From snapshot information to long-term population dynamics of Acacias by a simulation model

Kerstin Wiegand[1,*], David Ward[2], Hans-Herman Thulke[1] & Florian Jeltsch[1,3]
[1]*UFZ Centre for Environmental Research Leipzig-Halle, Department of Ecological Modelling, Leipzig, Germany;*
[2]*Mitrani Department of Desert Ecology & Ramon Science Center, Blaustein Institute for Desert Research, Ben Gurion University of the Negev, Sede Boqer, Israel;* [3]*Present address: Plant Ecology and Nature Conservation, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany;* *Present address: Department of Ecology and Evolutionary Biology, Princeton University, Guyot Hall, Princeton, NJ 08544-1003, USA, (E-mail: kwiegand@eno.princeton.edu)*

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 well understood. The main idea of our study is to learn more about the long-term population dynamics of these trees using snapshot information in the form of size frequency distributions. These distributions are highly condensed indices of population dynamics acting over many years. In this paper, we analyse 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 these live history processes that are based on the analysed field evidence. The main properties of simulated as well as observed tree size frequency distributions are characterised with Simpson's index of dominance and a new permutation index. 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. Finally, the size frequency distributions observed in the Negev reveal the information that, in this harsh environment, mortality of adult *A. raddiana* is independent of tree size (age).

> '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)

Introduction

In Africa, the genus *Acacia* is widely distributed (Ross 1981) and of great ecological and economic importance. *Acacia* trees 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). They provide food, shade, shelter, perch, nest, and roost sites to many animals (Leistner 1967; Ashkenazi 1995; Milton 1995). *Acacia* seed pods are of high nutritive value and an important food source to wild and domestic browsers especially 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 1970; Ashkenazi 1995; Miller 1996) and as medicinal plants (Boulos 1983; Ashkenazi 1995).

There is fear that the abundance of these trees might be declining in some regions (Young & Lindsay 1988; Mwalyosi 1990; Ashkenazi 1995). 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, 1995; Ward & Rohner 1997; Rohner & Ward 1999; Wiegand K. et al. 1998). 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 (Ashkenazi 1995). 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.

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 modeling studies refer to Acacias (Pellew 1983; Grice et al. 1994).

In this paper, we address the questions 'Which mechanisms can cause a certain type of size distribution?' and 'What kind of size distribution results from a certain mechanism?' by a combined field study and modelling approach. SAM is an existing simulation model of the spatio-temporal population dynamics of *Acacia raddiana* (considered a sub-species of *A. tortilis* by Ross 1979) in the Negev desert, Israel (Wiegand K. et al. 1999). We analyse additional field data on recruitment, growth, and mortality of *A. raddiana* in order to design biologically possible model scenarios of these processes. Then, we run the SAM model under these different scenarios and determine the resulting size frequency distributions. First, we investigate the effects of different processes (i.e., recruitment, growth, and mortality) on pattern (i.e., simulated size frequency distributions). Second, we 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. We infer long-term processes from snapshot patterns.

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 1999). The reason for restricting this study to the wadi area is that in arid regions *A. raddiana* grows only inside wadi beds (Figure 1). Mean annual precipitation is 38 mm, most of which falls during winter months (October–April). In Nahal Katzra, trees suffer relatively high infestations of the semi-parasitic mistletoe *Loranthus acaciae* and are frequently browsed by domestic (goats, camels, sheep) and wild (gazelle *Gazella dorcas*) mammalian herbivores. Size frequency distributions of live and dead *A. raddiana* have been determined in further sites throughout the Negev (Nahal Saif, Nahal Bitaron, Nahal Roded, Shezaf, and Hai-Bar). Furthermore, a lumped size frequency distribution of *Acacia* trees in 75 plots throughout the Negev (Ward & Rohner 1997) has been used for a model parameter fit (see *Results*: *Model scenarios*: *Mortality*).

Materials and methods

Field data collection: recruitment

Periodic tree regeneration has been hypothesised as the cause of irregular size distributions of *Acacia* trees (Mwalyosi 1990; Prins & Van der Jeugd 1993; Kiyiapi 1994; Sinclair 1995). Therefore, recruitment of *Acacia* trees has been monitored over the years 1994–1998 in 75 populations throughout the Negev (not all plots in each year; Ward & Rohner 1997; Rohner & Ward 1999, Ward, unpubl. data).

Field data collection: growth

Variable tree growth is also suspected to cause irregular tree size frequency distributions (Grice 1984;
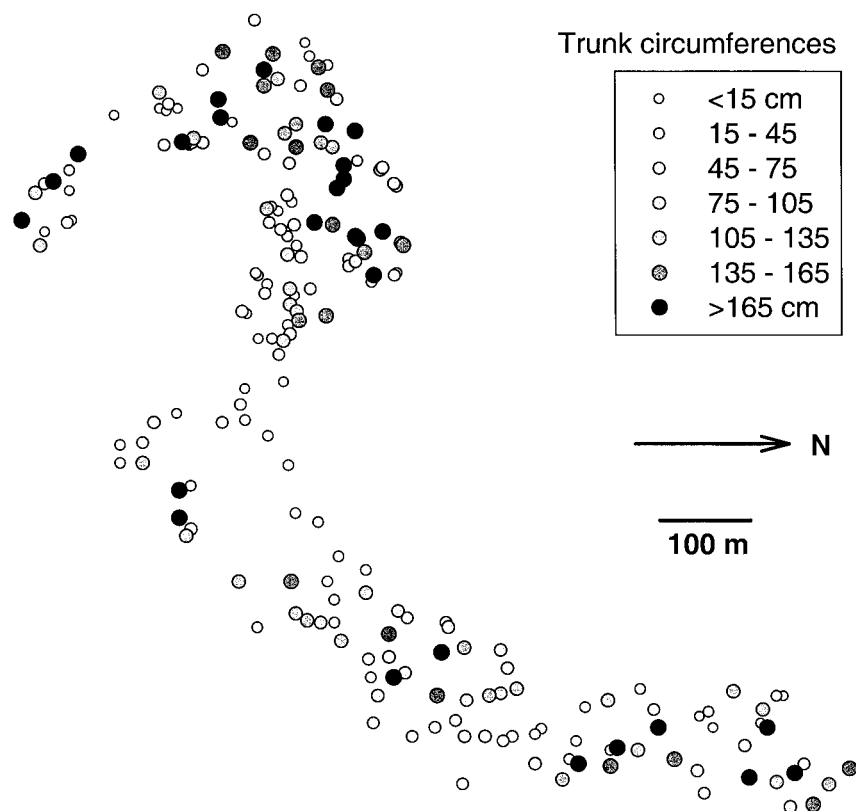
Figure 1. Spatial tree distribution in Nahal Katzra. The legend indicates the trunk circumference of the trees.

Ruess & Halter 1990; Grice et al. 1994; Rohner & Ward 1999). 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. We first determine average growth of *A. raddiana* and second how these factors influence tree growth. Trunk circumference (*TC*) was used as an index of tree size. We measured trunk circumferences at breast height of about 200 trees in Nahal Katzra on an annual basis from 1996 to 1998. In the case of multistemmed trees we used an aggregate trunk circumference calculated from the total area of combined trunks (Coughenour et al. 1990). All measurements were done by the same person and a strip was painted around each tree trunk to show the exact location of the annual measurements. The correlation between trunk circumference and trunk diameter (another common index of tree size) is very high ($R^2 = 0.988$, $n = 200$; Ward unpubl. data). 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 Katzra (Ward, unpubl. data).

$$\log_{10} TC = 1.15 * \log_{10} CD - 1.54. \tag{1}$$

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. Nevertheless, we restricted some analysis (section *Tree growth pattern*) to trees where trunk size was measured directly.

Trees was were visually classified as 'heavily browsed' if many branches show 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 1).

Average growth. The interpretation of size frequency distributions of African *Acacia* trees is complicated by the fact that size-age relationships are largely un-

Table 1. Summary table of tree size distribution, mistletoe infestation, moisture status, and browsing pressure for the 187 trees studied in Nahal Katzra.

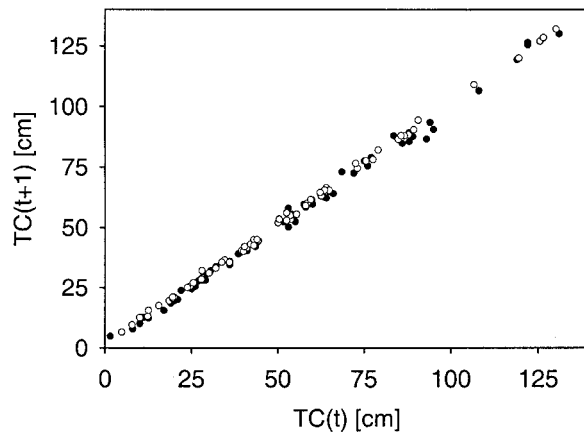| Trunk circumference	Number of trees	Attribute of trees	Number
<15 cm	10	Many mistletoes	15
16–45 cm	45		
46–75 cm	35	Poor moisture status	12
76–105 cm	33		
106–135 cm	38		
136–165 cm	14	Heavily browsed	109
>165 cm	12		

Figure 2. Trunk circumference (*TC*) at time t in Nahal Katzra vs. circumference at time *t*+1. Closed symbols: *t* = 1996, open symbols: *t* = 1997.

known. The classical method 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 (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 of single-stemmed trees in Nahal Katzra at *t* = 1996 vs. *t* + 1 = 1997 and at *t* = 1997 vs. *t* + 1 = 1998 (Figure 2). From the graph, a linear relation appears to be an appropriate approach to derive a basic growth function in time:

$$TC(t + 1) = a \times TC(t) + b, \qquad (2)$$

where *TC* is the trunk circumference in cm, *t* the time in years, and *a*, *b* are constants (cf., Wiegand T. et al. 2000, this volume). Note that the resulting size-

age relationship will be polynomial of power age-1 (Wiegand K. 1999).

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 an increase in trunk circumference. As a first step, we analyse whether browsing, mistletoe infestation, and moisture status interact. It appears (heavy browsing and poor moisture: 10 trees, heavy browsing and many mistletoes: 9 trees, poor moisture and many mistletoes: no trees; see also Table 1) that they are not significantly interrelated (χ^2-test, Yates correction; browsing–mistletoe, $\chi^2 = 0.018$, $P = 0.89$, $1 - \beta = 0.05$; browsing–moisture, $\chi^2 = 2.299$, $P = 0.13$, $1 - \beta = 0.31$; mistletoe–moisture, $\chi^2 = 0.258$, $P = 0.61$, $1 - \beta = 0.08$). Note that the power of the test to reject a false null hypothesis that there is no significant interrelationship is not high. Thus, further field studies are needed to test the reliability of these conclusions. We tested the influence of each characteristic on the growth increment separately (using a Mann–Whitney Rank Sum Test). This must be done for both growth periods separately because of the possible influence of 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, $P > 0.05$) Therefore, we neglected tree size when analysing the effect of rainfall, browsing, mistletoes, and moisture status on tree growth. However, remember that average growth increment is modelled as a function of tree size (Equation (2)).

Field data collection: 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. Range of sample sizes at these sites = 27–53 alive trees and 10–31 dead trees). 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 small 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).

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 basic model structure is presented in the following text. A full description is available in Wiegand K. et al. (1999). For biological information, see also Ward & Rohner (1997) and Rohner & Ward (1999).

The aim of the SAM model is to capture the main mechanisms that determine the population dynamics of *Acacia raddiana*, to understand the relative importance of these mechanisms, and to develop possible management strategies for the conservation of this species. In order to be accurate at small population sizes and to allow for the consideration of several parameters of interest (location, size, moisture status, mistletoe coverage, . . .), SAM is individual-based (Judson 1994). Tree moisture status is classified as good or poor, representing trees with less or more than 50% dry branches, and infestation by mistletoes (*L. acaciae*) is simulated in terms of the proportion of the canopy covered by these parasites in units of quarters of the canopy volume. However, canopy volume is not modelled explicitly. The destiny of each seed is followed individually. The consideration of spatial variation in seed distribution and of local interaction between trees is enabled by the spatially-explicit design of the model. Basically, SAM subdivides the wadi into a grid of cells that are 5 m×5 m in size and thus represent the typical size of a young, 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.

Figure 3 shows the causal structure of the factors and processes considered by the SAM model. Here, we give a description of the model version published in Wiegand K. et al. (1999), further model scenarios will be developed 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 3). Recruitment of trees is initially influenced by germination and seedling mortality. One 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 actual 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; drawn from an equal distribution) 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. Trees larger than 15 cm in trunk circumference can already reproduce, but full sexual maturity is reached at a trunk circumference of 45 cm. As a 'poor' tree moisture status means that many (>50%) branches are dry, SAM reduces the seed crop produced by a tree proportionally to the canopy volume unavailable to seed production due to 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* (Rohner & Ward 1999). The amount of seeds available at a specific location is altered by seed dispersal by flood events and large mammalian herbivores consuming *Acacia* pods. Floods and wadi morphology are not modelled explicitly. However the resulting distribution of *Acacia* seeds is qualitatively modelled via the definition of 'normal' and 'seed attractive' areas. Furthermore, tree establishment also depends on seedling mortality, which is higher for smaller seedlings and in years with lower water availability.

Once a tree is established we assume a constant growth rate based on field data. 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.

Description of size frequency distribution

We deal with hundreds of size frequency distributions and must condense the information contained in these distributions. We find that commonly used indices
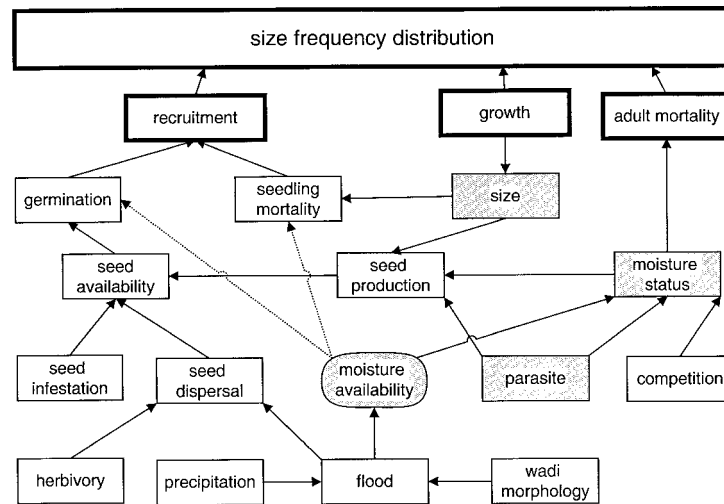
Figure 3. Graphical model of the factors structuring the population size-frequency distribution of *A.raddiana* in the Negev. Arrows point in the direction of the respective effects. Alternative scenarios: Dashed arrows indicate relations that are removed in the 'constant recruitment' scenario and hatched factors influence growth in the 'variable growth' scenario. Further explanations are given in the text.

(mean, standard deviation, skewness, kurtosis, or Gini coefficient; Turner & Rabinowitz 1983; Hara 1984; Weiner & Solbrig 1984; Dixon et al. 1987; Bendel et al. 1989) do not adequately characterise irregular size distributions, because they do not describe the deviation from a monotonically declining shape (see Appendix 1). We describe the size distributions resulting from single simulation runs with Simpson's index of dominance and a new permutation index. For both indices the trunk circumference data are 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.

(i) Simpson's index of dominance

$$C = \frac{1}{N(N-1)} \sum_{i=1}^{20} N_i(N_i - 1), \qquad (3)$$

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 4).

(ii) Permutation index

$$P = \sum_{i=1}^{20} |J_i - i|; \quad J_i = 1, \dots, 20, \qquad (4)$$

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 than a preceding size class, the ranking differs from enumeration, resulting in a greater permutation index (Figure 4).

Results

Field data: recruitment and growth

Only 3 germination events were observed in the entire Negev over the years 1994–1998 (1995: Hai-Bar, 1997: Nahal Zeelim, Nahal Saif).

Average growth. From 1996 to 1997 trees in Nahal Katzra grew slowly ($a = 0.9984$, $b = 0.2409$, 67 trees, $R^2 = 0.996$). 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, $R^2 = 0.999$). Combining data from both growth periods ($a = 1.0013$, $b = 0.7393$, $R^2 = 0.997$), yields a growth regime that is slightly lower than the growth measured for *A. tortilis* in the
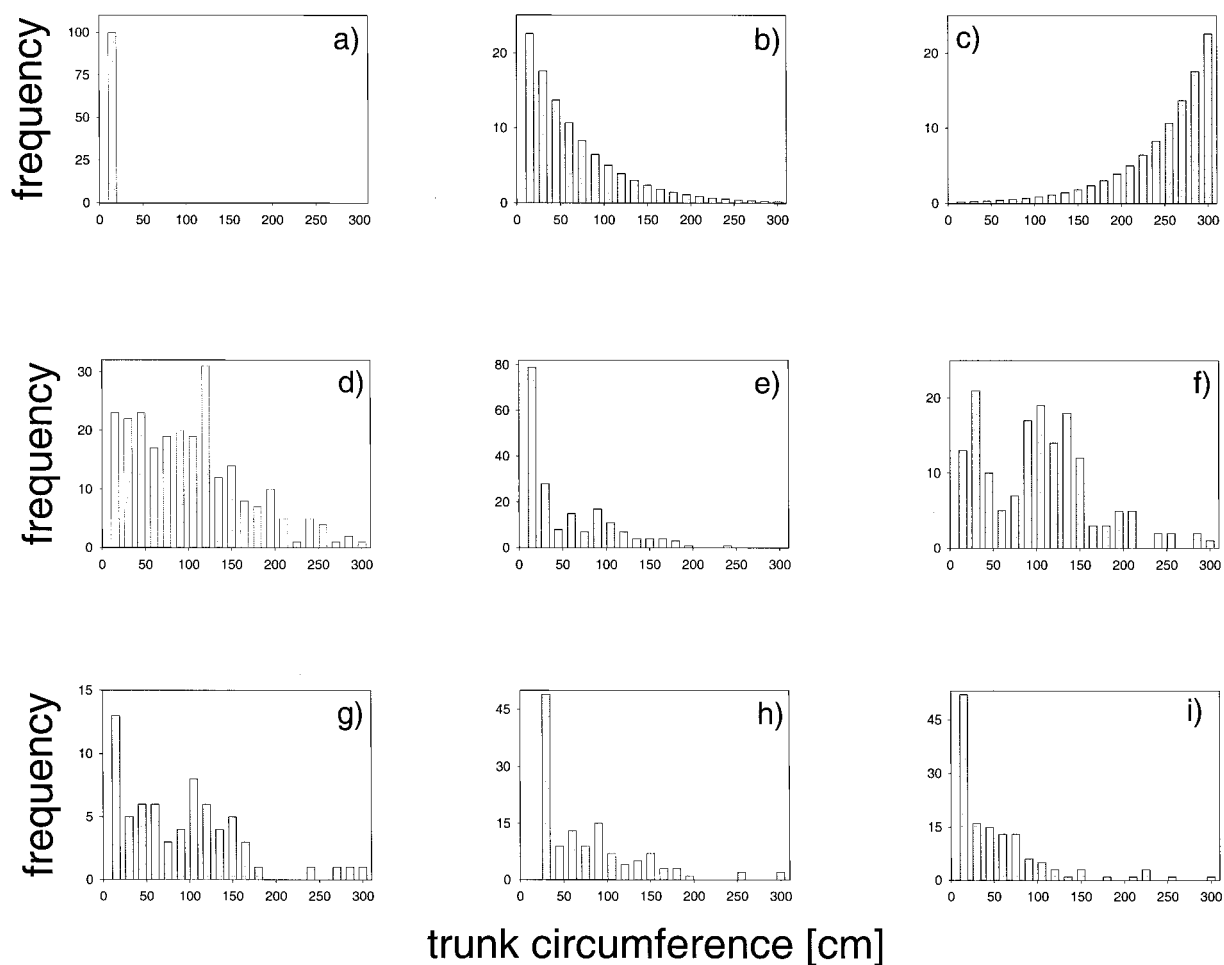
Figure 4. Hypothetical (a–c), real (d–f), and model (g–i) size frequency distributions and their respective indices of dominance (C) and permutation (P). (a) C = 1, P = 0 ; (b) C = 0.1, P = 0; (c) C = 0.1, P = 200; (d) Nahal Katzra: C = 0.07, P = 30 ; (e) Nahal Saif I: C = 0.25, P = 14; (f) Nahal Saif II: C = 0.08, P = 60; (g) C = 0.08, P = 52; (h) C = 0.18, P = 50; i) C = 0.20, P = 30. The model distributions (g–i) are produced under the rare recruitment – variable growth – moisture-dependent mortality – scenario.

Njemps Flats, Kenya ($a = 1, b = 1.36$; Kiyiapi 1994) and slightly higher than the growth of (3 year old) trees at an experimental site in Sede Boqer, Israel (Ward, unpubl. data).

Tree growth pattern. 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 ($T_{143,13} = 650.5$, $P = 0.317$). The reliability of measurements was checked on several occasions and found to be high (Ward, unpubl. data).

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 $\rho_s = -0.228$, $P = 0.0048$). Summarising, it appears that growth is influenced by water availability only, because the only differences we found were between
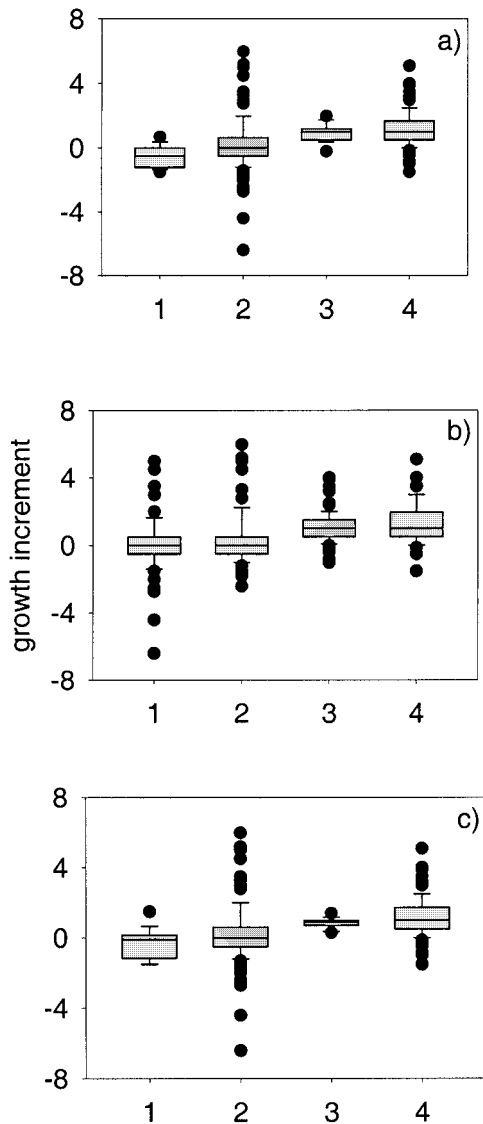
Figure 5. Tree growth increments in terms of trunk circumference in Nahal Katzra for growth periods 1996–1997 (numbers 1 and 2) and 1997-1998 (3, 4) under different tree conditions. (a) Mistletoes (many: 1, 3; none or few: 2, 4). (b) Browsing (heavy: 1, 3; none or moderate: 2, 4). (c) Moisture status (poor: 1, 3; good: 2, 4). Boxes summarise the inner 50% and whiskers the inner 80% of the data.

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). 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.

Field data: mortality

At first glance, the ratio of live to dead trees seems to be size-dependent ($\chi^2 = 26.580$, df $= 14$, $P = 0.022$, $N= 7$ sites for which adequate data were available). 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 $= 12$, $P = 0.060$, $N=7$).

Model scenarios

In the following sections, we use our results from the field data analysis to derive contrasting modelling scenarios of recruitment, growth, and mortality 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 2.

Model scenarios: recruitment

The 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 favourable. However, it is not clear whether this paucity of seedlings is a normal feature or a sign of decline (Ashkenazi 1995). Therefore, we wish to contrast a rare event scenario with a constant recruitment scenario, i.e., a scenario where germination takes place every year. The constant recruitment scenario corresponds to a removal of the dependence of germination and seedling mortality on moisture availability (dashed arrows in Figure 3).

*Rare recruitment scenario (*see Wiegand K. et al. 1998; Wiegand K. et al. 1999*).* In years with good weather, 15.6% of seeds germinate (Rohner & Ward 1999). During their first 5 half- years, seedling mortality depends on rainfall. In good years, seedlings undergo a semi-annual mortality of 60% (Rohner & Ward 1999, 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

Table 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 Equation (2) deterministically
	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

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.

Model scenarios: growth

We contrast a stochastic growth scenario that follows the observed growth pattern as closely as possible 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. By running the model under both scenarios we will be able to determine the effect of growth variability on size frequency distributions. Whereas the deterministic growth scenario is shown in Figure 3, the variable growth scenario would correspond to the introduction of a direct dependence of growth on tree size (cf., Equation (2) because of the size-age relation), moisture availability, parasite 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)).

Variable growth scenario. This scenario combines deterministic average growth *d* (following Equation (2)) with stochastic deviation *f* from this average.

$$g = d + f; \quad f \in F. \tag{5}$$

The modulations $F = F$(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 6, a description of how we set up the distributions *F* is given in Appendix 2). 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).

Model scenarios: mortality

The field study gives ambiguous answers on whether or not mortality is a function of tree size depending on in- or exclusion of small trees. Therefore, we investigate two mortality scenarios with the model: the so-called moisture status-dependent mortality scenario, which 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
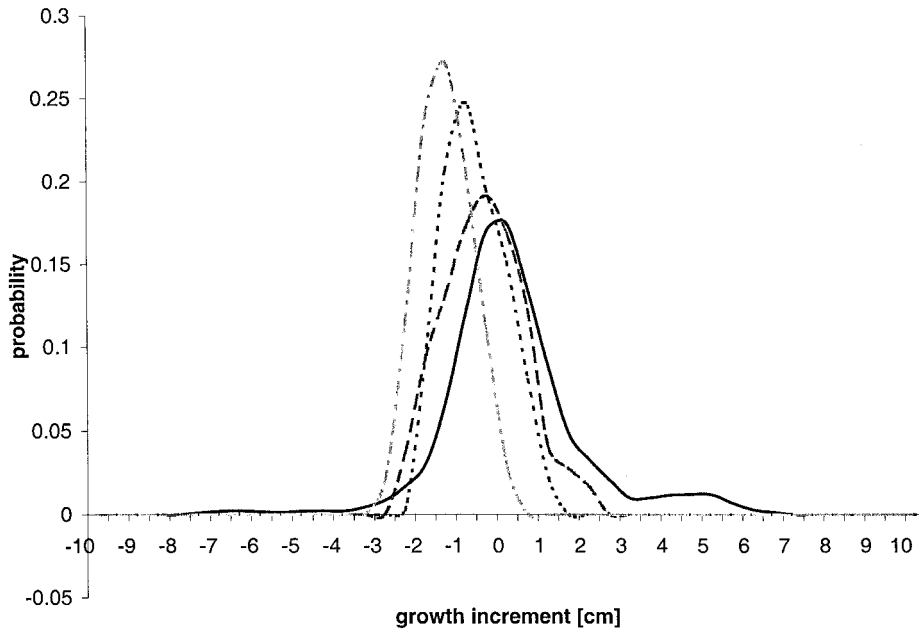
Figure 6. Sample probability distributions F from which deviations f from average growth d are drawn every year for each tree. The distributions given are $F = F$(intermediate year, tree condition), based on the growth period 1996-1997 in Nahal Katzra. $F_{\text{intermediate year}}$ (good moisture status, without many mistletoes): black solid line, F_{iy}(poor moisture status, without many mistletoes): grey dashed line, F_{iy}(good moisture status, many mistletoes): grey dotted line, and F_{iy}(poor moisture status, many mistletoes): light grey dashed-dotted line.

two scenarios to the size distributions observed in the field.

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

$$mortality = 1-vitality; \qquad (6)$$

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 (different from the data given here) as described in Wiegand K. et al. (1999):

$$vitality = 0.97+0.025\times ms. \qquad (7a)$$

For this parameter fit, we used a cumulative size frequency distribution of living *Acacia* trees in 75 plots throughout the Negev (Ward & Rohner 1997). The fitting procedure had to be repeated for the different scenario combinations. However, parameter changes are below the accuracy of the numbers given in Equation (7).

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

$$vitality = 0.98 + 0.025 \times ms + 0.05 \left(\frac{TC}{250}\right)^{4} \quad (7b)$$

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. The field distribution of dead trees is the lumped distribution of all dead tree measurements given in this paper.

Model runs

From the cross-combination of the scenarios described above (Table 2) eight model scenarios result (cf., Figure 8). By running the model under these scenarios and comparing the tree size distributions resulting from both modelling 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. All model outputs are measured in the year 200 (from the beginning of the simulations). We chose the year 200 because this time span ensures that the tree size distribution is not determined by the initial conditions of the simulations, which are based on the actual data from the trees in Nahal Katzra.

Figure 7 shows results of a typical simulation run of SAM under the rare recruitment scenario. The number of seedlings (trunk circumference <15 cm) over
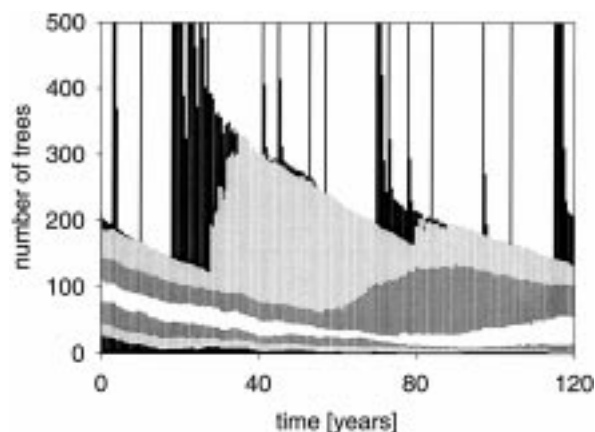
Figure 7. Typical time series showing the number of trees in the modeled area of Nahal Katzra under rare recruitment, variable growth, and size-dependent mortality. The size structure is indicated by grey shading (from top to bottom: black: <15 cm, grey: 16–45 cm, dark grey: 46–75 cm, light grey: 76–105 cm, grey: 106–135 cm, light grey: 136–165 cm, black: >165 cm trunk circumference).
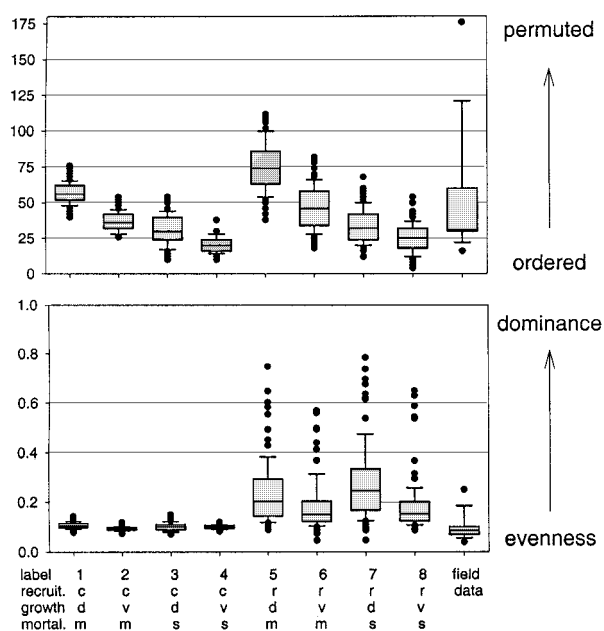

Figure 8. Summary of size distributions resulting from the 8 model scenarios and as found in the 10 field sites given in *Materials and Methods: Field data collection: mortality.* a) Permutation index. b) Simpson's index of dominance. Category axis labels describe the model scenarios: recruitment (*recruit.*): 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 2. Box plots as in Figure 2. Each simulation consists of 100 runs.

time has high peaks due to mass germination events. However, not all germination events result in recruitment, i.e., an increase in tree (>15 cm) 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.

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 8 displays the main characteristics of the size-frequency distributions resulting from the model simulations.

Each box plot represents the permutation index (Figure 8a) or Simpson's index of dominance (Figure 8b) for one scenario combination. If we compare the permutation index for the same growth and recruitment scenarios combined with different mortality scenarios (1 vs. 3, 2 vs. 4, 5 vs. 7, 6 vs. 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.

Finally, we compare the patterns produced by the SAM model to size-frequency distributions observed in the field (also shown in Figure 8). This way, we gain information about the processes acting in the field populations. From Figure 8, we hypothesise 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 modelled 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 8, which differ in the type of mortality scenario. Because box plot 6 (moisture dependent mortality) gives a better agreement for the permutation index, we conclude that mortality effects that are dependent on tree size are negligible.

Discussion

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) led 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 K. et al. 1999) 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. (1999) 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.

Can rare recruitment cause irregular size distributions?

There is a large body of literature on *Acacia* tree size frequency distributions reporting mostly irregular patterns. Many authors hypothesise periodic tree regeneration as the cause for irregular size distributions (Mwalyosi 1990; Prins & Van der Jeugd 1993; Kiyiapi 1994; Sinclair 1995; Ward & Rohner 1997; Rohner & Ward 1999). In our study we tested this hypothesis and showed that periodic tree regeneration is indeed a major factor forming tree size frequency distributions. Even though we associated periodic tree regeneration with rare recruitment events driven by weather, it is quite possible that the driving forces are a combination of both weather and herbivory on seeds and seedlings. The design of our recruitment scenarios leaves this interpretation open. A clear distinction between these two factors will be possible after further field studies on the effect of weather and herbivory on recruitment.

Can the mortality regime cause irregular size distributions?

Pellew (1983), Walker et al. (1986), Ruess & Halter (1990), Shackleton (1993), and Dublin (1995) discuss high mortality due to disturbances, e.g., caused by elephants at very high population densities or by human harvesting as a further factor causing irregular size distributions. 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.

The field study gave ambiguous results on the size-dependence of *Acacia* mortality. An analysis of all trees showed size-dependence, which was no longer the case when small trees were neglected. 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. Therefore, it is more likely that tree mortality does not explicitly depend on tree size. The model results confirm that notion. 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.

Can variable growth cause irregular size distributions?

Irregular tree growth due to growth suppression by herbivores has been discussed as another factor shaping tree size distributions (Ruess & Halter 1990; Rohner & Ward 1999). 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 (1999) and Ruess & Halter (1990) examined tree height. Therefore these studies cannot be directly compared to our study. Indeed, Rohner & Ward (1999) 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.

Our results are in agreement with another study discussing the effect of irregular tree growth due to an episodic rainfall regime 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.

An unexpected result is that tree moisture status and mistletoe infestation reduce the inter-tree variability in tree growth (see Figure 5). 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 in further studies. In summary, the fact that we found rare recruitment and irregular growth to shape irregular *Acacia* size distributions is not a surprise, because others have suggested that before. However, most authors mentioned above are merely speculating on the factors causing size frequency distributions different from a monotonically declining shape. The achievement of this study is to test these hypotheses and to evaluate the relative effect of the single factors.

What kind of size distributions result from certain mechanisms?

The effects of recruitment, growth, and mortality on the size-frequency distributions observed by us are biologically reasonable. Size-dependent mortality gives greater order in the size frequency distributions. 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 variablity 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.

Summarising, recruitment is the most important mechanism shaping size frequency distributions in the Negev desert.

Is it possible to learn about long-term dynamics from snapshot pattern?

Snapshot data are inherently weak data. However, in conservation biology it is often not possible to wait until long-term data sets have accumulated, because the species under study might have gone extinct by then. Models are a means to reduce this dilemma, because they can extrapolate short-term information to time scales appropriate to the study of long-lived species (Wiegand et al. 1995; Jeltsch et al. 1997). However, models cannot completely solve the problem, because they frequently rely on incomplete field data. In order to gain some insights, it is important to extract a maximum of information from the snapshot data available.

The major objective of our investigations was to understand the mechanisms underlying 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 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; Bendel et al. 1989). Because we found that these indices do not adequately

characterise irregular size distributions, 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 permutation index turned out to be a powerful descriptor of size frequency distributions. With these indices it is possible not only to learn about the effects of different processes on size distributions, but also to make statements about the processes probably acting in real populations.

When field data are scarce, there might be overlaps between data used for model development and snapshot data to be compared to model outputs. In our study, this is partly true for size distributions. Our main snapshot data are size frequency distributions and we also used size frequency distributions for a parameter fit. However, first, we used different data sets and second, the parameter fit is done with a cumulative size distribution that is composed of data from many different field sites, resulting in a smooth, declining size distribution (Wiegand et al. 1999). Therefore, we did not use information on the irregularity of single size frequency distributions for the fitting procedure.

A combination of short-term field investigations and pattern-oriented modelling (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. For example, in our study, 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 average growth relationship used in this study is based on two growth periods and one location. Because the growth of Acacias depends on precipitation (see also Milton 1988; Gourlay 1995a; Gourlay 1995b), the present growth regime cannot be more than a first estimation. Clearly, neither experimental nor theoretical studies provide a complete view of the question under study, but promote each other's findings (cf. Moloney et al. 1992). In the course of a few more years, we will be able to establish a more accurate estimation of the growth of *A. raddiana*.

Appendix 1

A population with constant birth, death, and growth rates has a size frequency distribution constant in time. The frequency of the smallest size class equals the number of births minus the number of trees dying or growing into the next larger size class. The frequency of any other size class equals the number of trees growing into the size class minus the number of trees dying or growing out of the size class. The death of trees results in a monotonic decline. This decline is exponential, because the death rate is constant (cf. radioactive decay).

Figure 9 provides indices of size frequency distribution as applied to the examples given in Figure 4. We discuss these indices with respect to their power to measure the deviation of a size frequency distribution from a negative exponentially declining distribution. This includes the shape (negative decline) of the size frequency distribution and the relative sizes (exponential decline) of the single columns.

The *arithmetic mean* of a size frequency distribution reflects deviations from a negative decline of the frequencies with tree size quite well. More frequent classes containing large trees result in higher average tree sizes. This can be seen by comparison of e.g., Figures 4b and c or Figures 4b and f. However, the average does not reflect the shape of the distribution only. Imagine two distributions declining monotonically with the same slope, but having different intercepts. The frequency distribution describing more trees, i.e. having a greater intercept will result in a higher average, because the relative sizes (frequencies) of the single columns are different. Or, imagine two monotonically declining size frequency distributions containing the same total number of individuals, but being different in slope. The distribution declining faster will result in a lower average. Therefore, the
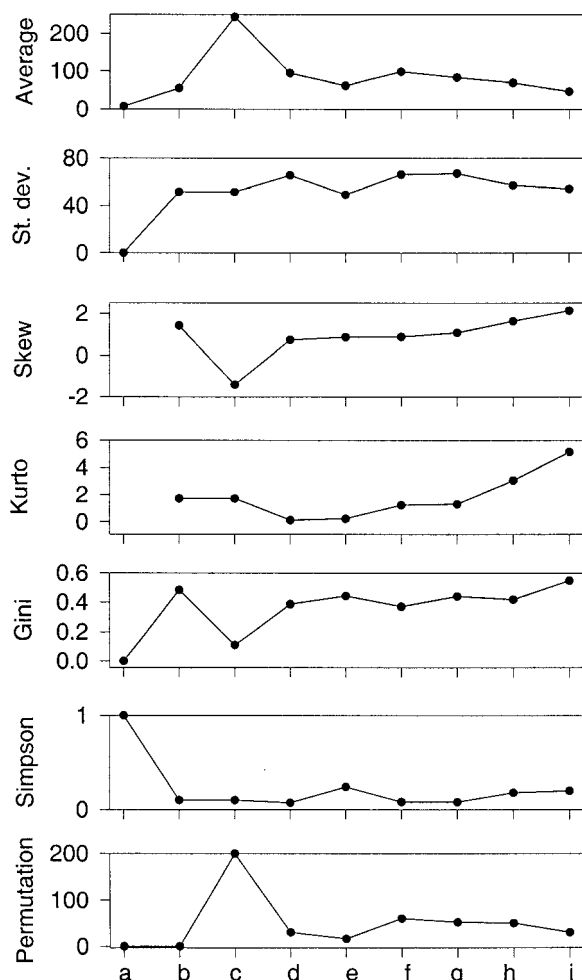
Figure 9. Indices of size frequency distributions given in Figure 4. *Average*: arithmetic mean, *St. dev.*: standard deviation, *Skew*: skewness, *Kurto*: kurtosis, *Gini*: Gini coefficient, *Simpson*: Simpson's index of dominance, *Permutation*: index of permutation. Labels refer to graphs in Figure 4.

deviation of a size frequency distribution from a negative monotonically decline, the slope of the decline and the total number of trees observed influence the arithmetic mean.

The *standard deviation* describes the deviation of measurements from the average. This is relevant for the study of even-aged plant populations (e.g., Hara 1984), but it is not a phenomenon we are interested in. The same holds true for variance and coefficient of variation (e.g., Huston 1986; Bendel et al. 1989).

The *skewness* characterises the degree of symmetry of a distribution around its mean. Monotonically declining distributions result in positive values (e.g., Figure 4b), while monotonically increasing size distributions give negative values (Figure 4c). However, the skewness is not sensitive to

differences in shape such as those between Figures 4d and 4f.

The *kurtosis* describes the flatness or peakedness of a distribution relative to a normal distribution. This does measure the relative size (frequency) of the single columns, but is intertwined with the underlying assumption that the 'ideal' distribution is a normal distribution. However, in our case, reference to an equal or an exponential decline would be sensible, but not reference to a normal distribution (see also Simpson's index of dominance).

The *Gini* coefficient is a measure of variation, formerly called 'coefficient of concentration', that has often been used in economics to measure the degree of inequality in the distribution of income in societies (Glasser 1962; Weiner & Solbrig 1984). The Gini coefficient is the average of the absolute difference of all pairs of values in a population divided by twice the average and the squared population size. The coefficient equals 0 when all trees are in the same size class and almost 1 when all size classes are equally represented. For the examples given in Figures 4d–i the Gini coefficient reflects the deviation from a monotonic decline. For example, Figures 4c,d,f deviate increasingly from a monotonic decline which results in declining values of the Gini coefficient (Figure 9). However, let us now consider two examples taken from Weiner & Solbrig (1984; Figure 1a, b): A population consisting of fifty individuals of size one unit and five individuals of size two units does not deviate from a monotonic decline (it would if we were interested in a strict monotonic decline; Weiner & Solbrig 1984, Figure 1a). Another population consisting of fifty individuals of size one unit and five individuals of size ten units deviates from a negative decline, because size ten units is more abundant than sizes two units through nine units (Weiner & Solbrig 1984, Figure 1b). However, the Gini coefficients of these two examples are (a) 0.075 and (b) 0.409. That is, here the Gini coefficient increases with increasing deviation from a negative decline. Given this ambiguous behaviour relative to different deviations from a monotonic decline, the Gini coefficient is not of interest to us.

Simpson's index of dominance (Pielou 1977) describes the probability that any two trees drawn at random from the same community are of the same size. Therefore, this measure ignores the order in which the columns of a size frequency distribution are arranged. Simpson's index tells us whether a size frequency distribution is steeper (if the columns are arranged in descending order) than expected from a exponentially declining distribution (values above 0.1; e.g. Figures 9a and e) or if tree sizes are more evenly distributed among trees (values below 0.1).

The *permutation index* measures the deviation from a monotonic decline. It is the sum of the absolute distances between the expected and the real location (rank) of all size classes (bars). Thus, it completely ignores the relative frequency of different size classes.

We chose to describe the size frequency distributions with both Simpson's index of dominance and the permutation index because each of them describes only one of the two properties of size frequency distributions we are interested in. We are interested in the deviation from a monotonic decline, because we expect 'ideal' populations to be monotonically declining (see above). This property is measured by the permutation index. Furthermore, we expected rare recruitment events to be an important factor shaping *Acacia* tree size frequency distributions (Mwalyosi 1990; Prins & Van der Jeugd 1993; Kiyiapi 1994; Sinclair 1995; Ward & Rohner 1997; Rohner & Ward 1999). Rare recruitment events favour the occurrence of dominant (more frequent) size classes, a property measured by Simpson's index of dominance. Therefore, our approach follows Dixon et al. (1987) who state '... parameters should be chosen to represent best the phenomenon of interest': The combination of these two indices best represents our objectives in this paper.

Appendix 2

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

$$h = 0.9\sigma n^{-1/5}, \tag{9}$$

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 respective 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 mistletoes only and dryness only.

References

Ashkenazi, S. (1995) *Acacia* trees in the Negev and the Arava, Israel: A review following reported large-scale mortality. Hakeren Hakayemet LeIsrael, Jerusalem (in Hebrew, with English summary).

Belsky, A. J., Amundson, R. G., Duxbury, J. M., Riha, S. J., Ali, A. R. & Mwonga, S. M. 1989. The effects of trees on their physical, chemical, and biological environment in a semi-arid savanna in Kenya. J. Appl. Ecol. 26: 1005–1024.

Belsky, A. J., Mwonga, S. M., Amundson, R. G., Duxbury, J. M. & Ali, A. R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. J. Appl. Ecol. 30: 143–155.

Bendel, R. B., Higgins, S. S. & Teberg, J. E. 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78: 394–400.

Boulos, L. 1983. Medicinal plants of North Africa. Medicinal plants of the world. Reference Publications Inc., Algonac, Michigan, USA.

Coe, M. & Coe, C. 1987. Large herbivores, *Acacia* trees and bruchid beetles. S. Afr. J. Sci. 83: 624–635.

Coughenour, M. B., Ellis, J. E. & Popp, R. G. 1990. Morphometric relationships and developmental patterns of *Acacia tortilis* and *Acacia reficiens* in Southern Turkana, Kenya. Bull. Torrey Bot. Club 117: 8–17.

DeAngelis, D. L. & Huston, M. A. 1987. Effects of growth rate in models of size distribution formation in plants and animals. Ecol. Modell. 36: 119–137.

Dixon, P. M., Weiner, J., Mitchell-Olds, T. & Woodley, R. 1987. Bootstrapping the Gini coefficient of inequality. Ecology 68: 1548–1551.

Dublin, H. T. 1995 Vegetation dynamics in the Serengeti-Mara ecosystem: the role of elephants, fire, and other factors. Pp. 71–90. In: Sinclair, A. R. & Arcese, P. (eds), Serengeti II: Dynamics, management, and conservation of an ecosystem. Chicago University Press, Chicago.

Ehleringer, J. R., Cook, C. S. & Tieszen, L. L. 1985. Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68: 279–284.

Glasser, G. J. 1962. Variance formulas for the mean difference and coefficient of concentration. Journal of the American Statistical Association 57: 648–654.

Gourlay, I. D. 1995a. Growth ring characteristics of some African *Acacia* species. J. Trop. Ecol. 11: 121–140.

Gourlay, I. D. 1995b. The definition of seasonal growth zones in some African *Acacia* species - a review. IAWA J. 16: 353–359.

Grice, A. C. 1984. The demography of the leguminous shrubs *Acacia victoriae, Cassia nemophila* and *C. phyllodinea* in semi-arid south-eastern Australia. PhD Thesis. Macquarie University, North Ryde, Australia.

Grice, A. C., Westoby, M. & Torpy, C. 1994. Dynamics and population structure of *Acacia victoria* Benth. Aust. J. Ecol. 19: 10–16.

Grimm, V. 1994. Mathematical models and understanding in ecology. Ecol. Modell. 75/76: 641–651.

Gwynne, M. D. 1969. The nutritive value of *Acacia* pods in relation to *Acacia* seed distribution by ungulates. E. Afr. Wildl. J. 7: 176–178.

Halevy, G. 1974. Effects of gazelles and seed beetles (Bruchidae) on germination and establishment of *Acacia* species. Isr. J. Bot. 23: 120–126.

Hara, T. 1984. A stochastic model and the moment dynamics of the growth and size distribution in plant populations. J. Theor. Biol. 109: 173–190.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Hauser, T. P. 1994. Germination, predation and dispersal of *Acacia albida* seeds. Oikos 71: 421–426.

Härdle, W. 1991. Smoothing techniques: With implementation in S. Springer-Verlag, New York.

Huston, M. 1986. Size bimodality in plant populations: an alternative hypothesis. Ecology 67: 265–269.

Huston, M. A. & DeAngelis, D. L. 1987 Size bimodality in monospecific populations: A critical review of potential mechanisms. Am. Nat. 129: 678–707.

Jeltsch F., Milton S. J., Dean W. R. J. & Van Rooyen N. 1997. Simulated pattern formation around artificial waterholes in the semiarid Kalahari. J. Veg. Sci. 8: 177–188.

Jeltsch F., Moloney K. A. & Milton S. J. 1999. Detecting process from snap-shot pattern - lessons from tree spacing in the southern Kalahari. Oikos 85: 451–466.

Judson, O. P. 1994. The rise of individual-based models in ecology. Trends Ecol. Evol. 9: 9–14.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology 65: 1874–1884.

Kiyiapi, J. L. 1994. Structure and characteristics of *Acacia tortilis* woodland on the Njemps Flats. Adv. Geoecol. 27: 47–69.

Leistner, O. A. 1967. The plant ecology of the southern Kalahari. Memoirs of the Bot. Soc. S. Afr. 38: 11–73.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

Martin, D. M. & Moss, J. M. 1997. Age determination of *Acacia tortilis* (Forsk.) Hayne from northern Kenya. Afr. J. Ecol. 35: 266–277.

Miller, M. F. 1996. *Acacia* seed predation by bruchids in an African savanna ecosystem. J. Appl. Ecol. 33: 1137–1144.

Milton, S. J. 1988. The effects of pruning on shoot production and basal increment of *Acacia tortilis*. S. Afr. J. Bot. 54: 109–117.

Milton, S. J. 1995. How useful is the keystone concept and can it be applied to *Acacia erioloba* in the Kalahari desert?. Z. Ökologie Naturschutz 4: 147–156.

Moloney, K. A., Levin, S. A., Chiariello, N. R. & Buttel, L. 1992. Pattern and scale in a serpentine grassland. Theor. Popul. Biol. 41: 257–276.

Mwalyosi, R. B. 1990. The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. Afr. J. Ecol. 28: 189–199.

Norton, D. A. & Carpenter, M. A. 1998. Mistletoes as parasites: host specificity and speciation. Trends. Ecol. Evol. 13: 101–105.

Obeid, M. & Seif, E. D. 1970. Ecological studies of the vegetation of the Sudan. I. Acacia Senegal (L) Willd. and its natural regeneration. J. Appl. Ecol. 7: 507–518.

Peled, Y. 1988. Mortality of *Acacia* trees in the southern Arava. MSc Thesis, Hebrew University, Jerusalem (in Hebrew, with English summary).

Peled, Y. 1995. Death of the *Acacias*. Eretz, Geogr. Mag. Israel 9: 63–65.

Pellew, R.A. 1983. The impacts of elephant, giraffe and fire upon *Acacia tortilis* woodlands of the Serengeti. Afr. J. Ecol. 21: 41–74.

Pielou, E. C. 1977. *Mathematical Ecology*. John Wiley & Sons, New York.

Prins, H. H. & Van der Jeugd, H. P. 1993. Herbivore population crashes and woodland structure in East Africa. J. Ecol. 81: 305–314.

Ratz, A. 1996. A generic forest fire model: spatial patterns in forest fire ecosystems. PhD thesis, Philipps-Universität Marburg, Germany.

Rhoades, C. 1995. Seasonal pattern of nitrogen mineralisation and soil moisture beneath *Faidherbia albida* (syn *Acacia albida*) in central Malawi. Agroforestry Syst. 29: 133–145.

Rohner, C. & Ward D. 1999. Large mammalian herbivores and the conservation of arid *Acacia* stands in the Middle East. Cons. Biol., 13: 1162–1171.

Ross, J. H. 1979. A conspectus of African *Acacia* species. Mem. Bot. Soc. S. Afr. 44: 1–155.

Ross, J. H. 1981. An analysis of the African *Acacia* species: their distribution, possible origins and relationships. Bothalia 13: 389–413.

Ruess, R. W. & Halter, F. L. 1990. The impact of large herbivores on the Seronera woodlands, Serengeti National Park, Tanzania. Afr. J. Ecol. 28: 259–275.

Shackleton, C. M. 1993. Fuelwood harvesting and sustainable utilisation in a communal grazing land and protected area of the eastern Transvaal Lowveld. Biol. Cons. 63: 247–254.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Monographs on statistics and applied probability. Chapman and Hall, London, New York.

Sinclair, A. R. 1995. Equilibria in plant-herbivore interactions. Pp. 91–113 In: Sinclair, A. R. & Arcese, P. (eds), Serengeti II: Dynamics, management, and conservation of an ecosystem University of Chicago Press, Chicago, London.

Turner, M. D. & Rabinowitz, D. 1983. Factors affecting frequency distributions of plant mass: the absence of dominance and suppression in competing monocultures of *Festuca paradoxa*. Ecology 64: 469–475.

Van Sickle, J. 1977. Mortality rates and size distributions. Oecologia 27: 311–318.

Walker, B. H., Stone, L., Henderson, L. & Vernede, M. 1986. Size structure analysis of the dominant trees in a South African savanna. S. Afr. J. Bot. 52: 397–402.

Ward, D. & Rohner, C. 1997. Anthropogenic causes of high mortality and low recruitment in three *Acacia* tree species in the Negev desert, Israel. Biodivers. Cons. 6: 877–893.

Weiner, J. & Solbrig, O. T. 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia (Berlin) 61: 334–336.

Weltzin, J. F. & Coughenour, M. B. 1990. Savanna tree influence on understorey vegetation and soil nutrients in northwestern Kenya. J.Veg. Sci. 1: 325–334.

Wiegand, K. 1999. A model of the spatio-temporal population dynamics of *Acacia raddiana*. UFZ-Bericht 15/1999, UFZ Centre for Environmental Research Leipzig-Halle GmbH, Germany.

114

Wiegand K., Jeltsch F. & Ward D. 1999. Analysis of the population dynamics of *Acacia* trees in the Negev desert, Israel with a spatially-explicit computer simulation model. Ecol. Modell. 117: 203–224.

Wiegand, K., Jeltsch, F., Ward, D. & Rohner, C. 1998. Decline of the Negev's Acacias – a spatially explicit simulation model as an aid for sustainable management. Pp. 63–72. In: J. L. Usó, J. L., Brebbia, C. A. & Power, H. (eds), Ecosystems and sustainable development, Computational Mechanics Publications, Southhampton.

Wiegand T., Milton S. J. & Wissel, C. 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. Ecology 76: 2205–2221.

Wiegand, T., Milton, S. J., Esler, K. J. & Midgley, G. 2000. Fast growth and early death: estimating size-age relations and mortality pattern of shrub species in the semiarid Karoo, South Africa. Plant Ecology, 150(1-2) in this issue.

Young, T. P. & Lindsay, W. K. 1988. Role of even-age population structure in the disappearance of *Acacia xanthophloea* woodlands. Afr. J. Ecol. 26: 69–72.