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## Minimum recruitment frequency in plants with episodic recruitment

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**Abstract** There is concern about the lack of recruitment of *Acacia* trees in the Negev desert of Israel. We have developed three models to estimate the frequency of recruitment necessary for long-term population survival (i.e. positive average population growth for 1,000 years and <10% probability of extinction). Two models assume purely episodic recruitment based on the general notion that recruitment in arid environments is highly episodic. They differ in that the deterministic model investigates average dynamics while the stochastic model does not. Studies indicating that recruitment episodes in arid environments have been overemphasized motivated the development of the third model. This semi-stochastic model simulates a mixture of continuous and episodic recruitment. Model analysis was done analytically for the deterministic model and via running model simulations for the stochastic and semi-stochastic models. The deterministic and stochastic models predict that, on average, 2.2 and 3.7 recruitment events per century, respectively, are necessary to sustain the population. According to the semi-stochastic model, 1.6 large recruitment events per century and an annual probability of 50% that a small recruitment event occurs are needed. A consequence of purely episodic recruitment is that all recruitment episodes produce extremely large numbers of recruits (i.e. at odds with field observations), an evaluation that holds even when considering that rare events must be large. Thus, the semi-

stochastic model appears to be the most realistic model. Comparing the prediction of the semi-stochastic model to field observations in the Negev desert shows that the absence of observations of extremely large recruitment events is no reason for concern. However, the almost complete absence of small recruitment events is a serious reason for concern. The lack of recruitment may be due to decreased densities of large mammalian herbivores and might be further exacerbated by possible changes in climate, both in terms of average precipitation and the temporal distribution of rain.

**Keywords** *Acacia* · Arid environments · Extinction · Simulation models

### Introduction

It is generally assumed that virtually all recruitment of long-lived plants in arid environments takes place during infrequent episodes (Crisp 1978; Walker 1993; Watson et al. 1997b). This has led to the term “event-driven dynamics” (Walker 1993), describing population dynamics determined by rare recruitment (and sometimes also mortality or management) events. Long-term population survival is considered possible under these conditions because long-lived plants, where individuals having reached the reproductive stage have high survivorship, store reproductive potential over decades (“storage effect”, Chesson and Warner 1981; Higgins et al. 2000a, 2000b). Watson et al. (1997b) followed the germination and (seedling) survival of two long-lived shrub species from arid environments over 11 years and found a combination of event-driven and continuous recruitment, with recruits being plants <10 cm in height or canopy width. According to Watson et al. (1997a), only 50–70% of the recruitment in this case study occurred during episodes. Also, a literature survey on arid environment shrub dynamics showed that recruitment appears to occur for most species outside large events (Watson et al. 1997a). However, Watson et al. (1997a) admit that differences in the

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definition of the term recruitment made comparisons among recruitment events described in different studies particularly difficult. Nevertheless, “event-driven and continuous processes must be end points of a continuum” of strategies realized in different species (Watson et al. 1997a).

Here, we are especially interested in the question of how often recruitment events are needed to ensure the long-term survival of plants with a given longevity and seed production and no seed bank. The starting point of our study concerns the *Acacia* trees in the Negev desert of Israel. A lack of recruitment leads to concern regarding the long-term survival of these trees in the Negev (Ashkenazi 1995; Ward and Rohner 1997; Rohner and Ward 1999). Wiegand et al. (1999, 2000a, 2000b) have developed a spatially explicit, individual-based simulation model, SAM, to better understand the population dynamics of the *Acacia* trees. These authors showed that there has been episodic recruitment for many decades (Wiegand et al. 2000b). This was done by comparing tree size-frequency distributions observed in the Negev to those produced under different SAM model scenarios. Wiegand et al. (2000b) investigated continuous and episodic recruitment. However, the episodic recruitment was not purely episodic in the SAM model for the following reason. Based on an annual time step (cf. Deterministic model section below in the Materials and methods), each germination event and subsequent survival was followed explicitly. Depending on the weather conditions, only some of these germination events led to major recruitment events while others lead to the survival of but a few individuals (Wiegand et al. 2000b). In the present study, we are interested in the question of how rare recruitment events may be and yet still sustain the Negev’s *Acacia* populations. Furthermore, we are interested in the importance of *Acacia* establishment in low numbers between major recruitment episodes. Due to data scarcity, these questions can be answered on a qualitative level only. The SAM model (Wiegand et al. 1999) serves as a basis for the present study as it is the best summary of the demography of the Negev’s *Acacias* to date.

To investigate the role of the temporal distribution of recruitment, we have developed three alternative models. As a baseline model, we use a deterministic approximation to determine the minimum frequency of episodic recruitment events yielding stable (in the sense of not declining) population size. Then, we conduct stochastic simulations under the extreme assumption that all recruitment occurs during rare, yet large recruitment events. Furthermore, acknowledging Watson et al.’s (1997a) results, we conduct simulations under the assumption of partly continuous and partly episodic recruitment. All simulations are conducted under a range of parameter values to ensure that our results are general enough that they can also be used as guidelines for episodically recruiting plant species with mainly local dynamics irrespective of the precise reason for recruitment being episodic.

## Materials and methods

### Model system

*Acacia raddiana* is one of the most dominant tree species among the sparse tree populations in the Negev desert of Israel. Apart from the northern Negev where annual rainfall exceeds 150 mm these trees grow in wadi beds only (Halevy and Orshan 1972). Our investigations mainly focus on two wadis near the Arava valley: a 1.5-km-long section of Nahal Katzra (35°08'E, 30°32'N) and a 2.0-km-long section of Nahal Saif (35°10'E, 30°52'N). Both sections included about 200 trees. The Negev is a winter rainfall area and annual precipitation is about 40 mm at both sites (Wiegand et al. 1999). Survival of trees in such a dry climate is possible because the wadis collect water from catchments, which increases soil moisture availability as compared to areas outside the wadi beds. On average, there are less than two flood events per year. The dynamics of the *Acacia* trees are primarily influenced by these surface flows in contrast to groundwater (BenDavid-Novak and Schick 1997).

Seed production of breeding *A. raddiana* is a function of tree size, tree moisture condition, and mistletoe infestation. Individual trees do not produce seed every year. However, the proportion of trees which produce seed is above 80%, except for very small trees (Wiegand et al. 1999). Seed infestation of *A. raddiana* in the Negev desert, mostly by *Bruchidius arabicus* and *Caryedon palaestanicus*, is as high as 95%–98% (Rohner and Ward 1999). In the SAM model, infested seeds were assumed not to germinate (Wiegand et al. 1999). A further 90% reduction of seeds is due to the transport of seeds out of wadis by floods and ungulates and the destruction of seeds chewed by rodents and ungulates (Miller 1994; Wiegand et al. 1999). Germination in arid environments depends primarily on local water availability (Wilson and Witkowski 1998). Thus, two conditions need to be fulfilled for the successful germination of a non-infested seed: sufficient rainfall and location of the seed at a safe site (Miller 1994). Under optimal conditions, about 16% of the non-infested seeds in safe sites germinate (Rohner and Ward 1999). Based on rainfall data, SAM included three classes of years: good (23% occurrence probability), intermediate (61%), and bad (16%) years (Wiegand et al. 1999). Seedling survival in the first 30 months is 40%, 20%, and 0% per half-year in good, intermediate, and bad years, respectively (Rohner and Ward 1999; Wiegand et al. 1999). Assuming a germination event and good moisture conditions for seedling survival, the number of seeds per tree of age  $T$  that develop into 5-year-old seedlings ( $O$ ) can be approximated by:

$$O \approx 0.12T/\Delta t \quad (1)$$

with  $T$  measured in steps of  $\Delta t=5$  years (Appendix, Wiegand et al. 1999).

Equation 1 has been derived based on the assumption that trees grow 1.5 cm in trunk circumference per year (cf. Kiyapi 1994). This will also be assumed in the models below resulting in a tight size-age relationship. The deviation from this assumed tight size-age relationship is probably moderate (cf. Wiegand et al. 2000b), in particular because of the wide spacing among trees, which prevents suppression of small individuals by larger individuals as found in forests. Annual survival of older trees has been estimated as 98% (Ward and Rohner 1997). The assumption of age-independent survival of older *A. raddiana* has been shown to be reasonable by Wiegand et al. (2000b) based on an analysis of the size distribution of dead trees in the field and based on simulation experiments. For further details on the life history of *A. raddiana* in the Negev see Ward and Rohner (1997), Rohner and Ward (1999), and Wiegand et al. (1999; 2000a; 2000b).

In the following, we present the three models. Central to all of the models are the parameters survival rate ( $s$ ), fertility factor ( $ff$ ; describing the number of offspring a tree of given age produces), and frequency of years with recruitment events (recruitment frequency;  $rec$ ). For all models presented, the aim is to determine for a given  $s$  and  $ff$  the minimum  $rec$  ( $rec_{\min}$ ) under which long-term population growth rate is  $>1$ .

### Deterministic model

In the SAM model of Wiegand et al. (1999), recruitment is modelled in several steps. The basic time step of the model is 1 year and years are classified into good, medium, and bad years. Germination takes place in good years only and, within the first 2.5 years, seedling survival is 40% in good, 20% in medium, and 0% in bad years. Thereafter, survival is assumed to be independent of the classification of the year. In the deterministic model introduced here, recruitment is modelled in one step. The basic time step is 5 years and only those seeds are considered that germinate and thereafter survive for 5 years. Recruitment is defined as germination and survival for 5 years. Furthermore, we consider germination events followed by optimal weather conditions only, meaning that only large recruitment events are considered. Survival is assumed to be size-independent.

The deterministic model describes the average dynamics of a large population starting at time  $t=0$  at population size  $N_0$ . After one time step,  $\Delta t$  (=5 years), population size changes to  $N_1$  due to the survival rate  $s$  and the establishment of new trees:

$$N_1 = N_0 s \Delta t (1 + \bar{O} \text{rec} \Delta t) \quad (2)$$

$\bar{O}$  is the average number of establishing recruits per tree and recruitment event (a variable) and  $\text{rec}$  is a parameter with a fixed value during each simulation run (see below) and describes the probability that such a recruitment event takes place.  $\bar{O}$  and  $\text{rec}$  can simply be multiplied because Eq. (2) describes average behaviour. In this model describing average dynamics, recruitment takes place every year, but the total level of recruitment is adjusted to the intended value by multiplication of  $\bar{O}$  with the parameter  $\text{rec}$ . Iteration of Eq. (2) gives:

$$N_T = N_0 (s \Delta t + s \Delta t \bar{O} \text{rec} \Delta t)^T \quad (3)$$

$\bar{O}$  can be calculated from a generalization of Eq. (1):

$$\bar{O} = ffT / \Delta t \quad (4)$$

Introducing average tree age,  $\bar{T}$ , leads to:

$$\bar{O} = ff\bar{T} / \Delta t \quad (5)$$

Due to the age-independent mortality, average tree age follows a (negative) exponential distribution and, therefore,

$$\bar{T} = \Delta t / (1 - s \Delta t) \quad (6)$$

(cf. Adler 1998, pp 578–580). Thus,

$$N_T = N_0 \left( s \Delta t + \frac{s \Delta t^2 ff \text{rec}}{1 - s \Delta t} \right)^T \quad (7)$$

Long-term survival is given if the term in the parentheses is  $\geq 1$ . From this condition, we derive:

$$\text{rec}_{\min} = \frac{(1 - s \Delta t)^2}{s \Delta t^2 ff} \quad (8)$$

For example, in the case of the *A. raddiana* in the Negev, with  $ff=0.12$  and  $s=0.90$  per 5 years (i.e. an annual  $s$  of 0.98, Ward and Rohner 1997), the  $\text{rec}_{\min}$  would be 0.09 per 5 years. In other words, on average, 1.85 recruitment events per century are necessary to sustain the population.

### Stochastic simulation model

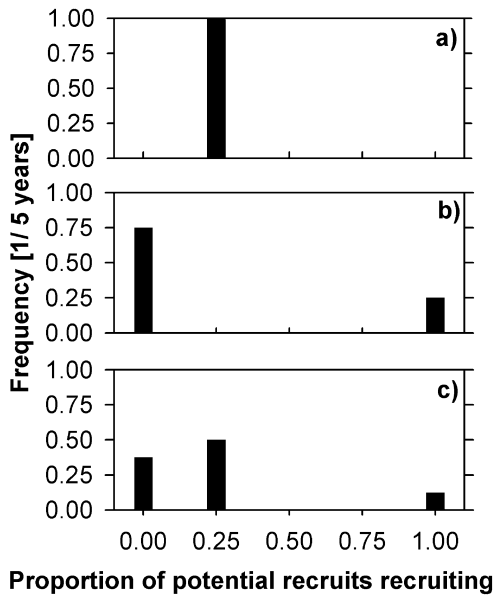
The stochastic simulation model is an i-state distribution model (Maley and Caswell 1993). Such models describe the population dynamics in terms of the distribution of individuals among categories. Here, individuals are categorized according to their age in units of 5 years. The last category is cumulative for all trees of age 256 time steps or more (an age rarely, if ever, reached). At each time step (5 years) survival, growth, and reproduction are simulated. As in the deterministic model above, survival is age independent. The number of survivors in a category is drawn from a binomial distribution or, in the case of few individuals ( $<30$ ), the survival of each individual is determined separately by random numbers according to the  $s$ .

Growth of surviving trees is modelled by shifting them into the next age class. We use random numbers to decide if recruitment occurs in the current time step based on the parameter  $\text{rec}$ . Thus, in the stochastic model,  $\text{rec}$  is included with respect to its original definition, i.e. the probability that a recruitment event (at a maximum level) takes place. In the case of recruitment, we calculate the number of recruits produced for each age class greater than age 2 (counting starts at zero) using Eq. 4. If the resulting number of recruits in an age class is not an integer, we randomly round up or down. As probability of rounding down, we use the difference between the exact number of offspring calculated and the nearest integer. This way, the number of recruits of extremely small populations is not automatically rounded down to zero and thus small populations still have a (small) possibility to recover. Note that, in contrast to the deterministic model, the actual number of recruits in the stochastic model changes with population age distribution and, as explained next, is restricted by an upper limit.

To avoid unrealistically high densities, we introduced density dependence (Henle et al. 2004). Due to the aridity and the large lateral root spread (D. Ward, personal observation of uprooted trees), it is most reasonable to apply the density dependence at the seedling stage. This is also in agreement with the spatial tree distribution in the field (clumped seedlings, randomly spaced adults: Wiegand et al. 2000a). Therefore, we limited the number of recruits per recruitment event (cf. Eq. 4) a priori to 5,000, corresponding to  $>540,000$  seedlings germinating in a wadi section envisaged to contain 200–1,000 trees. Thus, 5,000 was deemed to be an exceptionally large density of recruits; this judgement was also based on the dynamics of the SAM model. The precise value of this upper limit does not influence the qualitative results of our study.

Each simulation consists of 350 time steps and 200 replicate runs. Runs are initialized with 1,000 trees, an initial population size which is quite robust against demographic stochasticity. Trees are distributed among age classes using a negative exponential distribution. Based on preliminary simulations, we discard the first 150 time steps of each run to ensure that results are independent of this initial distribution. Simulation output includes the population growth rate, the population size including all ages, and the number of recruits for every 20th time step. Results are given as averages over time (time steps 150–350) and replicate runs.

Simulations are run for a range of values of  $s$  and  $ff$ . The  $\text{rec}_{\min}$  is estimated by a parameter fit. This was done by running a first simulation using the value for  $\text{rec}$  calculated by the deterministic model. Thereafter, if the average population growth rate over the 200 years analysed was  $<1.0$ ,  $\text{rec}$  was increased by 0.05 as many times as was necessary to yield a growth rate  $\geq 1.0$ . In addition, there was a requirement that populations survived in at least 90 of the 100 replicate runs. Earlier simulations without this supplementary requirement often led to parameter fits with positive average population growth but with  $<50$  out of 100 simulated populations surviving, which is due to the high degree of stochasticity and thus sometimes vast differences in population trajectories.



**Fig. 1a–c** Frequency of recruitment events (*rec*) of a certain size under three scenarios. A “potential recruit” is a seed that will germinate and survive for 5 years if the weather is favourable. The *x*-axis gives the size of the recruitment event expressed relative to the number of recruits produced by all trees. **a** Under the deterministic model, average behaviour is considered only and therefore recruitment takes place every time step at a relative size [*rec*]=0.25]. **b** Under the stochastic model, either all (probability *rec*) or no potential recruits recruit (probability 1–*rec*). **c** The semi-stochastic model is a mixture of **(a)** and **(b)**

Semi-stochastic simulation model

Before introducing the semi-stochastic model, we take a look at the deterministic and stochastic models from a different angle. Equation 4 gives the number of potential recruits produced by one tree during one time step. Under the deterministic model, we assumed that in each time step the proportion *rec* of these potential recruits does actually recruit (Fig. 1a). Under the stochastic model, however, in a proportion *rec* of the years all of those recruits will recruit, while there is no recruitment in the remaining time steps (Fig. 1b). The semi-stochastic model combines properties of both the deterministic

and the stochastic model. For each time step, there is a 50% chance that the model will behave like the deterministic model. In the remainder of the time steps, survival and growth are modelled as in the stochastic model. In time steps following the deterministic model there is always recruitment, yet at the low level of *rec* multiplied by the number of recruits produced. In time steps following the stochastic model, recruitment is at the highest level and takes place with probability *rec* (Fig. 1c). As a result of these rules, the average number of recruits for a given set of parameters is comparable across the models. Note that the main cause for between-year differences in the size of recruitment events is the weather (as described in the Deterministic model section above). However, in the semi-stochastic model we consider temporal variations in the number of recruits on a simplified phenomenological level only. In other words, we mimic the outcome of infrequent years which are optimal (or unfavourable) for recruitment via application of the rules of the stochastic (or the deterministic) model. The parameter *rec* is fitted as described for the stochastic model.

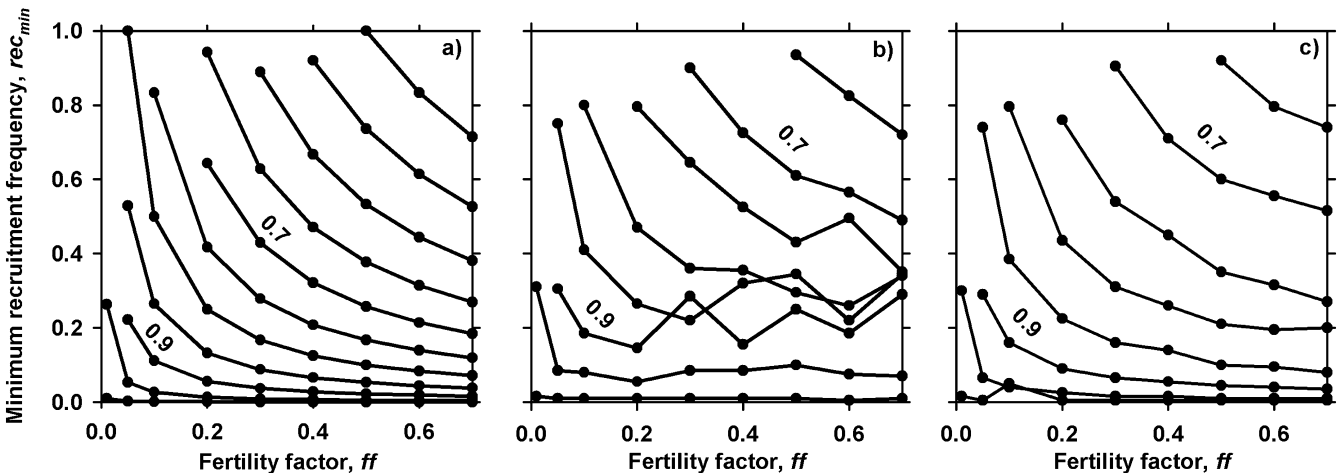
**Results**

Deterministic model

Within the range of *ff* s investigated (0.01–0.70), long-term population growth was positive for *s* >0.5 per 5 years (Fig. 2a). Lines join points with the same tree survival. Combinations of *ff* and *s* not shown on the left of these lines are not viable. These parameter combinations led to recruitment frequencies >1.0. As expected, with increasing survival, and increasing *ff*, the *rec*<sub>min</sub> decreases. For example, at *ff* =0.1, and *s* =0.9 per 5 years at least 0.11 recruitment events per 5 years, or 2.22 events per 100 years, are necessary to sustain the population.

Stochastic simulation model

An example of a time series including the total population and the number of recruits under the stochastic simulation model is given in Fig. 3a. The time series shown



**Fig. 2** Minimum *rec* (*rec*<sub>min</sub>) (per 5 years) ensuring long-term survival under the **a** deterministic, **b** stochastic, and **c** semi-stochastic models. Each point represents a (simulation) result for a combination of the fertility factor (*ff*) and the survival rate (*s*) (per

5 years) for which the *rec* ≤1.0 per 5 years. Points with the same *s* are joined by lines. *s* from bottom to top: 0.99, 0.95, 0.9, 0.85, 0.8, 0.75, 0.7 etc. *s* =0.9 per 5 years and *s* =0.7 per 5 years are indicated above the corresponding lines

exemplifies population dynamics under rare, yet large recruitment events. Each peak in the number of recruits is translated directly into a pronounced increase in total population size. Unless a further recruitment event follows soon thereafter, population size declines rapidly, e.g. from 1,286 individuals at time step 98 to 115 at time step 121. This corresponds to a decrease of 1,171 individuals within 23 years. Under this model, positive long-term population growth is possible for  $s > 0.65$  per 5 years only (Fig. 2b). The  $rec_{min}$  necessary is greater than under the deterministic model. For example, at  $ff=0.1$ , and  $s=0.9$  at least 0.19 recruitment events per 5 years, or 3.7 events per 100 years are necessary to sustain the population. In contrast to the deterministic model, results are somewhat noisy, as indicated by lines of equal  $s$  which cross. However, similar to the deterministic model, the trend is for a decreasing  $rec_{min}$  with increasing  $s$  and  $ff$  (Fig. 2b).

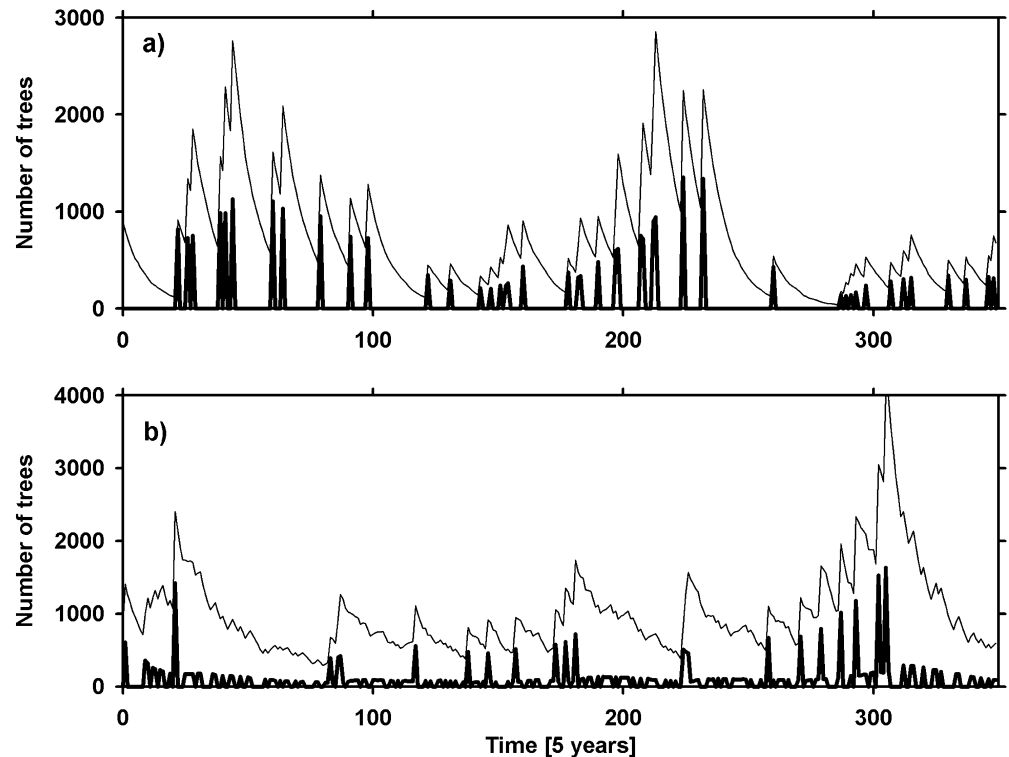
The fitting procedure exhibits high sensitivity with respect to both the number of populations and the population growth rate (Figs. 4, 5). For example, at a  $s$  of 0.9, we find that the condition of at least 90 simulated populations surviving is fulfilled relatively rapidly. That is, increases in  $rec$  translate into clear increases in the number of simulated populations surviving simulations (Fig. 4). At the same time, the increase in the population growth rate is quite rapid. However, when 90 populations survive, the growth rate remains below the target value of 1.0, except for small  $ff$  in the range of  $ff=0.05-0.2$  (Fig. 4). For  $ff \geq 0.3$ , a further increase in  $rec$  leads to the survival of all populations ( $ff=0.3-0.7$ ; Fig. 4). However, the concurrent increase in population growth rate is small and a drastic increase in the  $rec$  is necessary to reach growth rates  $>1$  ( $ff=0.3-0.7$ ; Fig. 4). At a  $s$  of 0.7, the deterministic value at

which the parameter fitting procedure is started is far too low to allow for population survival (Fig. 5). However, as soon as some populations survive, further increases in  $rec$  lead to both a rapid increase in the number surviving and the growth rate (Fig. 5). The sensitivity of the model output (number of populations and their growth rate) is of ecological significance in that these variables tell us that changes in (environmental) factors influencing  $rec$  may have a large impact on long-term population survival.

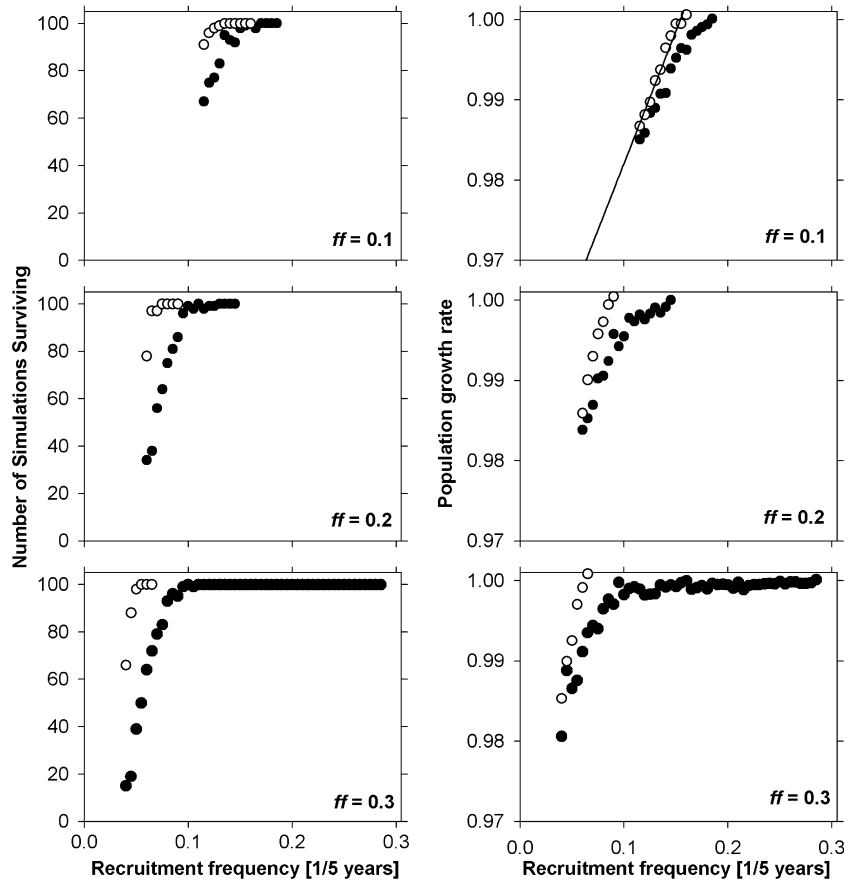
Finally, we examine the population sizes and the number of recruits under the fitted values of  $rec$  (the probability that a recruitment event takes place). Under the stochastic simulation model and, for example, a  $s$  rate of 0.9 per 5 years, overall average population size is 9,997.5 trees, with no significant relationship between average population size and  $ff$  (Pearson product moment  $\rho=0.611$ ,  $P=0.108$ ) but with fluctuations reflecting the fluctuations in  $rec$  (Fig. 2b). Under the same scenario and a  $s$  of 0.7 per 5 years, average population size is 11,961.4 trees at  $ff=0.3$  and decreases approximately linearly to 6,755.8 trees at  $ff=0.7$ . Again, this decrease in population size mirrors the decrease in  $rec$  (Fig. 2b). The counter-intuitive finding that the average population size decreases with increasing fertility is a result of the decreasing probability that a recruitment event takes place ( $rec$ , Fig. 2b). If the  $ff$  increases, a lower recruitment probability ( $rec$ ) is sufficient to guarantee a sustainable population. As a consequence, the average population size is smaller. Testing the significance of these results for natural systems would require evolutionary models and is thus currently unknown.

To avoid unrealistically high densities, we restricted the number of recruits per recruitment event to 5,000. This

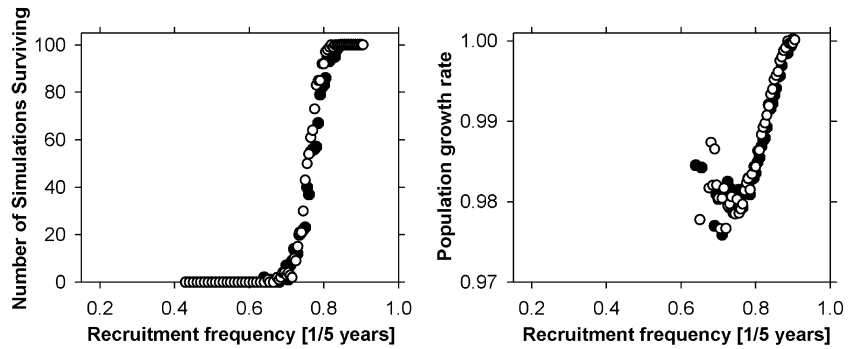
**Fig. 3** Number of trees over time for an example simulation run under **a** the stochastic and **b** the semi-stochastic models (note the different scales). Thin line all trees, thick line first-year trees only. The parameter settings were  $ff=0.12$ ,  $s=0.9$  per 5 years,  $rec=0.125$  per 5 years. Note that simulations with relatively small population sizes are shown because we are mainly interested in presenting the effect of single recruitment events on the immediate change in population size, which can be seen more easily if the range of values on the y-axis is small



**Fig. 4** Number of simulations in which the populations survive for all 350 simulated time steps (*left*) and average population growth rate from time step 150–350 (*right*) for  $s=0.9$  per 5 years and three different recruitment factors  $ff$  (cf. Eq. 4). ● Stochastic model, ○ semi-stochastic model. Results obtained with  $ff < 0.1$  and  $ff > 0.3$  were similar to those obtained with  $ff = 0.1$  and  $ff = 0.3$ , respectively. Concerning the growth rates, note that there were no values observed outside the range of the y-axis. As for greater values this is because simulations were stopped when a growth rate beyond 1.0 was reached. The line in the graph where  $ff = 0.1$  is given by:  $y = 0.95 + 0.33x$



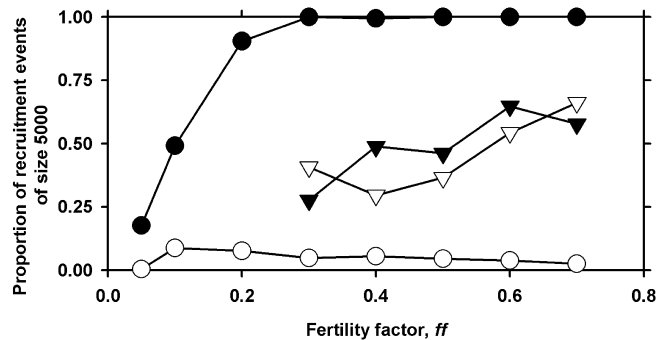
**Fig. 5** As for Fig. 4, but for survival  $s=0.7$  per 5 years and  $ff=0.3$ . Graphs for  $ff=0.1$  and  $ff=0.2$  (cf. Eq. 4) are not shown because of the negative long-term population growth rates under these  $ff$  and all  $ff \leq 0.1$ . Concerning the growth rates, note that all values below the range of the y-axis are zero



upper limit is reached quite often (Fig. 6). At a  $s$  of 0.9 per 5 years, the proportion of recruitment events of size 5,000 starts at about 0.1 at  $ff=0.05$  and rapidly approaches 1.0 at  $ff=0.3$ . At a  $s$  of 0.7 per 5 years, the proportion of maximum recruitment events is of the order of 50% (Fig. 6).

*Semi-stochastic simulation model*

A time series of the total population size and the number of recruits under the semi-stochastic simulation model shows rapid increases in total population size after large recruitment events (e.g. >5,000 trees, Fig. 3b), as seen under the stochastic model (Fig. 3a). However, due to the frequently interspersed small recruitment events, the



**Fig. 6** Proportion of recruitment events of size 5,000 versus  $ff$ . The maximum number of recruits allowed per recruitment event in the simulation models was 5,000. The numbers were estimated from the size of the recruitment events recorded every 20 time steps, starting at 160. ●, ▼ Stochastic model; ○, ▽ semi-stochastic model; ●, ○  $s = 0.9$  per 5 years; ▼, ▽  $s = 0.7$  per 5 years

decrease in population size after large recruitment events is rather slow, e.g. from 1,264 individuals at time step 87 to 577 at time step 110. This corresponds to a decrease of 687 individuals within 115 years, which is about half as rapid as under the stochastic model. Positive long-term population growth is possible for  $s > 0.65$  per 5 years (Fig. 2c). Values for  $rec_{min}$  are similar to or lower than under the stochastic model (Fig. 2b). For example, at  $ff = 0.1$ , and  $s = 0.9$ ,  $rec_{min} = 0.16$  per 5 years, or  $rec_{min} = 3.2$  per century. Note that this means that 1.6 large episodes per century are necessary to sustain the population. The main difference from the stochastic model is that the results are not as noisy; lines of equal  $s$  do not cross.

The parameter fit shows, for example for a  $s$  of 0.9 per 5 years, the following difference from the same scenario under the stochastic model: with increasing  $rec$ , both the number of simulated populations surviving simulations (Fig. 4) and the population growth rate (Fig. 4) increase rapidly and hit their target values (of 90 and 1.0, respectively) earlier than under the stochastic model (Fig. 4). These differences disappear at a  $s$  of 0.7. Here, the fitting of the semi-stochastic model proceeds more or less as under the stochastic model (Fig. 5).

As for population size, under the semi-stochastic simulation model and, for example a  $s$  of 0.9 per 5 years, overall average population size is 6,412 trees. This is less than the equivalent value under the stochastic model (9,998) and, as in the stochastic model, there is no significant relationship between average population size and  $ff$  ( $\rho = 0.315$ ,  $P = 0.448$ ). In contrast to the stochastic model, fluctuations in population size with  $ff$  are negligible. With a  $s$  of 0.7 per 5 years, population size lies at 11,500 except for 14,330 trees at  $ff = 0.3$ .

The upper limit of 5,000 recruits is reached less often under this model than under the stochastic model. At a  $s$  of 0.9 per 5 years, the proportion of recruitment events of size 5,000 is  $< 0.07$  (Fig. 6). Interestingly, at a  $s$  of 0.7 per 5 years, the proportion of maximum recruitment events is about 0.5 and thus higher than under an  $s$  of 0.9 per 5 years (Fig. 6). Thus, the trend of the effect of the  $s$  on the proportion of maximal recruitment events is inverted under lower survival (Fig. 6).

## Discussion

We have presented three models of the population dynamics of long-lived trees without a seed bank. The deterministic model is a baseline model estimating the conditions in terms of fertility and survival under which long-term survival is possible and the minimum recruitment necessary for positive population growth. This simple model is useful for rapid estimates of population viability. However, the recruitment frequencies estimated with this model are too low. Among other reasons, this is because the deterministic model operates with a continuous inflow of new trees. An alternative deterministic model which would relax this assumption would be the Lotka-Euler equation (Euler 1760; Lotka 1907) with

fecundity ( $b_x = 0$  for all ages ( $x$ ) with  $x \pmod n > 0$  (where  $n$  is a natural number), and  $b_x = O$  (Eq. 4) otherwise. Thus, recruitment would be assumed to occur every  $n$ th year. A  $rec_{min}$  can be estimated by calculating the sum in the Lotka-Euler equation for a range of values of  $n$  and selecting the maximum value ( $n_{max}$ ) under which the sum is  $> 1$  (e.g. Case 1999). The  $rec_{min} = 1/n_{max}$ . The results of this model are somewhat more realistic than our deterministic model but still more optimistic than the stochastic and semi-stochastic models.

Our stochastic model also relaxes the assumption of a continuous inflow of new trees and models recruitment as a rare, stochastic event. Recruitment in the stochastic model differs from the SAM model in that the detailed SAM model allows for recruitment events smaller than the number of offspring given in Eq. 4 (Wiegand et al. 1999). This happens when the good year during which germination occurs is followed by two intermediate years with lower seedling survival or by one intermediate and one good year. In this respect, the recruitment regime of the SAM model is intermediate to our stochastic and semi-stochastic models, which acknowledges Watson et al.'s (1997a, 1997b) observation of a mixture of continuous and episodic recruitment in arid environments.

An important step towards deciding whether the lack of recruitment of *Acacia* trees in the Negev is a reason for concern would be to know if recruitment of viable *Acacia* populations tends to be episodic or continuous. Both this study and Wiegand et al.'s (2000b) support the hypothesis that recruitment of *Acacia* trees in the Negev has encompassed rare, large recruitment events and that such events can be considered a normal feature of the dynamics of these trees. Episodic, large recruitment peaks create the characteristic features of the tree size-frequency distributions that are also found in natural populations, i.e. high variability in both the distribution among size classes and the deviation from a monotonic decline in size class occupancy with increasing size (Wiegand et al. 2000b). The SAM model, and the stochastic and semi-stochastic models, all include large recruitment events (cf. Fig. 3) and are therefore in agreement with natural size frequency distributions.

The most pragmatic approach to dealing with a system with fluctuating recruitment, both for modelling and field studies, is to focus on the episodic, large recruitment peaks. This is the case for the stochastic model and simplifies field surveys in that monitoring of recruitment can be restricted to easily detectable mass recruitment. Following such an approach, low levels of recruitment are noise that can be neglected. In the following, we will argue that this assumption leads to unrealistic model dynamics and that a lack of small yet continuous recruitment in field surveys is a serious reason for concern.

The assumption of rare, large recruitment events in the stochastic model leads to rapid declines in population size in periods without recruitment (Fig. 3a). As is typical for models with density dependence at high densities, populations cannot fully balance the more rapid decline by the greater increases in population size following larger

recruitment (Henle et al., [in press](#)). As a consequence thereof, despite a population growth rate near 1 (e.g. 0.99), the risk of extinction within the 350 years simulated is quite high (Figs. 4, 5; closed symbols). With increasing *rec* the duration of such unfavourable periods decreases, and, on average across all replicate runs, population size increases. Unless fertility and/or survival are low, a large population size is sustained until the next recruitment event (due to survival) and the number of recruits is large (due to fertility). This has led to a great proportion of recruitment events at the maximum size permitted. What was meant to serve as an upper limit for rare, large events resulted in a frequently applied upper limit. The long tails with little increase in population growth rate in the fitting of the stochastic model (Fig. 4; closed symbols) are due to the fact that the increase in population growth resulting from more frequent recruitment was restricted to the positive effect of the increased frequency of recruitment. However, these populations could not profit, in terms of recruitment, from their larger size because the number of recruits produced remained constant. However, large population size is *the* prerequisite for long-term survival because it improves the chances that the population will survive periods without recruitment (cf. Fig. 3a). Stochasticity in the timing of the recruitment events explains the noise in the increase in the population growth rate (Figs. 4, 5; closed symbols) and consequently the noise in Fig. 2b.

In the absence of suitable data, we do not know what the historical recruitment regime of *Acacia* trees is in the Negev. However, the dynamics resulting under the stochastic model, i.e. exclusively due to episodes of recruitment at maximum density appear unrealistic to us. Clearly, such episodes must be large to balance their rarity. However, based on our previous experience with the SAM model and a lack of reports of such extreme events, we expected most recruitment episodes to be noticeably below the maximum density. Thus, we follow Watson et al. (1997a, 1997b) and propose that recruitment in long-lived plants in arid environments is determined by both rare, large and more frequent, smaller recruitment events. The rare, large events are more spectacular and clearly have a pronounced effect on population dynamics (Fig. 3a). However, the relatively frequent occurrence of a few recruits here and there are important to the population dynamics because they slow down the decay of the population, making longer periods between large recruitment events possible (Fig. 3b). They constitute an “ecological buffer” (sensu Jeltsch et al. 2000), preventing rapid decline and even extinction in tree populations in periods without large recruitment events. As a consequence, the lack of large recruitment events is no reason for concern as they are expected to occur, on average, 1.6 times per century only, assuming that 50% of the years have episodic and 50% continuous recruitment (see the Semi-stochastic model section in the Results). A period of, say, 25 years without a large recruitment event can be considered normal. However, if the proportion of years with small recruitment events is indeed of the order of 50%, and assuming that recruitment is not completely

synchronized within the Negev, germination should have been observed in more than three out of 75 locations within 1994–1998, a reported by Wiegand et al. (2000b). Regular surveys for new plants were conducted at our permanent sites Nahal Saif and Nahal Katzra. Of these, one localized germination event was observed in 1997 in Nahal Saif. However, all seedlings died within the same winter (Wiegand et al. 2000b). Further monitoring of permanent sites will be necessary for a better estimate of current continuous and episodic recruitment because even a 5-year study is not sufficiently long.

The distinction between “large” and “small” recruitment events is artificial and these categories are not easily applied to field data (cf. Fig. 7). However, this does not affect our main conclusion that a virtually complete lack of recruitment over prolonged periods indicates population decline and an increased risk of extinction. Also, our semi-stochastic model gives a conservative estimate of the minimum recruitment because it does not consider demographic stochasticity, as observed in small (<200) populations. However, this might be counterbalanced if *Acacia* populations in different wadis form metapopulations. In this case, small populations could be saved from extinction, or (in the case of local extinction) re-colonized by introduction of seeds from other populations in nearby wadis (Levins 1969; Hanski 1999). This would necessitate movement by large mammalian herbivores that disperse the seeds among wadis. This possibility may be small due to great declines in the populations of these animals in the Negev over the twentieth century (Rohner and Ward 1999).

Lahav-Ginott et al. (2001) report an increase in population size at two sites observed via aerial photographs taken in 1956 and 1996. Based on an early estimate of the average life span of *Acacia* trees in the Negev of 42 years by Ward and Rohner (1997), Lahav-Ginott and Kadmon (2001) interpreted this population increase as evidence of recent recruitment. However, more recent estimates of the *Acacia* life span based on data on *Acacia* growth indicate that these trees probably reach 200 years of age frequently (Wiegand 1999; Wiegand et al. 2000b). Assuming that the survival estimate of Ward and Rohner (1997) was incorrect by 1% only (i.e. annual survival is

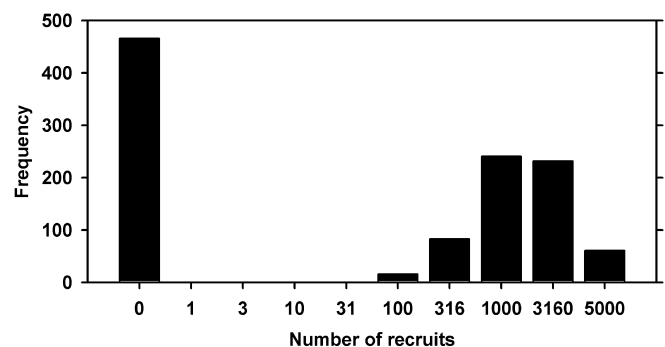


Fig. 7 Frequency of recruitment events of certain sizes under the semi-stochastic model summarizing a total of 1,100 data points. Classes are 0, 1, 2–3, 4–10, 11–31, 32–100, etc. ( $ff=0.1$ ,  $s=0.9$  per 5 years,  $rec=0.16$ )



99% which corresponds to 0.95 per 5 years), the average life span would be 100 years. Thus, many of the trees observed on the 1996 photographs were probably already present on the 1956 images and the increase in tree numbers could be fully explained by trees already present in 1956 yet too small for detection (a size threshold of 6 m<sup>2</sup> canopy size was used for the automated detection of individual *Acacia* trees on the aerial photographs).

Thus, unfortunately, the seemingly positive results of Lahav-Ginott et al. (2001) are not in disagreement with our impression of a severe lack of recruitment. Insufficient recruitment of *Acacia* trees in the Negev may be caused by factors additional to soil moisture availability. Seed infestation by bruchid beetles (family Bruchidae) has been and still is extremely high at 70–98% (Halevy 1974; Rohner and Ward 1999). Most of these seeds are not viable (Halevy 1974; Lamprey et al. 1974; Rohner and Ward 1999). These high attack rates might be related to decreased numbers of large mammalian herbivores in the Negev. This is because bruchids initially attack fresh green *Acacia* pods on the tree. If mammalian herbivores do not consume the seed pods, bruchid reinfestation following emergence may occur on mature, dry pods on the tree or ground (Miller 1994; Or and Ward 2003). Consumption of *Acacia* seeds by ungulates is advantageous to germination since passage of the hard, indehiscent *Acacia* seeds through the gut of ungulates results in an increased germination rate due to the scarifying action of digestion on the hard seed coat (Coe and Coe 1987; Rohner and Ward 1999). Thus, the decline of pastoralism in the Negev since the 1940s might be of particular importance (Danin 1983). The decreasing camel numbers might be a key to explaining a decrease in *Acacia* recruitment (Rohner and Ward 1999) and domestic camels could be used as a management tool to maintain these tree populations by introducing them to wadis after the occurrence of winter floods. However, removal of the camels after defecation seems advisable because of possible negative browsing effects (Milton 1995; Rohner and Ward 1999).

Another factor influencing the future survival of the Negev's acacias is the climatic change in the Negev. It is as yet unclear what the predominant pattern of climate change is in the Negev: average annual precipitation is considered to be increasing (Otterman et al. 1990; Steinberger and Gazit-Yaari 1996; Perlin and Alpert 2001) or decreasing (Alpert et al. 2002). High-intensity rains have increased in frequency, with fewer rains of moderate and weak intensity (Alpert et al. 2002), while the length of the rainfall season might be decreasing (Kutiel 2001) or increasing (Steinberger and Gazit-Yaari 1996). More data are needed from a greater range of rainfall stations to fully ascertain the predominant climatic changes. In any case, small changes in average precipitation may already have pronounced negative or positive effects on the survival of acacias in the Negev. This can be seen from Fig. 4 ( $\beta = 0.1$ ). The slope of the relationship between the population growth rate and the *rec* is 0.33 per 5 years and thus quite high. However, an increase in average precipitation, combined with a shorter rainy

season and fewer rains of moderate and weak intensity, may actually lead to an overall disadvantageous effect on *Acacia* survival in the Negev. This is because a decrease in small recruitment events (caused by the shorter rainy season and the decrease in rains of moderate and weak intensity) would weaken the buffer provided by this contribution to population dynamics. It is very unlikely that this could be counterbalanced by the expected increase in large recruitment events due to the envisaged increase in high-intensity rains (Otterman et al. 1990; Steinberger and Gazit-Yaari 1996; Perlin and Alpert 2001). Certainly, the cautionary principle requires us to assume that average precipitation is decreasing. Therefore, we have to fear decreases in *Acacia* densities due to both decreased average precipitation and a decrease in small recruitment events. Furthermore, there is more alarming news. Winters have become colder while summers have become warmer (Ben-Gai et al. 1998). Due to the effects of temperature on soil moisture status and plant water demand, this should cause lower winter and higher summer mortality. The net effect is likely to increase overall mortality.

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## Appendix

Assuming that trees grow 1.5 cm in trunk circumference per year (cf. Kiyiapi 1994) and using age  $T$  in units of 5 years, trees can be classified into non-reproducing seedlings (<15 cm,  $T/5$  years=0, 1), subadults with low seed production (15 cm–45 cm,  $T/5$  years=2, 3, 4, 5), and adults ( $\geq 45$  m,  $T/5$  years  $\geq 6$ ) with full seed production (Wiegand et al. 1999). The number of seeds produced by a tree ( $S$ ) of trunk circumference ( $tc$ ; cm) is:

$$\log S = 3.8 + 1.1 \log tc$$

(Wiegand et al. 1999) or, in terms of age  $T$  (5 years):

$$\log S = 4.8 + 1.1 \log T$$

Thirty-five percent of the subadult and 84% of the adult trees reproduce in a given year. On average, the number of seeds produced is reduced by 84% (subadults) and 75% (adults) due to mistletoe infestation and unfavourable moisture status (Wiegand et al. 1999).

Given a germination event under optimal weather conditions, a certain seed has a chance of  $1.8 \times 10^{-6}$  to evolve into a 5-year-old seedling. This is because 96.5% of the seeds are infested by seed beetles, 93% of the seeds get lost, 50% land at a safe site, 15.6% of the seeds at safe sites germinate, and semi-annual seedling mortality is 60%

within the first 2.5 years and 1.74% over the following 2 years (Wiegand et al. 1999).

Thus, the number of offspring ( $O$ ) produced by a subadult tree for a potential recruitment event is:

$$\log O = -1.5 + 1.1 \log T$$

and the number of offspring produced by adults is:

$$\log O = -1.1 + 1.1 \log T$$

Plotting number of offspring versus age reveals a linear relationship, which is approximately:  $O \approx 0.12 T / \Delta t$ .

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