Modeling seed dispersal in a variable environment: a case study of the fleshy-fruited savanna shrub Grewia flava

Jörg Tews a,b, Kirk Moloney b, Florian Jeltsch a

a Institute of Biochemistry and Biology, Plant Ecology and Nature Conservation, University of Potsdam, Malzherallee 2, D-14467 Potsdam, Germany
b Department of Botany, Iowa State University, 144 Beatty Hall, Ames, IA 50011-1020, USA

Received 5 March 2003; received in revised form 2 September 2003; accepted 27 October 2003

Abstract

In ecology much attention has been paid towards seed dispersal of fleshy-fruited plants, however, knowledge is lacking about the long-term demographic consequences of variation in dispersal distance and fruit removal rate, particularly given the natural variability of the environment the organism lives in. In this study we used a spatially explicit, two-level stochastic computer model to simulate population dynamics of a fleshy-fruited shrub living in the sub-canopy of solitary savanna trees. On the landscape level we implemented three realistic scenarios of savanna landscape dynamics for a period of 500 years with equal inter-annual mean of environmental variables. The first scenario is representative of a relatively constant environment with normal variability in precipitation, constant tree density and random tree recruitment pattern. The second and third scenarios represent positive auto-correlated, cyclic patterns with alternating phases of tree cover increase and decrease corresponding with favorable and unfavorable rain phases. Our simulation experiments show that when fruit removal rate is extremely low, population persistence is enhanced under relatively constant rain conditions, while alternating rain phases of the cyclic scenarios lead to a significant population decrease. This result confirms previous findings that periodically fluctuating environments may increase local extinction risk. However, when dispersal distance is a limiting factor (whilst removal rate was sufficiently high), tree clumps typically forming in wet phases of both cyclic scenarios compensated for the negative effect of low dispersal distances, while the constant scenario with random tree pattern and larger inter-tree distances resulted in a significant population decline.

Keywords: Dispersal distance; Environmental variability; Periodically fluctuating environments; Spatial-explicit simulation models; Woody plants

1. Introduction

Seed dispersal is widely believed to be a fundamental element of plant population ecology and has received much scientific attention in the last decades (e.g. Howe and Smallwood, 1982; Herrera et al., 1994; Fuentes, 2000; Nathan and Muller-Landau, 2000). It is a crucial ecological process that maintains the diversity of plant communities (Christian, 2001; Webb and Peart, 2001). This becomes relevant when the set of potential seed-dispersal agents of a plant species is small and loss of a single agent may affect abundance and long-term persistence (Loiselle and Blake, 2002). However, the link between both the process and spatial pattern of seed dispersal and their demographic and genetic consequences still requires investigation.
(Schupp and Fuentes, 1995; Willson and Travesset, 2000). In particular, knowledge is lacking about the ecological importance of removal rate, i.e. percent of total crop removed from an individual plant (Willson and Whelan, 1993) and seed-dispersal distance, since this requires experimental modifications of seed distributions (Portnoy and Willson, 1993). Considering long-term population dynamics, possible effects are hard to judge, as both habitat mosaics and dispersal processes are likely to change. Nowadays implications of global climate change may raise even more questions.

In the context of our study we describe environmental variability as spatial and temporal variance in the distribution and density of habitat patches available for plant recruitment. For instance, in arid savanna of southern Africa, large, solitary Acacia trees act as recruitment foci for bird-dispersed, fleshy-fruited plant species where seed deposition is generally higher under the trees than in the open grassland habitat (Leistner, 1967; Dean et al., 1999). This pattern is typical for bird-mediated seed rain (e.g. Herrera et al., 1994; Dean and Milton, 2000; Jordanano and Schupp, 2000) and may be generally more common than expected (Kollmann, 2000). However, from a long-term perspective, the ratio of open habitats to Acacia microsites and the spatial distribution of trees is unstable as a result of extrinsic factors such as precipitation (supports increase in woody plant cover), fire (reduces woody plant cover) or herbivory (may support both increase and reduction) (Jeltsch et al., 1999, 2000).

In arid savanna, recruitment of fleshy-fruited plant species not only depends on the general availability of favorable microsites and, e.g. key processes such as precipitation (supports increase in woody plant cover), fire (reduces woody plant cover) or herbivory (may support both increase and reduction) (Jeltsch et al., 1999, 2000). There is general agreement that tree–grass ratios in arid savanna vary in the form of long-term cyclical phases (see Belsky, 1990, 1995) triggered by ecological buffering mechanisms, which may prevent the system from converting to either a stable grassland or a forest state (Jeltsch et al., 2000).

In arid savanna, recruitment of fleshy-fruited plant species not only depends on the general availability of favorable microsites and, e.g. key processes such as germination and survival—seeds also have to be distributed away from the parent plant in order to guarantee recruitment success. Each dispersal agent is characterized by a specific fruit handling behavior and consumption rate, and thereby produces a distinct seed-dispersal pattern, which in turn may alter plant population dynamics (e.g. Bleher and Böhnig-Gaese, 2000). For many fleshy-fruited plant species there is a wide range of potential seed dispersers and dispersal patterns vary between and within species depending on, e.g. the abundance of dispersal agents and the composition of dispersal guilds. In addition, in savannas where rainfall is unpredictable, many bird species show nomadic and erratic movement patterns (Tyler, 2001). Frugivorous birds directly affect seed dispersal through the number of seeds they remove (quantity component) and to where, and in what condition, those seeds are deposited (quality component) (Losselle and Blake, 1999). High temporal and spatial variation of removal rates can be observed among individual plants in the same year and site (e.g. Alcántara et al., 1997) or between years and sites (e.g. Ortiz-Pulido and Rico-Gray, 2000; Parciak, 2002) with rates varying by several orders of magnitude. Besides highly variable removal rates, one must consider the distances of seed dispersal, as this may determine whether a seed reaches a suitable site or not. For instance, dispersal distance depends on species-specific movement patterns, activity ranges and gut retention times. Both dispersal distance and removal rate form the shape of the seed-dispersal curve for a parent plant, which is usually described as leptokurtic with a higher peak (near the parent plant) and longer tail than a normal distribution (Willson and Travesset, 2000).

It is difficult to evaluate the relative importance of seed-dispersal components for plant population dynamics when environmental conditions change. Furthermore, from a logistical perspective, long-term experiments are time consuming and demand considerable human resources. Consequently, computer simulation tools provide a practical means for analyzing the implications of long-term environmental change. For the purposes of this study we used Spatial Grewia Model (SGM), an existing spatial simulation model which has been developed to simulate dispersal processes and population dynamics of the fleshy-fruited raisin bush Grewia flavescens D.C., Tiliaceae (Tews et al., in press). G. flavescens is a prominent, long-lived shrub in southern Kalahari savannas and is usually found beneath the canopy of other woody plants (Leistner, 1967; Dean et al., 1999)—only a few seeds are deposited in the open grassland matrix. However, empirical data show that Grewia emergence rates are similar between sub-canopy habitats and matrix vegetation (Schurr, 2001).
In this study we explore how varying seed removal rate and dispersal distance may affect long-term population dynamics of G. flava for three possible habitat scenarios. To our knowledge this is one of the few attempts to investigate long-term consequences of seed dispersal under variable environments (however, see Kriticos et al., 2003). We analyze population dynamics for a 500-year period for a static and two-cyclic environmental scenarios where tree density and precipitation periodically change. Here we focus on ecological thresholds of both components, i.e. when either removal rate or dispersal distance is too low to allow long-term persistence. For both cases we expect the population to decrease or even go extinct. Of particular interest is whether population response is similar in all three environmental scenarios, i.e. whether environmental variability may alter population dynamics.

2. Methods

2.1. Spatial Grewia Model

In this study we used SGM, a two-level, rule-based simulator operating on a 200 x 200 cell grid and on annual timesteps (see Tews et al., in press). SGM has been previously validated with empirical data (see Schurr, 2001) and simulates population dynamics of G. flava under specific land use, fire and rain scenarios in southern Kalahari semiarid savannas. On the landscape level, each grid cell represents 5 m x 5 m of savanna vegetation defined as either Acacia cell type (A) or grassland matrix type (M). Once an Acacia tree dies, its cell type switches from A to M status and vice versa where a new tree establishes. A second layer simulates annual population dynamics of Grewia individuals, which are described in five discrete stages: seeds, seedlings, and adults, i.e. small-, medium- and large-sized shrubs. The first step during each iteration computes the annual rainfall type at the beginning of the wet season. Default values derived from precipitation records from 1940 to 2000 of the study region correspond to 14.7% probability for ‘poor’ rainfall years (droughts), 72.2% for ‘average’ years and 13.1% for ‘good’ years. In SGM, rain determines shrub growth (i.e. the probability of transition into the next size class) in the early wet season and fruit crop size of each shrub (depending on individual size class) in the mid wet season. Furthermore, the annual rainfall type determines the probability of Grewia emergence (0, 1–2, and 3–4% in ‘poor’, ‘average’, and ‘good’ years, respectively), drought mortality (3% for adult shrubs in ‘poor’ years, 50, 90, and 100% for seedlings in ‘good’, ‘average’, and ‘poor’ years, respectively) and the likelihood of a fire in the dry season. After fruit production in the mid wet season, fruits are dispersed according to specific rules (see Section 2.2) and may be subsequently consumed by seed predators. Seedling emergence rates are generally low, corresponding with the slow population dynamics of Grewia (Schurr, 2001). Fire may kill shrubs occasionally (probability of 4% for adults and 95% for seedlings in M cells, 0 and 75% in A cells, respectively). However, in most cases Grewia quickly re-sprouts and reaches the pre-fire aboveground biomass after two years. Grewia plants are noted for clonal, multi-stemmed growth forms (Schurr, 2001). Hence, the model does not consider seedlings that emerge beneath a parent plant, due to adult plant shoots that usually develop in the former sub-canopy after a fire. Furthermore, each cell can only hold a certain carrying capacity of shrubs, i.e. additional recruits may not establish if total cover of all shrubs in one cell equals the size of a grid cell. If shrub cover exceeded carrying capacity, individuals in the cell died. This was simulated annually by removing the smallest individuals first, i.e. in descending order of size class, until shrub cover is smaller than the carrying capacity.

2.2. Seed dispersal

Deposition of G. flava seeds into the grassland matrix is very low (Schurr, 2001). Matrix deposition mainly occurs through carnivorous mammals like Yellow Mongoose (Cynictis penicillata), Bat-eared Fox (Otocyon megalotis) or Black-backed Jackal (Canis mesomelas) which occasionally feed on Grewia fruits. In our model we annually vary $P_{\text{depo}}$, i.e. the probability that a fruit is deposited in a randomly selected M cell, uniformly random around a mean estimate with $P_{\text{min}} = 0.0001$ and $P_{\text{max}} = 0.001$. The main dispersal vectors for Grewia seeds to Acacia cells are small birds (e.g. Acacia Pied Barbet Tricholaema leucomelas, Wattled and Glossy Starling Creatophora cinerea and Lamprotornis nitens, occasionally White-Browed Scrub-Robin Cercotrichas...
leucocephry, Milton and Dean, 1995). The annual proportion of fruits (each fruit contains two seeds) removed from an individual plant and dispersed to neighboring A cells is determined by \( P_{\text{deposition}} \). This parameter excludes the proportion of seeds dropped during fruit handling prior to distribution. Empirical data suggest \( P_{\text{deposition}} \) to be 0.16 (Schurr, 2001). However, as long-term variability of removal rates, mean dispersal distance, and the relationship between annual fruit production and dispersal rate are unknown, we used two modeling approaches. For the first approach, we performed uniform random parameter variation per year for \( P_{\text{deposition}} \) between 0.01 and 0.3 and for \( D_{\text{max}} \), the maximal dispersal distance, between 20 and 200 m. In a second step, we then combined a set of fixed values of \( D_{\text{max}} \) and \( P_{\text{deposition}} \) according to \( D_{\text{max}} = 20, 30, 50, 100, 200 \) m and \( P_{\text{deposition}} = 0.01, 0.05, 0.15, 0.3 \). The actual probability of arrival of a Grewia fruit in a neighboring A cell is then computed by using the equation

\[
P_{\text{deposition}}(N) = \frac{1 - m_j}{\sum_j 1 - m_j},
\]

where \( j \) denotes an A cell within \( D_{\text{max}} \) and \( m_j \) is the proportion of the sum of distances of all A cells to the cell of removal. The dispersal procedure first detects all A cells within \( D_{\text{max}} \) and their distance to the center by means of a moving window algorithm. \( P_{\text{deposition}} \) is then computed as a weighted probability where A cells near the cell of removal have the highest seed deposition probability. For the case of one A cell, i.e. \( N = 1 \), probability of deposition equals 1. For the case of \( N = 0 \) within \( D_{\text{max}} \), we assume that all removed fruits are dropped beneath large Grewia shrubs.

2.3. Environmental scenarios

Recent studies using spatially explicit simulation tools emphasize cyclic, non-stable patterns of long-term tree-grass ratios in semiarid savannas (e.g. Jeltsch et al., 1996, 1999). The patterns generated show increased tree densities in wet climate phases, alternating with reduced tree recruitment in drier phases. This corresponds with cycles of low and high rainfall known for Southern Africa (Tyson, 1987). While increased fire frequencies in wet phases favor tree recruitment near adult patches resulting in clumped tree distributions (Jeltsch et al., 1999), dry phases may support a random recruitment pattern, as fire frequencies are generally low. Although savanna systems are likely to show this long-term pattern, one may only guess the relevance of spatial and temporal scales, i.e. how strong (magnitude of variance) and for how long (length of cycles) rain conditions and corresponding tree-grass ratios may oscillate. Based on these assumptions we established three hypothetical scenarios where tree cover and rain conditions periodically change over the course of time (Fig. 1). Besides a stable landscape scenario with constant tree density and rain conditions (scenario a), we developed two scenarios with variation of tree establishment rate fitting a cyclical tree density curve (scenario \( \beta \) and \( \gamma \), see Fig. 1). Similar periodic-type habitat models with oscillatory perturbations have been also applied for beetle populations (e.g. Henson et al., 2002). For scenario (a) the default parameter set of rainfall probabilities and mean tree density of \( \bar{x} = 5 \) trees per hectare typical for southern Kalahari dry savannas (see, e.g. Jeltsch et al., 1996, 1999) was held constant. For scenario (\( \beta \)) and (\( \gamma \)) phases of tree cover increase characterized by high recruitment rates and aggregated pattern alternated with phases of tree cover decrease with low recruitment and random pattern (half-cycle length \( \delta_{\beta} = 50 \) years, \( \delta_{\gamma} = 125 \) years; for visualization see Fig. 1). Clumped tree pattern in wet phases was incorporated through recruitment restriction within a radius of 10 m (two cells) of each tree. The variance of tree density \( \gamma \) was two trees per hectare in the \( \beta \)-scenario (i.e. 4-6 trees per hectare) and five trees hectare in the \( \gamma \)-scenario (i.e. 2.5-7.5 trees per hectare). In phases of tree cover decrease the probability of ‘good’ rainfall years was 50% higher than the default value, at the cost of ‘average’ years, and ‘poor’ rainfall years had a 50% higher probability in phases of tree cover decrease. Through these procedures we kept inter-annual mean of tree density and rain probability constant. For all model scenarios we performed 25 replicate runs with initial population of 1000 individuals for \( t = 500 \).

2.4. Time series and point pattern analysis

As Grewia abundance largely depends on the number of available Acacia micro-sites, we analyzed time series trends through calculating total plant numbers in years where tree density (\( x_t \)) at time step \( t \) was sim-
Fig. 1. Scenarios of constant (a) and periodically oscillating tree density (b) and (c) used in the simulation model. Upper graphs show mean tree density $\bar{x} = 5$ trees per hectare according to: constant tree density with default rain type probabilities (a); weak environmental fluctuation with variance of magnitude $\lambda = 2$ trees per hectare (4–6 trees per hectare) and half-cycle length $\delta = 50$ years (b); strong fluctuation with $\lambda = 5$ trees per hectare (2.5–7.5 trees per hectare) and $\delta = 125$ years (c). Arrows indicate time step $t$ where $\chi(t) = \bar{x}$.

Lower graphs indicate sample simulation run of univariate point pattern analysis as a function of time and scale for the spatial distribution of Acacia trees. For the spatial pattern, black cells indicate significant clustering of trees, gray cells indicate no significant spatial relation (random), and cells in dark-gray indicate significant hyperdispersion. While trees are randomly distributed in scenario (a) they temporally form aggregates in scenario (b) and (c).

ilar to the mean tree density. For scenario (b) this was valid for $t = 25, 75, 125, 175, 225, 275, 325, 375, 425, 475$, for scenario (c) for $t = 63, 188, 313, 438$ (see arrows in Fig. 1). To determine and compare population trends we then used simple linear regression to calculate the $z$-value, i.e. the slope of the time–abundance relationship. In this study we also focus on how the spatial pattern of Grewia shrubs changed over time, i.e. where (on which spatial scale) and when (on which temporal scale) clustering occurred in relation to the distribution of Acacia trees. Beyond considering population abundance over time, the question of whether shrub aggregates occur gives additional information about the influence of spatio-temporal variation in tree densities and short dispersal ranges on shrub establishment. For instance, population dynamics in terms of population numbers in two model scenarios may be the same, even though spatial pattern over time may differ and hence factors that affect both populations may not correspond. For data analysis in our model we used Ripley’s $L(h)$ function (Ripley, 1976; Wiegand et al., 1998), to characterize spatio-temporal patterns of shrubs and Acacia trees across a range of scales $h$ in the model output. Here $h$ is the radius of a circular area around each point (i.e. cell) of the pattern being analyzed. If the distributional pattern of shrubs is random, the expected value of $L(h) = 0$, otherwise $L(h) > 0$ for a clustered pattern and $L(h) < 0$ for a hyperdispersed pattern. We assessed statistically significant departures from a random pattern using Monte Carlo simulation techniques (Ripley, 1981; Cressie, 1991; Bailey and Gatrell, 1995). For each pattern analysis, 99% confidence intervals were constructed by randomizing the location of the points in the pattern 99 times, calculating $L(h)$ values for each resulting pattern and determining the minimum and maximum values for $L(h)$ from among all 99 randomized patterns. An $L(h)$ value lying above the maximum value obtained through the 99 randomizations was considered to be significantly clustered, whereas values lying below the minimum value were considered to be significantly hyperdispersed (Haase, 1995). The computer routines used in our analyses were developed through a modification of computer code provided in Venables and Ripley (1994).

3. Results

In the first step of this study we focused on how populations may respond to random variation of removal probabilities and dispersal distances within a realiz-
tic range. This is reasonable due to the high natural variability of these factors. In the second step, we applied fixed parameter values, which may indicate how the system reacts when, for example, either dispersal distance or removal rate show a constant pattern over longer time periods.

For a random parameterization of $P_{acacia}$ and $D_{max}$, the time series of environmental scenarios ($\alpha$, $\beta$, and $\gamma$) showed similar population trends (Fig. 2). Even though sub-populations of smaller and medium-sized shrubs oscillated substantially, mean abundance of *Grewia* amongst the scenarios was similar. These results are consistent with the fact that mean environmental conditions in all three scenarios were the same, i.e. tree density and inter-annual mean of rain (shown here as numbers of ‘good’ years per decade).

Surprisingly, when keeping dispersal components constant we found a striking discrepancy among environmental scenarios ($\alpha$, $\beta$, and $\gamma$) (Fig. 3). Although population trends for most of the parameter combinations were similar to the random parameter set (see, e.g., $z$-values of scenario A in Fig. 3; results of combinations between $D_{max} = 30, 50, 100, 200$ m and $P_{acacia} = 0.05, 0.15, 0.30$ are not shown), remarkable differences occurred when either dispersal distance or removal probability was limiting for *Grewia* popula-

---

**Fig. 2.** Typical time series of *Grewia* population dynamics for environmental scenarios: constant (\(\alpha\)), five-cyclic (\(\beta\)), and two-cyclic (\(\gamma\)) (see Fig. 1). Trends of sub-populations of seedlings, large, medium-sized, and small shrubs are shown as one typical simulation run. For the total population typical time series (top) and means of 25 replicate runs (bottom) are given. Mean $z$-value, i.e. the slope of the population trend, was 17.14, 19.48, and 3.192 for the ($\alpha$, $\beta$), and ($\gamma$) scenarios, respectively. Both dispersal distance and removal probability vary randomly per year (see text). The lower three figures indicate temporal rain pattern given as the number of ‘good’ rain years per decade and tree density over time (dotted line).
Fig. 3. Mean time series trends of total population for fixed dispersal parameter sets (A–D). Scenarios (a), (b) and (c) indicate the constant, five-cyclic and two-cyclic scenario, respectively (see Fig. 1). Row A shows the case when both dispersal distance and removal rate are sufficient ($D_{\text{max}} = 200 \text{ m}; P_{\text{acacia}} = 0.3$), B represents limitation by removal rate ($D_{\text{max}} = 200 \text{ m}; P_{\text{acacia}} = 0.01$), C represents limitation by dispersal distance ($D_{\text{max}} = 20 \text{ m}; P_{\text{acacia}} = 0.3$) and D refers to the case when both dispersal distance and removal rate are extremely low ($D_{\text{max}} = 20 \text{ m}; P_{\text{acacia}} = 0.01$). Mean population trends with standard deviations are indicated as the mean $z$-value of 25 replicate runs.

For parameter set B (limitation through removal rates, here $D_{\text{max}} = 200 \text{ m}; P_{\text{acacia}} = 0.01$) scenario (a) performed a slight positive trend with $z = 18.2$ while scenario (b) and (c) produced a population decrease. For parameter set C (limitation through dispersal range, here $D_{\text{max}} = 20 \text{ m}; P_{\text{acacia}} = 0.3$) we found the opposite effect: while populations in scenario (a) strongly decreased with a mean $z$-value of $-90.8$, scenarios (b) and (c) generated a steady population growth. In this case sufficiently high numbers of seeds are distributed each year, however, limited dispersal range prevents seeds from reaching a recruitment site. For parameter set D where both removal rate and dispersal range in-
hibit shrub recruitment all scenarios performed a similar population decrease. In the latter case, too few seeds are dispersed and dispersal vectors are only occasionally permitted to reach possible host trees.

In order to explore the surprising effects described for recruitment limitation through parameter combinations B and C it is important to explore whether population increase in the constant scenario of B (henceforth B-α) and decrease in the constant scenario of C (henceforth C-α) is due either to annual variability of tree density or rainfall. For population increase in B-α (and respective decrease in B-β and B-γ), we hypothesized that rainfall variability was likely to be more effective for population dynamics, since a dispersal range of 200 m may compensate for spatially varying tree densities. In contrast, for population decrease in C-α (and increase in C-β and C-γ), we supposed that the respective trends may be attributable to annual variability and spatial distribution of trees rather than to precipitation. To prove these hypotheses, we developed two complementary scenarios where we modified the constant scenario of parameter sets B and C, respectively. For the constant scenario of B (B-α) we created a scenario were we kept tree density constant but varied rain according to scenario (β) and (γ) (scenario B-αβ and B-αγ in Fig. 4). For the constant scenario of C (C-α) we performed simulation runs where we kept rain event probabilities constant but modified tree density according to (β)- and (γ)-type (see C-αβ and C-αγ in Fig. 4).

As hypothesized both B-αβ and B-αγ (i.e. scenario (α) of parameter set B with rain according to scenario β and γ) lead to a population decrease with a mean z-value of −9.9 and −40.7, respectively. In other words the positive population trend of B-α shown in Fig. 3 could be directly attributed to the low variability of precipitation. Interestingly, populations in scenario B-αγ showed a stronger decrease than in B-αβ, with shorter periods of either ‘bad’ or ‘good’ rain phases. For modifications C-αβ and C-αγ (i.e. scenario (α)}

![Fig. 4. Time series trends of total Grewia population of modified environmental scenarios B-α and C-α (see Fig. 3). For B-αβ and B-αγ tree density is kept constant, however, rain varies according to scenario (β) and (γ). For C-αβ and C-αγ rainfall probabilities are constant, but tree density varies according to scenario (β) and (γ). Mean population trends with standard deviations are indicated as the mean z-value of 25 replicate runs.](image-url)
of parameter set C with tree pattern according to scenario β and γ we found populations to increase, as expected. Here, variation in the spatial distribution of trees was the primary cause for population increase.

This is also clear from the spatio-temporal pattern of Grewia plants of parameter set C (see Fig. 3) shown in Fig. 5. Significant clustering of trees in wet phases (compare again lower graph in Fig. 1) led to the formation of Grewia clumps on most of the spatial scales.

4. Discussion

As evidenced by empirical studies, fruit removal rates and dispersal distances of fleshy-fruited plant species show a high degree of variability over the course of time (e.g. Alcántara et al., 1997; Ortiz-Pulido and Rico-Gray, 2000). Moreover, parameter estimates based on seed trap data may be inconsistent (see Stoyan and Wagner, 2001) and rare dispersal events (that may be accidentally neglected in empirical studies) have a considerable influence on plant populations (Malanson and Armstrong, 1996). Thus, seed dispersal models often face the problem of bridging the gap between empirical data and general model validity. In our study we therefore created several theoretical dispersal scenarios that may be realistic in terms of the environmental conditions of G. flava.

Besides variability and uncertainty in fruit removal rates, the spatial pattern and density of microhabitats where seed deposition is concentrated can also vary, i.e. in our study the distribution of Acacia trees within an otherwise, relatively homogenous grassland vegetation (Belsky, 1995). The results generated by our model were remarkable: even though we kept the inter-annual mean of environmental variables constant we found Grewia population trends to differ noticeably between environmental scenarios with dispersal limitation. However, this was not the case when both the number of distributed seeds and dispersal ranges were sufficient for recruitment and population growth, i.e. combinations of \( D_{\text{max}} > 30 \text{ m} \) and \( P_{\text{acacia}} > 0.05 \) or random parameterization resulting in an inter-annual mean of \( P_{\text{acacia}} = 0.15 \) and a mean maximal dispersal distance larger than 100 m. In the latter scenarios, Grewia populations exhibited no limitations in terms of available recruitment habitat (determined by the dispersal distance) and number of seeds distributed into these habitats.

When fruit removal rate was a limiting factor over extended periods populations were more vulnerable under periodically fluctuating rain conditions with longer periods of either ‘good’ or ‘bad’ rain conditions (see parameter combination B in Fig. 3). In the cyclic scenarios the temporal rain pattern was more strongly auto-correlated, i.e. for instance a ‘poor’ rainfall year in a ‘bad’ phase has a higher probability of being followed by another ‘poor’ year than in the weakly auto-correlated scenario (α) (see also rain data in Fig. 2). In other words, unfavorable effects associated with ‘bad’ periods seem to override favorable effects occurring in ‘good’ periods. This is likely
due to a saturation effect occurring in favorable rain phases, as the number of available *Acacia* recruitment sites is limited. In the model, population growth is indirectly regulated by total shrub cover in each cell, i.e. once shrub cover reaches the carrying capacity in a cell potential recruits in ‘good’ periods that fail to establish in terms of density regulation may not contribute to the total population size. However, when rain conditions are poor and recruitment generally low, no limit regulates the number of mortality events until the population is extinct. Although we did not test it, we believe that this mechanism may also hold for other plant population parameters that limit population growth, such as the probability of emergence.

This negative influence of periodically fluctuating environments has also been reported, e.g. for light-limited phytoplankton in a study by Huisman (1999). Higher mixing depth, i.e. longer periods with either favorable or unfavorable light conditions, led to population decrease of algae. The same relationship was demonstrated by Wichmann et al. (2003) using an individual-based, stochastic model: for the extinction risk of a raptor species in arid savanna they showed that periodically fluctuating environments with long periods of low rain conditions decreased persistence time. Based on a theoretical approach, Ripa and Heino (1999) generally demonstrated that while overcompensated populations gain viability from positively auto-correlated environments, undercompensating populations experience increasing extinction risk as the environmental autocorrelation increases. Taking these conclusions into account, our model results support additional evidence that increased environmental autocorrelation may have a negative impact on population persistence. However, at this point we want to emphasize that we do not intend to explicitly quantify the impact of cycle length (i.e. strength of autocorrelation, here $\delta_{0} = 50$ years; $\gamma_{0} = 125$ years) and magnitude of variance of precipitation (here CV = 50%).

Interestingly, variable environments were favorable for *Grewia* when removal rates were sufficient, yet the range of dispersal low (parameter combination C in Fig. 3). Although little is generally known about the distances moved following fruit consumption prior to defecation (see Stanley and Lill, 2002) and bird movements in general (Tyler, 2001), this parameter combination may occur when the composition of the bird disperser guild shifts towards smaller species with shorter dispersal ranges (through shorter gut retention times and activity ranges) or long-term tree densities become more sparse. In this case birds may be more attracted to perch in large, adjacent *Grewia* shrubs in the open, rather then flying towards distant canopy trees. Here, population trends were negative for the constant scenario (with random tree pattern) and positive for the cyclic scenarios (with tree clumping in wet phases).

Our additional simulations showed that the underlying cause could be due to the forming of tree aggregates in wet phases, which reduced local inter-tree distances and thereby enabled ample recruitment events even though dispersal ranges were low. Obviously, spatial tree distribution rather than varying tree density increased *Grewia* population when dispersal distances were low. Although not shown here, we believe that fluctuating tree densities may even adversely affect the population viability of *Grewia* to some extent. For example, this may be relevant when a good rain year with high fruit production and fruit removal coincides with low tree density (i.e. reduced number of potential recruitment sites) instead of a high tree density year with a high number of potential recruitment sites. Moreover, under natural conditions, *Grewia* population dynamics may be subject to response lags between *Acacia* tree density and favorable rain conditions, as this process may decouple *Grewia* dispersal and microsite availability. Generally, our results agree with findings of a recent theoretical model approach employed by Johst et al. (2002). They demonstrated that dispersal distance combined with the spatial pattern of recruitment patches are crucial ecological parameters for meta-population persistence.

Clearly, one can only speculate how long-term changes of tree/grass ratios may develop in a changing climate and how dispersal components may be affected through extrinsic factors. This is particularly true in the case of human impact. For instance, land use in the form of cattle farming has nowadays heavily degraded many parts of Southern African savannas, including extensive areas with increased *Grewia* cover due to overgrazing (Trollope, 1982; Skarpe, 1990; Moleele and Perkins, 1998; Dougill and Trodd, 1999; Tews et al., in press). Grazing by domestic livestock has completely changed typical dispersal characteristics of many fleshy-fruited woody plant species by increasing seed deposition in open grassland habitats (Grice, 1996; Brown and
Carter, 1998; Kriticos, 2001; Tiver et al., 2001; Radford et al., 2001). Furthermore, default conditions of spatio-temporal rain and tree pattern applied in scenarios α, β, and γ represent a simplified and substitutional version of the actual spatial dynamics that may occur. We thus do not claim to predict *Grewia*’s response to future conditions. However, even though long-term spatial dynamics are largely unpredictable, we were able to reveal important ecological processes that result from specific constellations of crucial environmental variables. By combining ecological knowledge and modeling tools we call for further studies on population-based consequences of seed dispersal. This would improve upon our current knowledge and enable enhanced decision-making in ecosystem management and nature conservation.

**Acknowledgements**

This work was funded by the German Ministry of Education and Research (BMBF) in the framework of BIOTA South Africa (01LC0024).

**References**


Bleher, B., Böhning-Gaese, K., 2000. *Seed dispersal by birds in a South African and a Malagasy forest.*


