----------|-------------|------|------|------|-----------|
| Katzra | 191 ± 12 | 320 | -0.0005 | 0.80 | 93.0 | 64.0 | 12.0 | 8.0 | 16.0 | 0.17 |
| field | 187 | | | | 94.0 | 66.0 | 16.3 | 10.5 | 7.2 | |
| Saif | 163 ± 11 | 250 | -0.0010 | 0.88 | 89.0 | 84.0 | 7.0 | 4.0 | 7.0 | 0.15 |
| field | 172 | | | | 89.0 | 85.5 | 7.3 | 2.2 | 5.0 | |

Table 2.2: Simulation outputs for standard parameters for Nahal Saif and Nahal Katzra (mean of 1000 simulation runs, year 200) compared with field data (Ward, unpubl. data). For simulated populations, the standard deviation of the average population size is given (\pm). *Moisture* = fraction of trees with good moisture status in %; *Mistle* = fraction of trees with $x/4$ mistletoe cover in %; D_{max} = Kolmogorov-Smirnov test statistic for the comparison of the tree size distribution resulting from the model to the field data (see *Methods* for further explanation).

measurements are probably higher than the assumed relative total range of 20%.

Modifications to initial conditions, i.e. randomization of initial trunk circumferences based on the average tree size distribution observed throughout the Negev and / or randomization of coordinates of simulated trees, had no major effect on survival of the *Acacia* trees. However, for Nahal Katzra, simulations with randomly drawn initial trunk circumferences lead to a slight decrease in number of trees below the 95% confidence limits (random tree sizes: 154 trees, random tree sizes and locations: 144 trees, while the lower 95% confidence limit was 173 trees). The same is true for the long-term growth rate of the population (random tree sizes: $-2.7 \cdot 10^{-3}$ per year, random tree sizes and locations: $-1.4 \cdot 10^{-3}$ per year, while the lower 95% confidence limit was $-1.3 \cdot 10^{-3}$). Actual size distribution in Nahal Katzra shows approximately equal numbers of trees in all age classes. This leads to a higher seed production and therefore a better survival than in the random scenarios.

2.4.3 Simulation experiments

Climatic changes, as well as changed utilization patterns of the wadis, have been discussed as possible contributing factors to the observed decline of *Acacias* in the Negev. However, a changed utilization pattern results in decreased large mammalian herbivore densities in the wadis and, consequently, in a decreased number of *Acacia* seeds consumed by herbivores. This, in turn, affects germination rates of *Acacia* seeds, which profit from passage through the digestion tract of herbivores (Coe and Coe, 1987; Hauser, 1994). Because both of these factors, i.e. weather and germination, proved to be important for survival of simulated populations of *A. raddiana* (see Table 2.1) and because, in nature, both can vary over large ranges (compare e.g. Lamprey et al. (1974); Karschon (1975); Coughenour and Detling (1986); Ernst et al. (1989); Tybirk (1991); Rohner and Ward, in press) we conducted further simulation experiments to explore their impact on survival of *A. raddiana*, both separately and in combination.

In a first simulation experiment we varied the probability of good and dry years, both separately and in combination (Fig. 2.6). Occurrence of good years is important for the survival of young seedlings and a prerequisite for germination. Thus, an increase in good years leads to a clear linear increase in tree numbers as well as in growth rate (Fig. 2.6). Similarly, a decreasing probability of dry years leads to a decrease in mortality of very young seedlings and reduces the

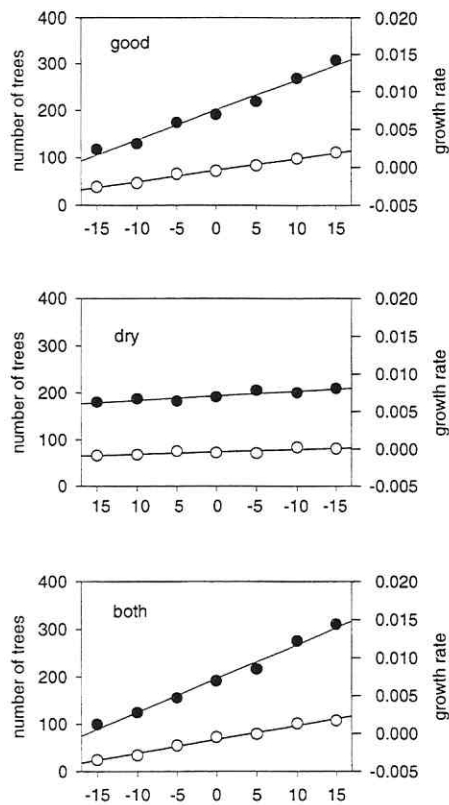


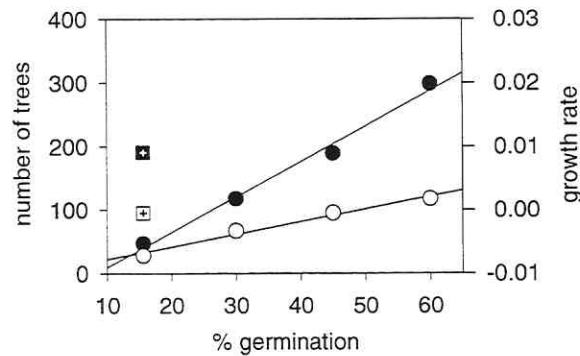
Figure 2.6: Number of trees (closed symbols) and long-term growth rate (open symbols) as a function of the weather regime. Changes in the weather are given on the abscissa in % of the standard occurrence probabilities. *Good* = occurrence of good years increases, *Dry* = occurrence of dry year decreases, *Both* = occurrence of good years increases whereas dry years decrease. The simulations were run under the standard parameters of Nahal Katzra and the mean was calculated for the year 200 of 500 simulation runs.

probability that adult trees worsen in moisture status. Again, the relationship between improving weather conditions, i.e. a decrease in dry years, and tree population size as well as population growth rate is linear. However, the effect is less pronounced than with an increase in good years. Therefore, correlation between weather conditions and tree population dynamics is similar to the 'good' scenario when both weather modifications occur together, i.e. when occurrence of good years increases at the same rate as frequency of dry years decreases (Fig. 2.6).

The previous simulation experiment indicates that minor changes in distribution of dry and good years may cause a long-term decline in the number of *Acacia* trees and population growth rate.

In a second simulation experiment, we simulate a pessimistic scenario with a relative reduction in frequency of good years by 40%. Simulations show that, despite the bad conditions, tree number and population growth rate could be increased to the value of the standard scenario if germination rate was about 45% (Fig. 2.7). Such high germination rates are probably unrealistic under natural conditions. However, germination rates can be significantly increased if *Acacia* seeds are consumed by large mammalian herbivores. Experiments have shown that the passage through the digestive tract may increase germination rates by up to 60% (Rohner and Ward, in press). For the purpose of comparison, Fig. 2.8 shows the population dynamics of *A. raddiana* for germination rates from 8.9% to 45% under unmodified weather conditions in Nahal Katzra. Fig. 2.8 shows that increased germination leads to a linear increase of the number of trees up to 800 and a slightly slower increase of long-term population growth rate to +0.0053.

Figure 2.7: Germination scenario under deteriorated weather conditions in Nahal Katzra. Occurrence of good years is diminished by 40% of the standard occurrence probability (which was 23%); squares give output under standard weather and germination; for remaining symbols and colors see Figure 2.6.

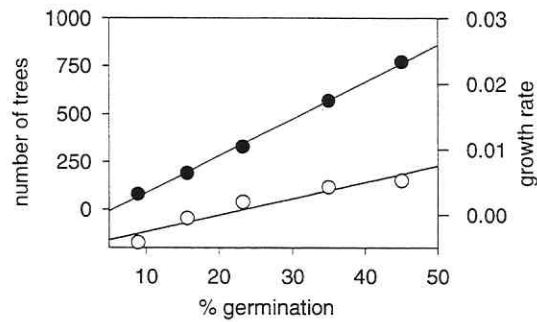


2.5 Discussion

2.5.1 Advantages and shortcomings of the model

We developed SAM, a grid-based simulation model of the spatially-explicit population dynamics of *A. raddiana* in wadis of the Negev desert. Despite many field studies of the population ecology of African *Acacia* trees there are few simulation models. Some model the interaction between browsers and biomass production of *Acacias* (Pellew, 1983; Teague et al., 1990; Teague and Walker, 1990), and others *Acacia* tree - grass - coexistence in Savannas (Jeltsch et al., 1996). But, to our knowledge, SAM is the only simulation model that focusses explicitly on the population dynamics of an African *Acacia* species. Spatially-explicit simulation models incorporating layout of the landscape are an increasingly used approach for simulation of animal populations (Dunning et al. 1995; Turner et al., 1995), but not yet often used for plants (Mladenoff et al., 1996). However, irrespective of the species under consideration, spatially-explicit models have great data requirements (Conroy et al., 1995; Ruckelshaus et al., 1997). As far as available, data for SAM were obtained from field studies and complemented by best guesses, often based on literature (Conroy et al., 1995). For parametrization of SAM, we have used field data not only for direct estimation of parameters, but also for a parameter fitting procedure. This way, we could use actual, easily obtainable data on e.g. moisture status or mistletoe infestation of *Acacia* trees to estimate corresponding rates for deterioration of the moisture status or infestation by mistletoes. To measure these rates in the field, long-term studies would have been necessary. However, parameter fit required the assumption that, on average, actual population size of trees remains fairly constant over time. If actual densities should be declining we would have underestimated mistletoe infestation, moisture status (both leading to higher mortalities), and seed loss and overestimated vitality of trees. Therefore, absolute values of population growth rate and number of trees may not resemble the situation of *A. raddiana* in the Negev. However, field studies (Ward and Rohner, 1997) and analysis of aerial photographs (Lahav-Ginott, pers. comm.) did not give any evidence for an increase in *Acacia* mortality. Nevertheless, we based our sensitivity analysis on changes in growth rate and tree density rather than on absolute values, thus further reducing risk of biased results.

Figure 2.8: Number of trees (closed symbols) and long-term growth rate (open symbols) vs germination rate in Nahal Katzra. Standard germination rate: 15.6%.



Model development forced us to compile present knowledge on population dynamics of *A. raddiana* and to give this knowledge a hierarchical structure. It was a first aim of this study, to present this knowledge in a clear and reasonable way. But we don't think this is sufficient, because it is also important to evaluate this knowledge. For evaluation, we need to know the accuracy of the parameter estimation and sensitivity of the system to this parameter. With help of our sensitivity analysis we are able to evaluate for which processes knowledge is reasonable and which deserve further studies. For example, there are some data on the germination-weather interaction, but it is not very accurate and the population dynamics of *A. raddiana* are very sensitive to this complex. Therefore, we need further field studies in this direction. On the other hand, seed production is reasonably well known and has some, but not too much effect on the long-term survival of the Acacias. Therefore, possible further field studies on seed production should have a low priority. But, even though sensitivity analysis did provide an idea on the relative importance of individual parameter values, we have to realize that this analysis relies on the structural assumptions of SAM and present knowledge. Furthermore, it would have been ideal to conduct a multi-factorial sensitivity analysis, but, because of the complexity of spatially-explicit models in general, these models are usually not suitable for such a thorough analysis. Even though we took care to design our model rather simple, this is also true for SAM. Therefore, we restricted our sensitivity analysis to an uni-factorial design, but we conducted it for two data points (Nahal Saif and Nahal Katzra data). The fact that sensitivities determined for these two Nahals are virtually the same (Table 2.1) and that modifications of initial conditions (i.e. trunk circumferences and / or coordinates of simulated trees) had no major effect on survival of *Acacia* trees means that the results shown in this publication are not bound to these two specific study sites but transferable to the entire Negev. However, before applying the results to African populations we recommend a comparison of the local life history traits.

2.5.2 Possible threats to *Acacia* survival

Basing the model on the assumption that the current status of the *A. raddiana* population in the Negev, as regards environmental quality, is still in a stable state, we evaluated the relative

importance of several natural factors and processes for survival of these ecologically important trees. In this study, we focussed on natural processes and neglected anthropogenic disturbances, such as road construction (discussed in Wiegand et al. (1998, Chapter 3 of this thesis) and aquifer depletion (see Ward and Rohner 1997). A detailed sensitivity analysis of the model indicates that, unexpectedly, mistletoe infection plays a minor role in long-term population dynamics of *A. raddiana*. Therefore, we reject the hypothesis (i) (see Chapter 1 of this thesis) that the mistletoe *L. acaciae* causes the decline of *Acacia* trees. On the other hand, we agree with the hypothesis (ii), that bruchids seriously delimit recruitment, because in addition to mortality and germination rates, production and survival of viable seeds reaching safe sites is one of the major bottlenecks for long-term survival of the *Acacia* populations in the Negev. Despite the production of a huge seed crop, recruitment is seed limited. In Negev *Acacias* close to 100% of the seeds do not germinate, mostly due to bruchid beetle predation. As simulations show, even small variations in this fraction have a major effect on the long-term trend and size of the tree population.

However, *Acacia* seed losses and germination rates are closely linked to plant-animal interactions. Many studies throughout Africa have shown that interactions between seed loss and germinability and herbivorous animals are quite complex: seed pods have been found to form an important part of herbivore diets when other food is short in supply (Gwynne, 1969). Small mammalian herbivores can destroy seeds during chewing and digestion (Miller and Coe, 1993; Miller, 1994) but digestion by large mammalian herbivores (Lamprey et al., 1974; Miller, 1995; Rohner and Ward, in press) and gnawing of the seed coat by rodents (Miller, 1995) may also enhance germination. In addition, mammalian herbivore faeces may enhance germination conditions (Coughenour and Detling, 1986; Mwalyosi, 1990) and improve seedling establishment (Coughenour and Detling, 1986). Consumption of seeds by mammalian herbivores may also remove bruchid beetles from infested seeds (Coe and Coe, 1987; Hauser, 1994). In general, bruchid beetle survival is probably not controlled by mammalian herbivores (Traveset, 1992; Rohner and Ward, in press); bruchids are attacked by parasitoid wasps (Traveset, 1991) and ants (Ashkenazi, 1995). However, seed infestation by bruchids is highly variable over time and space (Karschon, 1975; Ernst et al., 1989; although not in our study areas) and seed infestation does not necessarily have a detrimental effect. Bruchids may improve germinability in those rare cases where the seed embryo is not destroyed by the beetle because the bruchid exit hole increases permeability of the seed coat and thus enhances germination (Halevy, 1974; Lamprey et al., 1974).

The mosaic of short-term studies of the complex seed-germination-herbivore systems in many different places under different, often non-comparable conditions, is very complex. There is a need for comprehensive long-term studies in specific locations to facilitate evaluation of the relative importance of the interaction of these factors at least for these study areas. Very importantly, such a study should be carried out in a manner that can also capture changes over time. A first step in this direction has been taken by Miller (Miller, 1994) by tracing the fate of seeds from a tree to the soil seed bank, including via herbivores.

2.5.3 Implications for management

Simulation experiments showed that an increase in germination rate of *Acacia* seeds in a sample Negev wadi may, to a certain extent, counteract the detrimental effect of climatic changes that lead to a decrease of those high rainfall years that are suitable for germination and seedling establishment. It is also shown that, contrastingly, a decrease in germination rates may significantly contribute to a possible decline of the Negev's *Acacias* even under unchanged

climatic conditions. This interesting result possibly provides a window of opportunity for managing for improved survival conditions of *A. raddiana* in the Negev: increases in germination rates are likely to be caused by increased mammalian herbivore densities via increased germination after ingestion and subsequent defecation (Rohner and Ward, in press). Consequently, management strategies that increase mammalian herbivore densities may enhance *Acacia* recruitment and long-term survival. Further field studies are necessary to evaluate this indicated benefit for the *Acacia* population resulting from an increased introduction of large mammalian herbivores into the wadis. Of course, such management strategies must ensure that introduced large mammals do not counterbalance seed germination with increased tree defoliation and seedling removal.

2.5.4 Future directions

Understanding the population dynamics of a long-lived species is enhanced by an integrated approach combining field studies and modelling; none of these approaches alone provides a complete view, but they mutually promote each other's findings. Field studies are necessary for development of the structure and parameterization of the model, whereas the model administers and evaluates the present knowledge, uncovers gaps in knowledge, extrapolates short-term information to meaningful time scales, and, by sensitivity analysis, indicates directions for future research. The present simulation study emphasizes the need for further investigations of seed production and mortality rates under different moisture and rainfall conditions. Such field investigations are currently in progress in the Negev and results will be used to improve the parameterization of SAM. Further investigations will have to include a study of spatial patterns arising from the population dynamics. SAM includes several rules that refer to space, as for example, the heterogeneous distribution of safe sites. With respect to investigations conducted in this paper, these rules proved not to be important for the total size of the population. Hence, currently it would not have been necessary to use a spatially-explicit model, but we chose a spatially-explicit approach, because this way we do have a sound basis for landscape related analyses and applications.

For example, SAM allows us to conduct a spatial pattern analysis, which we will use to gain a better understanding of the local recruitment process in time as well as in space. Further examination of spatial interaction will require information on the wadi profile. For example, in a shallow, wide part of the river bed the water flow will be slow, and will create more safe sites as well as leaving more seeds in situ. SAM facilitates such a study, because it is designed to read in data on wadi morphology from a GIS. The feature of being linkable to a GIS will be useful in future use of SAM as a management tool for specific wadis.

Note: A simplified version of the source code is given in the appendix of this thesis.

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2.7 Link to the following chapter

Chapter 2 has been an extensive presentation and thorough analysis of the model. The model is a well organized summary of the present knowledge on the population dynamics of *A. raddiana*. From the sensitivity analysis, we've learned about the relative importance of the different processes to the survival and recruitment of the *Acacia* trees. For example, it turned out that,

contrary to popular perception, mistletoe infection is not a threat, but that the availability of germinable seeds is a major bottleneck. An increase in germination rate could counteract the shortage of viable seeds. Reintroduction of large mammalian herbivores would cause such an increase in seed germination and is therefore a suitable management measure. In short, Chapter 2 has already been a big step towards the aim of understanding population dynamics of the *Acacia* trees and finding management measures.

In the following chapter, I will present a more applied study on the effects of roads crossing populations of *A. raddiana*. Historically, this study was conducted at an earlier stage of model development than Chapter 2. Therefore, some of the rules are different. This involves a different way of distributing seeds. In Chapter 2, they were distributed completely independent of tree locations, while in the following chapter seed density will be higher in the vicinity of seed-producing trees. Both points of view are in agreement with knowledge from the field. Furthermore, weather was modeled more simple, because weather data were not yet available when the investigations of Chapter 3 were conducted. In this simpler approach, we distinguished between good years (good for germination) and bad years (five or more consecutive bad years lead to a higher risk of tree moisture status deterioration) only. This is fair enough for the investigations conducted in the following chapter which are not as detailed as the sensitivity analysis of Chapter 2. Due to the simpler weather model, seedling mortality is independent of actual weather in Chapter 3. Finally, adult mortality is age-dependent in Chapter 3. The dependence of tree mortality on tree size or age will be investigated more thoroughly in Chapter 5. At the present stage, both possibilities are reasonable. Even though these differences between the two model versions have some impact on the exact results of simulations conducted, they are far from changing any of the results of Chapter 3 qualitatively.

Readers having read Chapter 2 may skip chapters 3.3.1 and 3.3.2, because they give a shortened description of the model, assuring that this chapter can be read independently. However, due to the above-mentioned differences the reader might like to look at the paragraphs *Seed distribution and germination*, *Seedling mortality*, and *Mortality of trees*. Simulations in the following chapter consist of 100 replications of 1000 year runs.

Decline of the Negev's Acacias - a spatially explicit simulation model as an aid for sustainable management¹

3.1 Abstract

In the Negev desert there is high concern about the high mortality and low recruitment of *Acacia* trees, a major source of livestock feed and firewood for the native Bedouins. The *Acacias* are mostly restricted to ephemeral riverbeds and areas with high ground water levels near oases. As the only trees in much of this desert, the *Acacias* constitute a major ecological concern in southern Israel.

To develop sustainable conservation and management strategies it is necessary to understand the population dynamics of the trees. A spatially-explicit, object-oriented computer simulation model is presented which is based on demographic data gained by field studies. As an example, we show first results of an application of the model to the ephemeral riverbed Nahal Saif which is cross-cut by a road. The road alters the flood regime. This leads to modifications in seed dispersal and reduces the water availability to the *Acacia* trees. It is shown that both factors have a negative impact on the population dynamics of *A. raddiana*. Culverts under the road would reduce the severity of this impact although this should be done in conjunction with the reintroduction of herbivorous mammals in order to facilitate seed dispersal and germination.

3.2 Introduction

In the Negev desert, Israel, most trees belong to the genus *Acacia*, with *A. raddiana* being the most abundant species in this genus. These trees are largely restricted in their distribution to wadi beds (Halevy & Orshan 1972). Providing food and shelter for many desert animals (Ashkenazi 1995) and ameliorating the soil for other plant species (Milton & Dean 1995), these trees are of great ecological importance for the Negev's ecosystems. Furthermore *A. raddiana* is a major source of fuel, fodder and remedies for the Bedouin people (Ashkenazi 1995, Ward & Rohner 1997).

There is concern about the high mortality of *Acacia* trees combined with low recruitment throughout the Negev (Ashkenazi 1995, Ward & Rohner 1997). Among other reasons, the decrease of *Acacia* populations in the Negev is explained by human impacts (Ashkenazi 1995, Ward & Rohner 1997). Ward & Rohner (1997) found that aquifer depletion does not significantly influence *Acacia* survival, which they explain by the fact that roots usually do not reach as deep as the aquifers. However, their results show a clear negative impact of roads cross-cutting wadis, thereby attenuating the water flow to the trees in the lower parts of the wadis.

The aim of this paper is to understand the influence of roads on the *Acacia* demography and

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to discuss management strategies that can counteract their negative effects. This task we address with the help of the spatially explicit, stochastic computer simulation model SAM. For this study we show first simulation results of SAM applied to a about 2 km long part of Nahal Saif, a wadi located near the Northern Arava valley (30°52' N, 35°10' E). This part of Nahal Saif is divided into two sections by a road (Figure 3.1), with about 100 trees of the species *A. raddiana* in each section. The road diminishes the amount of flood water reaching the downstream section of Nahal Saif. We assume that this causes a negative effect on the moisture status of the trees in the lower section. We also assume a significant influence on seed distribution:

- (1) The downstream transport of seeds by flood water will be disturbed by the road, thus reducing the number of seeds transported from the upper section of the wadi;
- (2) The reduced flood intensity and frequency will leave a higher amount of seeds clumped beneath the trees.

We studied the effect of reduced moisture availability and modified seed distribution on the population size dynamics of Nahal Saif separately and thereafter the combination of both and discuss their relative influences on *Acacia* survival. Management strategies are proposed on the basis of the results of the model.

3.3 The model

3.3.1 Aim and general features of the model

The aim of the SAM model is to capture the main mechanisms that determine the population dynamics of *Acacia raddiana*. The distribution of *A. raddiana* in the Negev is dominated by the landscape because in most areas these trees do not grow outside the wadis. Inside the wadis the population dynamics of the trees is largely influenced by tree spacing and seed distribution. For example, seeds will germinate mostly in sites providing enough water and light. Therefore, any model that attempts to explain the population dynamics of *A. raddiana* needs to be spatially explicit. Grid-based simulation models have been shown to be an appropriate approach to model spatial vegetation dynamics in arid and semi-arid systems (Thiéry et al. 1995, Jeltsch et al. 1996, Wiegand et al. 1995). Thus, SAM subdivides the wadi into a grid of cells (total number: 7168) of 5m*5m, a typical canopy size of a young adult tree (Figure 3.1).

Modeling small population sizes requires an individual-based approach (DeAngelis & Gross 1992). In SAM, this is realized by an object-oriented implementation of the individual trees. Each specimen is represented as an object with the properties of one of 3 classes. SAM distinguishes: 'seedlings', 'subadult and adult trees' and 'dead trees'. Trees of all three classes are characterized by the attributes: (1) trunk circumference, (2) location of the cell the plant grows in. The choice of the class depending on the actual trunk circumference. Further, for dead trees, the time since death is recorded. For living trees, SAM records the moisture status and the cover of mistletoes hosted by the tree.

For plants, demographic parameters are determined by the life history stage or size of an individual rather than by its age (Harper 1977). SAM records the trunk circumference, which is representative of the overall size of *A. raddiana*, because these trees grow allometrically (Ward & Rohner 1997).

The simulations presented in this paper are based on field studies conducted in Nahal Saif and other wadis. One simulation consists of 100 replications of 1000 year runs. The initial distribution of the trees coincides with the actual distribution in Nahal Saif.

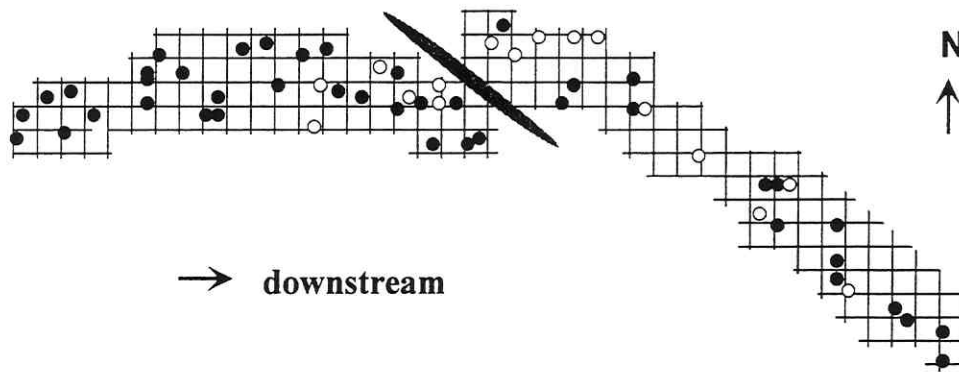


Figure 3.1: Simulation output showing a detail of a typical spatial pattern in Nahal Saif taken from the simulation shown in Figure 3.2a (year 10). One square corresponds to 4*4 cells. Black circles: trees; open circles: dead trees; dark shaded: road.

3.3.2 Model description

In SAM, a year is divided into two periods, summer and winter. In each period different life history events take place. In summer, seeds become distributed and germinate. In both periods we employ successively the modules for growth and mortality of seedlings, for growth of trees, infestation of trees by mistletoes, deterioration of trees' moisture status' and for mortality of trees. Additionally, in winter the 'ageing' and removal of dead trees takes place, seeds are produced, suffer infestation and can get lost.

3.3.2.1 Seed distribution and germination

Distribution SAM follows the destiny of each seed individually. It is assumed that 70% of the *Acacia raddiana* seeds are clumped beneath the trees, the density decreasing exponentially with distance from the tree. The other 30% of the seeds are equally distributed throughout the wadi. This simulates distribution of seeds by animals, water and other agents.

Germination Seed germination in arid environments depends primarily on water availability. In terms of the model 'germination' means the germination of a seed and the survival of this seedling for half a year. We assume that germination in this sense takes place only in 'good' years with high rainfall. SAM distinguishes between good and bad years; good years occur randomly with a probability of 8%, which has been estimated from the size distribution of the trees in Nahal Saif (Ward, unpubl. data). Secondly, we assume that germination takes place only in safe sites, that is, microsites that provide optimal nutrient, water and shade conditions. There are three classes of grid cells depending on the availability of safe sites: (1) 90%, (2) 50% or (3) 10% of the cell area offer suitable germination conditions. Patches of 16 cells (Figure 3.1), having the same safe site density, are distributed randomly throughout the wadi. This represents the inhomogeneous distribution of safe sites within the wadi. Finally, in good years, seeds that

are at a safe site have a germination probability of 15.6% (Rohner & Ward, in press).

3.3.2.2 Seedling growth and mortality

Growth In SAM the trunk circumference of seedlings and of trees increases by 0.68 cm per six months (Kiyapi 1994, Ward, unpubl. data).

Mortality 0.5, 1 and 1.5 year old seedlings have a mortality rate of 89%, 75% and 55% respectively (Rohner & Ward, in press). Older seedlings are assumed to follow the half-annual mortality of 0.87% measured for *A. raddiana* trees with a trunk circumference greater than 8 cm (Ward & Rohner 1997).

3.3.2.3 Mistletoe infestation, moisture status and mortality of trees

Mistletoe infestation Mistletoes are known to reduce the seed production of *A. raddiana* trees in the Negev (Ashkenazi 1995). Additionally they are suspected to reduce the viability of infested trees. SAM models a simple population dynamics of mistletoes. A tree becomes infested by a mistletoe with a semi-annual probability of 0.3%. The mistletoe may grow in size (0.2% per half year) and dies once the host tree dies. These dynamics are fitted from the actual abundance of mistletoes living on *A. raddiana* in Nahal Saif (Ward, unpubl. data).

Moisture status In Nahal Saif 6.8% of subadult and 14.1% of adult *A. raddiana* have a low moisture status; that is many dry branches (Ward, unpubl. data). SAM assumes a good moisture status for seedlings, but trees' moisture status' may decrease at rates fitted to the field data, dependent on long term weather, number of trees in neighboring cells and mistletoe infestation.

Mortality Tree mortality is modeled via a vitality function of the trees. The vitality of a tree decreases with its trunk size (age), with the deterioration of the moisture status and with increasing mistletoe infestation. Over the wadi this leads, on average, to a semi-annual mortality rate of 0.87% as measured by Ward & Rohner (1997).

3.3.2.4 'Ageing' and removal of dead trees

Once a year the time since death of the dead trees is updated. Dead trees in the Negev desert remain standing for about 10 years (Ward & Rohner 1997). Therefore in the model dead trees have a probability of 10% of falling.

3.3.2.5 Seed production and infestation

Seed production The seed production of breeding trees in good moisture condition and without mistletoes depends on the trunk circumference tc . A regression of unpublished data (Ward) from Nahal Saif gives for the number of produced seeds S :

$$\log S = 3.65 + 1.19 * \log tc$$

SAM uses this regression, but reduces S for trees with a poor moisture status, trees infested by mistletoes, and for trees that have not yet reached the full maturity (subadults).

Seed infestation Seed infestation of *A. raddiana* in the Negev desert by seed beetles, mostly *Bruchidius albosparsus*, is as high as 98% (Rohner & Ward, in press). Infested seeds are assumed not to be germinable.

Seed loss Very high seed loss rates have recently been reported for African indehiscent *Acacia* trees (Miller 1994). *Acacia* seeds may be transported out of the wadis by floods and by ungulates, seeds eaten by rodents are destroyed, and on the ground they can decompose or get buried (Miller 1994). Following Miller (1994), we assume a seed loss rate of 96%, which is not yet supported or disproved by data from Nahal Saif.

| scenario | | g | d | c | short description |
|----------------|---|-----|-------|------|---|
| normal | | 100 | 96.00 | 70.0 | road neglected |
| moisture | 1 | 95 | 96.00 | 70.0 | less good years in the lower wadi => germination events less frequent; trees with bad moisture status more likely |
| | 2 | 85 | " | " | |
| | 3 | 70 | " | " | |
| | 4 | 40 | " | " | |
| seed dispersal | 1 | 100 | 96.08 | 70.6 | less seeds in the lower wadi; more seeds remaining beneath trees |
| | 2 | " | 96.20 | 71.5 | |
| | 3 | " | 96.40 | 72.5 | |
| | 4 | " | 96.80 | 76.0 | |
| combined | 1 | 95 | 96.08 | 70.6 | assumptions of coresponding moisture and seed dispersal scenarios at the same time |
| | 2 | 85 | 96.20 | 71.5 | |
| | 3 | 70 | 96.40 | 72.5 | |
| | 4 | 40 | 96.80 | 76.0 | |

Table 3.1: Parameter values for trees in the downstream wadi section for the different scenarios described in the text, given in % (g: ratio of number of years good for the upper wadi to years good for the entire wadi; d: seed loss rate; c: percentage of seeds remaining beneath trees)

3.3.3 The influence of the road

The road cross-cutting Nahal Saif into two sections (Figure 3.1) alters the flood regime of the lower section. A part of the flood water drains into the roadside ditch thus reducing the water availability of the trees growing downstream of the road and thereby altering seed dispersal. Less water and therefore fewer seeds flow into the lower section. On the other hand, due to the lower water flow, fewer seeds produced in the lower section become transported outside the modeled area. However, the total number of seeds will be reduced. Furthermore, more seeds will remain in the vicinity of their tree.

We studied four different types of road influence scenarios - a normal scenario, moisture scenarios, seed dispersal scenarios and combined scenarios. Each of the scenarios is simulated in 4 steps of 'severity' (see Table 1). In the normal scenario, we assume that the road does not have any effect on the population dynamics of *A. raddiana*. The moisture scenarios are based on the assumption of SAM that seed germination takes place only in good years, that is in years with floods of sufficient magnitude. Even in some good years, the amount of flood water crossing the road will be insufficient. Thus we distinguish between years that are good for the whole wadi and years that are good for the upstream wadi section only. The population

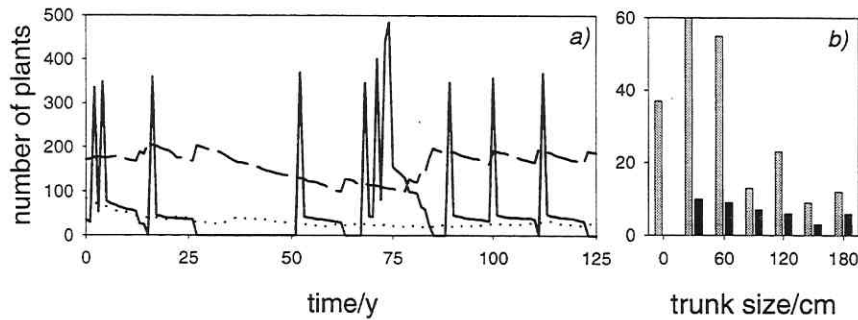


Figure 3.2: a) Typical time series showing the number of seedlings (solid), trees (dashed) and dead trees (dotted) in the modeled area of Nahal Saif for the normal scenario. b) Size distribution. The number of seedlings (dark gray, leftmost bar), trees (dark gray) and dead trees (light gray) is given at the year 25 of the simulation shown in a).

downstream of the road experiences diminished long-term water flow, which leads to a higher probability of deteriorating water status for these trees. The seed dispersal scenarios assume a decrease in the proportion of seeds that are randomly distributed instead of remaining close to the trees and they assume a higher seed loss rate because of the prevention of seed input from the upper wadi. Finally, in the combined scenarios, all assumptions of the moisture and of the seed dispersal scenarios are considered. Parameter values are given in Table 1.

3.4 Results

As already noted in Chapter 2, for individual runs of SAM, the number of seedlings over time has high peaks (Figure 3.2a) due to rare events of high germination. For living and dead trees this is buffered because of the high longevity and stochastic mortality of *Acacia raddiana*. The irregular size distributions (Figure 3.2b) are similar to the size distributions observed in the field.

Relative to the normal scenario, the number of trees in the downstream section of Nahal Saif (mean over 100 simulation runs) is reduced due to the effects of the seed dispersal scenarios as well as of the moisture scenarios (Figure 3.3a,b). In both cases, small parameter changes lead to a reduction of the population size over time. In the combined scenarios (Figure 3.3c) the negative effects are amplified.

3.5 Discussion

The time series for seedlings and trees shown in Figure 3.2a are typical for event-driven systems (Wiegand et al. 1995). The behavior of the model is clearly dominated by the assumption of germination events occurring only in good years. This is indirectly supported by several field studies showing little or no recruitment (Ashkenazi 1995, Ward & Rohner 1997) because these field studies might not have included any of the scarce good years. The discontinuous size distribution found in the model and in the field can be explained by mass germination. However, a discontinuous size distribution may also result from growth suppression by herbivores (Ward & Rohner 1997). This clearly deserves further investigations. However, we believe that rare germination events play an important, and perhaps controlling, role in the population dynamics of *A. raddiana*.

In a 'normal' scenario we studied the population dynamics of *A. raddiana* disregarding the road that cross-cuts Nahal Saif. The population size stayed approximately constant. For the moisture scenarios, we assumed that the road cross-cutting Nahal Saif reduces the number of good years in the downstream section. Since small reductions in the number of good years reduce the population size, culverts under the road allowing more flood water to pass to the lower side of the road would be of great value to the survival of *A. raddiana*.

However, the seed dispersal regime might still be disadvantageous. Lots of material gets stuck in the culverts and prevents seeds from crossing the road. Even if the amount of water is about the same the water might be much more canalized by the culverts than before the road construction accelerating the seed flow towards much lower parts of the wadi, and not distributing seeds lying clumped beneath trees. Thus, the assumptions of our seed distribution scenarios would still be valid. That means that the road would still have a noticeable negative impact on the population dynamics of *A. raddiana*.

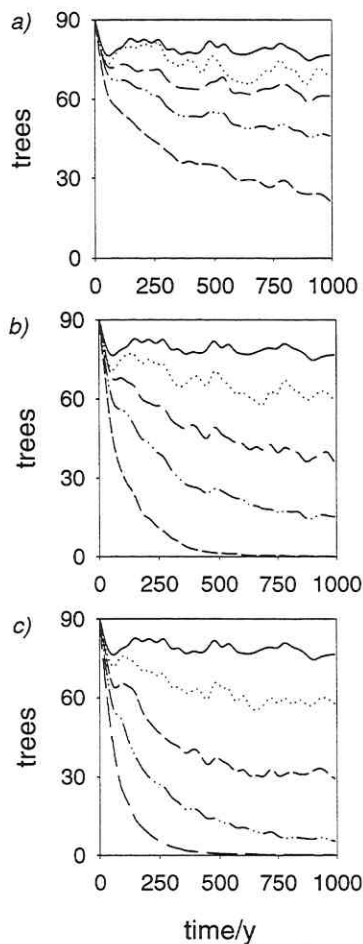


Figure 3.3: Mean number of trees over 100 simulation runs in the downstream section of Nahal Saif over time. a) seed dispersal scenarios, b) moisture scenarios, c) combined scenarios. Each graph shows the result of the normal scenario (solid lines). Parameter values of the scenarios are given in Table 1 (row 1: dotted, row 2: long dashes, row 3: dash-dot-dotted, row 4: dashed)

Care would have to be taken in the design of the culverts to ensure adequate distribution of water to the downstream side of the road to avoid canalization and, therefore, localized recruitment of trees. The problem of inadequate water distribution might be diminished by the reintroduction of herbivorous mammals. Herbivores feeding on *Acacia* seeds facilitate seed germination because their gut action scarifies the hard seed coat and they disperse the seeds throughout different regions of the wadis.

We have presented first results of SAM, a spatial model for *Acacia* population dynamics in arid environments discussing a case study. SAM summarizes the actual knowledge of the population dynamics of *A. raddiana* in the Negev on the basis of field investigations. Most parameters are quite well known, but some are only estimates, requiring long-term field studies. Hence, at present, the SAM model allows only for qualitative results. Nevertheless, investigating different scenarios, we gained a further understanding of the influence of the road on the population dynamics of *A. raddiana*.

SAM can be run on any wadi. It needs data on the spatial course of the wadi and the actual population distribution. This model is currently being expanded towards the consideration of other factors that may influence the population dynamics of *A. raddiana* such as browsing by herbivores or geomorphic features of the wadi. SAM will be developed into a management tool that allows case studies that address questions such as 'Should we build the road on location route A or B?' or 'How many camels do we need to compensate the negative impact of a road?'. As a step towards this goal, SAM will be linked to a geographical information system (GIS) providing geomorphological data.

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3.7 Link to the following chapter

In the discussion of Chapter 3, it has been said that SAM was meant to be expanded towards the consideration of geomorphological wadi features in order to develop the model into a management tool that allows us to conduct case studies. Therefore, I planned to link SAM to a geographical information system (GIS) providing geomorphological and remotely sensed data. This linkage between model and GIS was one of the reasons for the spatially-explicit design of SAM.

GIS and remote sensing are techniques of increasing importance to modelers, but are still far from being well-known to all of them. Furthermore, one purpose of dissertations is to introduce other students and colleagues to (new) methods. Therefore, I decided to give a quite extensive introduction to GIS (Chapter 4.2.2) and remote sensing (Chapter 4.2.3) with respect to ecological modeling. Then, I analyze the available data on wadi morphology and investigate the relationship between wadi morphology and actual tree distribution. The identification of a clear relationship is an important prerequisite for the implementation of a link between SAM and GIS, because it means that wadi morphology is indeed a determinant of the spatial population dynamics of *Acacia* trees.

In Chapters 2 and 3, the location (and size) of trees has been measured directly in the field (by D. Ward). Another possibility to determine tree distributions would be the analysis of remotely sensed data. In Chapter 4, I will investigate whether this method is more efficient than a direct measurement in the field.

Reflections on linking a spatially-explicit model of Acacias to GIS and remotely-sensed data¹

4.1 Abstract

The distribution of *Acacia* trees in the Negev desert is dominated by landscape features. Because of the arid climate, the trees are largely restricted to ephemeral river beds (wadis). We assume that the establishment and survival and thus the density of trees within the wadis is influenced by the morphology of the wadis.

SAM, an existing model of the population dynamics of *A. raddiana* is spatially-explicit and has been constructed in a way allowing us to link the model to Geographical Information System (GIS) containing data on wadi morphology and spatial tree distribution. Currently, the model considers wadi morphology in a very simple way only and spatial tree distributions are mapped in the field. A linkage to GIS would be desirable, because, in the Negev, morphological data are available in the form of a GIS only and a linkage would allow us to initialize and parameterize the model in an effective way and to run the model for different wadis. The latter would facilitate the study of applied management aspects. These aims are followed on basis of readily available GIS and remotely-sensed data.

We give an introduction to the basic principles of GIS and remote sensing with respect to the specific aims of our study. In order to find ways to relate the population dynamics of *A. raddiana* to wadi morphology, we compare the wadi morphology characterized by wadi width, slope, and curvature to the current tree distribution based on two study sites. However, based on the data currently available to us, there was no relationship between wadi morphology and tree distribution and therefore we preliminarily retreat from the idea of extending the SAM model with an explicit morphological component. A regression analysis relating a vegetation index derived from satellite images (NDVI) to the tree distributions in our study sites shows a weak correlation between the two. Several possibilities for improving the relationship are discussed. However, these methods would considerably increase the time used for image analysis. Therefore, we conclude that it is more effective to measure the tree distribution directly in the field.

4.2 Introduction

4.2.1 Aim

SAM (Spatial Acacia Model) is a spatially-explicit simulation model of the population dynamics of *Acacia raddiana* in the Negev desert of Israel (Wiegand *et al.*, in press, Chapter 2 of this thesis). The main aim of the model is to gain an understanding of the processes occurring during the life cycle of *A. raddiana*, to put them into a conceptual framework, and to investigate their relative importance to the long-term survival of *A. raddiana*. An understanding of the population dynamics regarding the long-term survival of these tree populations is of special interest, because these ecologically important trees (Danin 1983) are believed to be declining on

¹Authors: K.Wiegand, H.Schmidt, F.Jeltsch & D.Ward. A combination of a summary of Chapter 2 and the Methods, Results, and Discussion of this paper has been submitted to *Folia Geobotanica*.

a large scale (Ashkenazi 1995). However, further to the general understanding of the problem, it would be desirable to be able to facilitate management decisions concerning particular populations in certain conditions. For example, management measures may need to be developed for a tree population that is threatened by the negative impact of a nearby road (cf. Wiegand *et al.* 1998, Chapter 3 of this thesis).

The distribution of *A. raddiana* in the Negev is dominated by landscape features. Because of the arid climate (mean annual rainfall: 20 - 100 mm) they are largely restricted to ephemeral river beds (wadis). After rain, run-off water from surrounding slopes flows through the wadis for several hours, and percolates into the soil. The amount of water stored in this habitat is much greater than in other habitats (Tadmor *et al.* 1962) and makes the survival of trees possible. The specific morphology of a particular wadi determines the distribution of both water and seeds, because the seeds lying beneath trees are washed away by floods. The wadi morphology determines where the seeds get deposited, if they will be supplied with sufficient water for germination and establishment, and if water will be sufficient for adult survival. In other words, the morphology is important to the distribution of establishing trees within the wadi bed and to the performance and survival of trees in specific locations. Thus, if one wants to apply the SAM model to a specific wadi, the morphology of that wadi has to be taken into account. Furthermore, the actual tree abundance and distribution needs to be known in order to make predictions for the future development of that wadi. However, it would be desirable to avoid intensive field studies prior to each simulation experiment. Therefore, we investigate the possibility to use information on wadi morphology and tree distribution from more-or-less readily available GIS and remotely-sensed data. In the following, we will give an introduction to the basic principles of GIS and remote sensing with regard to the idea of linking the grid-based SAM model to such data. A complete linkage would include an initialization of the tree distribution based on remotely sensed data, a determination of the wadi morphology, and the revision of some model rules (e.g. seed distribution, germination) towards an explicit consideration of the wadi morphology by these rules. Firstly, linking the model to remotely sensed data makes sense if the determination of the tree distribution is more effective than a direct measurement of tree locations in the field. Therefore, we analyze remotely-sensed data in order to find out if they allow us to determine the tree distributions effectively. Secondly, if wadi morphology is as important as suggested above, we should be able to find relationships between wadi morphology and actual tree distribution. These relationships would indicate to us how to consider wadi morphology in the model rules. Therefore, we analyze topographic wadi characteristics with respect to the actual tree distribution. The next step would be to revise the model rules. However, as we can not find the relationship between wadi morphology and tree distribution, there is no need to take this final step.

4.2.2 Geographic Information Systems (GIS)

A GIS is an organized collection of computer hardware, software, geographic data, and personnel designed to efficiently capture, store, update, manipulate, analyze, and display all forms of geographically-referenced information (Environmental 1995, see also Bartelme 1995, p.12-13). GIS are a further development of maps. A map is an abstract representation of the physical features of a portion of the Earth's surface graphically displayed on a planar surface. Maps typically emphasize, generalize, and omit certain features from the display to meet design objectives (e.g. railroad features might be included in a transportation map but omitted from a highway map; Environmental 1995). A main idea behind the development of GIS is the aim not to start all over again if one wants to display other features or if just some details have changed

with time (Stahl & Henneberg 1997). Thus, historically, the development of GIS has been motivated by the improvement of the efficiency in storing and displaying information. Due to the high computational demands, GIS is a very young discipline with the first applications dating back to the 1970's (Bartelme 1995).

GIS store both locational and attribute (feature) data of the objects under consideration. The association of the attribute data with the locational data is usually done by using relational database management systems (RDBMS). The basis of a RDBMS is the collection of objects described by the same attributes into 'entities'. A RDBMS can then be thought of as a set of tables, where the rows are entities (e.g. represented by an identification number) and the columns are attributes (e.g. name, weight, height,...) of these entities. RDBMS have the capability to recombine the data items from different files (tables), providing powerful tools for data usage. (Bailey & Gatrell 1995; Environmental 1995).

GIS generally use one or both of two types of data formats: vector and grid formats. Vector formats are build upon points, lines, and areas to which attributes are assigned. In the present context, the grid formats are of specific importance. Grid formats subdivide the area under consideration into a mosaic of subareas, which in most systems are square 'grid cells' of the same size. The attributes are then assigned to the grid cells. A special form of grid formats are Digital Elevation Models (DEM). These DEMs are raster representations of continuous variables (e.g. elevation) over a two-dimensional surface, usually referring to the surface of the Earth (Bartelme 1995; Environmental 1995). An alternative to the regular raster of DEMs are Triangulated Irregular Networks (TIN). In a TIN model, the data sampling points are connected by lines to form triangles with a plane surface defined by the elevations of the three corner points. Small triangles are used to describe terrain that is rugged and larger triangles to describe flatter terrain. Altogether, the triangles build a continuous mosaic surface (Zhou 1998). However, the use of DEMs and TINs is often closely interlinked. For example, a common method to generate DEMs of the Earth's surface is to digitize the contour lines of topographic maps. Instead of directly converting contour lines into a grid, a TIN is calculated and subsequently converted into an elevation grid (DEM). This is done, because direct interpolation procedures from contour lines have a low performance (Radeloff *et al.* 1997).

A very common application of DEMs is the generation of slope (maximum change in elevation between the focus and the 8 neighboring cells) and aspect (direction of normal vector in degrees clockwise from North) information. A more sophisticated application is the derivation of drainage networks, including the determination of watersheds and streams. A watershed is an attribute of each point, which defines the region upstream of that point. The delineation of watersheds from DEM data-base is based on the assumption that water follows the steepest downhill path. Thus, after assigning a flow direction to each cell by determining the lowest of the eight neighboring cells, a watershed is determined as the set of all cells draining through a given cell. A stream is a (one-cell-wide) line of cells whose flow accumulation exceeds a specified upstream drainage area threshold. The procedures being developed for determination of watersheds and streams have to face many problems. A common problem is the occurrence of depressions (areas surrounded by higher elevation values only, often caused by data errors) corrupting the algorithms designed to extract the drainage network. Furthermore, the grid resolution of the DEM data profoundly influences both the spatial pattern and the frequency distribution of derived topographic attributes. Another problem is the choice of the threshold area defining the streams, because the threshold is critical for the congruence between reality and the stream network derived from a DEM (Jenson & Dominigue 1988; Moore *et al.* 1991 and references therein; Gallant & Hutchinson 1996; Maidment 1996; Martínez-

Casasnovas & Sturmer 1998; Zhou 1998).

GIS are not just tools for the storage, retrieval, and display of geographic information, but offer also analytical capabilities. However, for example in the field of statistical spatial analysis, these capabilities are not yet as sophisticated as desirable (Bailey 1994). Even though some GIS offer a programming language (e.g. Arc Info Macro Language AML of Arc Info) that enables the user to write his/her own modules, it would be desirable to have ready modules for most standard methods. An overview of statistical spatial analysis techniques, the potential benefits in linking such techniques to GIS, and the current availability of these techniques in different GIS packages is given by Bailey (1994), see also Ding & Fotheringham (1992) and Goodchild (1993). Currently, this is more of interest to people working mainly with(in) GIS, because their possibilities are gradually expanded. Modelers will still find it easier to write their own modules for spatial analysis in their 'daily-use' environment than to invest the time to acquaint themselves with a complex GIS package and then use just a few routines.

Another branch of further development and expanded application of GIS is the combination of dynamic modeling and GIS. At a first glance, it seems easy to link grid-based GIS and grid based simulation models, because of their common (grid) philosophy. However, an as-yet insufficiently-solved problem is the lack of interfaces for the exchange of data between different GIS packages or between GIS and common programming languages as C++ (Stahl & Henneberg 1997). In 1994, a trade association, The Open GIS Consortium, was founded in order to generate a standard for spatial data exchange (Gardels 1996; Open GIS Consortium 1998). Furthermore, specific methods are being developed for the generic data exchange between simulation models and GIS, for example methods for individual-based (DeAngelis *et al.* 1998; Gross 1998) or hydrological models (Djokic *et al.* 1996). There are also solutions found by specific GIS software. For example, GRASS and MapInfoProfessional allow programmers to integrate modules of these packages into applications written in programming languages as C++. However, only a few studies have taken advantage of this possibility (e.g. Baker *et al.* 1991). Currently, GIS data is mostly used to parameterize simulation models while the very simulation takes place outside the GIS (e.g. Coughenour 1992; Akcakaya *et al.* 1995; Liu *et al.* 1995; Akcakaya 1996; Rushton *et al.* 1997).

However, there are also some models developed within GIS packages which provide their own object oriented programming language (e.g. AML, e.g. used by Yarie 1996, Wu 1998). Nevertheless, modeling within GIS is problematic. Programs are very slow, because grids are always updated on disk instead of storing them temporarily in memory. Another major drawback is the current philosophy used to update cells. Cells sequentially become focus cells, based on the state of the focus cell and the neighborhood calculations are performed, and then the state of the focus cell is changed. Therefore, if one wants to model seed distribution of a plant, it is impossible to focus on the cell containing that plant and distribute the seeds to the neighboring (not focused) cells. Instead, it is necessary to calculate, at each location, the plants that are contributing seeds to that location (Slothower *et al.* 1996).

Returning to the specific case of linking the SAM model to morphological data, we had to decide what kind of data we needed and how to get it. The most basic information is the wadi area within which the population dynamics of *Acacia* trees will be followed. Unfortunately, the delineation of watersheds and streamlines in a DEM is inadequate, because a streamline is located within a riverbed which itself is located within a watershed, but the riverbed is not identical to either of the two. Therefore, we had to use a different approach to identify the wadi area (see below). Further morphological features of interest are the width and the slope of the wadi bed and the complexity of channels within the wadi. All of these features determine the

water velocity. Low water velocity allows more water to percolate into a given soil area, and more seeds to become deposited. While the spatial variability of the wadi width and complexity is rather high, the wadi slope is relatively constant (pers. obs.), emphasizing the need for information on wadi width and complexity. While the wadi width can be derived from the wadi area, we tried to deduce the complexity of the channel network within the wadi from a DEM which is available at a scale of 25 m * 25 m * 10 cm (see below). The within-wadi morphology is variable over time (Akhtar & Kuschetzki 1990), but these changes should be moderate only. Therefore, it was no major drawback that the DEM is available for a certain point in time only. However, the availability of just one DEM means that there is no point in maintaining the communication between GIS and SAM model. Instead, the DEM data was planned to be used for model initialization and revision of model rules only.

What are the possibilities provided by the SAM model for linkage with GIS data? The spatial units of SAM are cells. Each cell represents an area of 5m * 5 m, corresponding to the typical canopy size of an adult tree. 16 cells are combined into a supercell. While the single cells have been designed to store information on the number of seedlings, trees, dead trees, and seeds, are the supercells meant to contain information on morphological attributes of the wadi under study. In Wiegand *et al.* (in press; Chapter 2 of this thesis) the supercells administer the biological attributes *seed attractiveness* (a 'seed attractive' supercell will contain more seeds after a seed distributing flood event than 'unattractive' supercells) and *density of safe sites* within the 20m * 20 m area represented by each supercell. These biological properties are associated with wadi morphology, but so far (Wiegand *et al.* in press; Chapter 2 of this thesis) these associations were based on plausible assumptions. Now, the idea was to establish (quantitative) relations between these biological properties and morphological data (see below). Furthermore, we needed to link the model with the morphological data. This would have been fairly easy; as SAM can read in a ASCII table containing for each supercell the locational coordinates and the attributes of interest (e.g. slope of supercell). To summarize, we wanted to use data on wadi morphology and to use these data to describe spatially-explicit, biologically meaningful characteristics of the wadi to be used for the simulation of the population dynamics of *Acacia* trees. Furthermore, we wanted to take the initial spatial distribution of the trees from remotely-sensed information. This would have enabled us to run our model for any location by linking the model to the respective morphological data and by initializing the tree distribution based on remotely-sensed data of the chosen wadi.

4.2.3 Remote Sensing

Remote sensing is the collection and interpretation of information about an object without being in physical contact with it (Weissel 1996). One prominent example having many applications is spectroscopy of radiation in the visible and Near-InfraRed (NIR) segments of the electromagnetic spectrum (e.g. Foley *et al.* 1998 and citations below). This technique is based on the fact that certain materials reflect solar energy differently than other materials. It is often possible to identify objects because of their characteristic reflectance properties. For example, the reflectance characteristics or 'signature' of a healthy Oak leaf is shown in Figure 4.1. Chlorophyll absorption dominates in the visible (0.4 - 0.7 μm), removing both red and blue reflectances, leaving green (0.50 - 0.58 μm) as the dominant spectral wave range. The sharp rise in reflectance at 0.7 μm , continuing well beyond 1.1 μm , is largely the result of light being reflected by the walls of multiple cells (mesophyll cells). At longer wavelengths, absorption by pigments and cellular matter (protein, lignin, and cellulose) are characteristic (NASA 1998).

We are especially interested in satellite remote sensing, i.e. the collection of multispectral

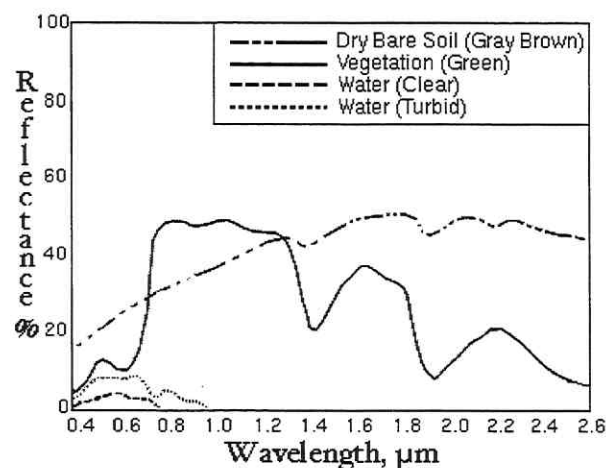


Figure 4.1: Spectral wavelengths of various Earth materials. Taken from NASA (1998).

reflectance data of a part of the Earth's surface by sensors mounted on satellites. However, much of the following considerations are also valid for data retrieval with ground based and airborne sensors. For example, the Thematic Mapper (TM) is a sensor used on a series of EOS satellites, called Landsat, acquiring seven bands of data from the visible through the thermal infrared spectral regions. Bands 3 and 4 cover the spectrum from 0.63 to 0.69 μm (visible red) and from 0.76 to 0.90 μm (NIR; Weissel 1996). For each band the reflectance intensity is recorded on a scale from 0 (no reflectance) to 255 Digital Numbers (DN). Each pixel of the images taken by these sensors represents an array of radiometric measurements (one for each band) for a certain location within the observed area (Bailey & Gatrell 1995). Thus, remotely-sensed images are raster-based and can easily be imported into grid-based GIS. The major conceptual difference between GIS and remotely-sensed images is that in remote sensing both locational and attribute information are collected simultaneously, while in GIS these two types of information are usually captured separately and associated with each other by relational database management systems (see above; Bailey & Gatrell 1995).

Remotely-sensed landscapes are multidimensional. The horizontal axis is given by the composition and position of land-cover elements within the landscape. The vertical domain is dominated by factors related to the height relative to the horizontal axis and extends into the atmosphere. Examples are topography, height of trees or other objects, and atmospheric elements as clouds or aerosols. The atmospheric elements which constitute the medium to be passed by the radiation are of special importance, because they may modify the reflectance (see Discussion). The third dimension is the multispectral axis as described above (Quattrochi & Pelletier 1990).

Obviously, remotely-sensed images are taken at different spatial, spectral, and temporal scales depending on the orbit the satellite is moving on and the properties of the sensor. If the spatial resolution is too coarse, signatures from independent objects on the ground are mixed into an aggregate spectral response for a particular pixel. On the other hand, if spatial resolution is too fine, misinterpretations are possible because objects may appear more heterogeneous than they really are (Quattrochi & Pelletier 1990) and analysis of large areas covered by many

images may become a logistical and financial problem (Tucker *et al.* 1985).

How can we learn from this technique about tree abundance and distribution within a specific wadi? The most obvious way is to make use of a vegetation index, that is a number generated by some combination of remote sensing bands that may have some relationship to the amount of vegetation in a given image pixel (Ray 1994). This is a rather cynical definition of these widely used indices that are generally based on empirical evidence, but not so much on basic biology, chemistry, or physics (Ray 1994).

The most common vegetation index is the Normalised Difference Vegetation Index (NDVI), a simple two-band spectral vegetation index computed from red and NIR reflectance exploiting differences in canopy reflectance in red and NIR wavebands to distinguish vegetation from other landscape components (Wessman *et al.* 1997). Returning to Figure 4.1, we see that vegetation has a lower reflectance than soil in the visible red wavelength, and a higher reflectance in the NIR. Thus, visible red radiation is highly absorbed by green plants (by scattering and absorption by photosynthetic pigments) and NIR radiation is strongly backscattered or reflected (by scattering in the absence of absorption; Tucker *et al.* 1986; Green *et al.* 1996; Peters *et al.* 1997). Given the definition

$$\text{NDVI} = (\text{NIR} - \text{red})/(\text{NIR} + \text{red})$$

with NIR and red being the amount of reflection in a band covering visible red and NIR radiation respectively, we find that vegetated areas will generally yield high index values, water will yield negative values, and bare soil will result in values near zero (Figure 4.1; Peters *et al.* 1997).

In the literature, the NDVI has been related to the fraction of photosynthetically active radiation (FPAR), green leaf biomass, Leaf Area Index (LAI), vegetation cover, primary production, biomass, annual aboveground net primary production (ANPP), precipitation, evapotranspiration, canopy structure, plant stress, photosynthetic potential, and chlorophyll concentration (Huete *et al.* 1984; Tucker *et al.* 1985; Tucker *et al.* 1986; Nicholson *et al.* 1990; Nicholson & Farrar 1994; Paruelo & Golluscio 1994; Gamon *et al.* 1995; Paruelo *et al.* 1997; Wessman *et al.* 1997). Many remote-sensing studies have been applied to grasslands due to the apparent simplicity of their structure and physiology (Paruelo *et al.* 1997; Wessman *et al.* 1997). In evergreen vegetation NDVI may not be a reliable estimator of photosynthetic performance, because seasonal reductions in photosynthetic radiation-use efficiency occur without substantial declines in canopy greenness (Gamon *et al.* 1995; Paruelo *et al.* 1997). On the other extreme, deserts and semi-deserts have low ground covers which leads often to problems interpreting satellite derived vegetation indices, because soil background may affect the signals (Graetz & Gentle 1982; Holben 1986; Huete & Jackson 1987; Graetz & Pech 1988; Peters *et al.* 1997, Saltz *et al.* in press). Even though temporal changes of the NDVI are very small in dry regions (Tucker *et al.* 1985), Peters (1997) was able to solve these problems by analyzing relative differences over time. While the soil signal is constant, the vegetation can be identified because of its variable signal in different seasons (Saltz *et al.* in press).

Given this background, the question arises if NDVI is a panacea or just humbug. Due to the fact that the Negev desert is very dry, it is quite possible that we will not be able to apply this vegetation index. However, one has to keep in mind that most studies cited above want to predict primary production whereas our aim is to gain a rough idea of the tree distribution within a wadi. It is not clear, but possible that this will work.

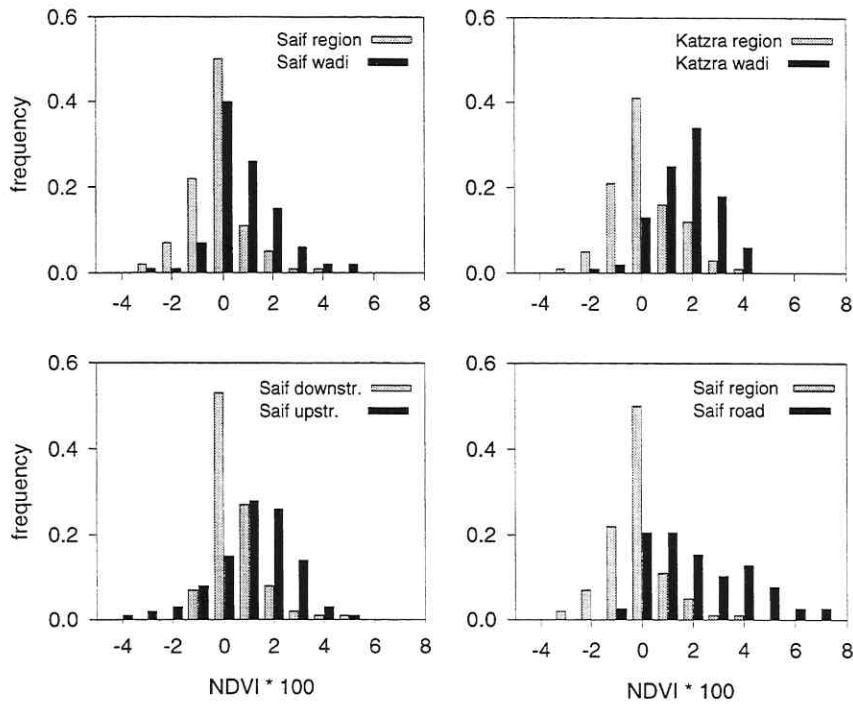


Figure 4.2: Frequency histograms of NDVI for different locations. Histograms shown in graphs are all significantly different (Mann-Whitney) a) Saif region - Saif, $T_{5828,521} = 2362094.500$, $P = <0.001$, b) Katzra region - Katzra, $T_{5543,550} = 2587835.500$, $P = <0.001$, c) Saif upstream - downstream, $T_{324,172} = 52085.500$, $P = <0.001$, d) Saif region - road, $T_{5828,39} = 97581.000$, $P = <0.001$. Median NDVI values: Saif region: -0.005, Saif wadi: 0.004, Katzra region: 0.000, Katzra wadi 0.011, Saif downstream 0.000, Saif upstream 0.009, road crossing Saif: 0.014. Subscripts n, m in $T_{n,m}$ give the sample sizes.

4.3 Methods

We investigated data from 2 study sites, Nahal Katzra and Nahal Saif. These wadis have been chosen, because we know the exact spatial tree distribution within these wadis (Figure 2 in Wiegand *et al.*, in press, Figure 2.2 in Chapter 2 of this thesis) as well as the sizes and moisture conditions of the trees. Trees have been classified into trees with many dry branches (->poor moisture status) and trees with none or few dry branches (-> good ms.). Knowledge on details of the tree distribution is an important prerequisite for the interpretation of the NDVI data. The average yearly precipitation in these areas is 38 mm (Katzra) and 45 mm (Saif), respectively. All rainfall occurs in winter and leads to floods within the ephemeral rivers. Nahal Saif is cross-cut by a road that reduces the amount of floodwater in the downstream section.

For the following analysis, we used two subsets of a Landsat-TM image taken at nadir view

on March 29, 1995, a year with very high rainfall (Katzra: 84 mm, Saif 64 mm), two DEMs, and two topographic maps (1:50000, Survey of Israel). The year 1995 has been chosen for the simple reason that it was the only image available. The DEMs have been created by the Geographical Survey Jerusalem with a resolution of 25m * 25m * 10 cm. The processing and analysis procedures have been performed using ARC/INFO Version 7.0 (ESRI, Redlands, California) and ERDAS-Imagine Version 8.2 (ERDAS Incorporated, Atlanta, Georgia).

First, we digitized the outlines of the two wadi sections and the road cross-cutting Nahal Saif. This was done by following the outlines on the topographic maps with a digitizer. Thus, we had three layers of maps and images: the outlines of the wadis, the DEM, and the remotely-sensed images. We rectified all maps (layers) based on well-distributed ground control points and a transformation first order, i.e. we established the relationship between the coordinates of these images (layers) and topographic coordinates. We converted the wadi area data from a vector format to a grid format and the pixel sizes of the other maps were resampled from 25m * 25m to 20*20m, corresponding to the supercell size in the SAM model.

The satellite images have been used to calculate the NDVI on the 20m * 20 m scale. From the DEM, we calculated the slope of each cell, i.e. the maximum change in elevation between the focus and the 8 neighboring cells (see Table 4.1). Finally, NDVI, slope, and wadi course data have been transformed into ASCII format and a C++ program was written for the reorganization of the data.

One of our aims is to establish relationships between the biological properties and wadi morphology. If there are such relationships (on the basis of the morphological data which was available to us), then these should be reflected by the current tree distribution or maybe also by the NDVI. Therefore, we tested for relations between slope and total vegetation cover (represented by NDVI) by determining the regression of NDVI on slope for both Nahal Saif and Katzra. Furthermore, we plotted the spatial slope and the tree distribution in order to find rules for the relationships between tree distribution and wadi morphology.

To assign a relationship between NDVI and the tree distribution, we calculated the following parameters for each cell from the field data: number of trees per cell, aggregate trunk circumference of all trees in a cell, aggregate ((trunk circumference)²), and aggregate (trunk circumference³). Gamon (1995) found that the NDVI is influenced by dead plant material. Therefore, we calculated a modified version of the three aggregate parameters by halving the circumference of trees in poor moisture conditions. All parameters based on trunk circumference are possible indicators of tree canopy size as observed by the TM sensor. As the original grain size of the satellite images was scaled from 25m * 25 m to 20m * 20 m, each new pixel contains information from neighboring pixels (resampling method Nearest neighbor was applied). Therefore, we recalculated all parameters derived from field data: this time we did not only look at the respective focus cell, but counted the number of trees or summed up the trunk circumferences in the focus and the 8 neighboring cells. We performed (multiple) linear regressions on all parameters and the respective NDVI values.

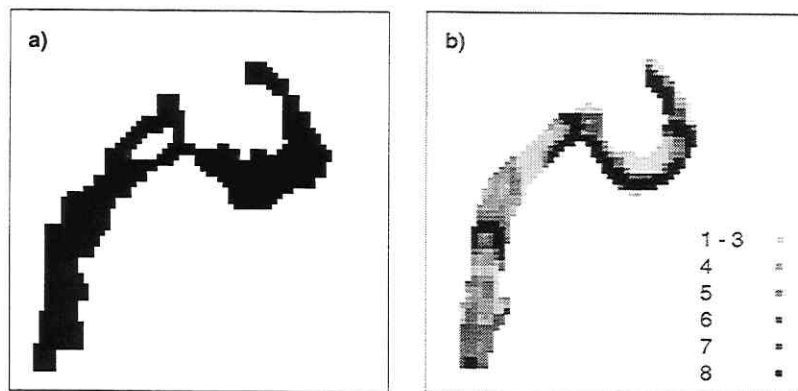


Figure 4.3: Nahal Katzra. a) Wadi area visually approximated on basis of the tree distribution, b) Slope distribution within wadi area. The legend gives slope classes as described in caption of Figure 4.4. The wadi area of b) has been derived from a topographical map (see text). Both details are 1120 * 1120 m in extend; the North is to the right.

4.4 Results

We used two independent definitions of the wadi areas. Firstly, we derived the wadi areas from the known tree distributions and secondly from topographical maps. The wadi areas derived by these two approaches are in qualitative agreement (Nahal Katzra: Figure 4.3). Due to the facts that i) an area estimation based on tree distribution will underestimate the wadi whenever there is a large gap in the spatial tree distribution and ii) the topographic maps give an idealized outline of the wadis, the exact wadi widths deviate from each other. This is especially true for Nahal Katzra, which has a more complex wadi shape than Nahal Saif. The riverbed of Nahal Katzra is surrounded by several rather steep hills, while Nahal Saif flows in largely flat terrain interspersed with some hills (pers. obs.). This is reflected in the distribution of slope classes of the areas around these two wadis (Figure 4.4; median slope class: Nahal Katzra 7, Nahal Saif 6, definition of slope classes is given in Figure 4.4). Within the wadi bed, Nahal Saif has a lower gradient than Nahal Katzra (median slope class: Nahal Katzra 6, Nahal Saif 4). This is not so much due to the overall inclination of the wadibeds, but is caused by the greater ruggedness of Nahal Katzra (the DEM has a height resolution of 10 cm). As expected, the wadi beds are generally more flat than the respective regions (Figure 4.4).

There is no significant correlation between NDVI and slope (linear regression: Nahal Katzra: $r^2 = 0.003$, Nahal Saif: $r^2 = 0.047$). However, we are mainly interested in the relationship

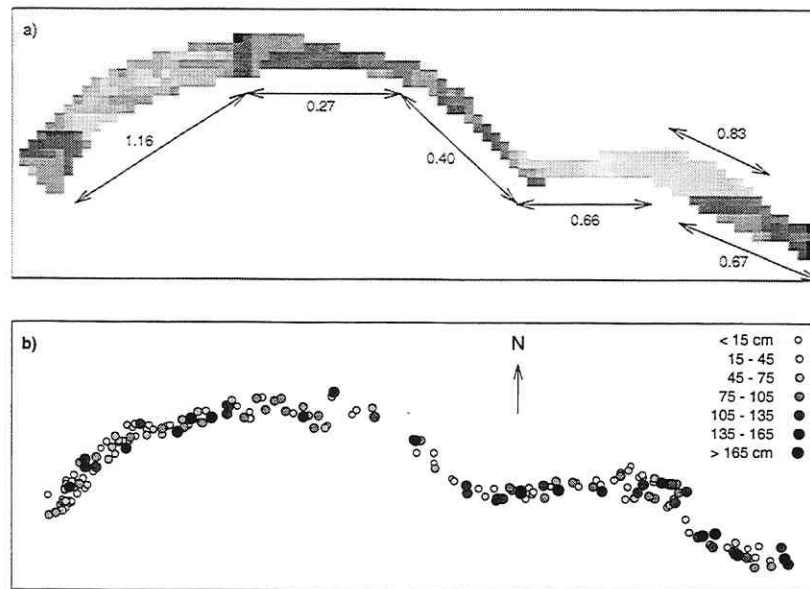


Figure 4.5: Nahal Saif. a) Slope distribution. The legend is given in Figure 4.3. The average number of trees per 20*20m within subsections of the wadi is marked by labelled arrows. b) Tree distribution. The legend gives the trunk circumference of the trees. Both details are 1800 * 600 m in extend.

Saif: wadi 0.004, region -0.005). In Nahal Saif, which is cross-cut by a road, NDVI values are significantly higher in the upstream (0.009) than in the downstream section (0.000) of the wadi bed. The road itself shows very high NDVI values (0.0142) due to sensitivity of the NDVI to dark surfaces (Huete & Jackson 1987, Saltz *et al.* in press).

NDVI, number of trees N (neighborhood included) and aggregate trunk circumference atc (neighborhood included, poor moisture status not considered) were linearly correlated (Nahal Saif upstream: $NDVI = -0.00118 + 0.000504 N + 0.0000255 atc$, $r^2 = 0.179$, $p(N) = 0.171$, $p(atc) = 0.006$; Nahal Katzra: $NDVI = -0.00817 + 0.000722 N + 0.0000125 atc$, $r^2 = 0.133$, $p(N) = 0.108$, $p(atc) = 0.002$) although with a large degree of scatter. Separate linear regressions are shown in Figure 4.6, see also Table 4.1 and show also weak linear relationships for all indicators of tree distribution investigated. For example, the consideration of tree moisture status slightly diminishes the r^2 values and basing the analyses on the focus cells only, clearly worsens the regressions (cf. Table 4.1).

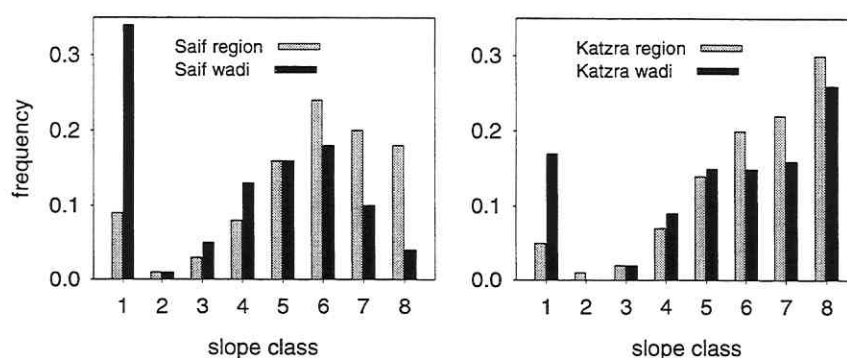


Figure 4.4: Frequency histograms of slope. The slope classes are: 1: $<0.57^\circ$, 2: $0.57^\circ - 1.23^\circ$, 3: $1.23^\circ - 2.66^\circ$, 4: $2.66^\circ - 5.71^\circ$, 5: $5.71^\circ - 12.13^\circ$, 6: $12.13^\circ - 24.89^\circ$, 7: -45° , 8: $>45^\circ$.

between wadi morphology and spatial tree distribution. Therefore, we visually tested a series of hypotheses regarding the relationship between wadi morphology and spatial tree distribution. For example, in wide wadi sections the water will flow slowly, allowing a lot of water to percolate into the soil and leaving behind many seeds, thus resulting in higher tree densities. In Nahal Saif (Figure 4.5), this is true in the leftmost area because this is both the widest and the most densely populated subsection of the wadi. However, in contrast to our hypothesis we find the lowest tree density (0.27 trees/supercell) at an intermediate (instead of the smallest) wadi width. Another hypothesis is that a higher curvature results in more turbulences and thrusts more seeds and more water into the curve, resulting in higher tree densities there. This seems to be true in Nahal Katzra, as tree density is higher in the curved half than in the relatively straight remainder of that wadi (cf. Figure 4.3b and Figure 2.2), but we could not detect a similar relationship in Nahal Saif. Furthermore, we expected higher slope values to represent the greater ruggedness of the wadi bed (note: the resolution of the DEM: $20 \times 20 \text{ m} \times 0.1 \text{ m}$). A greater ruggedness means that there are more little depressions and therefore more puddles that are optimal for tree establishment (cf. Rohner & Ward in press). However, to the right hand side of Figure 4.5 we see a very shallow and a very rugged area containing basically the same tree density (0.66 and 0.67 trees/supercell). Therefore, we could not establish any relationship between wadi morphology and tree distribution.

Typical NDVI values observed in this study range from -0.02 to 0.04. This is similar to the ranges observed by Markham (1986) and by Tucker (1985) in the Sahara and Namib deserts. The negative values are due to the lack of radiometric and atmospheric correction of the images. NDVI values within the wadi beds and in the areas around the wadis ('regions' of 1-2 km² size) are significantly different in both Nahals Saif and Katzra (Figure 4.2). Values are higher within the wadi beds, especially in Nahal Katzra (medians: Katzra: wadi 0.011, region 0.000;

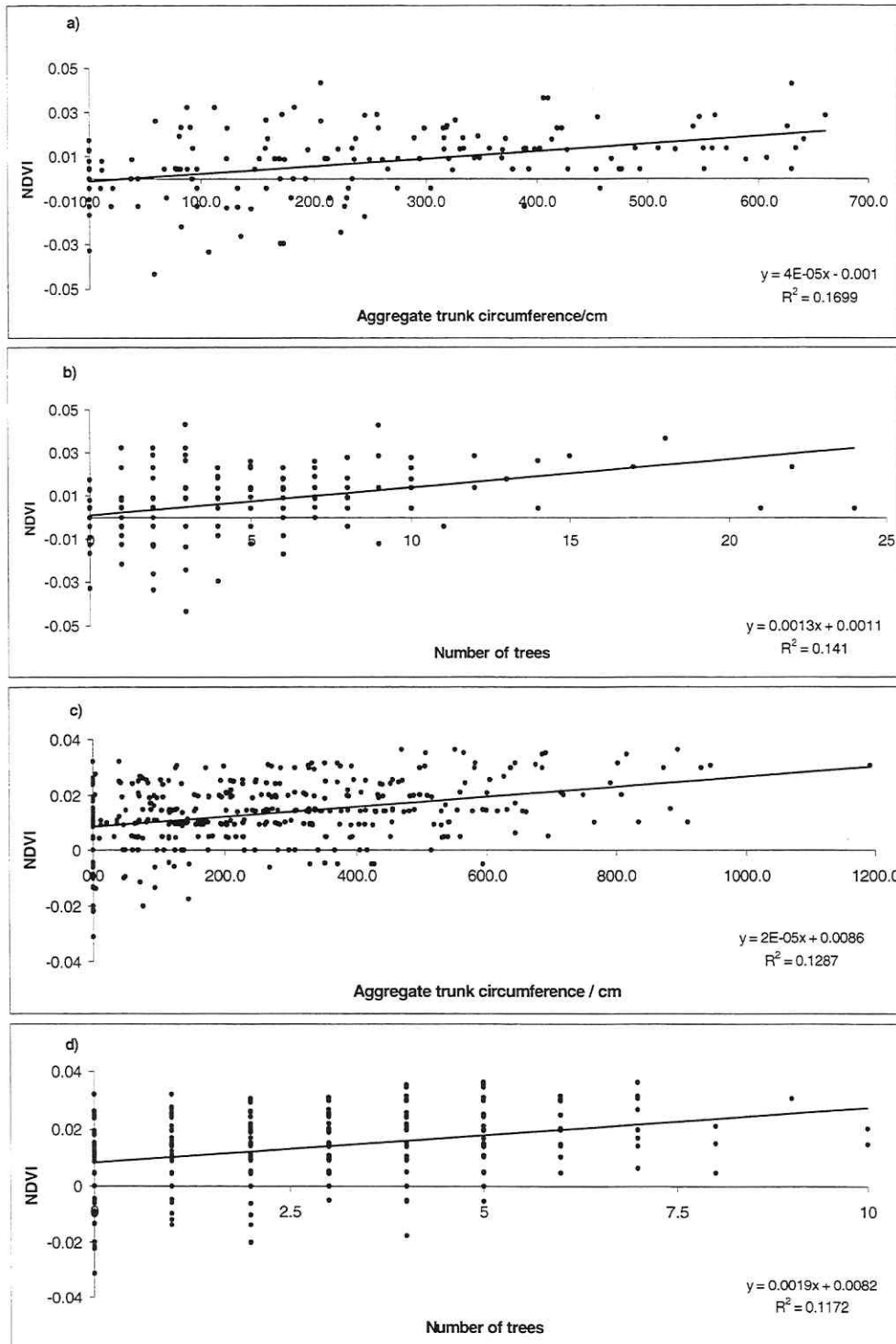


Figure 4.6 (overleaf): Scatter plots of NDVI vs. indicators of tree distribution. a) Number of trees in Nahal Saif upstream, b) Aggregate trunk circumference in Nahal Saif upstream, c) Number of trees in Nahal Katzra, d) Aggregate trunk circumference in Nahal Katzra vs. the corresponding individual NDVI value.

All parameters have been calculated on the basis of the focus cell and the 8 neighboring cells. Nahal Saif downstream has been omitted from the analysis because of the low NDVI values. Furthermore, the first 200 m above the road have been neglected because of the extremely high shrub density in that area (pers. obs.). In Nahal Katzra a group of 11 trees in the northwestern part of the wadi have been omitted from the analysis because of an apparent mismatch between their location as recorded in the field and the satellite image.

4.5 Discussion

The first aim of this study was to investigate possibilities of gaining efficient information on the spatial tree distribution of *A. raddiana* for subsequent initialization of the SAM simulation model. Therefore, we analyzed NDVI data derived from satellite images. We expected the NDVI of a certain image pixel to be related to the total volume of tree canopies in the area described by that pixel. However, the relationship between NDVI and tested indicators of tree distribution were extremely weak. This could be due to the fact that there are also shrubs and annuals growing within the wadis. However, the shrub density is relatively low. Therefore, we believe that shrubs obscure the relationship between NDVI and trees, but we expect the effect to be rather weak. Unfortunately, the satellite image available was taken just after a very wet winter. Therefore, there must have been a high cover of annuals there, worsening the power of the NDVI to indicate the tree distribution. Furthermore, the existence of dead and structural plant material, for example dead trees or dead branches and stems of living trees, might have had a negative influence on our results. We partly tested the influence of dead material by investigating the influence dead branches (expressed as poor moisture status which is associated with many dead branches) on the predictive power of the NDVI (see Table 4.1). However, the effect of the tree moisture status was negligible. Thus, we assume that the few dead trees in Nahals Saif and Katzra were of no importance to our investigations.

The road cross-cutting Nahal Saif reduces the amount of floodwater reaching the downstream wadi section. It is most likely that this leads to lower densities of annuals downstream from the road. However, in our case this does not mean that we can distinguish trees in the downstream section more easily, because trees of the downstream section received less water over many years, leading to deteriorated moisture conditions (in other words to a higher stress) which results in low NDVI values (cf. *Introduction*). Even though the stress of the trees and the reduced density of annuals explain the low NDVI values in the downstream section, we were still surprised by the extremely low NDVI values in that area. It is usually easy to discern areas within and outside wadi beds by means of the NDVI from the image used by us (see Figure 4.2b). However, in most areas of Nahal Saif downstream, the NDVI is as low as in the barely vegetated surrounding areas (cf. Figure 4.2c). Therefore, these trees are either extremely stressed or the percentage cover of the *Acacia* trees is generally too low to be tracked with remotely-sensed data as discussed here.

Several methods exist which could help to enhance the predictive power of the NDVI. A generally applied method is 'ground truthing', that is the collection of information about the actual conditions on the ground in order to be able to establish better relations between remote

Table 4.1: Results of the regression analysis between indicators of tree distribution (x) and NDVI (y) using Nahal Saif upstream section as an example. Nahal Saif was chosen because of the good congruence of the wadi area approximated from the tree distribution compared to the area approximated from the topographic map (cf. Figure 4.3). However, results from Nahal Katzra are of the same order of magnitude. Analysis of Nahal Saif has been restricted to the section upstream of the road, because of the extremely low values in the downstream section (cf. Figure 4.2c). N gives the number of trees, atc^n the aggregate (trunk circumferenceⁿ), consideration of tree moisture status in the regression is denoted by 'yes', and *no. of cells* indicates if the indicators of tree distribution have been determined on basis of the focus cell only (1) or on basis of the focus and the 8 neighboring cells (9).

| parameter | moisture status | no. of cells | regression equation | r^2 |
|------------------|-----------------|--------------|----------------------------------|--------|
| N | - | 1 | $y = 0.0046 x + 0.0048$ | 0.1037 |
| | - | 9 | $y = 0.0013 x + 0.0011$ | 0.1410 |
| atc | no | 1 | $y = 8 \cdot 10^{-5} x + 0.0051$ | 0.0805 |
| | no | 9 | $y = 3 \cdot 10^{-5} x - 0.0011$ | 0.1722 |
| | yes | 1 | $y = 8 \cdot 10^{-5} x + 0.0052$ | 0.0752 |
| | yes | 9 | $y = 4 \cdot 10^{-5} x - 0.0001$ | 0.1699 |
| atc ² | no | 1 | $y = 5 \cdot 10^{-7} x + 0.0062$ | 0.0362 |
| | no | 9 | $y = 3 \cdot 10^{-7} x + 0.0016$ | 0.1158 |
| | yes | 1 | $y = 5 \cdot 10^{-7} x + 0.0063$ | 0.0336 |
| | yes | 9 | $y = 3 \cdot 10^{-7} x + 0.0018$ | 0.1115 |
| atc ³ | no | 1 | $y = 2 \cdot 10^{-9} x + 0.0068$ | 0.0155 |
| | no | 9 | $y = 1 \cdot 10^{-9} x + 0.0035$ | 0.0777 |
| | yes | 1 | $y = 2 \cdot 10^{-9} x + 0.0068$ | 0.0146 |
| | yes | 9 | $y = 1 \cdot 10^{-9} x + 0.0037$ | 0.0735 |

sensing data and the objects observed (Graetz & Gentle 1982; Graetz & Pech 1988). Ground truth data in this study contain the spatial distribution and the moisture conditions of the trees. However, no data on percentage vegetation cover was available at the time the TM images were taken and no measurements of the spectral characteristics of trees, shrubs, grasses and soil, and so on were carried out.

Spectral differences in satellite images are not only due to different target objects, but are also caused by many other factors such as sensor characteristics, viewing directions, illumination (topographic) effects, and atmospheric noises (water vapor absorption and aerosol

scattering). Radiometric calibration of the TM sensor is used to derive quantitative relations between the data collected by the sensor and the Earth's surface and to convert the DNs into more meaningful physical quantities, such as radiances and reflectances. However, satellite measured radiances are modified according to the direction of both solar and view angles, because these are critical for the illumination and the perspective of the 3-dimensional landscape (as seen by the sensor; Jackson & Huete 1991). Furthermore, atmospheric constituents such as aerosols and water vapor modify the reflectances. Therefore, radiometric calibration of the sensor, atmospheric correction, and topographic corrections are usually applied during digital image analyses (Jackson & Huete 1991; Quattrochi & Pelletier 1990; Hill 1993; Nicholson & Farrar 1994; Radeloff *et al.* 1997; Wessman *et al.* 1997).

Another method for improving image quality is the analysis of several images. This can be done in two ways. First, using images taken within a short time period, a composite image can be derived. For NDVI analysis, this is done by selecting the maximum NDVI value for each pixel, which represents a defined time period. This technique reduces directional reflectance and off-nadir viewing effects and minimizes sun-angle and shadow effects (e.g. Holben 1986; Tucker *et al.* 1986; Paruelo & Lauenroth 1995). Satellite images, taken during different seasons, make it possible to estimate and monitor the seasonal variation of vegetation and to separate different vegetation components. In principle, this method is applicable in our study. However, we need to keep in mind the relationship between our aims and the amount of effort required to achieve these aims, particularly when no method is 100% accurate (see below).

As already discussed in the *Introduction*, problems arise from the spatial resolution of satellite images, which are mostly too coarse for the monitoring of sparse vegetation. In our case the spatial resolution of 25 * 25 m is too coarse to allow the correspondence of an image pixel and a single tree. Each pixel may combine information on several plants and in particular on the soil background. As this is a common problem, methods for unmixing of the image pixel have been developed. The linear mixture model is based on the physical assumption that there is no significant amount of multiple scattering between the different cover types, so that the signal measured by the sensor on a given pixel can be considered as the sum of the signals received from each of the constituent cover components weighted by their respective areal proportions within the pixel (Quaidrari *et al.* 1996). The cover components considered are called 'endmembers'. For example, we would use four endmembers: trees, shrubs, annuals, and soil. Knowing the total spectral response within a pixel and the spectral response of the endmembers for at least as many channels than endmembers, we would obtain a linear equation system with a unique solution for each pixel (Smith *et al.* 1990; Wessman *et al.* 1997).

Another possibility for enhancing the predictive power of our NDVI data would be to not scale the image resolution to the SAM model, but to change the resolution of the SAM model. This would avoid the blurring of information due to rescaling from 25 * 25 m to 20 * 20 m. However, we do not expect much improvement from this approach, because it would remove blurring on a small scale, but not change the overall characteristics of the spatial distribution of the NDVI.

Obviously, there is a large range of possibilities for improving our method of deducing the tree distribution from remotely-sensed data. Given the weak relationship between NDVI and tree distribution gained from our currently simple analysis, we probably would have to apply several methods in order to receive satisfying results. However, the time necessary to perform such an intensive image analysis is far beyond the time demand for measuring the spatial tree distribution directly in the field (at least in our specific case). Therefore, we retreat from the idea of initializing the tree distribution of the SAM model with the help of Landsat TM images.

Our second aim has been to deduce information on wadi morphology and to investigate possibilities of integrating the morphological data to SAM. It has been rather easy to gain information on wadi morphology, but the next step is rather tricky. We have to determine the biological significance of the wadi morphology and then to translate the significance into model rules. Our initial idea was that wadi morphology is important to the distribution of establishing trees and to the performance and survival of trees in specific locations. If this is true, there should be a relation between tree distribution and wadi morphology. However, we could not detect such a relationship. This could be because slope, wadi width and curvature do not adequately represent wadi morphology, at least not at the scales investigated by us. On one hand, it is possible that the morphological determinants for seedling establishment operate at a scale of a few centimeters. The distribution of safe sites may well be determined by the existence of a stone whose shade helps to retain soil moisture for a longer time or by small pieces of organic matter contributing to the local nutrient availability. The morphological determinants of the survival of both small and large trees definitely act on larger scales. Nevertheless, chances are high that these scales are clearly below our spatial resolution of 25 * 25 m. On the other hand, it is also quite possible that details of the tree distribution are simply stochastic, while the only features that may explain something about overall tree density on a wadi level are wadi slope, width, curvature and catchment area on a really large scale, because these features determine the amount and flow velocity of the water running through the riverbed. Furthermore, we need to keep in mind, that wadi morphology changes with time (Akhtar & Kuschetzki 1990) and that tree distribution could be determined by the morphological history of the wadi.

Unfortunately, we cannot currently easily test these possibilities, because we do not have historical data, a very fine-scaled DEM, or data on tree distribution for many wadis with different large-scale morphological features. Even though there are no historical data on wadi morphology, in principal it would be possible to collect these spatial data on present morphology. Large-scale morphological data can be derived from the DEMs used in this study, tree densities can be counted in the field, and small scale morphological data could be collected using airborne camera imaging (Chagarlamudi & Plunkett 1993; King *et al.* 1994).

Our plan was to link the SAM model to morphological data; we therefore tried to find a relationship between wadi morphology and tree distribution. While we clearly concluded from the analysis of the NDVI that it will be more effective to collect the data on tree distribution directly in the field (or at most from aerial photographs taken at moderate heights), the conclusions for the study of wadi morphology are not as clear. We will have to weigh up the costs (money, labor) and gains (improvement of the SAM model) of a more intensive study of wadi morphology.

The present study suffers from a problem that is typical to the use of remotely-sensed and GIS data. That is, due to financial constraints, users often have a limited choice of images available to them and often they must rely on published topographic maps and DEMs. As a consequence, the scales of investigation are predetermined by the remotely-sensed or GIS data available. However, the scales of investigation should be determined by the phenomena in question. Unfortunately, the spatial and temporal scales of interest to ecologists are often different to the remotely-sensed or GIS data available (Moore *et al.* 1991; Mack *et al.* 1997). Therefore, the promising idea of 'readily' available data covering large areas may easily turn out to be a fallacy. Even though field studies may be labor intensive, they are often more efficient because the information content of field studies can be targeted more precisely to the needs of the ecologist. This does not imply that remote sensing and GIS technology would be useless to

ecologists. GIS can be tailored to the needs of the question under study and there are many ecological studies successfully applying remote-sensing techniques, but most of the successful studies have been conducted on large spatial scales. However, with increasing resolution of satellite images one can expect that in the near future it will be easier to conduct studies on smaller spatial scales.

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4.7 Link to the following chapter

The aim of this thesis was to gain an understanding of the long-term population dynamics of *A. raddiana* in the Negev desert and to investigate potential management measures. In Chapter 2, a simulation model was developed for this purpose. Furthermore, the model was analyzed thoroughly in Chapter 2. In Chapters 2 and 3, management related aspects, namely the influence of a potential change in climatic conditions, the influence of roads cross-cutting wadis on the population dynamics of the *Acacia* trees, and the use of large mammalian herbivores as a management measure counteracting these negative effects, were investigated. In Chapter 4, the possibilities of linking the model to GIS were explored. Such a linkage would have led to the construction of a management tool making it possible to run the model on any specific wadi. However, in Chapter 4, we could not detect any important effects of site-specific wadi morphology on tree population dynamics. A strong relationship between site specific wadi morphology and population dynamics would have been an important prerequisite for a linkage between model and GIS. Given that this prerequisite was not fulfilled, I retreated from completing the linkage. Is this a major drawback? No, because the fact that I could not determine a relationship between wadi morphology and *Acacia* population dynamics presumably means that site-specific parameters are not very important to the tree dynamics. Otherwise, results of investigations conducted for specific wadis would have been valid for that specific site only. Therefore, and because I could show in Chapter 2 that the exact initial tree distribution both in terms of tree positions and tree sizes, as well as model rules referring to space (e.g. the heterogeneous distribution of safe sites) are not important for the long-term survival of the *Acacia* trees, model investigations conducted for a certain location are not bound to the specific study site, but transferable to the entire Negev.

Given the urgency of the *Acacia* decline problem, it is important to use every piece of information to learn more about the factors and processes driving the population dynamics of *A. raddiana*. This is the idea behind Chapters 5 and 6. In Chapter 6, I will use the spatial distribution of *A. raddiana* within the wadibeds in terms of clumping and even spacing while in Chapter 5 I focus on size-frequency distributions. Starting from the model version described in Chapter 2, I will develop model scenarios in order to learn from these scenarios about the processes shaping size-frequency distributions and furthermore, from a comparison between simulation results and field data, I improve the knowledge on the processes acting in the field. For example, we will find out if recruitment has always been a rare event.

I would like to mention some details of Chapter 5. Tree mortality has been modeled differently in Chapters 2 and 3. In Chapter 3, I employed an age-dependent mortality regime, while mortality was independent of age in Chapter 2. Initially, I did not know which of these two plausible hypotheses was valid; this point will be clarified in Chapter 5. Furthermore, tree growth was based on data from Kenya until this point. At the time investigations of Chapter 5 started, field information from the Negev had been collected and was used to model *Acacia* growth more realistically. Only this way is it possible to compare tree size-frequency distributions observed in the field and produced by the model as mentioned above. The new knowledge on tree growth will also serve to tackle the question "How old are these trees?".

From snap-shot information to long-term population dynamics of *Acacias* by a simulation model¹

It is wholly unrealistic and very dangerous to assume any relation between the size of trees and their age, other than the vague principle that the largest trees [...] are likely to be old.' (Harper 1977)

5.1 Abstract

The African Acacia species *A. raddiana* is believed to be endangered in the Negev desert of Israel. The ecology of this species is not yet well understood. The main idea of our study is to learn more about the long-term population dynamics of these trees using snap-shot information in the form of size frequency distributions, because these distributions are highly condensed indices of population dynamics acting over many years. In this paper, we analyze field data on recruitment, growth, and mortality and use an existing simulation model of the population dynamics of *A. raddiana* (SAM) to produce contrasting scenarios of recruitment, growth, and mortality that are based on field evidence. The main properties of simulated as well as observed tree size-frequency distributions are characterized with Simpson's index of dominance and a new index of disorder. Finally, by running the SAM model under the different scenarios, we study the effect of these different processes on simulated size frequency distributions (pattern) and we compare them to size distributions observed in the field, in order to identify the processes acting in the field.

Our study confirms rare recruitment events as a major factor shaping tree size frequency distributions and shows that the paucity of recruitment has been a normal feature of *A. raddiana* in the Negev over many years. Irregular growth, e.g. due to episodic rainfall, showed a moderate influence on size distributions, and has the potential to be a largely overlooked factor in regions with higher rainfall than in the Negev. Finally, the size frequency distributions observed in the Negev reveal the information that, in this harsh environment, tree size (age) plays a negligible role in the mortality of adult *A. raddiana*.

5.2 Introduction

In Africa, the genus *Acacia* is widely distributed (Ross 1981) and of great ecological and economic importance. *Acacia* trees are known to ameliorate the soil near their bole, thus increasing the density, and altering the composition of plants below their canopy compared to the tree interspaces (Belsky *et al.* 1989; Weltzin & Coughenour 1990; Belsky *et al.* 1993; Milton 1995; Rhoades 1995). Furthermore, they provide food, shade, shelter, perch, nest, and roost sites to many animals (Leistner 1967; Ashkenazi 1995; Milton 1995). Their seed pods are of high nutritive value and an important food source to wild and domestic browsers that is much sought after when grass is short in supply (e.g. Gwynne 1969; Halevy 1974; Coe & Coe 1987; Hauser 1994). Additionally, Acacias are used for fuel and timber wood (Obeid & Seif

¹Authors: K. Wiegand, D. Ward, H.-H. Thulke & F. Jeltsch. A similar version will be published in *Plant Ecology*

1970; Ashkenazi 1995; Miller 1996) and as medicinal plants (Boulos 1983; Ashkenazi 1995). According to Brennan (foreword to Ross 1979) "there is probably no group of trees and shrubs in Africa that can rival the *Acacia* spp. in their combined importance of their ecology and extent of their geographical range".

In some regions, there is a fear that the abundance of these trees might be declining on a large scale (Young & Lindsay 1988; Mwalyosi 1990; Ashkenazi 1995). For example, after reports of high mortality and low recruitment in Israeli *Acacia* trees, a series of field and simulation studies on the population dynamics of these trees have been conducted (Peled 1988; Peled 1995; Ward & Rohner 1997; Rohner & Ward 1998; Wiegand *et al.* 1998, Chapter 3 of this thesis). However, it takes many years of field research to improve the understanding of the population dynamics of long-lived trees and the present ecological knowledge is rather poor (New 1984). Possible keys to gain rapid insights into the long-term dynamics of Acacias are size frequency distributions, because they are the result of recruitment, growth, and mortality (Kirkpatrick 1984) acting over many years. Indeed, there is a large body of literature on size frequency distributions reporting mostly irregular, *Acacia* tree-size patterns. Many authors hypothesize periodic tree regeneration as the cause for irregular size distributions observed by them (Mwalyosi 1990; Prins & Van der Jeugd 1993; Kiyapi 1994; Sinclair 1995; Ward & Rohner 1997; Rohner & Ward 1998). Others discuss high mortality due to disturbances, e.g. caused by elephants at very high population densities or by human harvesting (Pellew 1983; Walker *et al.* 1986; Ruess & Halter 1990; Shackleton 1993; Dublin 1995), or irregular tree growth due to an episodic rainfall regime or growth suppression by herbivores (Grice 1984; Ruess & Halter 1990; Grice *et al.* 1994; Rohner & Ward 1998).

Size frequency distributions are highly condensed indices of population dynamics acting under variable biotic and abiotic conditions over many years. In field studies, it would take many years to identify relationships between population processes and size distributions. Consequently, most authors mentioned above are merely speculating on the factors causing size frequency distributions different from a monotonically declining shape. Therefore, several mathematical models of plant growth have been developed for the study of the connection between plant growth and size frequency distributions. The questions that have been studied are: "What kind of size distribution results from a certain mechanism?" (Pellew 1983; DeAngelis & Huston 1987) "Which mechanisms can cause a certain type of size distribution?" (Huston 1986; Huston & DeAngelis 1987; Grice *et al.* 1994), and "Under which conditions are certain mechanisms likely to be important?" (Huston & DeAngelis 1987). Typically, these models focus on processes such as intraspecific competition or different size-dependent growth regimes, but largely ignore the effects of mortality (but see Van Sickle 1977) and recruitment. Furthermore, they mostly investigate even-aged populations and just two of the modelling studies refer to Acacias (Pellew 1983; Grice *et al.* 1994).

In this paper, we study the long-term population dynamics of *Acacia raddiana* (considered a sub-species of *A. tortilis* by Ross 1979) in the Negev desert, Israel, by a combined field study and modelling approach. From field data, we generate biologically possible model scenarios of recruitment, growth, and mortality of the *Acacia* trees. Running the model under the different scenarios we gain a better understanding of the effects of different processes on pattern (i.e. simulated size frequency distributions), and we are able to assign the underlying processes to the particular pattern observed in the field (i.e. observed size frequency distributions) by comparing observed and simulated size frequency distributions.

5.3 Materials and Methods

5.3.1 Site description

The main study site is a 1.5 km-long section of the ephemeral river (wadi) Nahal Katzra (35° 08' E, 30° 32' N) which is located near the Arava valley. The wadi has been subjected to intensive field studies since 1994 (Ward & Rohner 1997; Rohner & Ward 1998). The reason for restricting the study to the wadi area is that *A. raddiana* grows only inside the wadi bed. Mean annual precipitation is 38 mm, most of which falls during winter months (October - April). In this wadi, trees suffer relatively high investigations of the semi-parasitic mistletoe *Loranthus acaciae* and are frequently browsed by domestic (goats, camels, sheep) and wild (gazelle *Gazella dorcas*) mammalian herbivores. Additional studies have been carried out in further sites throughout the Negev (Nahal Saif, Nahal Bitaron, Nahal Roded, Shezaf, and Hai-Bar; see section *Mortality*).

5.3.2 SAM model description

SAM is a stochastic, individual-based, spatially-explicit simulation model developed for the study of the population dynamics of *A. raddiana* in the Negev. It is based on tree size in terms of trunk circumference and not on age, a quantity almost impossible to measure in the field. A description of the model structure is presented in the following text with further details available in Wiegand et al. (in press; Chapter 2 of this thesis). For biological information, see also Ward & Rohner (1997) and Rohner & Ward (1998). The model version described in this section 5.3.2. is exactly the same as used in Chapter 2.

Figure 5.1 shows the causal structure of the factors and processes currently considered by the SAM model; further contrasting model scenarios are given below. Size frequency distributions of populations of *A. raddiana* are mainly determined by the establishment of tree seedlings and the growth and mortality of trees (Figure 5. 1).

Recruitment of trees is initially influenced by germination and seedling mortality. On one hand, a prerequisite for germination is the availability of seeds and moisture. Sufficient moisture depends on the occurrence of winter floods, which in turn depends on the amount of precipitation, and also on the wadi morphology. Based on an evaluation of rainfall data with respect to the biology of *A. raddiana*, SAM distinguishes between 'good', 'intermediate', and 'dry' years (probability of occurrence: 23%, 61%, and 16%, respectively) and allows for germination in 'safe sites', i.e. optimal water and shade conditions, only. The other prerequisite for germination, the availability of seeds, is determined by seed production which is a result of the size, the moisture status, and the degree of infestation by parasites (i.e. mistletoes) of the seed-producing trees. More explicitly, trees larger than 15 cm may already reproduce, but full maturity is reached at a trunk circumference of 45 cm. As we define a tree's moisture status as 'poor' when many (>50%) branches are dry, SAM reduces the seed crop produced by a tree proportionally to the canopy volume unavailable to seed production because of dry branches or occupation by mistletoes. However, only those seeds produced by the tree that are unharmed by seed predators (i.e. bruchid beetles) are available for germination. In the Negev desert, bruchids infest up to 98% of the seed crop of *A. raddiana*. The amount of seeds available at a specific location is altered by seed dispersal by flood events and large mammalian herbivores consuming *Acacia* pods. The resulting distribution of *Acacia* seeds is qualitatively modelled via the definition of 'normal' and 'seed attractive' areas. On the other hand, tree establishment also depends on seedling mortality which is higher for smaller seedlings and in years with lower water availability.

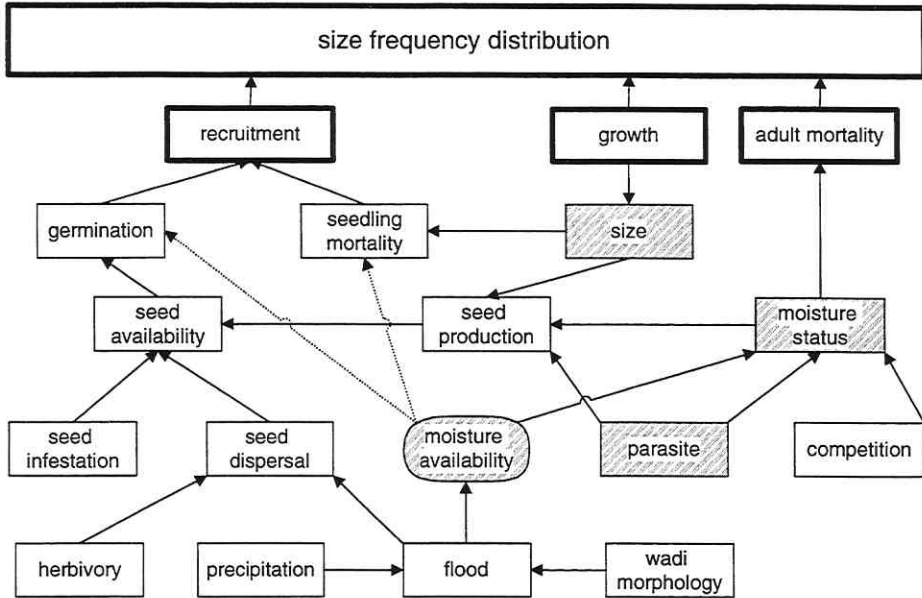


Figure 5.1: Graphical model of the factors structuring the population size-frequency distribution of *A. raddiana* in the Negev. Arrows point in the direction of the respective effects. Alternative scenarios: Dashed arrows indicate relations that are removed in the ‘constant recruitment scenario’. Hatched factors influence growth in the ‘variable growth scenario’. Further explanations are given in the text.

Once a tree has established we assume a constant growth rate, resulting in changes of the size of the tree. Due to the current lack of knowledge on the growth of *A. raddiana* in the Negev, we based our estimates on data for *A. tortilis* from Kenya (Kiyiapi 1994). Finally, the mortality of adult trees depends mainly on the moisture status of the trees. The moisture status may deteriorate if moisture availability is low and the degree of infestation by parasites (i.e. mistletoes) high. In SAM, infestation by mistletoes (*L. acaciae*) is simulated in terms of the proportion of the canopy covered by these parasites.

In the following sections, we will analyse field data on recruitment, growth, and mortality and derive contrasting modelling scenarios suitable for gaining an understanding of the roles these processes play in the evolution of size frequency distributions. For an overview of the model scenarios see Table 5.2.

5.3.3 Recruitment

In our comprehensive studies on *Acacia* trees in 75 populations in the Negev (Rohner & Ward 1997; Ward & Rohner 1997; Rohner & Ward 1998), we observed only 3 germination events in the entire Negev over the years 1994 - 1998 (1995: Hai-Bar, 1997: Nahal Zeelim, Nahal Saif). The extreme paucity of *Acacia* seedlings suggests that germination and establishment are rare events in this harsh environment and that they take place only if rainfall and temperature are favorable. However, it is not clear whether this paucity of seedlings is a normal feature or a sign of decline (Ashkenazi 1995). Therefore, we want to contrast a rare event scenario with a constant recruitment scenario, i.e. a scenario where germination takes place every year. The

rare recruitment scenario corresponds to a removal of the dependence of germination and seedling mortality on the moisture availability (dashed arrows in Figure 5.1).

Rare recruitment scenario (see Wiegand *et al.* 1998, Chapter 3 of this thesis; Wiegand *et al.* in press, Chapter 2 of this thesis). In years with good weather, 15.6% of seeds germinate (Rohner & Ward 1998). During their first 5 half-years, seedling mortality depends on rainfall. In good years, seedlings undergo a semi-annual mortality of 60% (Rohner & Ward 1998, Ward, unpubl. data). In intermediate and dry years, seedlings are assumed to suffer mortalities of 80% and 100%, respectively.

Constant recruitment scenario There is germination every year, but the germination rate is reduced to 3.6% (= germination rate * frequency of good years of the rare recruitment scenario). This leads to the same average recruitment success as in the rare recruitment scenario. Seedlings younger than three years undergo a semi-annual mortality of 80%, which corresponds to the mortality in intermediate years.

5.3.4 Growth

As mentioned in the Introduction, variable tree growth is suspected to cause irregular tree size frequency distributions. Possible factors causing irregular growth in Negev Acacias are the highly episodic rainfall regime, growth suppression by herbivores, mistletoe infestation, or poor tree moisture status. Our first aim is to determine by field studies if and what kind of influence they have on tree growth. We also estimate a first size-age relation for *A. raddiana* in the Negev.

Field data collection We measured trunk circumferences of about 200 trees in Nahal Katza on an annual basis from 1996 to 1998. Trunk circumference (TC) was used as an index of tree size. In the case of multitemmed trees we used an aggregate trunk circumference calculated from the total area of combined trunks (Coughenour *et al.* 1990). If trunk size could not be measured, because the trunk was too thorny or covered in branches, we used the maximum canopy diameter (CD) to estimate trunk circumference (TC) based on an empirical relation found for trees of known trunk size in Nahal Katza

$$\log_{10} TC = 1.15 * \log_{10} CD - 1.54 \quad (1)$$

This relationship is a reliable estimate, because trunk circumference and canopy diameter are strongly positively correlated (Ward & Rohner 1997). Furthermore, we determine growth increment from year t to $t+1$ as the absolute increase in trunk circumference in that year or, in the case of an indirectly measured trunk size, as the increase in the circumference of a major branch.

Trees have been visually classified as 'heavily browsed' if many branches showed signs of browsing, as infested by 'many mistletoes' if three quarters of the canopy is covered by mistletoes, and as having a 'poor moisture status' if many branches are dry (see Table 5.1).

Size-age relation The interpretation of size frequency distributions of African *Acacia* trees is complicated by the fact that size-age relationships are largely unknown. The classical method

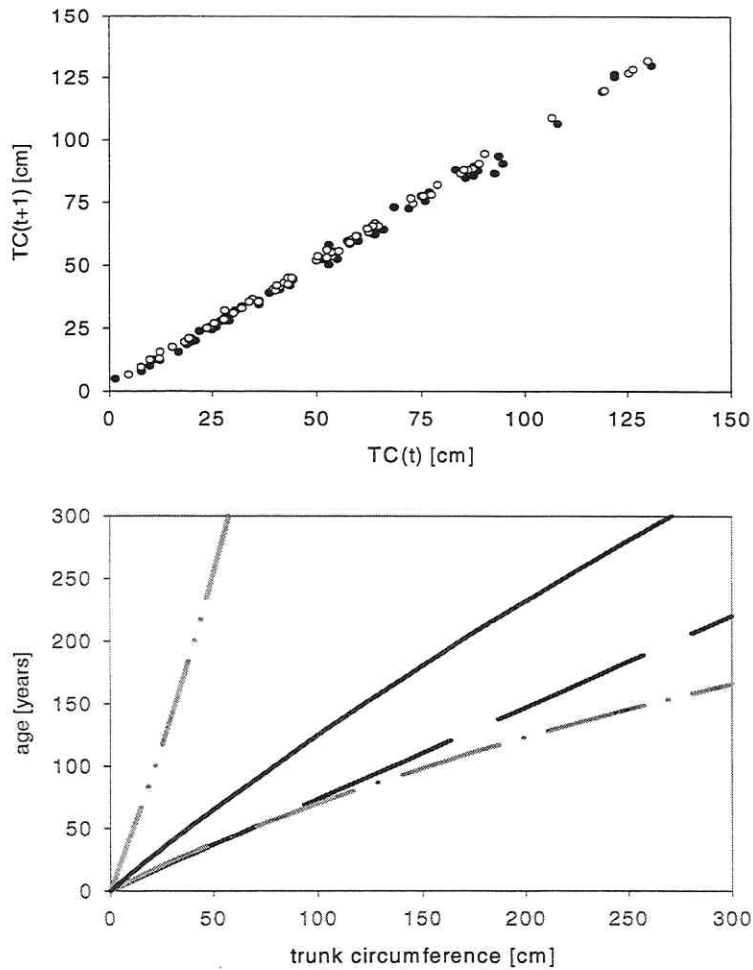


Figure 5.2: a) Trunk circumference (TC) at time t in Nahal Katzra vs. circumference at time $t+1$. Closed symbols: $t = 1996$, open symbols: $t = 1997$. b) Size-age relationships as follow from 1996-1997 growth period in Nahal Katzra (gray dash-dot-dotted line), 1997-1998 growth period (gray dash-dotted line), both growth periods combined (black solid line), and from Kiyapi (1994; black dashed line).

of investigating tree rings, used in temperate zones, is difficult to apply under tropical and subtropical climates without clear seasons because trees build less-pronounced tree rings, which are difficult to discern and are usually not formed annually (for further discussion see Gourlay 1995b; Martin & Moss 1997).

Therefore, we use an alternative method that is based on the relation of trunk circumference of trees at time t relative to their circumference at time $t+1$. We plotted trunk circumference

| trunk circum. | number | attribute | number |
|---------------|--------|----------------------|--------|
| <15 cm | 10 | many mistletoes | 15 |
| 16-45 cm | 45 | poor moisture status | 12 |
| 46-75 cm | 35 | heavily browsed | 109 |
| 76-105 cm | 33 | | |
| 106-135 cm | 38 | | |
| 136-165 cm | 14 | | |
| >165 cm | 12 | | |

Table 5.1: Summary tables of tree size distribution, mistletoe infestation, moisture status, and browsing pressure for the 187 trees studied in Nahal Katzra. Numbers given denote absolute tree numbers.

of single-stemmed trees in Nahal Katzra at $t = 1996, 1997$ vs. $t+1 = 1997, 1998$ (Figure 5.2a). From the graph, a linear relation appears to be an appropriate approach to derive a basic growth function in time:

$$TC(t+1) = a * TC(t) + b \quad (2)$$

where TC is the trunk circumference in cm, t the time in years, and a, b are constants. From 1996 to 1997 trees in Nahal Katzra grew slowly ($a = 0.9984, b = 0.2409$, 67 trees). However, in the following year, growth was much more rapid and the absolute growth increment was larger for bigger trees ($a = 1.0045, b = 1.2182$, 67 trees). This coincides with a higher amount of rainfall in the second growth period (see below). Combining data from both growth periods ($a = 1.0013, b = 0.7393$), yields a growth regime that is slightly slower than the growth measured for *A. tortilis* in the Njemps Flats, Kenya ($a = 1, b = 1.36$; Kiyapi 1994) and slightly higher than the growth of (3 years old) trees at an experimental site in Sede Boqer, Israel.

To establish a size-age relation we expand the regression of annual growth by iteration. Given the simple linear regression (2) and $TC(t=0) = 0$ we yield by iteration for the trunk circumference TC at time $t+1$:

$$TC(t+1) = \frac{a^{t+1}-1}{a-1} * b \quad a \neq 1 \quad (3a)$$

$$TC(t+1) = (t+1) * b \quad a = 1 \quad (3b)$$

Introducing the estimated constants a, b of the different growth periods in Nahal Katzra and

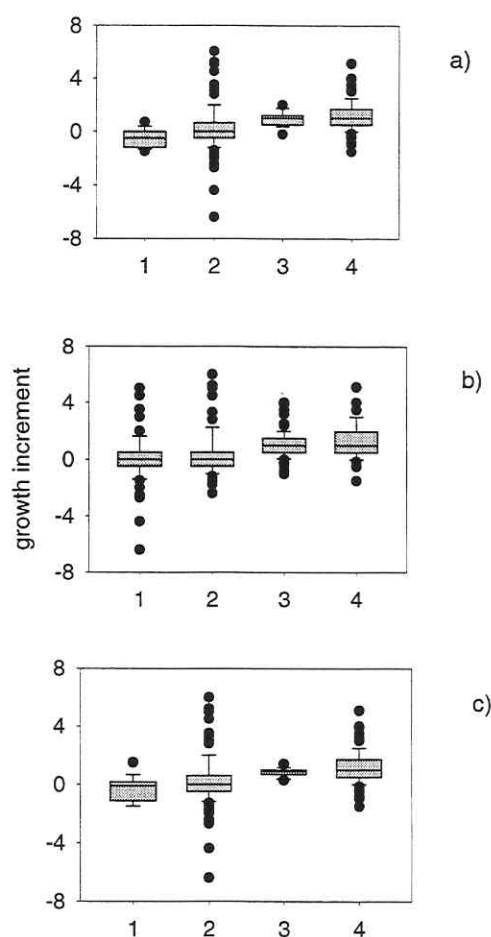


Figure 5.3: Tree growth increments in terms of trunk circumference in Nahal Katzra for growth periods 1996-1997 (numbers 1 and 2) and 1997-1998 (3, 4) under different tree conditions. a) Mistletoes (many: 1, 3; none or few: 2, 4). b) Browsing (heavy: 1, 3; none or moderate: 2, 4). c) Moisture status (poor: 1, 3; good: 2, 4). Boxes summarize the inner 50%, whiskers the inner 80% of the data, and data points beyond the 5th and 95th percentile are given as closed circles.

in Kenya (Kiyapi1994) given above we get the size-age relations shown in Figure 5.2b. The size age-relations from 1996-1997 and 1997-1998 (Figure 5.2b) give an idea of the possible range of growth of trees under different (extreme) rain conditions. A mixture of the conditions of the years 1996-1998 is currently the best approximation of the real size-age relation. We see,

for example, that under the combined scenario the 12 trees bigger than 165 cm (Table 5.1) can be expected to be about 200 years old. The establishment of a size-age relation is an important by-product of our study (Crisp & Lange 1976), because until now the age of *A. raddiana* in the Negev has not been known.

Tree growth pattern We now investigate if irregular rainfall, heavy browsing, high mistletoe infestation, or poor tree moisture status have an effect on growth in terms of increase in trunk circumference. As a first step, we analyze whether browsing, mistletoe infestation, and moisture status interact. It appears (heavy browsing & poor moisture: 10 trees, heavy browsing & many mistletoes: 9 trees, heavy browsing & many mistletoes: no tree; see also Table 5.1) that they are not significantly interrelated (χ^2 -test, Yates correction; browsing - mistletoe, $\chi^2 = 0.018$, $P = 0.89$, $1-\beta = 0.74$; browsing - moisture, $\chi^2 = 2.299$, $P = 0.13$, $1-\beta = 0.31$; mistletoe - moisture, $\chi^2 = 0.258$, $P = 0.61$, $1-\beta = 0.08$). We therefore tested the influence of each characteristic on the growth increment separately (using Mann-Whitney Rank Sum Test). This must be done for both growth periods separately because of the possible influence of the annual rainfall. One would expect that the growth increment is a function of absolute size. However, growth increment is only weakly correlated with tree size (Spearman Rank Order Correlation Test: 1996-1997, $\rho_s = -0.194$, $P = 0.012$; 1997-1998, no significant relationship, $P > 0.05$) and therefore, we neglected tree size in our analysis.

The described methods above lead to the following results: Tree growth differed significantly between growth periods (Mann-Whitney; $T_{169,154} = 32034.500$, $P = <0.001$); the median growth increment [cm] increased with total annual rainfall [mm] (1996-1997, -0.5 cm, 31 mm; 1997-1998, +0.5 cm, 68 mm).

During 1996-1997, mistletoes had a significant effect on growth ($T_{155,13} = 650.5$, $P = 0.008$). Trees infested by many mistletoes tend to shrink if rainfall is insufficient (median growth: many mistletoes, -0.5 cm; few or no mistletoes: 0.0 cm). However, in 1997-1998 there was no significant difference in growth due to mistletoe infestation ($T_{143,13} = 650.5$, $P = 0.317$).

Furthermore, heavy browsing as well as poor moisture status did not have an effect on tree growth (browsing: 1996-1997, $T_{98,70} = 6029$, $P = 0.715$; 1997-1998, $T_{93,63} = 5081$, $P = 0.626$; moisture: 1996-1997, $T_{156,12} = 767.500$, $P = 0.130$; 1997-1998, $T_{145,11} = 658$, $P = 0.156$).

The growth of trees is weakly negatively autocorrelated between the two periods (Spearman rank order correlation $\rho_s = -0.228$, $P = 0.0048$). Summarizing, we note that growth is influenced by water availability only, because the only differences we found were between years with clearly different rainfall and between trees with different levels of mistletoe infestation and thus with different levels of water loss (Ehleringer *et al.* 1985; Norton & Carpenter 1998:Box 1).

In order to develop a complete picture of the influence of browsing, moisture status and mistletoe infestation we also examined box plots of tree growth increments under the different characteristics (Figure 5.3). We found that whereas browsing has no noticeable effect on the tree growth pattern, both infestation by many mistletoes and a poor moisture status lead to a reduction in variability of tree growth.

For modeling, we contrast a stochastic growth scenario that uses the observed growth pattern extraordinarily closely with a scenario of deterministic average growth. The stochastic growth scenario reproduces the high variability of the annual growth increment due to rainfall, mistletoe infestation and tree moisture status demonstrated from the field data. From the field study, we know that growth is variable, but we do not know the effect of this growth regime on the size-frequency distribution. Therefore, we also need a scenario without variable growth, i.e. the deterministic growth scenario (see below). By running the model under both scenarios we

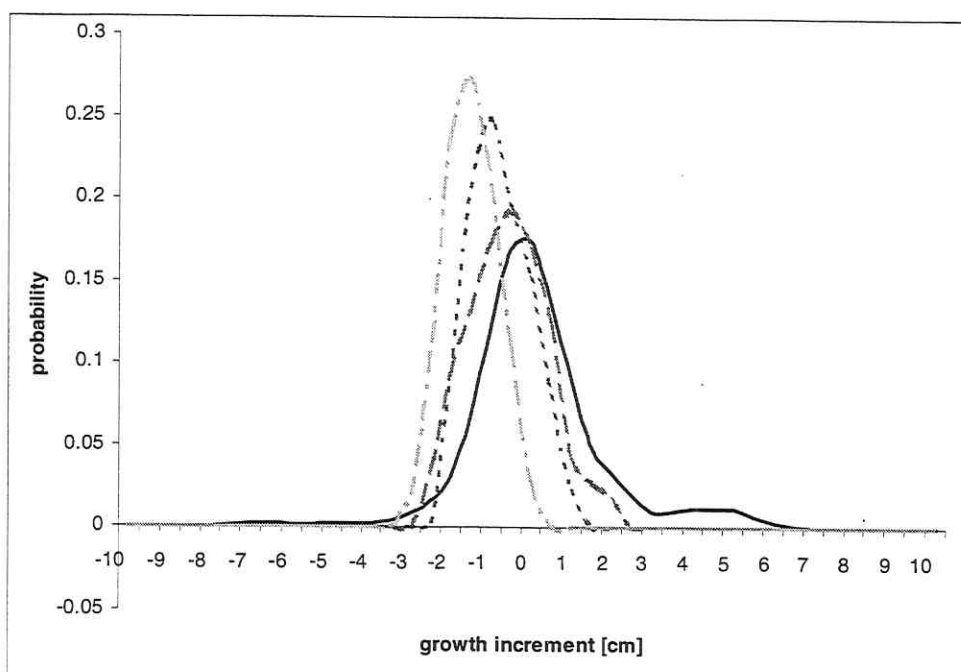


Figure 5.4: Sample probability distributions F from which deviations f from average growth d are drawn every year for each tree. The distributions given are $F = F(\text{intermediate year, tree condition})$, based on the growth period 1996-1997 in Nahal Katzra. $F_{\text{intermediate year}}(\text{good moisture status, without many mistletoes})$: black solid line, $F_{\text{poor moisture status, without many mistletoes}}$: gray dashed line, $F_{\text{good moisture status, many mistletoes}}$: gray dotted line, and $F_{\text{poor moisture status, many mistletoes}}$: light gray dashed-dotted line.

will be able to determine the effect of growth variability on size frequency distributions. Whereas the deterministic average growth scenario is shown in Figure 5.2, the variable growth scenario would correspond to the introduction of a direct dependence of growth on tree size (because of the size-age relation), moisture availability, mistletoe infestation, and tree moisture status.

Deterministic growth scenario Yearly tree growth simply follows the average growth d determined for Nahal Katzra ($a = 1.0013$, $b = 0.7393$; Equation (2); Figure 5.2b).

Variable growth scenario The basic idea of this scenario is to combine deterministic average growth d (following Equation (2)) with stochastic deviation f from this average.

$$g = d + f; \quad f \in F \quad (4)$$

The modulations $F = F(\text{weather, tree condition})$ of this growth regime represent probability distributions of the observed impact of the factors investigated in this study (good, intermediate, or bad year, many or no mistletoes, and good or poor tree moisture status). For each tree, we draw the deviation f from the respective distribution F every year (see Figure 5.4,

a description of how we set up the distributions F is given in the Appendix). The estimation of the distributions F for good and intermediate years is based on the field data from the 1996-1997 (an intermediate year according to our rainfall classification) and the 1997-1998 (good year) growth periods. For bad years, we assume that trees do not grow at all ($g=0$). The variable growth scenario has been implemented for trees bigger than 15 cm only, whereas smaller seedlings grow according to Equation (2).

5.3.5 Mortality

In the Negev desert, it has been estimated that dead trees remain standing for about 10 years before they fall down or get washed away by a flood (Ward & Rohner 1997). This estimation facilitates the study of the relationship between mortality and tree size. In order to be able to test if tree mortality is size dependent we measured the trunk circumference of living and dead trees at 10 field sites (Nahal Katzra, 1; Nahal Saif, 2; Nahal Bitaron, 4; Nahal Roded, 1; Shezaf, 1; Hai Bar, 1). For analysis, we lumped trunk circumference data from all 10 study sites, grouped them into classes of 15 cm width and conducted a χ^2 -test. Due to sample sizes in the large size classes, we excluded trees above 225 cm trunk circumference from our analysis (total number of trees: alive 329, dead 142).

At a first look, the ratio of live to dead trees seems to be size-dependent ($\chi^2 = 26.580$, $df = 14$, $P = 0.022$). However, if we only take (dead and alive) trees greater than 30 cm in trunk circumference, we find that mortality is size-independent ($\chi^2 = 20.365$, $df = 12$, $P = 0.060$). The discrepancy can be explained by the greater likelihood that small dead trees will be washed away by floods (small dead trees are relatively rare). That is, if they remain standing for a shorter period, their total mortality rate would be underestimated.

Thus, the field study indicates that mortality of *A. raddiana* is size-independent. However, because the relationship between tree size and the length of time that dead trees remain standing is not known, we cannot take this result for granted. Therefore, in the model, we investigate the so-called moisture status-dependent mortality scenario, which corresponds to the field studies described above and does not explicitly depend on size, as well as a size-dependent scenario. These contrasting scenarios refer to trees larger than 15 cm only. Mortality of seedlings (i.e. trees smaller than 15 cm) has been considered in the recruitment scenarios (see above). By running the model under both scenarios, we will be able to tell whether either of the mortality regimes has an effect on the tree-size frequency distribution. Thus, we might be able to find the 'true' mortality regime by comparing tree-size distributions under the two scenarios to the size distributions observed in the field.

Moisture status-dependent mortality scenario In this scenario, semi-annual tree mortality is modeled via a vitality function:

$$mortality = 1 - vitality \quad (5)$$

where vitality depends on the actual moisture status ms of the tree ($ms=1$: good; $ms=0$: bad) and has been determined by a fitting procedure of the size-frequency distributions of living trees in the model to field data as described in Wiegand *et al.* (in press, Chapter 2 of this thesis):

$$vitality = 0.97 + 0.025 * ms \quad (6a)$$

Table 5.2: Overview of model scenarios.

| process | scenario | description |
|-------------|--------------------------|--|
| recruitment | r- rare | germination takes place in good years only, young seedling mortality is weather dependent |
| | c- constant | seeds germinate every year, young seedling mortality constant |
| growth | d- deterministic | growth follows deterministically size-age relation, equ. (2) |
| | v- variable | growth depends on weather, and tree condition |
| mortality | m- moisture dependent | mortality is a function of tree moisture status |
| | s- size dependent | mortality is a function of tree moisture status and tree size |

Size-dependent mortality scenario We add size-dependent mortality to the previous mortality scenario:

$$vitality = 0.98 + 0.025 * ms + 0.05 * \left(\frac{TC}{250}\right)^4 \quad (6b)$$

The numbers in this equation again have been determined by a fitting procedure, this time not only of living but also of dead tree distributions.

5.3.6 Model runs - output

From the cross-combination of the scenarios described above (Table 5.2) eight model scenarios result (Figure 5.7). By running the model under these scenarios and comparing the tree size distributions resulting from both modeling and field data we establish the link between pattern and process. For each of the eight scenario combinations we ran the SAM model 100 times for 200 years. The actual weather regime differs between the simulation runs according to the simple weather model described in section 5.3.2. All model outputs are measured in the year 200 (from the beginning of the simulations). We chose the year 200 because on one hand, this time span ensures that the tree size distribution is basically not determined by the initial conditions of the simulations, which are based on the actual data from the trees in Nahal Katzra. On the other hand, 200 years still lead to moderate simulation times.

To describe the size distributions resulting from single simulation runs we use 2 indices. For both indices the trunk circumference data is grouped into classes of 15 cm width. In the SAM model, the upper size limit is 300 cm. Larger trees observed in the field are put in the [275, 300] size class.

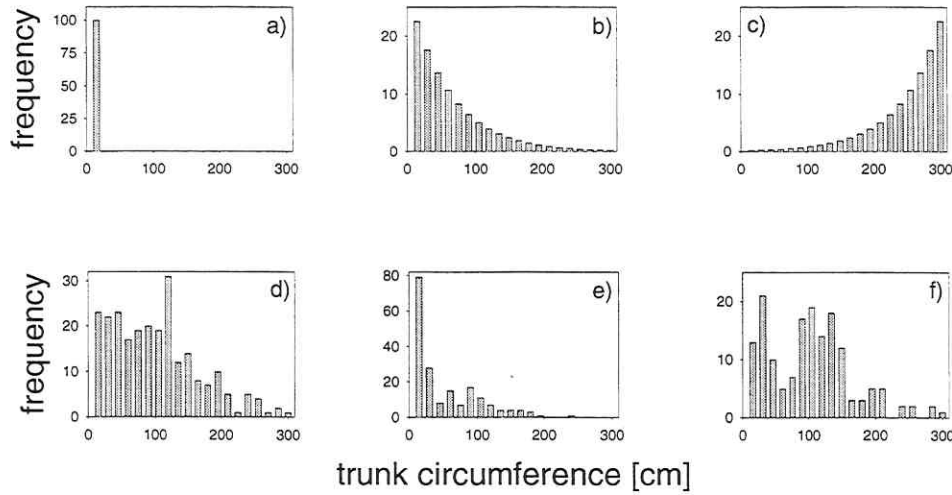


Figure 5.5: Hypothetical and real size frequency distributions and their respective indices of dominance (C) and disorder (IOD). a) $C = 1$, $IOD = 0$; b) $C = 0.1$, $IOD = 0$; c) $C = 0.1$, $IOD = 200$; d) Nahal Katzra: $C = 0.07$, $IOD = 30$; e) Nahal Saif I: $C = 0.25$, $IOD = 14$; f) Nahal Saif II: $C = 0.08$, $IOD = 60$.

(i) Simpson's index of dominance

$$C = \frac{1}{N(N-1)} \sum_{i=1}^{20} N_i(N_i-1) \quad (7)$$

where N is the total number of trees and N_i the number of trees in class i . In this study, the Simpson index (Pielou 1977) is a measure for the evenness of the occupation of the size classes (Figure 5.5).

(ii) Index of disorder

$$IOD = \sum_{i=1}^{20} |J_i - i| ; \quad J_i = 1, \dots, 20 \quad (8)$$

where J_i is the rank of size class i ($i=1$ for the smallest trees), with the highest rank ($J_i = 1$) given to the most frequent size class. We developed this index based on the idea that the size distribution of an undisturbed *Acacia* population should decline monotonically (Ward & Rohner 1997). Thus, in this ideal case, the ranking is equivalent to enumerating the size classes from the class representing the smallest (most frequent) to that representing the biggest (least frequent) trees. If a size distribution is discontinuous, i.e. with bigger trees being more frequent

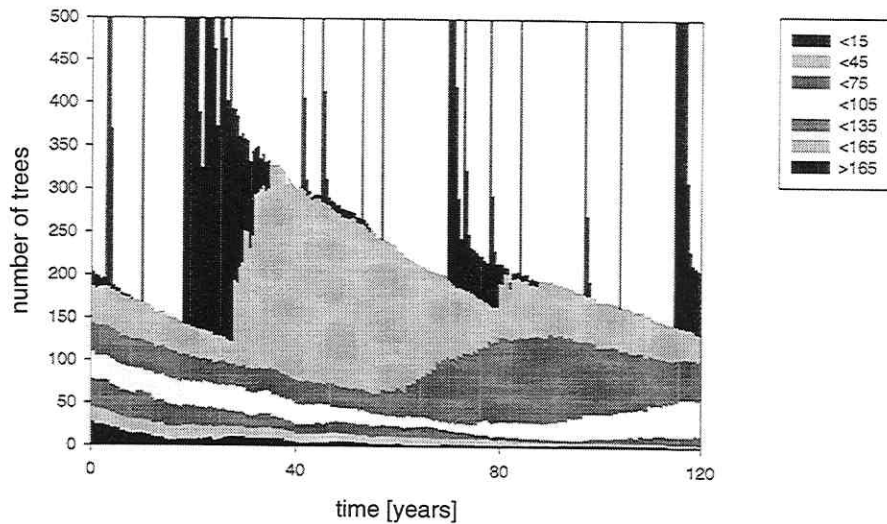


Figure 5.6: Typical time series showing the number of trees in the modeled area of Nahal Katzra under rare recruitment, variable growth, and size-dependent mortality. The size structure is indicated by grey shading (from top to bottom: black: <15 cm, grey: 16-45 cm, dark grey: 46-75 cm, light grey: 76-105 cm, grey: 106-135 cm, light grey: 136-165 cm, black: >165 cm trunk circumference).

than a preceding size class, the ranking differs from enumeration, resulting in a greater index of disorder (Figure 5.5).

5.4 Results

Figure 5.6 shows a typical simulation run of SAM under the rare recruitment scenario. The number of seedlings (trunk circumference <15 cm) over time has high peaks due to mass germination events. However, not all germination events result in recruitment, i.e. an increase in tree (>15cm) numbers, because of the weather-dependent mortality of very young seedlings. It can be seen that cohorts recruiting into the population shift with time towards larger size classes and decrease in number. Furthermore, from this graph it becomes clear that it would not have been reasonable to run the model for less than 200 years, because this period is necessary for the development of size distributions largely independent of the initial conditions.

The first questions we want to address are with regard to the effect of rare vs. constant recruitment, variable vs. deterministic average growth, and size-dependent vs. size-independent mortality on the size frequency distributions of *A. raddiana* in the Negev. Figure 5.7 displays the main characteristics of the size-frequency distributions resulting from the model simulations. Each box plot represents the index of disorder (Figure 5.7a) or Simpson's index of dominance (Figure 5.7b) for one scenario combination (see Table 5.2). If we compare the index of disorder for the same growth and recruitment scenarios combined with different mortality

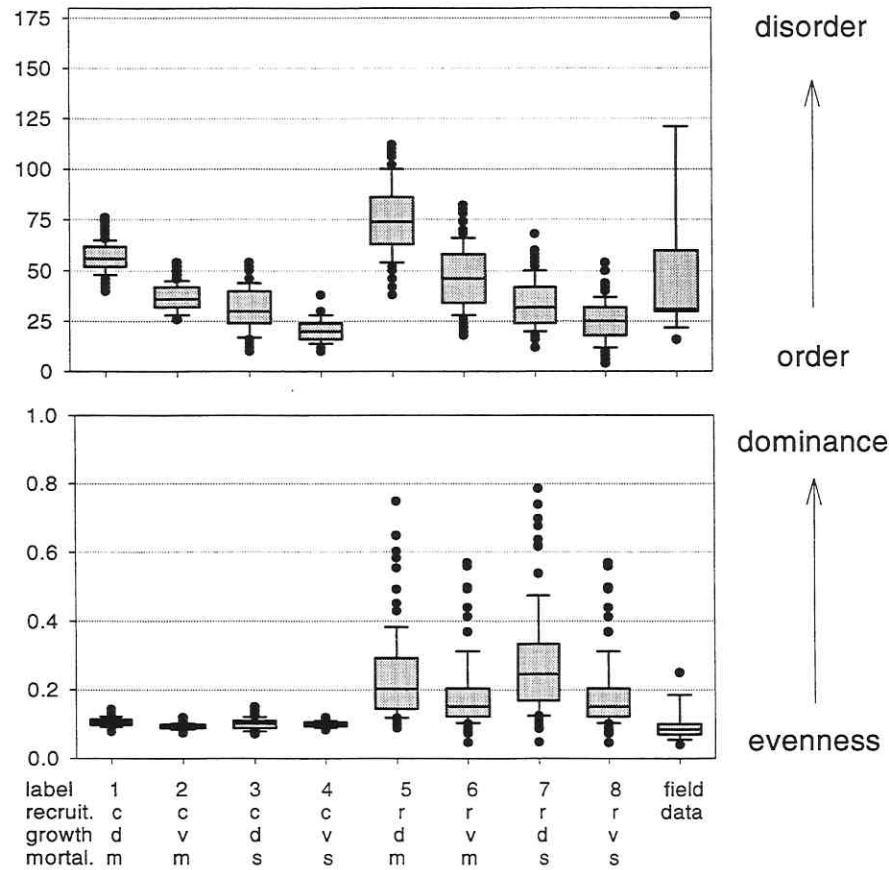


Figure 5.7: Summary of size distributions resulting from the 8 model scenarios and as found in the field. a) Index of disorder. b) Simpson's index of dominance. Category axis labels describe the model scenarios: recruitment (*recruit.*): rare (*r*) or constant (*c*), growth (*growth*): deterministic (*d*) or variable (*v*), mortality (*mortal.*) moisture dependent (*m*) or size dependent (*s*). The last category represents field data (*field data*). For a further description see Table 5.2. Box plots as in Figure 5.2. Each simulation consists of 100 runs.

scenarios (1-3, 2-4, 5-7, 6-8), we find that size-dependent mortality (3,4,7,8) gives greater order in the size-frequency distributions. That is, distributions are closer to the ideal negative exponential distribution than under the moisture status-dependent mortality scenario (1,2,5,6) whereas the dominance remains basically unchanged. Similarly, variable growth (2, 4, 6, 8) results in a greater order and a slightly decreased, but basically unchanged, dominance. On the other hand, under rare recruitment (5, 6, 7, 8) the size-frequency distributions show a somewhat greater disorder as well as a clearly greater index of dominance. The most pronounced

difference between the two recruitment scenarios is that the interquartile range of the box plots under rare recruitment is much larger than under constant recruitment, representing a high plasticity of the size-frequency distributions under rare recruitment.

The observed effects of these processes on the size-frequency distributions are biologically reasonable. If mortality depends explicitly on tree size, very large trees become less frequent. This means that it is more unlikely that a very large size class is more frequent than a preceding class, or in other words, the order of the frequency distribution is higher. As size-dependent mortality differs from size-independent mortality mainly at large tree sizes, which are generally rather infrequent, the dominance is not affected by the mortality regime. Significant variability of tree growth tends to blur a given pattern and thus levels out irregularities in the size-frequency distributions. This results in a lower disorder as well as in a slightly reduced dominance. If recruitment is a rare event, there is sometimes an outbreak of small trees (resulting in high order and dominance). Over time, trees of this very frequent size class grow and die (thus decreasing order and dominance). This explains the high variability of the shapes of the size-frequency distributions under the rare recruitment scenario.

Finally, we compare the patterns produced by the SAM model to size-frequency distributions observed in the field (also shown in Figure 5.7). This way, we gain information about the processes which may be acting in the field populations. From Figure 5.7, we hypothesize that recruitment in *A. raddiana* in the Negev is a rare event because the field size distributions show a large interquartile range in their disorder as well as in dominance. Comparing the dominance in the four box plots under rare recruitment to the field data, we find that variable growth shifts the evenness of modeled populations towards the lower evenness observed in the field. This is congruent with the non-deterministic model scenario and shows that the growth regime indeed has an effect on the size-frequency distributions. Thus, the factors acting in the field are represented by box plots 6 or 8 of Figure 5.7, which differ in the type of mortality scenario. Because box plot 6 (moisture dependent mortality) gives a better agreement for the index of disorder, we conclude that mortality effects that are dependent on tree size are probably negligible.

5.5 Discussion

The aim of this study was to learn more about recruitment, growth, and mortality of *A. raddiana* in the Negev desert, Israel. Because we do not have long-term data, we combined short-term information and modeling in order to gain insights into the mechanisms underlying the patterns we observed in the field. The major pattern of our investigations was tree size-frequency distributions. Surprisingly, we found that most studies working with such distributions use graphical displays instead of condensing the information in indices (e.g. Huston 1986; Huston & DeAngelis 1987; Grice *et al.* 1994). Studies that do use indices such as the mean, standard deviation, skewness, kurtosis, or the Gini coefficient are typically interested in patterns arising in even-aged plant populations (Turner & Rabinowitz 1983; Hara 1984; Weiner & Solbrig 1984; Dixon *et al.* 1987), see also (Bendel *et al.* 1989). Since we found that these indices do not adequately characterize the phenomenon of irregular size distributions, because they do not describe the deviation from a monotonically-declining shape, we developed our own method. We took up the idea of Ratz (1996) of describing the size-class distribution with an index of evenness and added an index capturing the irregularities in size class allocation. The combination of Simpson's index of dominance and our index of disorder turned out to be a powerful description for size frequency distributions. With these indices we

could not only learn about the effects of different processes on size distributions, but also could make statements about the processes probably acting in real populations.

In the *Introduction*, we mentioned that some studies on size-frequency distributions examined the question which mechanisms cause a certain type of size distribution. We were able to identify rare recruitment, variable (i.e. stochastic) growth (depending on precipitation, mistletoe infestation, and tree moisture status), and size-independent mortality as mechanisms causing the size distributions observed in the Negev desert. Thus, we confirmed periodic tree regeneration as a major factor forming tree size frequency distributions. In the literature, high mortality (e.g. due to elephants, see *Introduction*) has been discussed as a further factor. In our study area, there are no such prominent causes of mortality (except for road building). Therefore, we tested moderate mortality scenarios only. Nevertheless, our results show that mortality does have a clear effect on the disorder of tree size distributions. Both, analysis of field data and a comparison between field data and model results indicate that mortality does not explicitly depend on tree age. Presumably, tree survival in a harsh environment such as the Negev desert is affected by problems such as diminished water supply long before ageing becomes a prominent cause of mortality. We are aware of just one study discussing the effect of irregular tree growth on *Acacia* size distributions (Grice 1984; Grice *et al.* 1994). Grice found evidence that *A. victoriae* in semi-arid Australia may grow rapidly after prolonged periods of very high rainfall and thus cause major changes in the population structure. In combination with our finding that growth irregularities due to rainfall, mistletoe infestation and tree moisture status do play a role in the disorder of the size distributions, we believe that the importance of the growth regime might sometimes have been underestimated.

Growth suppression by herbivores has been discussed as another factor shaping tree size distributions (Ruess & Halter 1990; Rohner & Ward 1998). From field data analysis, we found that browsing does not influence tree growth. When interpreting this unexpected result, one needs to keep in mind that we measured tree size in terms of trunk circumference, while Rohner & Ward (1998) and Ruess & Halter (1990) examined tree height. Therefore these studies cannot be directly compared to our study. Indeed, Rohner & Ward (1998) found an influence of browsing on tree height of *A. raddiana* in the Negev, i.e. the same species as in our study and at a nearby location. This means that in the presence of heavy browsing, trunk circumference is an useful estimator of tree age while tree height is rather unsuitable. Another unexpected result is that tree moisture status and mistletoe infestation do not have much effect on median trunk circumference growth, but that they do reduce the inter-tree variability in tree growth. These patterns of growth are consistent within Nahal Katzra and have also been observed in another study site, Nahal Saif (results not shown here). Therefore, we believe that this interesting growth regime is a general pattern and it will be interesting to gain further understanding of these observations. For example, does heavy mistletoe infestation diminish tree growth flexibility or are inflexible trees more susceptible to mistletoe infestation? Why do trees grow a lot in one year, but shrink in the next year even if rainfall is higher? Is this pattern related to seed production? In the last-mentioned case, a strong negative correlation (i.e. trade-off) between reproduction and growth could lead to this result.

Even though our study is not designed to establish correlations between tree growth and rainfall, we made an observation which is very interesting in this context. Median (and average) growth of our populations in Nahal Katzra and Nahal Saif (data of the latter location not shown here) in the two investigated growth periods were clearly positively related to local annual rainfall. Nevertheless, we found high inter-tree variability in growth. This high variability has also been observed by Mariaux (1975) and Martin (1995, cited in Martin & Moss 1997), both investigating tree ring widths of *A. tortilis* in Senegal, Niger, and Kenya. Unfortunately,

Martin(1997) gives no *details* on his study, but Mariaux's (1975) investigations were motivated by the idea of relating tree ring width to known annual rainfall data in order to reconstruct unknown rainfall patterns from tree ring widths of old trees. While ring widths of single trees were highly uncorrelated between trees and with rainfall, an average over ring widths of 3 trees already coincided quite well (50%) with annual precipitation (Mariaux 1975). Mariaux (1975) interpreted these results as a failure of his idea and argued that tree water availability was dependent on many factors such as rooting depth, or losses due to run-off, thereby obliterating the influence of rainfall. However, in the light of our study, it seems that Mariaux's idea of reconstructing rainfall data from tree ring widths of old trees would be possible only if the number of trees investigated is sufficiently high.

In the *Introduction*, we also asked what kind of size distributions result from certain mechanisms. We are able to give answers for recruitment, growth, and mortality mechanisms investigated in this study. For example, we found that age dependence in mortality and variable growth tend to increase the order of size-frequency distributions. However, we cannot give a general answer to the question under which conditions certain mechanisms are likely to be important. But we can say that the recruitment is the most important mechanism shaping size-frequency distributions in the Negev desert.

The rather good agreement between size frequency patterns observed in the field and resulting from the model under rare recruitment, variable growth, and moisture dependent mortality can have two, not necessarily mutually exclusive, implications:

- (1) The size frequency distributions have been shaped over many years. Extrapolating the variable growth regime and rare recruitment observed during the last few years in the Negev with the help of the model to a meaningful time scale (200 years) lead to very similar size frequency patterns. Thus, we can conclude that these factors have indeed been acting in the Negev for many years. This is very interesting, because it means that rare recruitment is not only a recent threat (*cf* (Ashkenazi 1995), but has been an integral part of the reproductive biology of *Acacia* trees in the Negev for many years. However, because of the great importance of recruitment to long-term population growth (Wiegand *et al.* in press, Chapter 2 of this thesis) even a slight shift in rarity of recruitment may have detrimental effects.
- (2) The good agreement between observed and modelled patterns may mask other factors contributing to the shape of the size-frequency distributions. In other words, demonstrating that a model can produce patterns consistent with observed patterns does not prove causality; quite different models can give rise to virtually identical patterns (Levin 1992; Moloney *et al.* 1992). For example, Jeltsch *et al.* (Jeltsch *et al.* 1998) investigating tree spacing of *Acacia erioloba* in the Kalahari with a comparable simulation study, found that vegetation patterns (tree spacing) were very sensitive to changes in processes (e.g. fire). Nevertheless, a given pattern was not necessarily diagnostic of the underlying processes, because different processes could lead to very similar spatial tree distributions. However, given our combined field and modeling approach, we are quite confident that we did not miss any major factor.

This approach of directly combining experimental and theoretical investigations is an integral part of the philosophy of an ongoing project on the demography of *Acacia* trees in the Negev desert. Field studies (Ward & Rohner 1997; Rohner & Ward 1998; Ward, unpubl.data) were the basis for the development of the model structure and parameterization of the SAM simulation model (Wiegand *et al.* 1998, Chapter 3 of this thesis; Wiegand *et al.* in press, Chapter 2 of this thesis). On the other hand, model development has been a means to administrate and evaluate the present knowledge, and to indicate directions for further field

research (see Wiegand *et al.* in press, Chapter 2 of this thesis). In the present study, field investigations and modelling were highly interlinked. Field investigations determined the size distribution patterns and narrowed the range of possible mechanisms acting in Negev Acacias (rare recruitment, and variable growth were observed in the field, but mortality was not well known). Furthermore, the field data were used to generate hypotheses that were subsequently investigated by the SAM model. Only by embedding the field knowledge into the model in this way, we were able to evaluate the importance of all mechanisms and furthermore to identify the as yet unknown mortality regime. Thus, neither experimental nor theoretical studies provide a complete view of the question under study, but both promote each other's findings. In a synthesis paper on multidisciplinary studies conducted in an annual grassland, Moloney *et al.* (1992) came to exactly the same conclusion. Nevertheless, Moloney *et al.* (1992) noticed that field experiments and modeling have been separate disciplines in traditional ecological research. Despite some exceptions, e.g. the present study, we cannot say that this would have changed much during the last years.

In this paper, we were able to learn from snap-shot information about the long-term population dynamics of *Acacia* trees. The combination of short-term field investigations and pattern-oriented modeling (Grimm 1994) has the power to extract the maximum of information available within a short-term study. Nevertheless, we believe that a study such as this cannot completely substitute for long-term investigations. One problem is that in contrast to the model, some field distributions might be correlated, because some sites are closely located and should hence experience similar weather regimes. In particular, recruitment events might have occurred simultaneously. This might explain why evenness is generally greater in the field than under the rare-recruitment model scenarios. Furthermore, the size-age relationship used in this study is based on two growth periods and one location. Because the growth of Acacias depends noticeably on precipitation (see also Milton 1988; Gourlay 1995a; Gourlay 1995b), the present size-age relationship cannot be more than a first estimation. However, in the course of a few more years, we will be able to establish a more accurate estimation of the growth regime of *A. raddiana*.

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5.6 Appendix

To set up the distributions F , we first shifted the respective growth increment data by the total average growth increment. Note that this is not the same as using the unshifted frequency distribution directly while retreating from the use of the average, size-dependent, growth d (Equation (2)), because the average growth increment is the average over all years and trees, i.e. a size-independent number. We then applied a Kernel density estimation technique to these deviation-from-average-growth-increments. The basic idea behind the density estimation is that

the data observed in the field are samples from an unknown probability density function F . Density estimation now gives an estimator of this probability function using the information of the frequencies of any observed value of increment. We chose Kernel density estimation, because it is a nonparametric approach allowing the data to speak much more for themselves in determining the estimated density F than would be the case if F were constrained to fall in a given parametric family (Silverman 1986; Härdle 1991). For the purpose of this study, we chose the Epanechnikov Kernel with the bandwidth h

$$h = 0.9 \sigma n^{-1/5} \quad (9)$$

where σ is the standard deviation, and n the number of data points of the original data (Silverman 1986).

As mentioned, these probability densities F are further used in SAM to fix respective actual growth scenarios. However, trees may have a poor moisture status and heavy mistletoe infestation simultaneously. This has not been observed in Nahal Katzra, probably because the sample size was not large enough to encounter this rare combination. For our purpose, we derived the according probability density functions F from two simple patterns observed in the field data: (1) growth variability, i.e. the width of the probability density function F , is reduced by poor moisture as well as by many mistletoes; (2) both factors reduce average growth. Assuming that variability as well as average growth will be reduced even further if a tree is infested with mistletoes as well as suffering from water shortage, we multiply the two probability density functions (reducing variability) and shift the product function (reducing average growth) toward smaller growth increments. More explicitly, we shift the distribution such that the average growth reduction as compared with trees in good condition is equal to the sum of the reductions due to pure mistletoes and pure dryness.

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5.8 Link to the following chapter

In Chapter 5, I succeeded in gaining a maximum of information on mortality and recruitment from tree size-frequency distributions. We've learned that age is not an important determinant of *Acacia* mortality in the Negev and that rarity of recruitment events has been a normal feature of the population dynamics of these trees for many decades. However, deduction of processes from observed patterns always carries the risk that other, unconsidered, processes may cause the same pattern. Therefore, such studies may not substitute for long-term investigations. Nevertheless, given the grave concern about the *Acacia* trees in the Negev, it has been important to conduct this investigation and to learn as much as currently possible.

The keys to the success of Chapter 5 have been the availability of field data from several sites and the idea of describing the size frequency distributions with indices retaining a maximum of information and that still allow us to compare model scenarios and field data. In Chapter 6, I will investigate the spatial tree distribution. In principle, I could imagine conducting a study similar to Chapter 5. However, currently, I have data from two study sites only and the starting point is quite different. For the size-frequency distributions, it has been known before that they are irregular and that they deviate from the ideal negative exponential shape. However, for the spatial tree distribution, I will have to address more basic questions such as "Are trees randomly distributed, clumped, or evenly spaced?", "At which scales does the distribution deviate from random patterns?", "For which tree sizes

can such a deviation be observed?", "Are small trees clumped with respect to each other or with respect to mature, seed producing trees?". Once I've analyzed the field data I will have to determine whether the model produces patterns in agreement with the field observations and design alternative model scenarios that might explain the observed patterns. In the current form of the model (as described in Chapter 2), one would expect that the rules for seed distribution and germination, because of the seed-attracting supercells and the supercells with many safe sites, will lead to a clumped distribution of seedlings. Furthermore, older trees might be regularly spaced due of competition between trees.

Do spatial effects play a role in the spatial distribution of desert dwelling Acacias?¹

6.1 Abstract

We investigated the spatial pattern of *A. raddiana* in the Negev desert of Israel in order to gain insights into the factors and processes driving the dynamics of this species. Using a scale-dependent measure, the ring statistic, we analysed both patterns observed in the field and time series of spatial tree distributions produced by a simulation model. In the field, random spacing was the predominant pattern observed, however seedlings were clumped on small scales. We ran the model under two contrasting scenarios representing hypotheses that explain the clumping of seedlings and the random distribution of trees. One hypothesis is that there is spatial heterogeneity in seed distribution, germination, and seedling mortality, but that these heterogeneities are not correlated with each other in space. The second hypothesis assumes a correlation between these heterogeneities leading to areas suitable for establishment and density-dependent tree mortality due to competition. Both hypotheses lead to spatial distributions that are in qualitative agreement with the patterns observed in the field. Therefore, the classical view that a clumped seedling distribution and a random pattern of older trees is due to clumped regeneration and density-dependent mortality may not hold for *Acacia* trees in the Negev.

6.2 Introduction

It is widely accepted that spatial aspects are important to the population dynamics of plants. For example, plants need safe sites for germination and they interact positively and negatively with neighbours, which influences their survival and growth (e.g. Harper 1977; Tilman 1988; Begon *et al.* 1996). These spatial influences result in temporally variable, spatial patterns of plant distribution. For example, competition may result in the death of weaker individuals and thus increase the overall spacing between these plants over time (Smith & Goodman 1987). If spatial aspects of population dynamics have a strong influence on spatial patterns of plant distribution, then spatial patterns do contain information on population dynamics in a highly condensed way. Therefore, it should be possible to learn about these factors by investigating spatial patterns of plant distribution. As the information is very condensed, one can not expect to clearly identify the set of underlying factors and processes (Leps & Kindlman 1987; Leps 1990), nevertheless a pattern analysis is useful for the generation of realistic hypotheses to be further investigated by other studies (Leps 1990; Levin 1992). Or in the words of Besag (see Ripley 1977): spatial statistical analysis usually provides helpful insight into situations rather than definitive conclusions.

Statistical pattern analysis has been employed for many years in field-oriented studies (Cottam 1955; Greig-Smith 1961; Sterner *et al.* 1986). Sometimes, several similar study sites are being investigated (Leemans 1991; Jeltsch *et al.* in press) in order to allow for safer

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conclusions. Other studies investigate several sites differing in one or more aspects (Phillips & MacMahon 1981; Skarpe 1991), thus facilitating the consideration of the influence of these aspects. However, patterns observed in the field, are always snap-shots and do not give information on the temporal variability of the system under study. From the pattern alone, it is not clear if the actual pattern observed represents typical characteristics or if these characteristics are highly variable over time. The latter is very likely in event-driven systems as can e.g. be found in (semi)arid regions (Wiegand *et al.* 1995; Wiegand, K. *et al.* 1998, Chapter 3 of this thesis). Information on temporal aspects of spatial patterns may be gained by the use of spatially-explicit simulation models (Jeltsch *et al.* in press; Wiegand, T. *et al.* 1998). This approach, however, implies that the population dynamics of the plants under study is already relatively well known. In simulation models, the inevitable gaps in the respective knowledge are filled by plausible assumptions and educated guesses of parameter values. The assumptions and the parameter values are then varied in different model scenarios. Runs of different model scenarios and comparisons of the resulting patterns to the patterns observed in the field may then reduce the range of possible scenarios, and thus increase our understanding of the processes driving the population dynamics.

In this paper, we try to uncover factors and processes driving the population dynamics of *Acacia raddiana* in the Negev desert of Israel with the help of a spatial pattern analysis of both field data and model results. Investigating the spatial pattern regarding the population dynamics of this species is highly relevant, because these ecologically important trees are believed to be endangered (Danin 1983; Ashkenazi 1995). In Israel, the distribution of *A. raddiana* is largely restricted to ephemeral riverbeds (wadis). We believe that the flash floods occurring in winter dominate the distribution of *A. raddiana* by re-distributing seeds that have fallen from trees. Wadi morphology is unlikely to be an important factor for tree distribution, because Wiegand *et al.* (unpubl., Chapter 4 of this thesis) could not find a relationship between tree distribution and wadi width, slope, or curvature. Therefore, we expect trees to be randomly distributed. We analyse mapped tree distributions of two study sites using a scale-dependent pattern analysis technique, the ring statistic (Wiegand, T. *et al.*, subm.). Furthermore, we use a simulation model to study the temporal development of the spatial pattern under two (seemingly) contrasting hypotheses. The patterns observed in the field and under the model are compared in order to evaluate the two model scenarios.

6.3 Methods

6.3.1 Study sites

The study has been conducted in two wadis, Nahal Katzra and Nahal Saif, near the Arava valley. All precipitation falls in winter (Katzra: 38 mm, Saif: 45 mm) and results on average in about one flood event per year (Stern *et al.* 1986). In both wadis, a section (Katzra: 1.5 km, Saif: 2 km) containing about 200 living trees has been mapped. The study areas were restricted to the riverbeds, because trees do not grow outside the wadis. The only tree species present was *A. raddiana*. The other plant species that occur there are mainly *Retama raetam*, *Ochradenus baccatus*, *Zilla spinosa* and *Anabasis articulatus*, all of which occur at low density (<5% total cover). Annual plants do not occur in the wadi in any significant density due to the erosive action of the annual floods.

6.3.2 Simulation model

An existing simulation model (SAM) of the population dynamics of *A. raddiana* in the Negev desert has been used to simulate the spatial dynamics of *A. raddiana* for 100 years, taking Nahal Katzra as an example. A description of the model is given below, with further details available in (Wiegand *et al.* in press, Chapter 2 of this thesis, Wiegand, K. *et al.* subm., Chapter 5 of this thesis). Except for the growth regime (slightly different growth rates), the version of the model used in this chapter does completely coincide with the model version used in Chapter 2. However, a contrasting model version is introduced in 6.3.3. A sensitivity analysis is given in Wiegand *et al.* (in press, Chapter 2 of this thesis) and Ward & Rohner (1997), Rohner & Ward (in press) provide further biological information.

General aspects SAM is a spatially-explicit, individual-based, stochastic simulation model. The model keeps track of the location and size of each individual and differentiates between seedlings (trunk circumference $TC < 15$ cm), subadult ($15 \text{ cm} \leq TC < 45$ cm) and adult trees ($TC \geq 45$ cm), and dead trees. Dead trees are considered, because they remain standing for about 10 years (Ward & Rohner 1997). SAM works on a yearly basis, each year being subdivided into a summer and a winter period. In both periods, growth and mortality of seedlings and trees and mistletoe infestation and deterioration in moisture status of trees take place. Seeds are produced in summer, while distribution and germination occur in winter. Furthermore, in winter, dead trees may fall down and hence become removed from the simulated population. It is assumed that seed distribution and the fall of dead trees are dominated by the flood events occurring in winter.

SAM is a grid-based model and consists of cells that are $5\text{m} \times 5\text{m}$ in size and thus represent the typical size of an adult tree. One cell may contain an arbitrary number of seedlings, trees, and dead trees, but due to the low plant density, cells rarely contain more than one living or dead tree. However, high numbers of seedlings are common after mass germination events. Patches of 4×4 cells are grouped into 'supercells'. Even though the entire modelled area is rectangular, plants may grow in supercells located within the wadibed only (for details of implementation see Wiegand *et al.*, in press, Chapter 2 of this thesis).

Weather The weather regime used in SAM works on a yearly basis. Based on an evaluation of rainfall data from weather stations close to Nahal Saif and Nahal Katzra with respect to the biology of *A. raddiana*, SAM distinguishes between good (23%), intermediate (61%), and dry (16%) years. The actual weather regime is determined at the beginning of each year. However, the sequence of good, intermediate, and dry years is the same for all simulations. This allows us to compare single simulation runs across different scenarios. The weather regime chosen is typical and includes periods of good as well as periods of bad long-term weather.

Seed distribution Seed distribution is considered in good years only, because only then seeds may germinate (see section *Seed germination*). SAM follows the destiny of each seed individually. It is assumed that, due to wadi morphology, seeds will be distributed by flood events in a spatially uneven fashion. This module is not meant to realistically simulate the distribution process but rather the essential features of its outcome. Numbers given below are educated guesses and will be varied in model scenarios. Seed distribution is modelled as a two-stage process. The first step consists of the identification of 'seed-attractive' and 'normal' supercells (patches of 16 cells). On average, seed numbers in attractive supercells are five times higher than in normal supercells. Based on the assumption that the current distribution of

seedlings in the field reflects seed-attractivity, we initially (year = 0) identify those supercells as seed-attracting, that contain at least one seedling (e.g. 20 of 669 supercells in Nahal Katzra). During the course of time, seed-attracting supercells become relocated. In years with good weather, that is with good rainfall resulting in heavy floods, each seed-attracting supercell has a 5% chance of relocation. Based on the actual seed production within the wadi and the ratio of seed-attracting to normal supercells, the average number of seeds per seed-attracting and per normal cell is calculated. In the second step, the actual number of seeds within a given cell is drawn from a negative exponential distribution with corresponding mean. This introduces a clumped seed distribution with many cells containing few seeds and few cells containing many seeds.

Seed germination In arid regions, germination primarily depends on local water availability (Coughenour 1986, Kenneni 1990). Local water availability is a result of both regional and local features. SAM considers the regional feature 'weather' representing the overall water availability and the local feature 'abundance of safe sites' representing the existence of microsites that provide optimal water and shade conditions (*cf.* Miller 1994). In SAM, only those seeds may germinate that encounter both a good year and a safe site. Note, that we do not consider a seed bank, because the survival of seeds into a second year is highly unlikely due to the extremely high seed infestation of bruchid beetles in the Negev (Rohner & Ward in press).

Again, the abundance of safe sites within the wadi is modelled outlining the essential features using educated guesses to estimate parameters. SAM assumes a heterogeneous distribution of safe sites within the wadi and divides supercells (patches of 16 cells) according to their availability of safe sites into three categories: (1) 90%, (2) 50%, or (3) 10% of the cell area provide conditions suitable for germination. Thus, a seed within a cell of category (1) has a 90% probability to be at a safe site. The classification of supercells is done randomly at the beginning of each simulation (year = 0; relative frequency of the three categories (1):(2):(3) = 1:2:1).

Mortality In SAM, mortality of up to 2.5 year old seedlings depends on rainfall. In good years, these seedlings undergo a semi-annual mortality of 60% (Rohner & Ward in press, Ward, unpubl.), while in intermediate and dry years 80% and 100% of the small seedlings die. Mortality of older seedlings and trees follows the semi-annual mortality of 0.87% measured for *A.tortilis* trees (Ward & Rohner 1997). Whereas the average mortality of trees follows that rate as well, the actual mortality risk of single trees depends on tree vitality.

Tree vitality is a function of tree moisture status. In Nahal Katzra, 3% of subadult and 8% of adult trees have a low moisture status, i.e. many dry branches. Therefore, SAM distinguishes between good and poor tree moisture conditions. It is assumed that trees in poor moisture conditions cannot recover to a good moisture status, while trees in good moisture conditions may deteriorate in moisture status depending on their infestation by mistletoes (trees have a semi-annual probability of 0.4% of becoming infested by the mistletoe *Loranthus acaciae*), due to competition with neighbours, and depending on the long-term weather regime. Every six months, the actual risk of moisture status decrease is recorded for each tree showing good moisture conditions. Each of the following factors adds one 'risk point' in the balance: (1) bad long-term weather (i.e. five or more consecutive dry years), (2) one or more subadult trees living within the eight cells that are adjacent to the cell containing the tree under consideration, (3) mistletoe infestation, and (4) other pooled undistinguished factors. Subadult trees located in the same cell and adult trees in adjacent cells result in 2 'risk points', whereas adult trees in the same cell account for 3 'risk points'. Hence, each tree has at least one risk point (factor 4). The

actual probability for each tree to worsen in moisture status is the sum of the 'risk points'. For example, in Nahal Katzra each 'risk point' represents a moisture status deterioration probability of about 1%, a value determined via parameter fitting (Wiegand *et al.* in press, Chapter 2 of this thesis).

Growth Based on field data from the Negev and Kenya, growth in trunk circumference has been approximated by a constant yearly increment of 1.36 cm for seedlings and 0.74 cm for trees (Wiegand, K., subm.: deterministic growth scenario (Chapter 5 of this thesis), Kiyiapi 1994).

Seed production For example in Nahal Katzra, 50% of subadult and 87% of adult trees reproduce within a given year. Potential seed production S of these trees depends on tree size (measured as trunk circumference TC):

$$\log S = 3.84 + \log TC * 1.11 \quad (1)$$

(Ward, unpubl. data). However, a poor moisture status as well as mistletoe infestation reduce the canopy volume available for seed production. Therefore, SAM reduces the number of seeds produced on an individual tree by 50% if it's moisture status is poor and additionally by the proportion of the tree canopy covered by mistletoes.

In the Negev desert, seed infestation of *A. raddiana* by bruchid beetles (mostly *Bruchidius arabicus* and *Caryedon palestinicus*) is as high as 97%. Furthermore, it has been determined that 93% of the seeds are lost for *Acacia* reproduction, because they are transported out of the wadi by floods and ungulates and many seeds eaten by rodents and ungulates are destroyed (Wiegand *et al.*, in press, Chapter 2 of this thesis; Rohner & Ward, in press), see also (Halevy 1974; Murray 1986; Hauser 1994; Miller 1994; Miller 1996).

6.3.3 Hypotheses and translation into model scenarios

Hypothesis 1 Our first hypothesis reflects our expectation of randomly distributed trees, as explained in the *Introduction*. We hypothesize, that there is spatial heterogeneity in seed distribution, germination, and seedling mortality, but that these heterogeneities are not correlated with each other. In SAM, seeds are most likely to become distributed into seed-attracting cells. Then, germination is best in cells with the highest density of safe sites. Survival of very small seedlings depends on weather, but is independent of location. Therefore, there is some degree of spatial heterogeneity in SAM. However, the rules introducing spatial heterogeneity are uncorrelated with each other. Therefore, the first hypothesis is realised in the model as described in section 6.2.2 and we will refer to this model version as scenario (1).

Hypothesis 2 Our second hypothesis is that there are areas suitable for establishment. Therefore, we will introduce a model scenario with correlation between seed-attractiveness, safe-site density and seedling survival. However, in this form, we would obtain an extreme tree distribution with most trees growing in those areas where establishment takes place. In the field, trees are not clustered in such an obvious way. Therefore, we assume that the suitability of specific wadi areas for establishment is temporally variable. Furthermore, we introduce a higher competition between trees. We expect the competition to counteract strong clustering of trees introduced by the correlation of the spatial aspects of tree establishment.

In scenario (2), five rules are altered in comparison to scenario (1). Comments in squared brackets refer to the respective circumstances valid under scenario (1).

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- (i) Average seed numbers in seed-attracting supercells are ten [five] times higher than in normal supercells.
- (ii) All seed-attracting supercells have the safe site density of category (1) 90% [uncorrelated].
- (iii) In intermediate years, small seedlings (first 2.5 years) suffer a mortality rate of 70% [80%] if they grow within a seed-attracting supercell. However, mortality of small seedlings in normal supercells is 100% [80%] in intermediate years. The mortality rate of 70% has been chosen, because this rate assures that adult tree densities differ only slightly from densities under scenario (1). Small seedling mortality in dry (or good) years remains unchanged since we assume that conditions are very bad (or good) for all seedlings in those years. In intermediate years, older seedlings might find more suitable conditions in seed-attracting supercells as well, but we assume that this is counterbalanced by competition due to higher seedling densities. Therefore, mortality of older seedlings remains unchanged.
- (iv) Seed-attracting supercells have a chance of 25% [5%] to become relocated in good years.
- (v) Trees receive more 'risk points' for deterioration in moisture status (resulting in a higher mortality risk) due to competition with nearby trees. Subadult trees located in the same cell and adult trees in adjacent cells result in 200 [2] 'risk points', whereas adult trees in the same cell account for 300 [3] 'risk points'. This seemingly strong increase in deterioration risk has been chosen, because it was known from simulation experiments not shown here, that a more moderate increase has no noticeable effect. Most importantly, one needs to keep in mind that the probability to deteriorate in moisture status is the sum of 'risk points' divided by 500.

In order to be able to evaluate the influence of each of the five rules that are different in the two scenarios, we will move from the first to the second scenario by changing the rules in a stepwise fashion until we've arrived at scenario (2).

6.3.4 Simulations

All simulations presented in this paper are based on Nahal Katzra, i.e. the wadi outline and the initial condition and spatial distribution of seedlings, trees, and dead trees corresponds to the situation in Nahal Katzra. Each simulation consists of a single run comprising 100 years. For all simulations, the weather regime is kept constant, that is the sequence of good, intermediate, and dry years is the same for each simulation.

6.3.5 Point pattern analysis

Both tree distributions observed in the field and produced by the model have been analysed using a derivative of the scale-dependent 'ring statistic' (Wiegand, T., *et al.*, *subm.*). The basic idea is to compare the number of trees that are concurrently within a ring and the wadibed to the number of cells within this ring and within the wadibed, thus calculating a density. This sampling technique involves the placement of a circular sample ring of radius $r \pm \Delta r/2$ around individuals of type A and counting the number of individuals of type B within the ring. Note, that this is not the same as counting the number of individuals within a circle. In this way, from the position of each individual of type A, the density of individuals of type B is determined for a range of discrete distances r from the location of that individual. Thus, the ring statistic is individual-centred (*sensu* Podani & Czaran 1997). Finally, the density profiles observed from all individuals of type A are summed up, resulting in the statistic $O_{AB}(r)$.

For ease of implementation we did not use smooth rings, but rather took advantage of the grid-based structure of the SAM model and used rings consisting of cells whose centre is located at a distance of $r \pm \Delta r/2$ from the centre of the cell containing an individual of type A. Thus, we chose $r = 0\text{m}, 5\text{m}, 10\text{m}, 15\text{m} \dots$ and $\Delta r = 5\text{m}$ or, in terms of cells, $r = 0, 1, 2, 3, \dots$; $\Delta r = 1$. Furthermore, we determine the density of individuals of type B by calculating the ratio of individuals of type B to the number of cells lying concurrently within the ring and within the wadibed. This includes edge correction, necessary when parts of the circle put around an individual of type A lie outside the study area, in a trivial manner (for problems of edge correction in the related K-function analysis see Haase 1995). More formally, our derivative of the ring statistic is defined as

$$O_{AB}(r) = \frac{\sum_{i=1}^{N_A} \sum_{j=1}^{N_B} \delta(c(p_i^A), c(p_j^B), r)}{\sum_{i=1}^{N_A} ny(i, r)} \quad (2)$$

with

$$\delta(c(p_i^A), c(p_j^B), r) = \begin{cases} 1 & r - \frac{\Delta r}{2} < \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2} < r + \frac{\Delta r}{2} \\ 0 & \text{all other cases} \end{cases} \quad (3)$$

and

$$ny(i, r) = \sum_{j=1}^N \delta(c_i^A, c_j, r) \quad (4)$$

where p_i^A represents the individual of type A with number i , $c(p_i^A)$ the cell containing individual p_i^A , c_i^A a cell containing at least one individual of type A, x_i, y_i the coordinates of cells $c(p_i^A)$ and c_i^A , N_A the number of individuals of type A, N the total number of individuals, and c_j an arbitrary cell within the wadibed. Per definition, O_{AB} is always positive, but unbounded upwards as cells may contain any number of individuals.

With the ring statistic, both univariate ($A=B$) and bivariate ($A \neq B$) analyses are possible. We conducted univariate analyses for living trees, dead trees, and living trees of certain size classes (for choice of size classes see *Results*) and bivariate analyses for small trees (seedlings) with respect to adult trees.

For each pattern analysed, we randomised the locations of all individuals 19 times (leaving all other attributes unchanged) using the pseudo-random generator r250 by Maier (Maier 1991) and recalculated the ring statistic for each of the resampled populations. The lowest and highest $O_{AB}(r)$ is used to define the lower and upper bound of a 95% confidence envelope for the null hypothesis that individuals of type B are randomly distributed at distance r from individuals of type A (cf. Haase 1995; Martens *et al.* 1997). Alternatively, it would have been possible to define the 95% confidence envelope via the 5th-lowest and 5-highest $O_{AB}(r)$ of 99

randomizations, because the probability that a observation is due to random among the 5 lowest (or highest) values is $5/100$ ($100 = 99$ randomization + 1 observation). However, due to the long simulation times involved, we decided to use 19 randomizations only (which gives a probability of $1/20$, with $20=19+1$). If at a given distance r , $O_{AB}(r)$ of the observed population is above (or below) the upper (or lower) limit of the confidence envelope, we say that the density of individuals of type B at a distance r from individuals of type A is significantly above (or below) the density expected from a random pattern. More briefly, we will say that B is clumped (or dispersed) with respect to A at the distance r .

6.4 Results

6.4.1 Field

The overall density of living trees is rather low in both Nahal Saif (0.03 trees/cell) and Nahal Katzra (0.02 trees/cell). Figure 6.1a shows the univariate ring statistic for all living trees (and seedlings) of Nahal Saif. At a distance of zero cells, tree density is significantly above densities expected from random patterns. In other words, trees are clumped within cells ($5\text{m} \times 5\text{m}$). At distances of up to 14 cells, trees are still clumped, even though clumping is not as distinct. At larger scales, trees are distributed randomly. In Nahal Katzra (Figure 6.1b), trees are randomly spaced at all scales. However, there is a tendency towards clumping at the smallest scale (within cells). Furthermore, in Nahals Saif and Katzra (Nahal Saif shown only: Figure 6.1c), dead trees are randomly distributed. The same holds true for the density of seedlings ($TC < 15\text{cm}$) as seen from the perspective of adult trees ($TC > 45\text{cm}$; Nahal Katzra shown only: Figure 6.1d).

Thus, *A. raddiana* follows largely our hypothesis of a random distribution. Only at very small scales, there is a clumped tree distribution for living trees. In the following, we want to find out if there are differences in clumping between age classes.

Seedlings ($TC < 15\text{cm}$) are significantly clumped at small scales in Nahal Saif, while trees ($TC \geq 15\text{cm}$) show a slight tendency towards clumping only (Figures 6.2a,b). We find the same pattern, if we look at *A. raddiana* with a trunk circumference smaller (Figure 6.2c) or greater than 45 cm (Figure 6.2d), but the pattern changes when we divide the population into trees smaller or greater than 75 cm (Figure 6.3a,b). Trees smaller than 75 cm in trunk circumference are significantly clumped at small scales, but larger trees are distributed randomly. A similar analysis for Nahal Katzra shows that small trees are clumped as well, but only up to a trunk circumference of 45 cm (Figure 6.3c,d).

6.4.2 Model scenarios

We have two contrasting model scenarios: (1) No correlation in factors determining tree establishment and (2) high spatial correlation in tree establishment, but a lower correlation between locations suitable for establishment in time and an increased competition between trees. In order to be able to evaluate the influence of each of the five rules that are different in the two scenarios, we will move from the first to the second scenario in a stepwise fashion. First, we will show results of scenario (1), then we will change rule (i), rule (i) and (ii), and so on until we've arrived at scenario (2). In the field, we observed some clumping for small trees and random distribution for large trees. Therefore, we show simulation results for univariate analyses of seedlings ($TC < 15\text{cm}$; Figure 6.4) and trees ($TC \geq 15\text{cm}$; Figure 6.5).

Figure 6.4a and 6.5a show the number of seedlings and trees over time. Rapid increases in seedling density are due to periods of good weather, but only longer periods of good weather

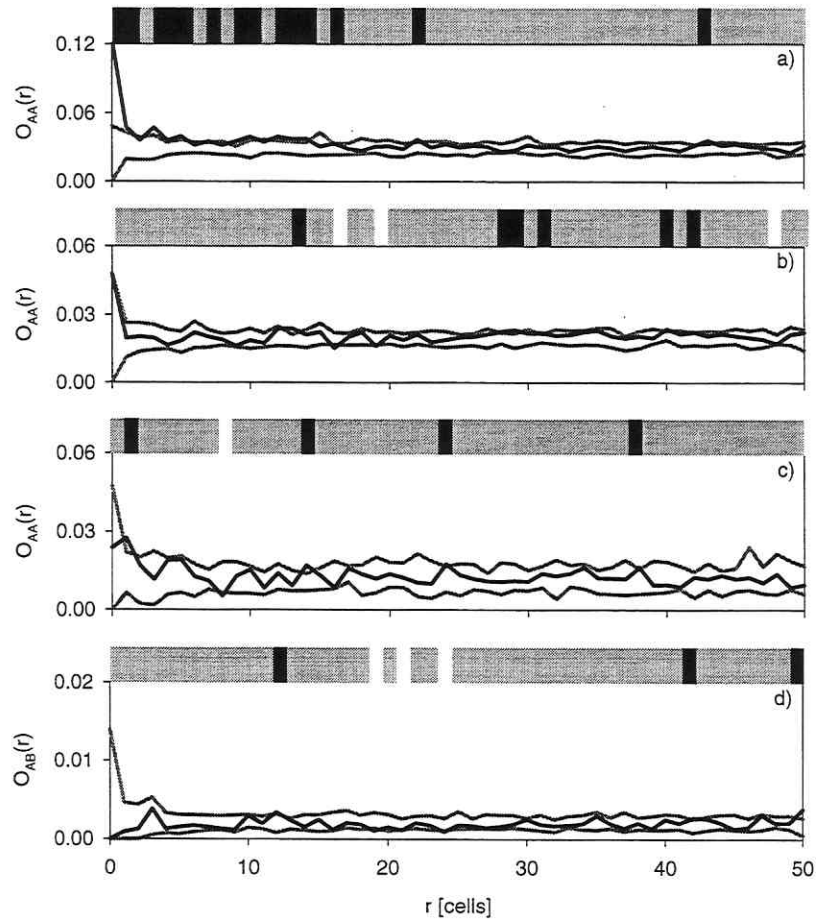


Figure 6.1: Analysis of patterns observed in the field. The ring statistic (black lines) has been plotted against the distance for each cell interval. The gray lines give 95%-confidence envelopes for complete spatial randomness. a) Nahal Saif, all living trees and seedlings; b) Nahal Katzra, all living trees and seedlings; c) Nahal Saif, dead trees; d) Nahal Katzra, seedlings (TC < 15 cm) relative to adult trees (TC \geq 45 cm). Bars above graphs summarize the spatial pattern shown in the graphs: significantly clumped (black), random (grey), or significantly even spaced (white).

lead to recruitment as is reflected in an increase in tree numbers starting in year 32. In scenario (1), we observe that seedlings are clumped at small distances in some years, but randomly distributed in others. Obviously, the appearance of clumping is related to germination events (Figure 6.4b). Besides some spots of clumping (e.g. at zero distance) and spacing, trees are

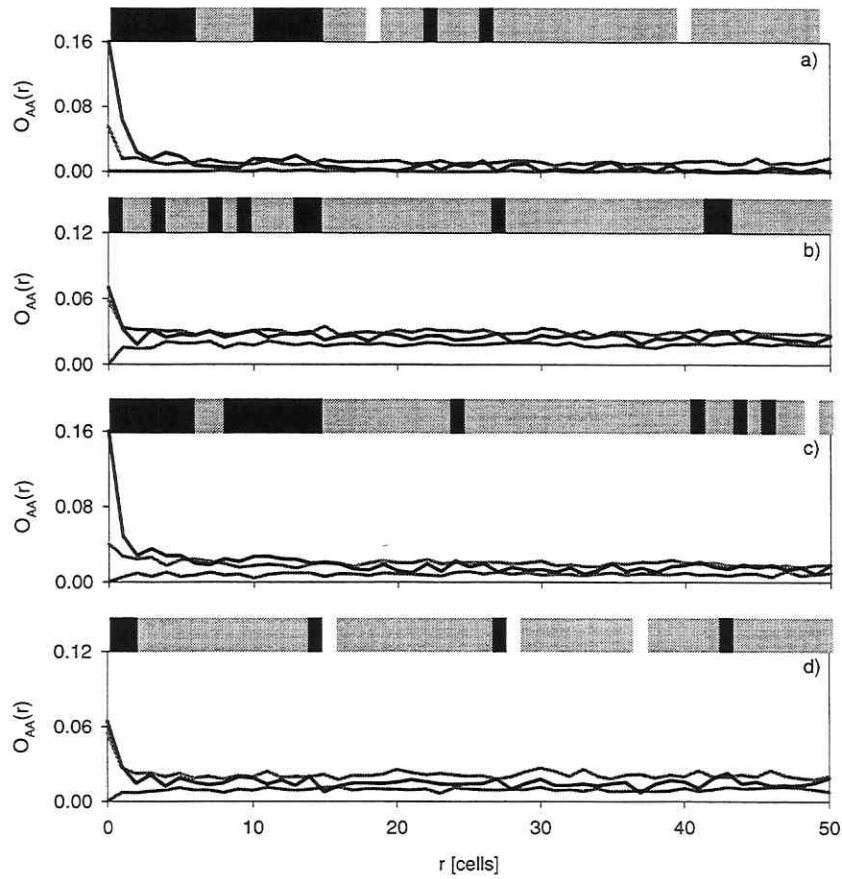


Figure 6.2: Analysis of patterns observed in Nahal Saif. a) Seedlings; b) trees; c) subadult trees and seedlings (trunk circumference $TC < 45$ cm); d) adult trees ($TC \geq 45$ cm). Bars as in Figure 6.1.

distributed randomly (Figure 6.5b). If we increase seed-attractivity (i), clumping of seedlings persists over longer time periods and leads to a more pronounced clumping of trees at large scales in the year 60, just after some good years (leading to recruitment; Figures 6.4c and 6.5c). The correlation between seed-attractivity and density of safe sites (ii) extends the range of scales at which seedlings are clumped, but does not change the pattern in time (Figure 6.4d). The clumped pattern of trees is changed only slightly (Figure 6.5d). Relating seedling mortality with both seed-attractivity and density of safe sites (iii) clearly increases clumping of seedlings in both time and spatial range (Figure 6.4d). After some years (necessary for seedlings to grow up and become trees), there is also a very pronounced clumping of trees (Figure 6.5d). This

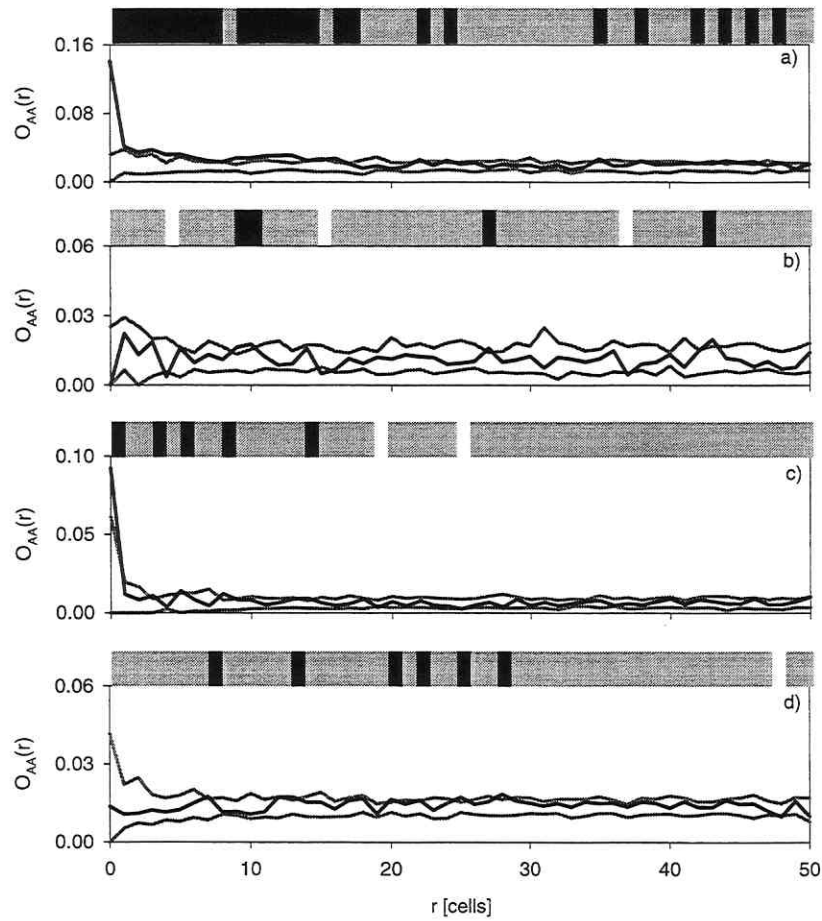


Figure 6.3: Analysis of patterns observed in the field. a) Nahal Saif, small trees and seedlings ($TC < 75$ cm); b) Nahal Saif, large trees ($TC \geq 75$ cm); c) Nahal Katzra, subadult trees and seedlings ($TC < 45$ cm); d) Nahal Katzra, adult trees ($TC \geq 45$ cm). Bars as in Figure 6.1.

clumping is reduced by a higher relocation rate of seed-attracting supercells (iv; Figures 6.4e, 6.5e). However, we observe also some regular spacing of seedlings at a scale of 5-14 cells. As expected, an increase in tree competition has no effect on clumping of seedlings (besides some changes due to random effects), but decreases clumping of trees over time notably (Hypothesis 2; Figures 6.4f, 6.5f). The pronounced clumping of trees at small scales after the year 60, is obviously due to the large recruitment event sustained by the occurrence of further good years. As these young trees grow up, they compete with each other, thinning the clumped pattern.

Figure 6.4 (caption on page 112)

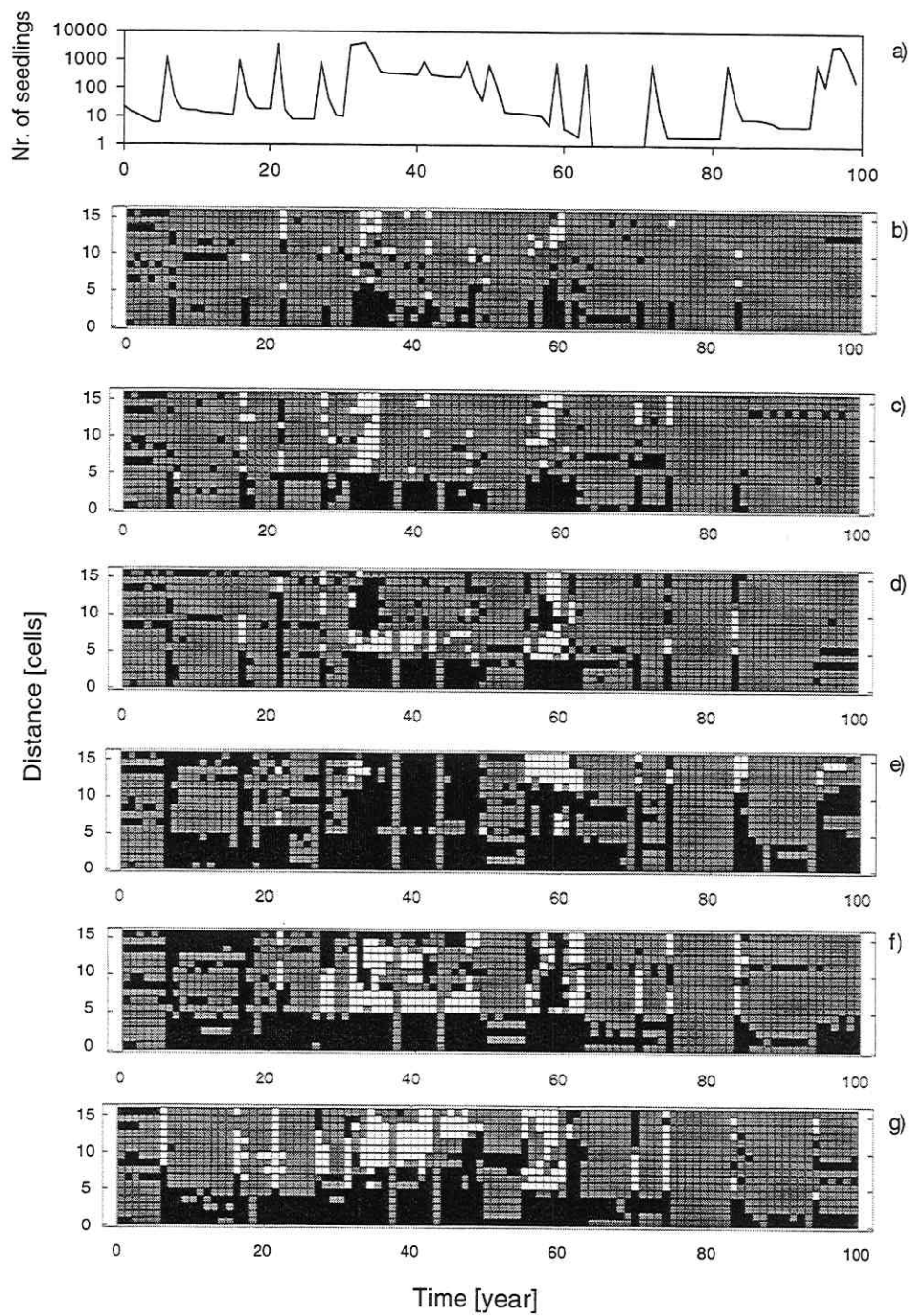


Figure 6.5 (caption on page 112)

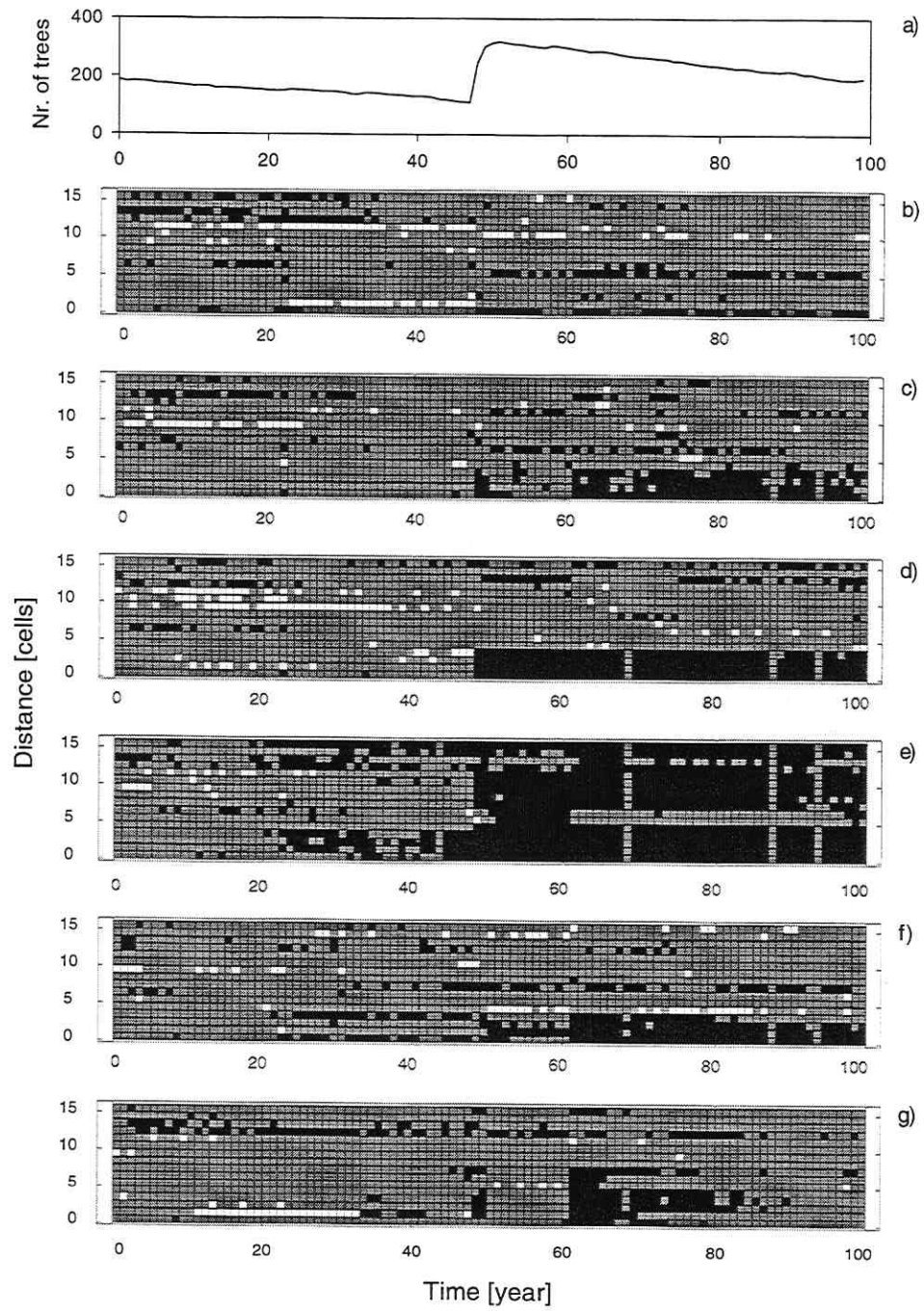


Figure 6.4 (page 110): Time series and analysis of spatial pattern of seedlings simulated over 100 years under different scenarios. a) Time series under scenario 1; b) - g) Change of the spatial pattern with time (x-axis) on a range of scales (y-axis). We distinguish whether the spatial distribution is significantly clumped (black), random (grey), or significantly even spaced (white) at the different scales. b) scenario 1; c) rule (i); d) rules (i, ii); e) rules (i - iii); f) rules (i - iv); g) scenario 2.

Figure 6.5 (page 111): As Figure 6.4, but for trees instead of seedlings.

6.5 Discussion

An interpretation of spatial patterns requires an understanding of the temporal variation of these patterns (Ives & Klopfer 1997). In all model scenarios, we observed that the spatial distribution of *A. raddiana* is highly variable in time. This variability is related to the high variability in seedling density over time and the resulting clumped spatial seedling distribution. We have snap-shots of the spatial tree distribution of two field locations only. Therefore, a comparison between field and model results has to be conducted cautiously. In the field, we observed clumping of small trees at small distances. 'Small' trees has different meanings in the two study sites. In Nahal Saif, trees of up to 75 cm trunk circumference exhibit clumping, but in Nahal Katzra clumping ceases at a size of 45 cm. This can be taken as a confirmation of our view that the spatial pattern varies over time, meaning that our two study sites are at different stages. From this point of view, the spatial patterns observed in the field and under scenario 1 coincide quite well. Random distribution dominates the spatial pattern, and seedlings exhibit some clumping at small scales. With an increasing degree of correlation between factors supporting establishment, clumping of seedlings as well as clumping of trees increases and leads to a persistent clumping of trees on all scales observed. The spatial decoupling of recruitment and competition between trees decreases the spatial range and temporal persistence of the clumping and leads back to patterns that coincide quite well with observations from the field. Therefore, both of our 'contrasting' scenarios seem possible.

The second scenario coincides well with the widespread opinion that a random distribution of adult trees and a clumped distribution of seedlings can be explained by clumped germination and subsequent thinning due to competition (e.g. Greig-Smith & Chadwick 1965, Phillips & MacMahon 1981; Prentice & Werger 1985, Sterner *et al.* 1986, Haase *et al.* 1996, Martens *et al.* 1997). However, even though we did not disprove this hypothesis, we showed that there is an alternative explanation: A decreasing aggregation with age can also be caused by relatively high, density independent mortality as given in SAM (hypothesis 1). Clearly, this hypothesis may explain the disappearance of clumping with tree age, but not even spacing of large trees. Thus, hypothesis 1 is not applicable to systems that show a transition from clumping to even spacing with increasing age as observed by Phillips & MacMahon (1981), Haase *et al.* (1996), and Martens *et al.* (1997), but not observed by Greig-Smith & Chadwick (1965). The transition to even spacing has been explained by competition for water (Phillips & MacMahon, 1981). However, even though water is scant in deserts, competition for water might not be a crucial factor to survival, because due to the harsh environment, many species seldom attain densities high enough to result in competition (Went 1955; Halevy 1971; Briones *et al.* 1998).

Clumping of *Acacia* seedlings has been observed in several studies (Greig-Smith &

Chadwick 1965; Smith & Goodman 1987; Kennenni & Van der Maarel 1990; Skarpe 1991; Milton 1995). *Acacia* seedlings are often absent beneath adult conspecifics but concentrated at the periphery of adults, which is due to a trade-off between the effects of seed distribution (leading to many seedlings beneath the seed-producing tree) and seedling mortality (which is highest beneath trees; Smith & Goodman 1987; Smith & Shackleton 1987; Kennenni & Van der Maarel 1990; Milton 1995). However, seed distribution is different in ephemeral riverbeds, because seeds are redistributed by flood events. This view is confirmed by our pattern analysis, because we found no significant departure from randomness when analysing seedling distribution relative to the distribution of adult trees. Further, this indicates that vegetative reproduction, e.g. observed by Halevy (1971) for *A. albida* in the Negev and by E. Schulz (pers. comm.) for *A. raddiana* in the Sahara, is absent in *A. raddiana* in the wadis of the Negev, because vegetative reproduction would have led to clumping of small trees beneath large tree.

From an analysis of size-frequency distributions we were able to show that recruitment of *A. raddiana* is heterogeneous in time (Wiegand, K., *et al.*, subm., Chapter 5 of this thesis). Here, we found that recruitment is also heterogeneous in space. Water is a factor crucial to germination and early seedling establishment of Acacias (Kennenni & Van der Maarel 1990; Wilson & Witkowski 1998, but see Smith & Goodman 1987) and can explain both temporal and spatial heterogeneity of *Acacia* establishment.

The motivation of our study was to improve our knowledge on the factors driving the population dynamics of *A. raddiana* in the Negev by investigating the spatial distribution of these trees. Even though our study could not reveal a unique set of processes underlying the observed patterns, it is an important step in our search for driving mechanisms. We learned that recruitment leaves tracks in spatial pattern of *A. raddiana* and we are confident that it will be possible to learn more about the recruitment from a more intensive study of spatial patterns. It would be interesting to investigate the spatial patterns of many locations that experienced different weather regimes over the last years and to study the relationship between weather and the tree size at which clumping of small trees ceases, because this may give new insights into the relation of weather and recruitment. Finally, an important contribution of scale-dependent pattern analysis towards future field studies is that pattern analyses give important indications for the scales at which future studies should be conducted (Getis & Franklin 1987).

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6.6 References

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7 Summary and Discussion

7.1 Abstract

In this thesis, I developed SAM, a spatially-explicit, individual-based, stochastic simulation model of *A. raddiana* trees in the Negev desert. To my knowledge SAM is the only model focusing on the population dynamics of an African *Acacia* species. The model is landscape related, a new approach not yet frequently used for plant models. SAM summarizes the actual knowledge on the population dynamics of *A. raddiana*, an ecologically important tree species that is believed to be endangered.

The model was thoroughly analyzed via a sensitivity analysis. A new idea in this sensitivity analysis has been the definition of 95%-confidence limits in order to determine whether changes in population characteristics are more likely to be caused by a change in a parameter than being due to purely random effects. From the sensitivity analysis, I evaluated the relative importance of different processes, and determined the major threats to the long-term survival of *A. raddiana* as well as possible management measures. I conducted further management related studies via simulation experiments concerning a possible climatic change and the effect of roads on the long-term survival of the *Acacia* trees.

A possible linkage between the simulation model and a geographical information system (GIS) has been investigated. This again is a very new technique. However, even though I constructed the technical prerequisites for this linkage, I decided to retreat from this linkage, because, surprisingly, my investigations showed that there was no relationship between the geomorphological data stored in the GIS and the population dynamics of the *Acacia* trees. Furthermore, in this context, I found out that in the case of the Negev's *Acacias* it is more efficient to measure the spatial distribution of the trees directly in the field than to determine the distribution from remotely-sensed images. During these investigations I acquired knowledge on GIS and remote sensing which I summarized in an introduction to these techniques specifically written as a starting point for modellers interested in linking their model to GIS.

In order to learn as much as possible about the population dynamics of *A. raddiana*, snap-shot patterns in the form of size-frequency distributions and spatial tree distributions were investigated. For the analysis of the size-frequency distributions I had to conduct some preparatory studies. First, I statistically analyzed patterns of *Acacia* tree growth. Second, I determined a preliminary size-age relation for these trees. Furthermore, I had to find a way to describe the size-frequency distributions that allowed me to make meaningful comparisons between distributions observed in the field and those produced by the model. A breakthrough in this study was the fact that I invented a new index of disorder. The most important result of this investigation is that recruitment has been a rare event for many decades. Therefore, a lack of recruitment, as currently observed in the Negev, is not necessarily a reason for concern.

Finally, I investigated the spatial pattern of tree distribution using a scale dependent method. Surprisingly, there have been very few modelling studies that have taken advantage of this technique. My analysis of field data showed that except for small trees, which are clumped, *A. raddiana* is randomly distributed in the Negev desert. Via simulation experiments, I could show that this might be caused by a combination of clumped recruitment and high density-independent mortality of *Acacia* trees. Thus, the widespread idea that density-dependent mortality is necessary for a transition from clumping of small trees towards a random distribution of large trees may not hold for *Acacia* trees in the Negev.

The random distribution of trees confirms my result from the GIS study that geomorphology does not affect the spatial distribution of the *Acacia* trees. The influence seems to be restricted to seedlings (which occur in clumps); because of the high seedling mortality these clumps fade out and it becomes difficult to determine any relationship between tree distribution and geomorphology.

The spatially-explicit design of SAM turned out to be less important than initially thought. I discuss the possibilities and dangers of spatially-explicit simulation models and further possible applications of the SAM model.

7.2 Summary

Acacia trees are the only trees in most parts of the Negev desert of Israel. Due to low precipitation (less than 100 mm/year), the distribution of these trees is restricted to ephemeral riverbeds (wadis). *Acacia* trees provide food and shelter to many animals and are a major source of livestock feed and firewood for the native Bedouin people. Despite of the important function these trees have in the Negev ecosystem, there has been little information on their demography. Furthermore, there have recently been alarming reports of large-scale mortality and low recruitment of the *Acacia* trees in the Negev.

The aim of this study was to gain an understanding of the long-term population dynamics of *A. raddiana*, the most abundant *Acacia* species in the Negev, and to investigate potential management measures to ensure the long-term survival of these trees. The chosen approach is the development, evaluation, and application of a simulation model accompanying ongoing field studies. Field studies covering a few years provide only short-term information, while the life-span of *Acacia* trees extends to several decades. With a model, it is possible to extrapolate from short-term information to time scales appropriate to the study of long-lived species.

A spatially-explicit, individual-based, stochastic simulation model, called SAM, has been developed. To my knowledge, it is the only simulation model that focuses on the population ecology of an African *Acacia* species. The model is landscape-related, an approach increasingly used to simulate animal populations, but not yet often used for plants. More exactly, the model is a further development of cellular automata models (CAM). In CAMs, the modelled area is usually represented as a regular mosaic of cells, the cell size being determined by typical biological scales. In the present case, the canopy size of an adult tree (5m*5m) is such a typical biological scale. However, in the Negev desert, trees may grow within distances of a few meters, but mean nearest-neighbour distance is as large as about 20 m. Furthermore, tree distribution is largely restricted to wadi beds. Thus, a standard CAM approach would result in a waste of computer memory and tremendous simulation times. Therefore, I introduced an irregular grid of supercells. A supercell represents an area of 20m*20m and serves to administer landscape data. Only those supercells located within the wadi area are subdivided into 16 cells, corresponding to the cells of classical CAMs. However, such a cell does not directly represent an ecological state (e.g. "no tree", "young tree", "adult tree") as in classical CAMs, but is mainly an administrative object. Given the small population sizes, I've chosen to model the *Acacia* trees via an object-oriented, individual-based approach. I distinguish between seedlings, trees, and dead trees. Each cell may contain one or several seedlings, live tree and dead tree objects. Dead trees are taken into account, because they remain standing for about 10 years.

In SAM, a year is divided into two periods, summer and winter. In each period, different life history events take place. In both periods, modules for growth and mortality of seedlings, for growth of trees, infestation of trees by mistletoes (*Loranthus acaciae*), deterioration of moisture status of trees and for tree mortality are successively employed. Additionally, in summer, seeds are produced, suffer predation by seed beetles (*Bruchidius arabicus*, *Caryedon palaestinus*; family Bruchidae) and disappear from the wadibed. In winter, seeds are dispersed and germinate, and the 'ageing' and removal of dead trees takes place.

For model parameterization, I used field data for direct and indirect estimation of parameters. Via a parameter fit, I could use actual, easily obtainable data on e.g. moisture status or mistletoe infestation of *Acacia* trees to estimate corresponding rates for deterioration of the moisture status or infestation by mistletoes. Model development forced me to compile and supplement

the present knowledge on the population dynamics of *A. raddiana* and to give this knowledge a hierarchical structure. The next step was to evaluate the relative importance of the different processes such as seed distribution and seed infestation by parasites, germination, mortality, and mistletoe infestation to the survival and recruitment of *Acacia* trees in the Negev. For two field sites, I conducted an uni-factorial sensitivity analysis with regard to the population size after a period of 200 years and relative to the long-term population growth rate. SAM is a stochastic model. Therefore, differences in the outcome of two simulation runs may be due to stochastic effects, due to a change in parameters, or due to both. This also holds true when comparing averages of two sets of simulations each consisting of hundreds of simulation runs under a fixed parameter set. Instead of neglecting this problem or conducting mega-replications, I decided to run simulations consisting of 500 runs 'only' and to determine 95%-confidence limits for the population size after 200 years and the long-term population growth rate under the two standard parameter sets (one for each field location). I consider only those parameters to have an essential influence on the population dynamics of the *Acacia* trees that have the power to alter the population size or growth rate beyond these confidence limits. Contrary to popular perception, the influence of infestation by mistletoes could not be discriminated from natural stochasticity. Mortality rates at different life stages, the production of uninfested seeds, and the weather regime were most influential.

The influence of a possible climatic change and a change in large mammalian herbivore densities have been investigated in simulation experiments. Both the climate and wadi utilization by large mammalian herbivores are possible contributing factors to a decline of *Acacias* in the Negev. It turned out that a decrease in the frequency of years with good rainfall, a prerequisite for germination and important for the survival of seedlings, has a pronounced negative effect on the long-term population growth rate of *A. raddiana*. Passage of seeds through the digestive tract of large mammalian herbivores is known to enhance seed germination. Most importantly, I could show that an increase in germination rate, as may result from increased large mammalian herbivore densities, may counteract the decremental effect of unfavourable climatic conditions.

Further simulation experiments deal with the negative effect of roads cross-cutting wadi systems. Roads alter the flood regime, which leads to modifications in seed dispersal and reduces the water availability to the *Acacia* trees. I could show that both factors have a negative impact on the population dynamics of *A. raddiana*. Culverts under the road would reduce the severity of this impact although this should be done in conjunction with an increase in density of herbivorous mammals, in order to facilitate seed dispersal and germination.

When investigating management-related aspects, I came to the conclusion that the most suitable management measure is the reintroduction of herbivorous mammals. This is because an increase in herbivorous mammal densities would lead to a pronounced increase in germination rates which has an overriding effect on the long-term population growth rate. This is a measure that can be put into practice relatively easily.

At this point we've already learned a lot about the population dynamics of *A. raddiana* and about suitable management measures. Nevertheless, there are still possibilities to improve our knowledge. For example, SAM considers the wadi morphology only implicitly. However, one might argue that wadi morphology is a determinant of where seeds get deposited by winter floods, if the seeds will be supplied with sufficient water for germination and establishment, and if water will be sufficient for adult survival. In other words, the morphology might be important to the distribution of establishing trees within the wadi bed and to the performance and survival of trees in specific locations. Thus, if one wants to apply the SAM model to a specific wadi, the

morphology of that wadi would have to be taken into account. Therefore, I investigated the possibility of expanding the model towards a direct consideration of wadi morphology. Furthermore, I considered the development of a method that allows me to initialize and parameterize the model in an efficient way in order to be able to run the model for different wadis which would be interesting for the study of applied management aspects regarding specific wadis. I followed these aims on the basis of readily available GIS and remotely-sensed data, methods that are of increasing importance to modellers, but still not well known to many modellers. Therefore, I gave an extensive introduction to the basics of GIS and remote sensing with respect to a linkage to grid-based simulation models. Then, I followed the idea of initializing SAM with the help of remotely sensed data and carried out a regression analysis relating a vegetation index derived from a satellite image to the tree distributions in two study sites. This study showed a weak correlation between the two. I discuss several possibilities for improving the relationship. However, these methods would considerably increase the time used for image analysis. Therefore, I conclude that it is more effective to measure the tree distributions in the field. In order to find ways to relate the population dynamics of *A. raddiana* to wadi morphology, I compared the wadi morphology characterized by wadi width, slope, and curvature to the current tree distribution of our study sites. However, based on the data currently available, I found that wadi morphology and tree distribution are not related to each other. This indicates that within-wadi morphology is not as important as hypothesized. Therefore, there is no point in extending the SAM model with an explicit morphological component.

Given the grave concern about *Acacia* trees in the Negev, it is important to learn as much as possible from the data currently available. Two types of snap-shot data suitable for an investigation towards an improved understanding of long-term population dynamics were available: tree size-frequency distributions and spatial tree distributions. Both are highly condensed indices of population dynamics acting over many years. Analyzing these distributions and comparing their characteristics to characteristics produced by simulated populations under different model scenarios allowed me to gain a further understanding of the population dynamics of *A. raddiana*.

The first step towards the investigation of the size-frequency distribution was the analysis of data on tree growth in terms of trunk circumference from two growth periods and two study sites. Previously, there was no knowledge on the relationship between tree size and age for *Acacia* trees in the Negev. Therefore, I determined a size-age relation using an iterative approach. I could show that the oldest trees can easily be 200 years old, instead of 50 years as previously thought. Then, I analyzed tree growth with respect to annual rainfall, mistletoe infestation, tree moisture status, and browsing by large herbivores. It turned out that rainfall has a pronounced effect on the average growth of a tree population, but that inter-tree variability in tree growth is very high. Most interestingly, infestation by mistletoes and a poor tree moisture status had a weak effect on average tree growth, but reduced inter-tree variability. Furthermore, and surprisingly, heavy browsing had no effect on tree growth in terms of trunk circumference. Knowledge on tree growth was the first prerequisite for my study of tree size-frequency distributions. A second prerequisite was to find a good way to describe the essential characteristics of these distributions. The basis for this description was the idea that the frequency of tree sizes should decline exponentially with tree size and the often reported observation that many *Acacia* populations throughout Africa and Australia deviate from this ideal showing irregular tree size-frequency distributions. I chose to describe the size distributions with Simpson's index of dominance (which should be high for an exponentially declining size distribution) and developed an index of disorder, measuring the deviation from a monotonous

decline. Equipped with knowledge on tree growth and indices describing tree size frequency distributions, I still had to design model scenarios before I could start with the very study of the size frequency distributions. The model scenarios consisted of: rare recruitment vs. yearly recruitment, age-dependent vs. age-independent tree mortality, and variable growth vs. deterministic average growth. Variable growth means stochastic growth with growth increments following the irregular growth patterns observed in the field. I implemented this by setting up several probability distributions allowing for a consideration of possible mistletoe infestation, tree moisture status, and for consideration of different years with low, intermediate, and high amounts of rainfall, all of which have an effect on *Acacia* growth (see above). For the probability distributions, I used a Kernel density estimation technique to transform growth measurements from the field into growth increment-probability distributions for tree growth.

I ran the model under the different scenarios and investigated the effect of the different processes such as recruitment, growth, and mortality on tree size-frequency distributions and compare the model results under the different scenarios to size-frequency distributions observed in the field. The study confirmed rare recruitment events as a major factor shaping tree size-frequency distributions and showed that the paucity of recruitment has been a normal feature of *A. raddiana* in the Negev over many years. Irregular growth showed a moderate influence on size distributions. A literature review showed that this factor might be an important, yet largely overlooked factor in regions with higher rainfall than in the Negev. Finally, the size frequency distributions observed in the Negev revealed the information that, in this harsh environment, possible age-dependent effects play a negligible role in the mortality of adult *Acacia* trees.

After the very successful investigation about the population dynamics of the Acacias from tree size-frequency distributions I turned to a study of the spatial distribution of *A. raddiana* in the Negev desert. However, this investigation has not been as extensive as the previous one. For the analysis of the spatial patterns, I used a scale-dependent, individual-centered method, the ring-statistic. This method involves the placement of circular sample plots around individual trees. The density of trees within these rings is calculated for different radii. This results in information on the density of plants of type A (whose density within the rings has been determined) relative to plants of type B (around which the sample rings have been placed). I determined both the density profiles of mapped tree populations and of randomized spatial distributions. A comparison between 'real' and randomized density profiles allowed me to determine if *Acacia* trees in the Negev are randomly dispersed, clumped, or regular spaced for a range of scales. I investigated the spatial pattern of trees of different sizes relative to the same size classes ($A=B$), the pattern of dead trees (again $A=B$), and the pattern of seedlings relative to mature, seed-producing trees ($A \neq B$). In the field, random spacing turned out to be the predominant pattern. However, on small scales, seedlings are clumped relative to other seedlings, but not relative to adult trees. This indicates clumped regeneration independent of the location of the seed-producing trees. The latter can be explained by the floods occurring during winter storms redistributing *Acacia* seeds within the wadibed. After analysis of field data I ran SAM under two contrasting model scenarios representing hypotheses explaining the clumping of seedlings and the random distribution of trees. One hypothesis is that there is spatial heterogeneity in seed distribution, germination, and seedling mortality, but that these heterogeneities are not correlated with each other. The second hypothesis assumed a correlation between these heterogeneities leading to areas suitable for establishment and density-dependent tree mortality due to competition. Both scenarios led to spatial distributions that were quite variable over time. Furthermore, both scenarios produced spatial patterns in qualitative agreement with field observations. Therefore, the classical view that clumped seedling

distribution and a random pattern of older trees is due to clumped regeneration and density-dependent mortality may not hold for *Acacia* trees in the Negev.

7.3 Discussion

7.3.1 This thesis

The investigations described in this thesis are part of an integrated approach combining field studies and modelling. None of these approaches alone provides a complete view, but they mutually promote each other's findings, which is very important when trying to understand the population dynamics of a long-lived species such as *Acacia raddiana*. Field studies (Ward & Rohner 1997; Rohner & Ward in press) are necessary for the development of the structure and parameterization of the model, whereas the model administers and evaluates the present knowledge, uncovers gaps in knowledge, extrapolates short-term information to meaningful time scales, and, by sensitivity analysis, indicates directions for future research (Chapter 2). The simulation studies conducted in Chapter 2 emphasize the need for further investigations of seed production and mortality rates under different moisture and rainfall conditions. Such field investigations are currently in progress in the Negev and results will be used to improve the parameterization of SAM.

The studies described in Chapters 2 and 4 describe the basic characteristics of SAM. This includes a description of the model rules (which actually form a structured summary of our present knowledge), a study of the relative importance of the single model parameters, an investigation of the possibilities for expanding the model from caricatured landscapes to the integration of real wadi morphology into the model, and the investigation of the possibilities to initialize the tree distribution via remotely sensed images. These studies contribute to the basic understanding of the model as well as the population dynamics of the *Acacia* trees.

Furthermore, the model has also been used for several further investigations. In simulation experiments, the influence of possible changes in climate (Chapter 2) and the influence of roads cross-cutting wadibeds (Chapter 3) have been studied. Both a decrease in the frequency of good years and the existence of roads which hinder the water flow in the wadi bed have pronounced negative effects. However, an increase in the germination rate of *Acacia* seeds, such as may result from passage through the digestive tract of large mammalian herbivores, is capable of counteracting the detrimental effect of e.g. unfavourable climatic conditions (Chapter 2). Two further modelling studies were conducted in order to learn more about the long-term population dynamics of *A. raddiana* from snap-shot patterns. Via the comparison of tree size-frequency distributions observed in the field and produced by SAM, it could be shown that rare recruitment has been an integral part of *Acacia* population dynamics in the Negev for many years and that mortality of *A. raddiana* is a function of tree moisture status, but independent of tree age. Thus, trees become weakened in the harsh desert environment and die before old age has an impact on survival (Chapter 4). Furthermore, the analysis of spatial tree distributions showed that *Acacia* trees are randomly distributed within the wadi bed with the exception of seedlings which occur in clumps. One model scenario shows that this can be explained by centers of recruitment (including higher seed numbers, better germination, and lower seedling mortality in these optimal locations) leading to seedling clumps and subsequent strong competition between trees which leads to a random distribution. However, another scenario showed that clumping of seedlings and random distribution of trees can also be explained by heterogeneous, but not spatially correlated, seed distribution and germination in combination

with weak competition between trees only. In this scenario, which is in agreement with the 'normal' model rules given in Chapter 2, clumped seedlings thin out due to the relatively high seedling mortality only. Hence, the pattern analysis of the tree distribution observed in the field indicates that spatial effects are most important during the recruitment phase and call for further field studies which may determine which of the two hypotheses generated by the model is correct (Chapter 6, Levin 1992).

The results of the pattern analysis (Chapter 6) give us a further hint as how to interpret the results of the GIS study. The random distribution of the trees confirms our presumption that wadi morphology does not affect the spatial distribution of the adult *Acacia* trees. The clumped distribution of seedlings indicates that wadi morphology might be important at early life stages. If there are centers of recruitment, as assumed in the first model scenario, it is most likely that these locations ideal for recruitment are closely related to wadi morphology. However, even if this was the case, it is extremely difficult to uncover the relationship between wadi morphology and seedling distribution because of the very low seedling densities.

A main reason for our spatially-explicit modelling approach was the idea of linking SAM to GIS. This idea was based on the expectation of a significant influence of wadi morphology on the performance of the *Acacia* trees. Furthermore, simulation models of plant population dynamics in semiarid regions revealed spatial aspects to be very important (Wiegand *et al.* 1995, Jeltsch *et al.* 1996). However, during the process of model development and evaluation we learned more about the importance of space for our specific system. As described above, it turned out that wadi morphology, at least at the scales studied by us, has a limited influence on *Acacia* population dynamics. Recruitment could be identified as a process heterogeneous in space and it turned out that population dynamics of established trees is mainly independent of spatial effects. One exception is the competition for moisture between trees growing close together. This seems to be of minor importance, because trees rarely live at short distances. However, our spatially-explicit modelling approach allowed us to quantify the effect of tree competition on tree moisture status and thus on tree mortality via a parameter fit (see Chapter 2).

7.3.2 Spatially-explicit modelling

It is important to reflect what we've learned, we also need to consider the disadvantages of our spatially-explicit modelling approach. The time demand for program implementation was clearly higher. This is partly due to the facts that *A. raddiana* lives mostly within wadi beds and that the model was supposed to be linked to GIS, both demanding a rather sophisticated model design. Furthermore, simulation times and computer memory demands were increased. In short, the disadvantages are mainly of a technical nature.

More generally spoken, are spatially-explicit models worth the effort? Do these models have tremendous data needs? There is no general answer to these questions. In the case of SAM one might argue whether the technical efforts were worth the results obtained from the model. However, for example, in a model of a shrub ecosystem in the semiarid Karoo, the spatially-explicit model design was a main key towards understanding the population dynamics of these shrubs. It was shown that some species need specific temporal and spatial conditions for recruitment (Wiegand *et al.* 1995). In models of savanna (e.g. Jeltsch *et al.* 1996, Hochberg *et al.* 1994) the spatial component is important because fire has different effects on single or grouped trees, the chance that a seed develops into an adult plant depends on the location of that seed and the probability that a seed arrives at a certain location depends on the location of the seed producing trees, competition between woody and herbaceous plants acts locally and is a very important factor due to the high plant cover. Additionally, Pacala & Deutschman (1995)

showed that forest ecosystem function depends on the spatial distribution of individual trees.

Whether or not the data needs of a model are great depends on the complexity of the model. Some spatially-explicit models are very simple and therefore have small data needs only (e.g. Bascompte & Solé 1996, Molofsky 1994). On the other hand, non-spatial models may be very complex and thus need many data for parameterization (e.g. Reuter 1996). That is, model complexity does not only depend on whether or not space is included. However, in general, rules for movement of animals or dispersal of plants are often a critical point of spatially-explicit models, because this information may be very important and yet difficult to obtain (Dunning *et al.* 1995, Lima & Zollner 1996, Ruckelshaus *et al.* 1997). In such a case, it is necessary to run the model with different parameter estimates and/or under different scenarios. From a sensitivity analysis we can learn whether the specific approach has a disproportionate impact on the model results. Only in that case it is important to conduct further field studies to improve the data basis. For example, the seed distribution rules of SAM proved to be of minor importance to the long-term survival of *A. raddiana* and therefore it is not worth the effort to study seed distribution in detail in the field (cf. *Sensitivity analysis* in Chapter 2, Dunning *et al.* 1995). This is not to say that seed distribution is not important, but that its effects are limited to the early life stages only.

Even though spatially-explicit models may often require more data for parameterization, they also offer more possibilities to gain information via the spatial patterns produced by the model. Examples are Chapter 6 of this thesis, a similar study by Jeltsch *et al.* (in press), or a study of pattern evolution in a plant community mediated by different disturbance regimes (Wiegand, T. *et al.* 1998). The comparison of (spatial) patterns observed in nature and produced by models are a central part of a modelling strategy, called pattern-oriented modeling (Grimm 1994). Another related advantage of spatially-explicit models is the possibility to produce outputs that visualize the spatiotemporal dynamics of populations under different scenarios (or management strategies). This may facilitate the communication between modellers and managers or field experts (Turner *et al.* 1995).

7.3.3 Future directions

In my thesis I showed that rare recruitment has been a normal feature of the population dynamics of *A. raddiana* for many decades, but the question remains how rare such events may be and still sustain *Acacia* populations. Therefore, I will soon address the question "How often do we need recruitment?".

Another idea is to use the model to look into the interactions between seeds, seed beetles, and large mammalian herbivores. At present, these interactions are modelled in a simplified way by considering a simple increase of the germination rate due to the passage of the seeds through the digestive tract of large mammalian herbivores and the assumption that all infested seeds are destroyed. For example, seed consumption by large mammalian herbivores has not only a direct positive effect on the germination rate of seeds, but also leads to a removal of seeds from seed beetles (cf. Halevy 1974, Coe & Coe 1987). The improvement in the germination rate of seeds due to consumption by large mammals is a function of the body mass of the mammal (Rohner & Ward in press). A modelling study of the influence of these aspects, in combination with possible negative effects of large herbivores on seedling survival, would give us deeper insights into the effects of possible reintroduction of large mammalian herbivores in the Negev. A further aspect of this triangular relationship between seeds, beetles and herbivores is the spatiotemporal dynamics of the seed beetles (in terms of seed infestation rate of trees at different time steps throughout the year). This would be especially interesting with respect to the

influence of the megaherbivores, because the megaherbivores remove the seeds before a second generation of beetles can attack as yet uninfested seeds and thus may influence the spread of the seed beetles in space and time.

Another study which would take full advantage of the spatially-explicit design of the SAM model would be a further analysis of the population dynamics of the mistletoes. The mistletoes are dispersed by bulbuls (*Pycnonotus xanthopygos*) and eaten by megaherbivores such as camels. A question that could be addressed might be "How many factors do we need to include in the model in order to describe the spread of the mistletoes as seen in the field data?" or in other words "What is the most simple explanation for the current distribution pattern?"

By this review of some possible applications of SAM, it should have become clear that even though SAM has not become a tool for the study of applied management aspects regarding specific wadis it is a tool that can be used to address many questions both of basic and applied character.

7.4 Conclusions

In this thesis, the knowledge on the population dynamics of *A. raddiana* and on possible management measures has been considerably improved. For example, it has been shown that recruitment of *A. raddiana* is seed limited and that rarity of recruitment has been a normal feature in the reproduction of these trees for many years. The reintroduction of large mammalian herbivores would considerably facilitate the regeneration of Acacias due to their positive effect on germination rate. Contrary to popular opinion, infestation by the mistletoe *L. acaciae* does not threaten the long-term population survival of *Acacia* trees.

In this thesis, I showed that it is possible to use snap-shot information such as size frequency distributions or spatial patterns to understand long-term population dynamics. However, a critical point in such analyses is the choice of indices retaining a maximum of information, as shown by the indices used in this thesis.

Statistics such as confidence limits are commonly used in many fields, but seldom in ecological modelling. I decided to make use of such basic statistics in this thesis because I believe that it is important to estimate the reliability of the conclusions drawn from modelling studies.

In my model of the population dynamics of *A. raddiana*, spatial aspects turned out to be of moderate importance only. However, this would not have been apparent if the model had not been spatially-explicit.

Spatially-explicit models are commonly believed to have tremendous data requirements. However, they may or may not need more data than non-spatial models, depending on the general complexity of the model.

7.5 References

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Deutsche Zusammenfassung

In meiner Dissertation entwickelte ich ein räumlich-explizites, individuenbasiertes Simulationsmodell (SAM) von Akazienbäumen (*Acacia raddiana*) in der Wüste Negev, Israel. SAM ist das einzige Simulationsmodell das sich auf die Populationsdynamik einer afrikanischen Akazienart konzentriert. Das Modell ist landschaftbezogen; ein Ansatz der selten auf Pflanzen angewandt wurde. Mit SAM wird das aktuelle Wissen zur Populationsdynamik von *A. raddiana*, einer ökologisch wichtigen und in Israel bedrohten Baumart, zusammengefaßt.

Das Modell wurde gründlich mit einer Sensitivitätsanalyse untersucht. Eine neue Idee bei der Ausführung dieser Sensitivitätsanalyse ist die Definition von 95%-Vertrauensintervallen, um Parameter-spezifische und stochastische Änderungen in den Populationscharakteristika trennen zu können. Mit Hilfe dieser Methoden wurden die relative Bedeutung der verschiedenen Prozesse bewertet, Faktoren für einen langfristigen einen Populationsrückgang von *A. raddiana* und mögliche Managementmaßnahmen ermittelt. Weiterhin wurden managementrelevante Simulationsexperimente durchgeführt, die sich mit einem möglichen Klimawechsel und dem Einfluß von Straßen (die das Wasserangebot für die Bäume verändern) auf das langfristige Überleben von *A. raddiana*, beschäftigen.

Eine mögliche Kopplung zwischen Simulationsmodell und einem Geographischen Informationssystem (GIS) wurde getestet. Auch dies ist ein sehr neuer Ansatz. Meine Untersuchungen haben jedoch zu dem überraschenden Ergebnis geführt, daß es keine Beziehung zwischen den geomorphologischen Daten des GIS und der Populationsdynamik der Akazien gibt. Deshalb wurde von dieser Kopplung Abstand genommen. In diesem Zusammenhang habe ich herausgefunden, daß es effizienter ist, die räumliche Verteilung der Bäume direkt im Freiland zu vermessen, anstatt die Verteilung mit Hilfe von Fernerkundungsbildern zu bestimmen. Die daraus gewonnenen Erkenntnisse über GIS und Fernerkundung wurden in Form einer Einführung in diese Techniken zusammengefaßt. Diese Einführung dient u.a. für Modellierer, welche an einer derartigen Kopplung mit GIS interessiert sind.

Um so viel wie möglich über die Populationsdynamik der bedrohten Akazien zu lernen, wurden snap-shot-pattern in der Form von Größenhäufigkeitsverteilungen und räumlicher Baumverteilungen untersucht. Für die Analyse der Häufigkeitsverteilungen von Baumgrößen wurden folgende Voruntersuchungen durchgeführt: 1. Untersuchung der Wachstumsdaten von *A. raddiana*. 2. Bestimmung einer Alters-Größen-Relation für diese Bäume. 3. Entwicklung einer Methode zur Beschreibung der Größenhäufigkeitsverteilungen, die es erlaubt, aussagekräftige Vergleiche zwischen im Feld beobachteten und vom Modell erzeugten Größenverteilungen aufzustellen. Der entscheidende Schritt der die Analyse ermöglichte, war die Definition eines neuen Index, dem 'Unordnungsindex'. Das wichtigste Ergebnis der Untersuchungen der Baumgrößenverteilungen ist, daß Neuetaulierungen schon seit vielen Jahrzehnten seltene Ereignisse sind. Deshalb ist ein Mangel an Neuetaulierungen, wie derzeit im Negev beobachtet, nicht nötigerweise ein Beweis einer langfristigen Populationsabnahme.

Schließlich habe ich mit Hilfe einer skalenabhängigen Methode die räumlichen Muster der Baumverteilungen untersucht. Von dieser Technik haben bisher nur sehr wenige Modellstudien Gebrauch gemacht. Meine Analyse der Felddaten hat gezeigt, daß, abgesehen von den kleinen Bäumen, die aggregiert auftreten, *A. raddiana* in der Wüste Negev zufällig verteilt ist. Mit Hilfe von Simulationsexperimenten konnte ich zeigen, daß dies durch eine Kombination von aggregierter Neuetaulierung und hoher, dichteunabhängiger Mortalität der Akazien verursacht sein kann. Deshalb trifft die weitverbreitete Idee, daß dichteabhängige (im Gegensatz zu dichteunabhängiger) Mortalität nötig ist, um einen Übergang von der Aggregation kleiner Bäume zu einer zufälligen Verteilung großer Bäume zu erzeugen, für Akazien im Negev möglicherweise nicht zu.

Die zufällige Verteilung der Bäume bestätigt das Ergebnis meiner GIS-Untersuchungen, daß die geomorphologische Faktoren keinen Einfluß auf die räumliche Verteilung der Akazien haben. Der Einfluß scheint sich auf die Keimlinge (die aggregiert auftreten) zu beschränken; wegen der hohen Keimlingsmortalität dünnen diese Anhäufungen aus, ein Zusammenhang zwischen Baumverteilung und Geomorphologie kann nur schwer festgestellt werden.

Die Bedeutung räumlicher Aspekte für die Populationsdynamik von *A. raddiana* stellte sich als geringer dar, als ursprünglich gedacht. Die Möglichkeiten und Gefahren räumlich-expliziter Simulationsmodelle und weitere mögliche Anwendungen des Modells SAM werden diskutiert.

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Appendix: SAM source code

```
//-----
//This listing is an illustration of the programm described in:
//K.Wiegand, F.Jeltsch, D.Ward (1999)
//Analysis of the population dynamics of Acacia trees in the Negev
//desert, Israel with a spatially-explicit computer simulation model
//Ecol. Modell. x:x-x
//
//The code is simplified; input, output, error management, protection,
//list management, and initializations are missing or incomplete.
//                                K. Wiegand, Leipzig, October 1998
//-----
//                                contents                                page
//-----
//
//    general variables, constants, type definitions II
//
//    main programm                                III
//
//    supercell            declarations            V
//                        definitions            VII
//
//    tree_base            declarations            XIII
//                        definitions            XIV
//
//    tree_base::seedling  declarations            XVI
//                        definitions            XVII
//
//    tree_base::tree      declarations            XXI
//                        definitions            XXIII
//
//    tree_base::deadtree  declarations            XXXIII
//                        definitions            XXXIV
//
//    random numbers                                XXXVII
//-----
```

II Appendix: SAM source code

```
//-----  
//    general variables, constants, type definitions  
//-----  
const int  width_A = 26; //Katzra    56; //Saif    26;  
const int  width_B = 105; //        57; //        105;  
  
// *** special variable types *****  
#ifdef __BORLANDC__  
enum type_weather      {BAD_W, MIDDLE, GREAT_W};  
enum type_moist_status  {POOR_M, GOOD_M};  
enum type_mistle        {NONE, ONE, TWO, THREE, FOUR}; //quarters of the canopy  
enum type_site_safety   {LOW, MEDIUM, HIGH};  
#endif  
  
#ifdef __UNIX__  
typedef int type_weather;  
const type_weather BAD_W      = 0; //dry  
const type_weather MIDDLE     = 1; //intermediate  
const type_weather GREAT_W    = 2; //good  
  
typedef int type_moist_status;  
const type_moist_status POOR_M = 0;  
const type_moist_status GOOD_M = 1;  
  
typedef int type_mistle;  
const type_mistle NONE        = 0;  
const type_mistle ONE         = 1;  
const type_mistle TWO         = 2;  
const type_mistle THREE       = 3;  
const type_mistle FOUR        = 4;  
  
typedef int type_site_safety;  
const type_site_safety LOW     = 0;  
const type_site_safety MEDIUM = 1;  
const type_site_safety HIGH    = 2;  
#endif  
  
//for super_cell see below  
typedef super_cell* coarse_grid[width_A][width_B];  
coarse_grid nahal; //array of pointers to super_cells  
  
int A, dA, B, dB;  
unsigned year, halfyear, runs;  
float zufall; //random number
```

```

//-----
//                               main programm
//-----
void main()
{
    super_cell::nahal_build();
    for(unsigned run_counter=0;run_counter<runs;run_counter++)
        onesimulation();
    super_cell::nahal_remove();
}

void onesimulation()
{
    year=0;halfyear=0;
    tree_base::nahal_startdistri();
    super_cell::nahal_set_attraction();

    for(year = 1 ; year <= g.maxyear ; year++ )
    {
        super_cell::make_weather();

        /*** SUMMER *****/
        halfyear++;

        /*** seedlings *****/
        seedling::growth();
        seedling::mortality();

        /*** trees *****/
        tree::growth();
        tree::growth_mistle();
        tree::alter_moist_status();
        tree::mortality();
        if(super_cell::weather==GREAT_W)
        {
            tree::seed_production();
            tree::seed_infestation();
            tree::seed_loss();
        }

        /*** deadtrees just once a year

        /*** WINTER *****/
        halfyear++;

```

IV

Appendix: SAM source code

```
/** seeds *****/
if(super_cell::weather==GREAT_W)
{
    super_cell::nahal_reset_attraction();
    tree::seed_distribution();
    seedling::germination();
}

/** seedlings *****/
seedling::growth();
seedling::mortality();

/** trees *****/
tree::growth();
tree::growth_mistle();
tree::alter_moist_status();
tree::mortality();

/** deadtrees *****/
deadtree::growth();           //counts time_since_death
deadtree::mortality();        //makes trees fall down

} //END OF YEAR-LOOP *****/

tree_base::cleanup_nahal();
}
```

```

//-----
//               declarations: super_cell
//-----
class super_cell
{
    public:
        super_cell* next;           // pointer to next super_cell
        static super_cell* sp_first; // to first super_cell
        static super_cell* sp_last;  // to last super_cell

        const int a;    //coordinates of supercell
        const int b;
        //each supercell is subdivided into 16 cells
        tree_base* cell[4][4];
        unsigned seed_cell[4][4];

        type_site_safety    site_safety; //LOW,MEDIUM,HIGH
        static float        site_safety_frequ[3];

        unsigned seed_attraction;    //0->normal, 1->attractive
        static float seed_attr_factor; //e.g.2: 2x as much seeds end up in attr cells
        static float seed_attr_change; //prob., for attr to move to different s-cell

        static type_weather    weather;
        static float            weather_prob[3];
        static unsigned         germinated_seeds;
        static unsigned         bad_yearsinarow; //bad for establishment and moisture

        //constructors etc.
        super_cell(int a=0,int b=0);
        ~super_cell();
        static void nahal_build();
        static void nahal_remove();

        //coordinate trafos x,y, <-> A,dA,B,dB
        static void coord_trafo(int x,int y){g.A=x/4;g.dA=x%4;g.B=y/4;g.dB=y%4;};
        static int coord_btrafo(int A,int dA){return(4*A+dA);}; //A,dA, -> x

        static unsigned cell_existence(int, int);           //x,y
        static unsigned super_cell_existence(int, int);     //g.A,g.B

        //seed attraction
        static void nahal_set_attraction();
        static void nahal_reset_attraction();
        static unsigned count_cells();
        static unsigned count_attr_cells();

```


VI Appendix: SAM source code

```
//weather
static void    make_weather();
};
```

```

//-----
//                      definitions: super_cell
//-----
super_cell::super_cell(int ax,int by)
: a(ax),b(by)
{
    next = NULL;
    for(int i=0;i<4;i++)
    for(int j=0;j<4;j++)
    {{
        cell[i][j]      = NULL;
        seed_cell[i][j] = NULL;
    }}
    site_safety = MEDIUM;
    seed_attraction = 0;
}

super_cell::~super_cell()
{
    next = NULL;
    for(int i=0;i<4;i++)
    for(int j=0;j<4;j++)
    {{
        cell[i][j]      = NULL;
        seed_cell[i][j] = NULL;
    }}
}

void super_cell::nahal_build()
{
    unsigned no_of_super_cells, flag;
    int f,ff;
    super_cell* this_ptr = NULL;

    //read source file with wadi data
    source>>no_of_super_cells;
    for(int i=0; i<no_of_super_cells; i++)
    {
        source>>f; source>>ff;
        //create super_cell
        nahal[f][ff] = new super_cell(f,ff);
    }

    //put super_cells into list
    sp_first=NULL; sp_last=NULL;

    flag = 0;

```

VIII Appendix: SAM source code

```

this_ptr = nahal[0][0];

for(i=0;i<width_A;i++)
for(j=0;j<width_B;j++)
{{
    if(super_cell::super_cell_existence(i,j))
    {
        if(flag==0)
        {
            sp_first = nahal[i][j];
            sp_last = sp_first;
            flag = 1;
        }
        else
        {
            this_ptr = nahal[i][j];
            sp_last->next = this_ptr;
            sp_last = this_ptr;
        }
    }
}}

//assign site safeties
super_cell* ptr = sp_first;
do{
    zufall = dr250();

    if(zufall < site_safety_frequ[0])
        ptr->site_safety = LOW;
    else if(zufall < site_safety_frequ[0]+site_safety_frequ[1])
        ptr->site_safety = MEDIUM;
    else
        ptr->site_safety = HIGH;

    ptr = ptr->next;

} while (ptr!=NULL);
}

void super_cell::nahal_remove()
{
    sp_first = NULL;
    sp_last = NULL;

    for(i=0;i<width_A;i++)
    for(j=0;j<width_B;j++)
    {{

```

```

        super_cell* ptr = nahal[i][j];
        delete ptr;
    }}
}

unsigned super_cell::cell_existence(int x, int y)
{
    if((x>=0)&&(x<4*width_A)&&(y>=0)&&(y<4*width_B)&&(nahal[x/4][y/4]!=NULL))
        return 1;
    else    return 0;
}

unsigned super_cell::super_cell_existence(int Aco, int Bco)
{
    if((Aco>=0)&&(Aco<width_A)&&(Bco>=0)
        &&(Bco<width_B)&&(nahal[Aco][Bco]!=NULL))
        return 1;
    else    return 0;
}

void super_cell::nahal_set_attraction()
{
    super_cell* ptr = NULL;
    unsigned ac;

    //init
    ptr = sp_first;
    do{
        ptr->seed_attraction=0;
        ptr = ptr->next;

    }while (ptr!=NULL);

    //increase attraction for supercells containing seedling(s)
    ptr = sp_first;
    do{
        for(int i=0;i<4;i++)
            for(int j=0;j<4;j++)
            {{
                if(ptr->cell[i][j]!=0)
                if(*(ptr->cell[i][j]->circum<subadult_circum_thresh)
                { //seedling present
                    ptr->seed_attraction = 1;
                    //one seedling per supercell is enough
                    i=4; j=4;
                }
            }}
    }
}

```

X

Appendix: SAM source code

```

        else if(ptr->cell[i][j]->base_trees_in_cell>0)
        { //seedling present, but not first in list
            tree_base* temp = ptr->cell[i][j]->next_base_tree;
            while(temp!=NULL)
            {
                if(temp->circum<subadult_circum_thresh))
                {
                    ptr->seed_attraction = 1;
                    i=4; j=4;
                }
                temp = temp->next_base_tree;
            }
        }
    }
    ptr = ptr->next;
} while (ptr!=NULL);
}

void super_cell::nahal_reset_attraction()
{
    unsigned xzufall,yzufall;
    unsigned sce; //super cell existence
    unsigned sa; //seed attraction
    super_cell* ptr = NULL;

    ptr = sp_first;
    do{
        if(ptr->seed_attraction==1)
        {
            if(dr250()<seed_attr_change)
            { //look for existing, not yet attractive, supercell
                do{
                    xzufall=r250n(width_A);
                    yzufall=r250n(width_B);

                    sce = super_cell_existence(xzufall,yzufall);
                    sa = 0 ;
                    if(sce==1)
                    {
                        if((nahal[xzufall][yzufall]->seed_attraction== 1)||
                           (nahal[xzufall][yzufall]->seed_attraction==11) )
                            sa = 1;
                        else sa = 0;
                    }
                } while((sce!=1)||sa==1);
            }
        }
    } while(ptr!=NULL);
}

```

```

        //old super cell becomes unattractive
        ptr->seed_attraction=0;
        //new attractive supercells become a preliminary attraction=11
        //->they will not be moved again in this time step
        nahal[xzufall][yzufall]->seed_attraction=11;
    }
}
ptr = ptr->next;

} while (ptr!=NULL);

ptr = sp_first;
do{    if(ptr->seed_attraction==11)
        ptr->seed_attraction=1;

        ptr = ptr->next;
    }while (ptr!=NULL);
}

unsigned super_cell::count_cells()
{
    super_cell* ptr = NULL;
    no_of_cells=0;
    ptr = super_cell::first;

    do{    no_of_cells+=16;
        ptr = ptr->next;
    } while (ptr!=NULL);

    return no_of_cells;
}

unsigned super_cell::count_attr_cells()
{
    super_cell* ptr = NULL;
    unsigned no_of_attr_cells = 0;

    ptr = sp_first;
    do{
        if(ptr->seed_attraction==1)
            no_of_attr_cells+=16;
        ptr = ptr->next;
    } while (ptr!=NULL);

    return no_of_attr_cells;
}

```


XII Appendix: SAM source code

```
}  
  
void super_cell::make_weather()  
{  
    zufall = dr250();  
    float a=0,b=0;  
  
    a=weather_prob[0];  
    b=weather_prob[1]+a;  
  
    if(year==1) super_cell::set_bad_yearsinarow(0);  
  
    if(zufall<a)    { weather=BAD_W; super_cell::bad_yearsinarow++; } //dry  
    else if(zufall<b){ weather=MIDDLE;super_cell::bad_yearsinarow++; } //intermediate  
    else          { weather=GREAT_W;super_cell::bad_yearsinarow=0; } //good  
}
```

```

//-----
//                      declarations: tree_base
//-----
class tree_base
{
    public:
    /*** variables: biological ***/
    const int x;    //coordinates
    const int y;
    float circum;

    /*** variables: technical ***/
    unsigned base_trees_in_cell; //counter
    tree_base* next_base_tree; //pointer to further seedling, tree or
                                //deadtree in the SAME cell
    static unsigned tc_random; //1 -> random circums, cf Ward&Rohner (1997)
    static unsigned xy_random; //1 -> coordinates randomly chosen in wadi

    /*** parameters: biological ***/
    static float growth_per_hyear;
    static float tc_cd_ordinate;
    static float tc_cd_slope;

    /*** procedures: technical ***/
    tree_base(int x_=0, int y_=0, float circum_=0);
    virtual ~tree_base();
    static void nahal_startdistri(); //allocates plant start distribution
    static void cleanup_nahal();    //removes all plants

    /*** procedures: biological ***/
    void apply_growth_formula(){circum+=growth_per_hyear;};
};

```

```

//-----
//                      definitions: tree_base
//-----
tree_base::tree_base(int x_, int y_, float circum_)
: x(x_), y(y_), circum(circum_),
  base_trees_in_cell(0), next_base_tree(NULL)
{}

tree_base::~~tree_base()
{
    circum          = 0;
    base_trees_in_cell = 0;
    next_base_tree   = NULL;
}

void tree_base::nahal_startdistrib()
{
    // allocate start distribution
    unsigned no_of_live_trees=0;   //"treesai*.txt"
    unsigned no_of_dead_trees=0;
    unsigned no_of_super_cells = count_cells()/16;
    float f, ff, t_c, f_temp, ff_temp;
    float help;
    super_cell* sc_temp = super_cell::first;

    /*** trees and seedlings ***/
    //read source file with wadi data
    source>>no_of_live_trees;

    for(int i=0; i<no_of_live_trees; i++)
    {
        source>>f; source>>ff;      //field coordinates
        source>>t_c;                //field trunk circumference
        //or random trunk circumference
        if(tc_random)
        {
            zufall = dr250(); help=0;
            do
            {
                treesize_negev>>t_c;
                treesize_negev>>help;
            }while(help<zufall);
        }
        //random x,y coordinates
        if(xy_random)
        {
            sc_temp = super_cell::first;

```

```

        zufall=r250n(no_of_super_cells);
        //move to randomly drawn super_cell
        for(int j=0;j<zufall;j++)
            sc_temp=sc_temp->next;
        //choose cell within super_cell
        f = 4*sc_temp->a + r250n(4);
        ff = 4*sc_temp->b + r250n(4);

        //create seedling or tree
        if(t_c<seedling::subadult_circum_thresh)
            seedling::snew(f,ff,t_c);
        else tree::tnew(f,ff,t_c);
    }
    //or field coordinates
    else
    { //create seedling or tree
        if(t_c<seedling::subadult_circum_thresh)
            seedling::snew(f,ff,t_c);
        else tree::tnew(f,ff,t_c);
    }
}

tree::set_moist_status();
tree::set_mistle();

/** dead trees **
source>>no_of_dead_trees;
for(i=0; i<no_of_dead_trees; i++)
{
    source>>f; source>>ff;
    source>>t_c;
    //create dead tree
    deadtree::dnew(f,ff,t_c);
}
deadtree::set_time_since_death();
}

void tree_base::cleanup_nahal()
{ //kills all plants
    seedling::cleanup_seedlings();
    tree    ::cleanup_trees();
    deadtree::cleanup_deadtrees();
}

```

```

//-----
//          declarations: seedling
//-----
class seedling : virtual public tree_base
{
    public:
    /*** variables: biological ***/
    /*** variables: technical ***/
    static int sAnzahl;           // number of seedlings
    long series_number;          // each seedling has a unique number
    static seedling* sfirst;      // pointer to beginning of seedling list
    seedling* next;              // pointer to next object in seedling list

    /*** parameters: biological ***/
    static float germination;
    static float site_safety_values[3];
    static float subadult_circum_thresh;
    static float good_year_mort[2]; //mortalities
    static float medium_year_mort;
    static float dry_year_mort;

    /*** procedures: technical ***/
    seedling(int,int,float);      //x,y,circum
    virtual ~seedling();
    static void snew(int,int,float); //x,y,circum
    static void sdelete(int,int,long,char*); //x,y,seriesnumber
    static void cleanup_seedlings(); //remove all seedlings

    /*** procedures: biological ***/
    static void germination();
    static void growth();
    static void mortality();
};

```

```

//-----
//                      definitions: seedling
//-----
seedling::seedling(int x_,int y_,float circum_)
: tree_base( x_, y_, circum_),
{
    init_obj(); //puts object in seedling list
    sAnzahl++;
}

seedling::~seedling()
{
    sremove_object(series_number); //removes object from seedling list
    sAnzahl--;
}

void seedling::snew(int _x,int _y,float _circum)
//creates new seedling
//puts seedling in cell and at the end of respective base_tree-list
{
    super_cell::coord_trafo(_x,_y); //x,y->A,dA,B,dB

    tree_base* ptr      = nahal[A][B]->cell[dA][dB];
    tree_base* pred      = nahal[A][B]->cell[dA][dB];
    seedling* ns         = NULL;

    //search end of base tree list of respective cell
    while(ptr!=NULL)
    {
        pred  = ptr;
        ptr    = ptr->next_base_tree;
    }

    //increase number of base_trees_in_cell
    nahal[A][B]->cell[dA][dB]->base_trees_in_cell++;

    //create new seedling
    ns = new seedling(_x,_y,_circum);
    //put new seedling at the end of the base_tree-list
    pred->next_base_tree = ns;
}

// *** seedling ***** sdelete ***
void seedling::sdelete(int _x,int _y,long _series_number)
//deletes seedling
{
    super_cell::coord_trafo(_x,_y); //x,y->A,dA,B,dB

```


XVIII Appendix: SAM source code

```

tree_base* ptr = nahal[A][B]->cell[dA][dB];
tree_base* pred = nahal[A][B]->cell[dA][dB];
//search
while( (ptr->series_number != _series_number)
{
    pred = ptr;
    ptr=(pred->next_base_tree);
}
//update base_tree list
pred->next_base_tree = ptr->next_base_tree;
nahal[A][B]->cell[dA][dB]->base_trees_in_cell--;
//remove seedling
delete ptr;
}

void seedling::cleanup_seedlings()
// kills all seedlings
{
    seedling* temp      = sfirst;
    seedling* next_temp = NULL;

    if(temp->next==NULL) temp = NULL;

    while(temp)
    {
        next_temp = temp->next;
        temp->sdelete(temp->x,temp->y,temp->series_number)
        temp = next_temp;
    }
}

void seedling::germination()
{
    int x_,y_;
    float eff_germ;
    super_cell* ptr = super_cell::first;

    do{
        //determine site_safety of super_cell
        switch(ptr->site_safety)
        {
            case 0: actual_site_safety= site_safety_values[0]; break; //LOW
            case 1: actual_site_safety= site_safety_values[1]; break; //MEDIUM
            case 2: actual_site_safety= site_safety_values[2]; break; //HIGH
        }
    }
}

```

```

//effective germination rate = germination rate * prob of safe site
eff_germ = germination*actual_site_safety;

if(eff_germ>0)
for(int di=0;di<4;di++)
for(int dj=0;dj<4;dj++)
{{{
    while(ptr->seed_cell[di][dj]>0)
    { //seed available in cell
        //remove seed
        ptr->seed_cell[di][dj]--;
        //germination?
        zufall = dr250();
        if(zufall<eff_germ)
        {
            x_ = coord_btrafo(a,di);
            y_ = coord_btrafo(b,dj);
            snw(x_, y_, growth_per_hyear;)
        }
    }
}}}
ptr = ptr->next;
}while (ptr!=NULL);
}

void seedling::growth()
{
    seedling *temp      = sfirst;
    seedling *next_temp = NULL;

    if(temp->next==NULL) temp=NULL;
    while(temp)
    {
        temp->apply_growth_formula();

        if(temp->circum<subadult_circum_thresh)
            temp = temp->next;

        else //seedling becomes an subadult tree
        {
            //safe pointer to next temp object
            next_temp = temp->next;

            //new tree
            tree::tnew(temp->x,temp->y,temp->circum);
            //delete seedling
            temp->sdelete(temp->x,temp->y,temp->series_number)

```

XX Appendix: SAM source code

```

        temp = next_temp;
    }
}

void seedling::mortality()
{
    seedling* temp      = sfirst;
    seedling* next_temp = NULL;
    float  ms; //mortality rate
    type_weather rw=super_cell::weather;

    if(temp->next==NULL) temp=NULL;

    while(temp)
    { //determine mortality rate
        if(temp->circum>5*growth_per_hyear)
            ms=good_year_mort[1];
        else //small seedling
        { //mortality weather dependent
            if(   rw==GREAT_W)   ms=good_year_mort[1];
            else if(rw==MIDDLE)  ms=medium_year_mort;
            else if(rw==BAD_W)   ms=bad_year_mort;
        }

        zufall=dr250();
        if(zufall<ms)
        { //death
            //safe pointer to next temp object
            next_temp = temp->next;
            temp->sdelete(temp->x,temp->y,temp->series_number);
            temp = next_temp;
        }
        else //survived
            temp = next_temp;
    }
}
```

```

//-----
//                      declarations: tree
//-----
class tree : virtual public tree_base
{
    public:
    /*** variables: biological ***/
    unsigned long      seed;
    type_mistle mistle; //0, 1, 2, 3, 4 quarters of the canopy
    type_moist_status moist_status; //0 POOR, 1 GOOD

    /*** variables: technical ***/
    static int tAnzahl;    //number of trees
    long series_number;    // each tree has a unique number
    static tree* tfirst;    //pointer to beginning of list
    tree* next;            //pointer to next object in tree list

    /*** parameters: biological ***/
    static float seed_equ_intercept;    //seed production
    static float seed_equ_slope;
    static float adult_circum_thresh;
    static float breeding_tree[2];    //subadult, adult
    static float seed_infest;
    static float seed_loss;
    static float init_mistle_sa[4];
    static float init_mistle_a[4];
    static float mistle_incr_prob[3];
    static float tgood_moist_sa;
    static float tgood_moist_a;
    static float worse_moist_scale;
    static float v_basic_vitality;
    static float v_moist_factor;

    /*** parameters: technical ***/
    static float max_tcircum;
    static float init_mistle_sa_cum[5];
    static float init_mistle_a_cum[5];

    /*** procedures: technical ***/
    tree(int,int,float);    //x,y,circum
    virtual ~tree();
    static void tnew(int,int,float);    //x,y,circum
    static void tdelete(int,int,long);    //x,y,seriesnumber
    static void cleanup_trees();

    /*** procedures: biological ***/
    static unsigned long seed_equation(float); //trunc circum => max. #seeds

```

```
static void seed_production();
static void seed_infestation();
static void seed_loss(); //due to water, animals,...
static unsigned seed_portion(long unsigned, float);
static void seed_distribution();
static void growth_mistle();
static void alter_moist_status();
static void growth();
        float vitality();
static void mortality();
};
```

```

//-----
//                      definitions: tree
//-----
tree::tree(int x_,int y_,float circum_,char* name)
: tree_base( x_, y_, circum_),
  moist_status(GOOD_M), mistle(NONE), seed(0),
{
    init_obj(); //puts object in tree list
    tAnzahl++;
}

tree::~~tree()
{
    tremove_object(series_number); //removes object from tree list
    tAnzahl--;
}

void tree::tnew(int _x,int _y,float _circum)
//creates new tree
//puts tree in the cell and at the end of the base_tree-list
{
    tree_base* temp=NULL;

    super_cell::coord_trafo(_x,_y);
    tree_base* ptr = nahal[g.A][g.B]->cell[g.dA][g.dB];
    tree_base* pred= nahal[g.A][g.B]->cell[g.dA][g.dB];
    tree*    nt = NULL;

    while(ptr!=NULL) //search end of base tree list of respective cell
    {
        pred = ptr;
        ptr = ptr->next_base_tree;
    }

    //create new tree
    nt = new tree(_x,_y,_circum,"tree");
    //update counter
    nahal[g.A][g.B]->cell[g.dA][g.dB]->base_trees_in_cell++;
    //put new tree at the end of the base_tree-list
    pred->next_base_tree = nt;
}

unsigned tree::tdelete(int _x,int _y,long _sn)
//deletes tree
//puts tree out of the cell
// or out of the base_tree-list
//decreases number of base_trees_in_cell

```


XXIV Appendix: SAM source code

//tree-list-management is done by the destructor

```
{
    tree_base* ptr = nahal[g.A][g.B]->cell[g.dA][g.dB];
    tree_base* pred = nahal[g.A][g.B]->cell[g.dA][g.dB];

    super_cell::coord_trafo(_x,_y);

    //search
    while( (ptr->series_number != _sn)
    {
        pred = ptr;
        ptr = pred->next_base_tree;
    }
    pred->next_base_tree = ptr->next_base_tree;
    nahal[g.A][g.B]->cell[g.dA][g.dB]->base_trees_in_cell--;

    delete ptr;
}
```

void tree::cleanup_trees()

// removes all trees

```
{
    tree* temp = tfirst;
    tree* next_temp = NULL;

    if(temp->next==NULL) temp = NULL;

    while(temp)
    {
        next_temp = temp->next; //safe pointer to next temp object
        tdelete(temp->x,temp->y,temp->series_number)
        temp = next_temp;
    }
}
```

unsigned long tree::seed_equation(float tc)

//calculates the number of seeds produced by a tree with trunc circumference tc

```
{
    return(pow(10,seed_equ_ordinate) * pow(tc,seed_equ_slope));
}
```

void tree::seed_production()

```
{
    tree *temp = tfirst;
    unsigned long s; //no. of seeds
    unsigned i;
    long double ls;
```

```

float reduction_factor, tc;

if(temp->next==NULL) temp=NULL;
while(temp)
{
    tc = temp->circum;

    if(tc<adult_circum) i=0;    //subadult
    else i=1;                  //adult

    zufall=dr250();
    if(zufall<breeding_tree[i]) //max. seed production
        s = seed_equation(tc);
    else s = 0; //not all trees breed

    //mistle & moisture influence
    reduction_factor = 1 - ((int)temp->mistle)/(float)4;
    if(temp->moist_status==POOR_M) reduction_factor -= 0.5;
    if(reduction_factor<0) reduction_factor=0;

    temp->seed = s*reduction_factor;

    temp = temp->next;
}
}

void tree::seed_infestation()
{
    tree *temp = tfirst;

    if(temp->next==NULL) temp=NULL;

    while(temp)
    {
        temp->seed = (1-seed_infest)*temp->seed;
        temp=temp->next;
    }
}

void tree::seed_loss()
{
    tree *temp = tfirst;

    if(temp->next==NULL) temp=NULL;

    while(temp)
    {

```

XXVI Appendix: SAM source code

```

        temp->seed = (1-seed_loss)*temp->seed;
        temp=temp->next;

    }
}

unsigned tree::seed_portion(long unsigned seeds_still_to_distribute, float mean)
{
    return min(seeds_still_to_distribute,(long unsigned)u_neg_exp_d(mean));
}

unsigned tree::seed_distribution()
{
    tree *temp = tfirst;
    super_cell* ptr = NULL;
    long unsigned seed_to_distribute=0;
    long unsigned seed_still_to_distr[2]={0}; //0->norm, 1->attr
    unsigned s; //for seed portion
    unsigned *seed_for_norm_cells;
    unsigned *seed_for_attr_cells;
    unsigned *help;
    float mean_seed_per_cell[2];          //0->norm, 1->attr
    unsigned cells[2];                    //0->norm, 1->attr
    unsigned remaining_cells[2];          //0->norm, 1->attr
    unsigned target_cell_index=0;
    unsigned c[2]={0};
    unsigned count[2]={0};                //counter, used when putting seed into field
    unsigned uzufall;

    cells[1] = count_attr_cells();
    cells[0] = count_cells() - cells[1];
    for(i=0;i<2;i++) remaining_cells[i] = cells[i];

    //define arrays for determination of seed portions that will
    //become distributed into the field
    for(j=0;j<2;j++)
    {
        //determine size of arrays
        i=0;
        while(cells[j]>c[j]){i++; c[j]=pow(2,i);}
    }

    seed_for_norm_cells = new unsigned[c[0]];
    seed_for_attr_cells = new unsigned[c[1]];
    help = new unsigned[ max(c[0],c[1])];

    //sum seed_to_distribute up
    seed_to_distribute = 0;

```

```

seed_test = 0;
if(temp->next==NULL)    temp=NULL;
while(temp)
{
    seed_to_distribute += temp->seed;
    temp=temp->next;
}

//divide seed_to_distribute into seed for norm. cells and for attr. cells
seed_still_to_distr[0]
    = seed_to_distribute*cells[0]
    /(cells[0]+cells[1]*super_cell::seed_attr_factor);

seed_still_to_distr[1]
    = seed_to_distribute - seed_still_to_distr[0];

//calculate mean seed number per cell
for(j=0;j<2;j++)
{
    if(cells[j]!=0)
        mean_seed_per_cell[j] = seed_still_to_distr[j]/(float)cells[j];
    else mean_seed_per_cell[j] = 0;
}

//put seed portions into array seed_for_*_cells[]
//must be done in random order, otherwise seeds might be concentrated
//help keeps track of elements that did not yet get seeds
for(i=0;i<cells[0];i++) seed_for_norm_cells[i] = 0;
for(i=0;i<cells[1];i++) seed_for_attr_cells[i] = 0;

for(j=0;j<2;j++)
{
    for(i=0;i<cells[j];i++) help[i] = i;

    for(i=0;i<cells[j];i++)
    {
        if(i==(cells[j]-1))
            s = (unsigned)seed_still_to_distr[j];
        else
            s = (unsigned)seed_portion(seed_still_to_distr[j],
                                      mean_seed_per_cell[j]);

        if(s>0) //do not put 0 into any element
        {
            //choose element of array
            uzufall = r250n(remaining_cells[j]);
            target_cell_index = help[uzufall];

```

```

        //put seed in that element
        if(j==0)
            seed_for_norm_cells[target_cell_index] = s;
        else
            seed_for_attr_cells[target_cell_index] = s;

        seed_still_to_distr[j] -= s;

        //overwrite that element of help with last element
        //and decrease remaining_normal_cells by 1
        //(makes shure, that each element get chosen exactly once)
        help[uzufall] = help[remaining_cells[j]-1];
        help[--remaining_cells[j]] = 0;
    }
}

//put seed from the arrays seed_for_norm_cells and
//seed_for_attractive_cells into the field
ptr = super_cell::first;
do{
    if(ptr->seed_attraction==0)
        for(int di=0;di<4;di++)
            for(int dj=0;dj<4;dj++)
                ptr->seed_cell[di][dj] = seed_for_norm_cells[count[0]++];
    else
        for(int di=0;di<4;di++)
            for(int dj=0;dj<4;dj++)
                ptr->seed_cell[di][dj] = seed_for_attr_cells[count[1]++];
    ptr = ptr->next;
} while (ptr!=NULL);

delete[] seed_for_norm_cells;
delete[] seed_for_attr_cells;
delete[] help;
}

unsigned tree::growth_mistle()
{
    tree* temp = tfirst;
    type_mistle MT; type_mistle MTA[4] = {NONE,ONE,TWO,THREE};

    if(temp->next==NULL) temp=NULL;

    while(temp)
    {

```

```

        zufall=dr250();

        for(i=0;i<3;i++)
        {
            if(temp->mistle==MTA[i])
            {
                if(zufall<mistle_incr_prob[i])
                {
                    MT=MTA[i+1];
                    temp->set_mistle(MT);
                    i=3;
                }
            }
        }
        temp = temp->next;
    }
}

void tree::alter_moist_status()
{
    const int step[2][ 8]={ { 1,1, 1, 0,-1,-1,-1,0},{ 1,0,-1,-1,-1, 0, 1,1 } };
    float risk_points;
    unsigned btic, rc;
    int sub, adu, dx,dy;
    tree_base *tbtemp;
    tree *temp = tfirst;

    //if there is just the tstartobject
    if(temp->next==NULL) temp=NULL;

    while(temp)
    {
        if(temp->moist_status==GOOD_M) !=POOR_M
        {
            //bad luck
            risk_points=1;

            //>=5 POOR_M years in a row
            if(super_cell::bad_yearsinarow>4) risk_points++;

            //mistletoe
            if((int)temp->mistle>0) risk_points++;

            //other trees
            super_cell::coord_trafo(temp->x,temp->y);
            //other trees in same cell
            btic = nahal[g.A][g.B]->cell[g.dA][g.dB]->base_trees_in_cell;

```

XXX

Appendix: SAM source code

```
if(btlic>1)
{
    tbtemp = nahal[g.A][g.B]->cell[g.dA][g.dB];
    //subtract temp
    rc=temp->circum;
    if(rc>=adult_circum)
        {adu=-1;sub=0;}
    else if(rc>=seedling::subadult_circum_thresh)
        {sub=-1;adu=0;}
    //count sub, adu
    for(int kj=0; kj<btlic; kj++)
    {
        rc=tbtemp->circum;
        if(rc>=adult_circum)
            adu++;
        else if(rc>=seedling::subadult_circum_thresh)
            sub++;
    }
    //further tree (adult) in cell
    if(adu>0) risk_points+=3;
    //further tree (subadult) in cell
    if(sub>0) risk_points+=2;
}
//other trees in neighbour cell
sub=0;adu=0;
for(i=0;i<8;i++)
{
    dx = step[0][i];
    dy = step[1][i];

    if(super_cell::cell_existence( (dx+temp->x),(dy+temp->y) ))
    {
        super_cell::coord_trafo((dx+temp->x),(dy+temp->y));

        if(nahal[g.A][g.B]->cell[g.dA][g.dB]!=0)
        {
            btlic = nahal[g.A][g.B]->
                cell[g.dA][g.dB]->base_trees_in_cell;
            tbtemp = nahal[g.A][g.B]->cell[g.dA][g.dB];

            //count sub, adu
            for(int kj=0; kj<btlic; kj++)
            {
                rc=tbtemp->circum;
                if(rc>=adult_circum)
                    adu++;
                else if(rc>=seedling::subadult_circum_thresh)
```



```

sub++;
    }
    }
    }
    //adult in neighbour cell
    if(adu>0) risk_points+=2;
    //subadult in neighbour cell
    if(sub>0) risk_points+=1;

    zufall = dr250();
    if(zufall<risk_points/= worse_moist_scale)
        temp->moist_status = POOR_M;
}
temp = temp->next;
}
}

void tree::growth()
{
    tree *temp = tfirst;
    float old_circum;

    if(temp->next==NULL) temp=NULL;

    while(temp)
    {
        temp->apply_growth_formula();
        temp = temp->next;
    }
}

float tree::vitality()
{
    return( v_basic_vitality + v_moist_factor*(float)moist_status);
}

unsigned tree::mortality()
{
    tree*   temp       = tfirst;
    tree*   next_temp  = NULL;
    float   mt         = 0;

    if(temp->next==NULL) temp=NULL;

    while(temp)
    { //determine mortality rate

```

XXXII

Appendix: SAM source code

```
mt = 1 - temp->vitality();

zufall = dr250();
if(zufall<mt)
{ //death
    //safe pointer to next temp object
    next_temp      = temp->next;

    //new deadtree
    deadtree::dnew(temp->x,temp->y,temp->circum);
    //delete tree
    temp->tdelete(temp->x,temp->y,temp->series_number);

    //go to next temp
    temp = next_temp;
}

else //survived
    temp = temp->next;
}
```

```

//-----
//                      declarations: deadtree
//-----
class deadtree : virtual public tree_base
{
    public:
    /*** variables: biological ***/
    unsigned          time_since_death;

    /*** variables: technical ***/
    static int dAnzahl;          // number of dead trees
    long series_number;          // each dead tree has a unique number
    static deadtree* dfirst;      // pointer to beginning of dead tree list
    deadtree* next;              // pointer to next object in dead tree list
    long series_number;

    /*** parameters: biological ***/
    static float  fall_deadtree;

    /*** procedures: technical ***/
    deadtree(int x, int y, float circum);
    virtual ~deadtree();
    static void dnew(int,int,float);          //x,y,circum
    static void ddelete(int,int,long);        //x,y,seriesnumber
    static void cleanup_deadtrees();

    /*** procedures: biological ***/
    static void growth();
    static void mortality();
};

```

XXXIV Appendix: SAM source code

```
//-----
//          definitions: deadtree
//-----
deadtree::deadtree(int x_, int y_, float circum_,char* name)
: tree_base( x_, y_, circum_),time_since_death(0)
{
    init_obj(); //puts object in dead tree list
    dAnzahl++;
}

deadtree::~deadtree()
{
    dremove_object(series_number); //removes object from deadtree list
    dAnzahl--;
}

void deadtree::dnew(int _x,int _y,float _circum)
//creates new deadtree
//puts deadtree in the cell and at the end of the base_tree-list
{
    super_cell::coord_trafo(_x,_y);

    tree_base* ptr = nahal[g.A][g.B]->cell[g.dA][g.dB];
    tree_base* pred = nahal[g.A][g.B]->cell[g.dA][g.dB];
    deadtree* nd = NULL;

    while(ptr!=NULL)
    {
        pred = ptr;
        ptr = ptr->next_base_tree;
    }

    //create new deadtree
    nd = new deadtree(_x,_y,_circum,"deadtree");
    //update counter
    nahal[g.A][g.B]->cell[g.dA][g.dB]->base_trees_in_cell++;
    //put new deadtree at the end of the base_tree list
    pred->next_base_tree = nd;
}

/**/ deadtree ***** ddelete ***
unsigned deadtree::ddelete(int _x,int _y,long _sn)
//deletes deadtree
//puts deadtree out of the cell removes it from base_tree list
{
    super_cell::coord_trafo(_x,_y);
    tree_base* ptr = nahal[g.A][g.B]->cell[g.dA][g.dB];
```

```

tree_base* pred = nahal[g.A][g.B]->cell[g.dA][g.dB];

//search
while(ptr->series_number!=_sn)
{
    pred = ptr;
    ptr = (pred->next_base_tree);
}

pred->next_base_tree = ptr->next_base_tree;
nahal[g.A][g.B]->cell[g.dA][g.dB]->base_trees_in_cell--;
delete ptr;
}

unsigned deadtree::cleanup_deadtrees()
// removes all deadtrees
{
    deadtree* temp = dfirst;
    deadtree* next_temp = NULL;

    if(temp->next==NULL) temp = NULL;
    while(temp)
    {
        next_temp = temp->next;
        temp->ddelete(temp->x,temp->y,temp->series_number);
        temp = next_temp;
    }
}

void deadtree::growth()
{
    deadtree *temp = dfirst;

    if(temp->next==NULL) temp=NULL;
    while(temp)
    {
        temp->time_since_death++;
        temp = temp->next;
    }
}

unsigned deadtree::mortality()
{
    deadtree* temp = dfirst;
    deadtree* next_temp = NULL;

```

XXXVI Appendix: SAM source code

```
if(temp->next==NULL) temp=NULL;
while(temp)
{
    zufall=dr250();

    if(zufall<fall_deadtrees)
    { //death
        //safe pointer to next temp object
        next_temp      = temp->next;
        //delete
        temp->ddelete(temp->x,temp->y,temp->series_number);
        //go to next temp
        temp = next_temp;
    }

    //survived
    else temp = temp->next;
}
}
```

```

//-----
//          random numbers
//-----
float neg_exp_d(float mean)
{ // negativ exponentially distributed randomnumbers
  return(-log(1-dr250()*mean);
}

/** Function prototypes for R250 random number generator, by W. L. Maier */

/**** Function: r250
      Description: returns a random unsigned integer k
                  uniformly distributed in the interval 0 <= k < 65536.
****/
unsigned int r250();

/**** Function: r250n Description: returns a random unsigned integer k
                  uniformly distributed in the interval 0 <= k <
****/
unsigned int r250n(unsigned n);

/**** Function: dr250
      Description: returns a random double z in range 0 <= z < 1.
****/
double dr250();

/**** Function: r250_init
      Description: initializes r250 random number generator.
****/
void r250_init(int seed);

```


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