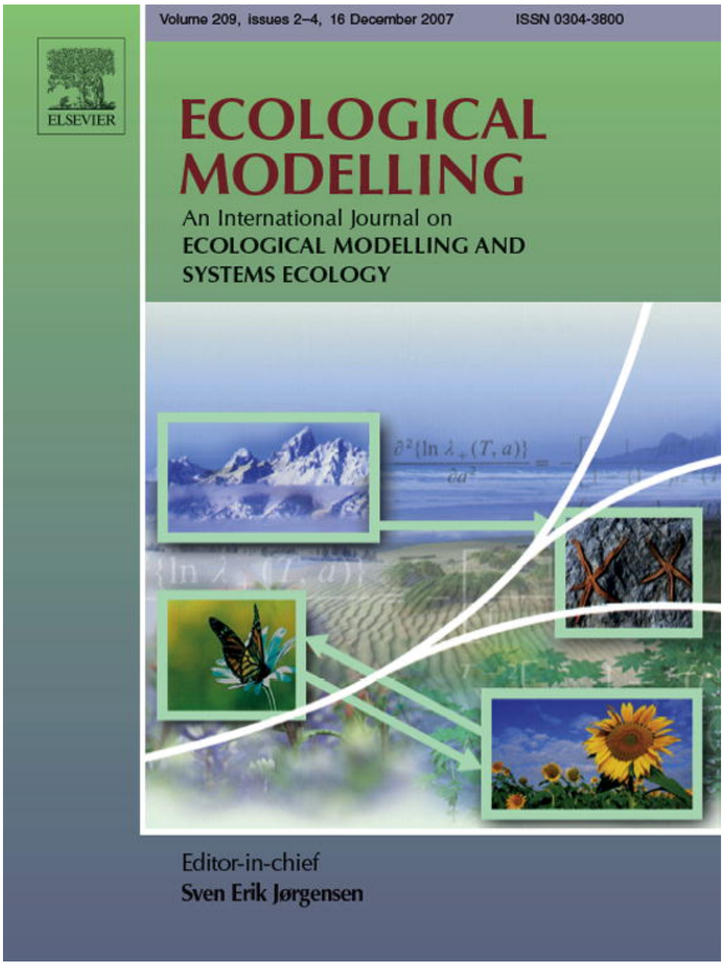

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SATCHMO: A spatial simulation model of growth, competition, and mortality in cycling savanna patches

Katrin M. Meyer[a,*], *Kerstin Wiegand*[a], *David Ward*[b], *Aristides Moustakas*[a,c]

[a] *Institute of Ecology, University of Jena, Dornburger Str. 159, D-07743 Jena, Germany*
[b] *School of Biological and Conservation Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa*
[c] *Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK*

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ABSTRACT

Many mechanisms have been suggested to explain the coexistence of woody species and grasses in savannas, yet, evidence from field studies and simulation models has been mixed. Shrub encroachment is an ecological and economic problem in savannas worldwide which generally is attributed to overgrazing. Patch-dynamics is a new mechanism explaining tree-grass coexistence and the natural occurrence of shrub encroachment in savannas. A patch-dynamic savanna consists of patches in which cyclical succession between grassy and woody dominance proceeds spatially asynchronously. The spatially explicit, individual-based patch-scale simulation model SATCHMO was developed to investigate cyclical succession in the paradigm of patch-dynamics for arid and semi-arid savannas. SATCHMO is designed to capture within-patch shrub population dynamics based on a grid of 51 m side length and a resolution of 10 cm. The model shrub characteristics were derived from *Acacia mellifera*, the main encroaching species in African savannas. The aim of SATCHMO is to give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the influence of precipitation and fire on patch transition frequencies, shrub growth rates, and shrub size frequencies. With SATCHMO, we want to identify the conditions leading to cyclical successions in general and shrub encroachment in particular. Soil moisture is the most important parameter in SATCHMO influencing growth, reproduction, and mortality of shrubs and grass tufts, and that mediates competition. To acknowledge the importance of belowground interactions in savannas, shrub root growth and competition are modelled spatially explicitly. The model output was successfully validated with morphometrical and spatial data from the field site in the South African Kalahari thornveld and with recent literature data on savanna woody species cover. Global sensitivity analysis with Latin hypercube sampling shows that soil moisture is the most important driver of shrub cover dynamics in semi-arid savannas.

1. Introduction

Savannas are ecosystems co-dominated by woody species and grasses in varying relative proportions. The widely discussed ‘savanna question’ is concerned with the factors that promote tree-grass coexistence and prevent savannas from being driven to open grassland or forests with a closed canopy. Many empirical studies and savanna models have proposed

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[*] *Corresponding author*. Present address: NIOO-KNAW, Centre for Terrestrial Ecology, Department of Multitrophic Interactions, Boterhoeksestraat 48, 6666 GA Heteren, The Netherlands. Tel.: +31 26 479 1208; fax: +31 26 472 3227.

E-mail address: k.meyer@nioo.knaw.nl (K.M. Meyer).

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solutions to the savanna question (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985; Menaut et al., 1990; Hochberg et al., 1994; Jeltsch et al., 1996, 1998, 2000; Higgins et al., 2000; Fernandez-Illescas et al., 2001; van Wijk and Bouten, 2001; van Langevelde et al., 2003). In the majority of studies, there is agreement on the four key factors determining savanna dynamics: water, nutrients, herbivory, and fire (Frost et al., 1986; Sankaran et al., 2004), but their relative importance has long been unclear. Recently, the analysis of data from 854 African field sites showed the paramount impact of mean annual precipitation (MAP) on woody cover as a switch effect at 650 mm MAP (Sankaran et al., 2005). Below this threshold, in arid and semi-arid savannas, herbivory, fire, and soil properties can only reduce woody cover below its maximum which depends linearly on MAP. Above this threshold, savannas are unstable and disturbances such as fire or herbivory are necessary to prevent canopy closure (Sankaran et al., 2005). The dominant role of water among the key determinants of savanna structure also highlights the greater importance of belowground interactions in arid and semi-arid savannas compared to aboveground interactions. Unfortunately, field methods for belowground investigations come at a much greater cost than aboveground methods so that simulation models provide an efficient alternative for capturing a reasonable amount of detail with similar effort for above- or belowground systems.

With respect to the mechanisms underlying tree-grass coexistence, both empirical evidence and model results are mixed and emphasize different aspects of savanna dynamics for the explanation of tree-grass coexistence. In their comprehensive review of savanna models, Sankaran et al. (2004) consider explanations focusing on the limiting role of demographic bottlenecks in woody species populations (Higgins et al., 2000; Jeltsch et al., 2000) to be superior to the traditional competition-based explanations (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985) because empirical evidence for rooting-niche separation and other competitive mechanisms is equivocal (Scholes and Archer, 1997; Sankaran et al., 2004; Wiegand et al., 2005) and resource competition alone does not produce coexistence in spatially explicit models (Jeltsch et al., 2000). Still, a unifying mechanism explaining tree-grass coexistence in savannas is lacking.

Furthermore, the ‘savanna question’ is not only an ecological issue but also has a socio-economic dimension. Shrub encroachment, i.e. the increase in density of woody plants often unpalatable to livestock, is observed in savannas all over the world reducing the amount and quality of grazing lands dramatically. So far, it was generally believed that overgrazing in combination with rooting-niche separation is primarily responsible for shrub encroachment. However, recent research has not only questioned the universality of the rooting-niche separation in particular and competition-based models in general but also the paramount importance of overgrazing for fostering shrub encroachment (Wiegand et al., 2005, 2006).

Wiegand et al. (2006) propose the patch-dynamics paradigm as a mechanism explaining tree-grass coexistence in arid savannas. The patch-dynamics concept is based on a cyclical succession that proceeds asynchronously in spatially distinct patches that constitute the savanna landscape. Patches cycle between woody and grassy dominance so that shrub encroachment is a natural phase in the cyclical succession. Patch-dynamics and overgrazing are not mutually exclusive explanations for shrub encroachment, but may enhance each other. If overgrazing occurs during the naturally encroached phase of the successional cycle, its effect on shrub cover increase will be greater than if it occurred during a non-encroached phase of the cycle. Moreover, the patch-dynamics paradigm does not exclude other theories about tree-grass coexistence, but can integrate many of the savanna theories put forward thus far because cyclical succession can be driven by a range of processes. For instance, the spatial and temporal overlap of localized rain events in arid savannas may induce mass germination of a shrub cohort and promote the transition of a grass-dominated patch to woody dominance. Empirical support for patch-dynamics is offered from paleoecological long-term studies in east African savannas that revealed cyclical changes in the relative abundance of trees and grasses at the local scale but stable proportions at the landscape scale (Gillson, 2004). The advantage – but also the challenge – of the patch-dynamics concept is its explicit consideration of spatial and temporal scales. While field studies are rarely able to cover several spatial and temporal scales (but see Gillson, 2004), simulation models do not suffer from such restrictions. In simulation models, processes can be implemented at one scale generating patterns at the next greater scale (Jeltsch et al., 1996; Wiegand et al., 2003). For this procedure to be successful, the processes prevailing at small scales have to be understood in detail before they can be generalized to larger scales. The great amount of detail necessary for a good understanding of small-scale processes with simulation models is supported by the accessibility of small-scale field data for model parameterization relative to data at larger scales.

In order to investigate cyclical succession at the patch-scale, we developed the small-scale spatially explicit, individual-based Savanna Patch Model (SATCHMO) for arid and semi-arid savannas (MAP < 650 mm). The focus of our model lies on savannas that receive less than 650 mm MAP because the continental-scale analysis of Sankaran et al. (2005) shows that water is the most limiting factor for woody cover and permits tree-grass coexistence in these savannas. The purpose of SATCHMO is to model within-patch population dynamics that give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the conditions leading to cyclical successions in general and shrub encroachment in particular.

2. Methods

2.1. Study area

SATCHMO is based on field data that were collected in semi-arid savanna in the Kalahari thornveld at Pniel Estates (28°35′S, 24°29′E), 30 km north of Kimberley, South Africa, between 2003 and 2005 (see also Meyer et al., 2005). Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September–March).

Blackthorn (*Acacia mellifera*) is the dominant plant species in the study area; camphor trees (*Tarchonanthus camphoratus*) and umbrella thorns (*A. tortilis*) are other important woody species.

2.2. Model description

The model description follows the ODD protocol that aims to standardize the description of individual-based simulation models (Grimm et al., 2006). The ODD protocol consists of the three parts Overview (containing purpose, state variables and scales, and process overview and scheduling), Design concepts, and Details (containing initialization, input, and submodels). The model was implemented in the programming language C++ with the help of the software package Borland Builder 6.0. The executable files of the model are available upon request from the corresponding author.

2.2.1. State variables and scales

The basic objects in SATCHMO are a shrub, a grass tuft, and the root of a shrub. Until the age of one year, shrubs and grasses are referred to as seedlings, thereafter as established shrubs and grass tufts.

Shrubs were modelled following the characteristics of the dominant species in the area, because one aim of SATCHMO is to identify conditions leading to shrub encroachment. Individual shrubs are characterized by the state variables location (xy-coordinate), canopy diameter, height, age, root system radius, and width of uptake zone. Each root is surrounded by an uptake zone in which water uptake occurs. If the uptake zones of two roots meet, an interaction scenario is activated. In scenarios with competition, the width of the uptake zone is a measure of the territoriality of the shrub. Aboveground, shrubs older than one year are represented by a circle with canopy diameter as diameter.

To acknowledge the predominant importance of soil moisture mediating plant interactions in semi-arid savannas, we modelled shrub roots spatially explicitly in two dimensions. We simplify the shrub root system by representing it with eight horizontal roots which initially radiate from the shrub base in the cardinal and intermediate directions at angles of 45° (Fig. 1). Roots are characterized by the state variables number and location of the shrub they belong to, root number (1–8), xy-coordinates of the most distant and second most distant cell of the root, whether they have stopped to grow, and whether

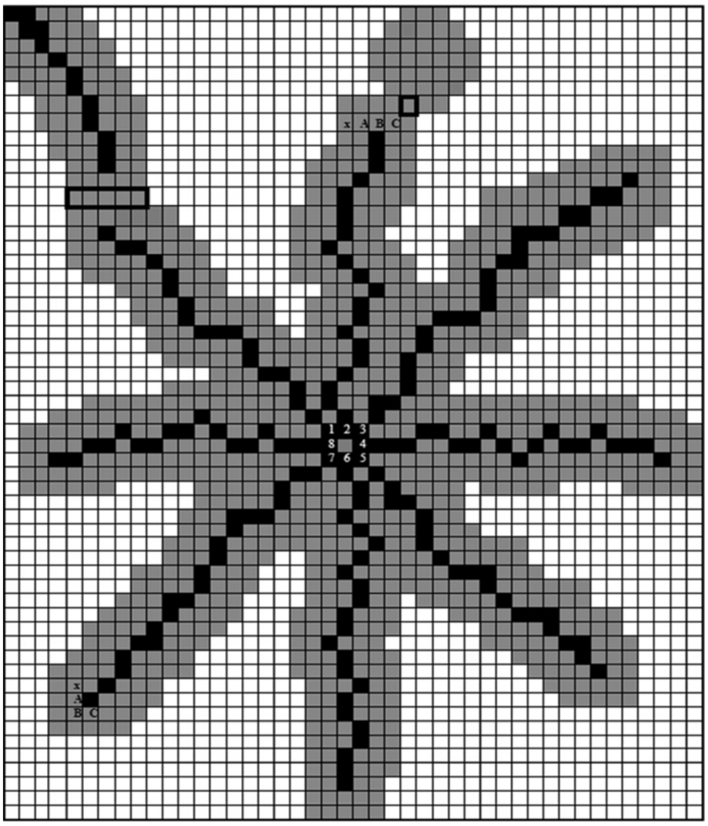

Fig. 1 – Schematic representation of belowground characteristics of a model shrub competing with a grass tuft (top right) and a root from another shrub (top left). The eight roots (black cells) of the model shrub are surrounded by their uptake zone (grey cells) with a width of two cells where water uptake occurs. If the uptake zone overlaps with uptake zones of other shrubs or grasses (black rectangles) competition takes place. Shrubs compete only indirectly with grasses by sharing the soil moisture in the overlapping cells. If two uptake zones of shrub roots meet, the result is determined by the competition scenario, e.g. asymmetric competition leads to a growth stop of the root of the smaller shrub. Numbers 1–8 refer to the starting point of the eight roots. The letters A, B, and C mark the possible cells to grow into during the next growth step in descending probability order for a root with cardinal original growing direction (number 2) and one with intermediate original growing direction (number 7). The × marks the original growing direction.

they grow in cardinal or intermediate direction. Roots are surrounded by an uptake zone whose width approximates the length of side roots responsible for water uptake.

Grass tufts serve as interspecific competitors for the shrubs. The grass state variables are individual number, location (xy-coordinate), canopy diameter, age, and width of uptake zone. Aboveground, grass tufts are represented by a circle with canopy diameter. Grass roots were not modelled spatially explicitly because grass was not in the focus of the model and because information on grass roots is scarce. Instead, water uptake occurs in a circular uptake zone around the canopy.

On a higher hierarchical level, all shrubs and all grasses in the simulated area constitute one population each. Populations are characterized by their number of individuals, the percentage ground covered by all canopies, and their canopy diameter-frequency distributions. Model outputs were analysed at the level of individuals and populations.

SATCHMO is based on a two-dimensional grid with 512 × 512 cells. The spatial extent of the grid corresponds to 51.2 m in reality. This side length conservatively corresponds to the sum of the maximum diameter of a shrub thicket (=patch) in the field of about 8 m, the maximum diameter of the root system of an individual shrub excavated in the study area of about 32 m (Meyer et al., 2005), and a buffer of about 10 m for patch edge effects. The side length of one cell corresponds to 10 cm which is the greatest common accuracy of all morphometric measurements in the field. We do not model soil depth explicitly because the roots of the plants modelled predominantly occur in the topmost soil layer where also the greatest part of the soil moisture and virtually all nutrients are restricted to (Evans and Ehleringer, 1993). The temporal resolution is daily for precipitation and annual for shrub and grass dynamics. The temporal extent of the simulations is 500 years to capture long-term savanna dynamics.

2.2.2. *Process overview and scheduling*

In SATCHMO, environmental processes (precipitation, soil moisture, and fire) are followed by the individual processes of shrub reproduction and mortality, grass reproduction and mortality, and shrub and grass growth (Fig. 2; for a detailed description of the model processes refer to Section 2.2.6). Sexual reproduction includes seed production, seed dispersal, and germination. Shrub growth is the core module of SATCHMO where above- and belowground regrowth are derived from individual water uptake, leading to mortality if regrowth is negative and to shoot and root growth if regrowth is positive. Root growth may be impaired in several mutually exclusive root competition scenarios. Time proceeds in discrete time steps (daily for precipitation, annual for all other processes).

2.2.3. *Design concepts*

Emergence. Maximum shrub age is an emergent property of SATCHMO, as well as population size and spatial shrub and grass patterns and all other population-level characteristics.

Sensing. Individual shrubs sense the soil moisture in the cells covered by their root uptake zones, their own height to produce the corresponding number of seeds, their location for aggregated seed dispersal, and their own canopy diameter as a proxy for maintenance costs in the calculation of regrowth from water uptake. Roots sense their original direction (cardinal or intermediate) and the contact of their uptake zone with the uptake zone of another root.

Interaction. Shrubs whose uptake zones overlap with other shrubs or grasses interact by sharing the soil moisture in the overlapping cells. If two uptake zones meet, the kind of interaction is determined by the specified competition scenario (see submodel *Root growth*). Aboveground contact of shrub or grass canopies does not lead to interactions.

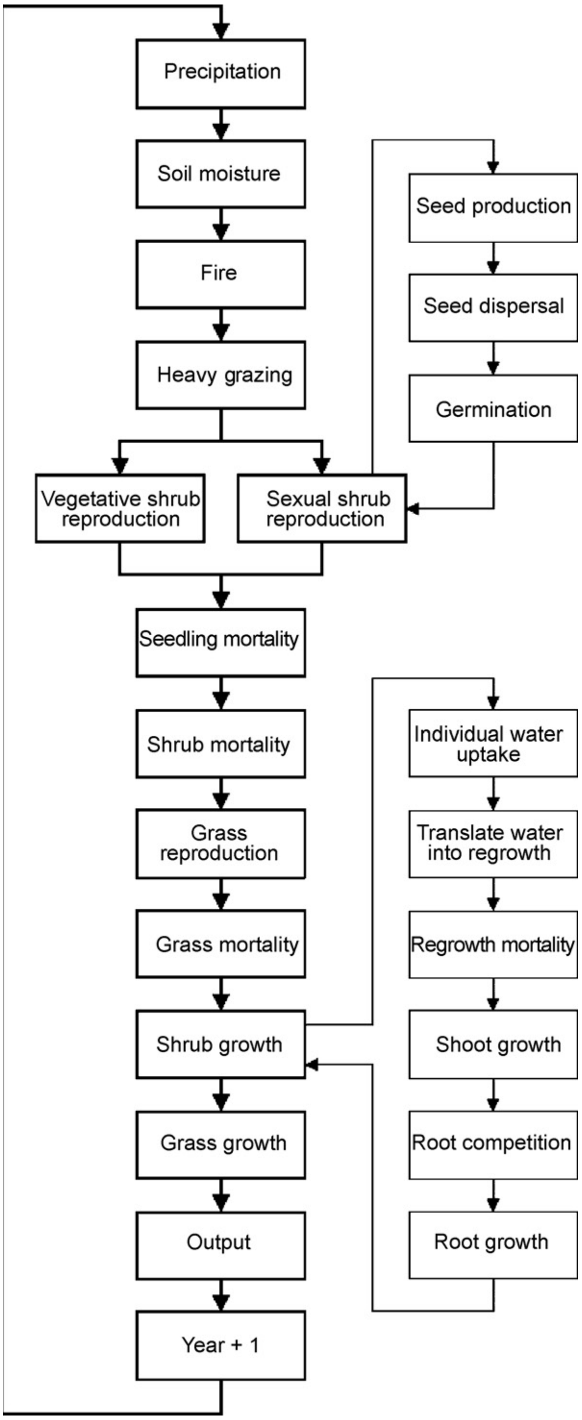

Fig. 2 – Scheduling of the main processes in SATCHMO.

Table 1 – SATCHMO model parameters

Parameter	Accur	Default	Source	Range	Distr	Source	Std RC N	Std RC Cover
Soil moisture parameters								
Long-term mean annual rainfall (mm)	1	377	Kimberley	203–553	n	SD, Pniel	ns	2.35
Long-term S.D. of annual rainfall (mm)	1	174	Kimberley	–	–	–	–	–
Interception $D(t)$ of grasses (mm)	3	1	Ref1	0.9–1.1	u	10%, EG	ns	ns
Interception $D(t)$ of shrubs (mm)	3	1.5	Ref1	0.85–1.15	u	10%, EG	6.79	3.65
Evapotranspiration, E_{max} (mm)	2	8	Kimberley[1]	7.1–8.9	n	SD, Kimberley	2.89	ns
Critical soil saturation s_c for grasses*	3	0.35	Ref2	0.15–0.5	e	Ref3	ns	ns
Critical soil saturation s_c for shrubs*	3	0.33	Ref2	0.15–0.5	e	Ref3	4.35	ns
Critical soil saturation s_c for bare ground*	3	0.33	Ref2	0.15–0.5	e	Ref3	ns	ns
Soil field capacity, s_{fc}*	2	0.442	Pniel	0.398–0.482	u	10%, EG	5.72	2.34
Soil porosity, n*	3	0.373	Ref4	0.373–0.48	e	Ref4	ns	ns
Maximum rooting depth, Z (mm)	2	700	Pniel	150–1050	u	Min–Max, Pniel	5.08	4.71
Relative water uptake of plants in grid cell	4	0.9	EG	0.81–0.99	u	10%, EG	3.73	2.79
Fire parameters								
Fire frequency (year^{-1})	2	0.006	Pniel	0.0006–0.06	e	*/10, EG	ns	ns
Maximum fire frequency (year^{-1})	2	1	Pniel	–	–	–	–	–
Shrub reproduction parameters								
Cumulative seed moisture threshold[2]	3	2.35	Kimberley	0.86–2.35	u	Min–Max, Kimberley	6.72	5.32
Cumulative shrub germination moisture threshold[3]	3	0.128	Kimberley	0.07–0.228	e	Min, Kimberley Max, EG	ns	ns
Shrub germination rain event (days)	4	3	Kimberley	–	–	–	–	–
Shrub germination probability	2	0.19	Pniel	0.09–0.19	u	Min–Max, Pniel	ns	ns
Vegetative reproduction probability	4	0.0005	EG	0.00005–0.05	e	*/100, EG	ns	ns
Number of vegetative seedlings (shrub^{-1})	4	15	EG	–	–	–	–	–
Shrub mortality parameters								
Seedling mortality coefficient, a (10^6)	3	75.953	Pniel	75.953–7595.3	u	Min, Pniel Max, *100	2.39	ns
Fire mortality of seedlings	4	0.65	EG	0.5–0.95	n	EG	ns	ns
Natural browsing mortality of seedlings	4	0.95	EG	0.5–0.999	e	EG	12.34	3.84
Basic mortality of established shrubs (10^{-3})	2	6.5	Ref9	5.85–7.15	e	10%, EG	ns	ns
Fire mortality of established shrubs	1	0.09	Ref6	0.081–0.099	e	10%, EG	ns	ns
Drought mortality of established shrubs	4	0.05	EG	0.04–0.06	u	20%, EG	ns	ns
Shrub growth parameters								
Regrowth probability	2	0.55	Pniel	0.46–0.62	u	Min–Max, Pniel	ns	ns
Line probability[4]	4	0.5	EG	0–1	n	EG	ns	ns
Width of shrub uptake zone (cells)	2	2	EG[5]	–	–	–	–	–
Competition scenario	4	Asymm	EG	–	–	–	–	–
Grass demography parameters								
Grass germination moisture[3]	3	0.128	Kimberley	0.07–0.228	e	Min, Kimberley Max, EG	3.09	3.20
Grass germination rain event (days)	4	3	Kimberley	–	–	–	–	–
Number of grass seedlings (m^{-2})	3	2.35	Ref7[6]	–	–	–	–	–
Grass seedling survival	3	0.72	Ref7[6]	0.65–0.79	n	10%, EG	ns	ns
Grass mortality	3	0.47	Ref8[6]	0.42–0.52	n	10%, EG	5.61	3.84
Grass regrowth length (cm)	3	5	Ref8	–	–	–	–	–
Width of grass uptake zone (cells)	3	2	EG[5]	–	–	–	–	–
Technical parameters								
Time steps (years)	–	800	Fig. 3	–	–	–	–	–
Number of runs	–	10	Results	–	–	–	–	–

Accur—estimated accuracy of standard values; Default—standard values of the parameters of SATCHMO; Source—sources of standard values; Range—range from which values were sampled for sensitivity analysis; Distr—distributions from which values were sampled for sensitivity analysis; Source—sources of ranges and distributions; Std RC—standardized regression coefficients representing the sensitivity of shrub cover (Cover) and shrub population size (N) to changes in the parameter values; asterisk (*) refers to sandy soil which is the main soil type of the study site at Pniel Estates; [1]long-term average evaporation; [2]minimum cumulative soil moisture between September and November needed for seed production; [3]minimum cumulative soil moisture per germination rain event between December and March needed for triggering germination; [4]probability of a root to maintain its growing direction; [5]corresponding to 20 cm length of (side) roots; [6]calculated with a mean annual precipitation of 377 mm (Kimberley weather data); asymm—asymmetric competition scenario; accuracy scale: 1—very well known, 2—well known, 3—approximately known, and 4—not well known; Ref1—Scholes and Walker (1993); Ref2—Laio et al. (2001); Ref3—Rodriguez-Iturbe et al. (1999); Ref4—Fernandez-Illescas et al. (2001); Ref6—Meyer et al. (2005); Ref7—O'Connor (1994); Ref8—O'Connor and Everson (1998); Ref9—Augustine and McNaughton (2004); Pniel—estimated from Pniel field data; Kimberley—estimated from Kimberley weather data; n—normal distribution; u—uniform distribution; e—exponential distribution; EG—expert guesses; SD—range refers to standard deviation; 10% or 20%—range refers to ±10 or ±20%; */10—range refers to *10 and /10; Min–Max—range refers to minimum and maximum; ns—not significant.

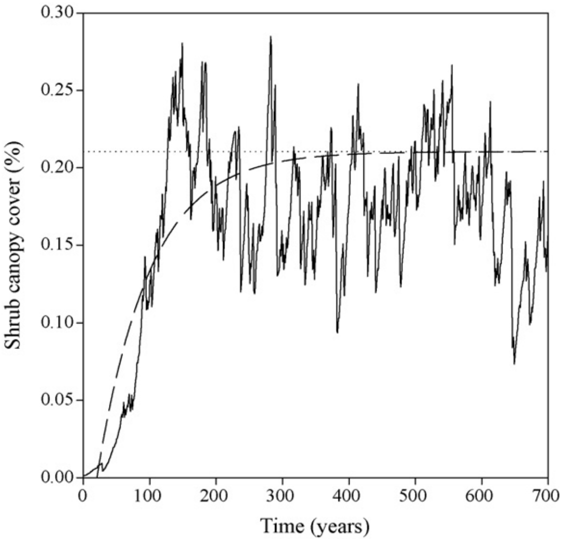

Fig. 3 – Simulated shrub canopy cover in % over time (solid line) with asymptotic regression model (dashed line). To exclude an effect of initial conditions, model evaluation starts only at year 300 when the regression line is sufficiently close to the asymptote (dotted line).

Stochasticity. All demographic parameters include stochasticity by handling them as probabilities to incorporate individual variability. Root growth follows a weighted random walk so that deviations of one cell to the right and to the left of the original growing direction of the root are possible (but less probable) than the original direction (see *line probability* in Table 1).

Observation. Individual shrub characteristics such as canopy diameter, height, age, location, and root system radius are determined every five years. Individual grass characteristics are collected every 100 years. Population-level outputs, i.e. population size and shrub and grass cover, are generated at the end of every year.

2.2.4. *Initialization*

Initially, one reproductively mature shrub with a height of 130 cm and a canopy diameter of 184.75 cm is located in the centre of the grid supplemented by 10 randomly arranged grass tufts whose canopy diameters are drawn from a normal distribution with mean and standard deviation from field data (20.88 ± 15.79 cm). The length of the shrub roots is calculated as a random number between the 0.9- and 0.5-quantile of the quantile regression of root length and shrub canopy diameter (Meyer et al., 2005). We included only quantiles for which the slope of the regression was significantly different from 0. Roots are initialized as if they had maintained their original direction without random deviation until the calculated root length was reached. Based on an asymptotic model of shrub cover over time (Fig. 3), model evaluation started after 300 years of pre-simulation to exclude an influence of initial conditions.

2.2.5. *Input*

Input environmental conditions that affect the state variables in SATCHMO are precipitation and fire. In semi-arid savannas, water limits plant growth much more than nutrients, and still noticeably more than fire or grazing (Sankaran et al., 2005). Hence, we do not explicitly take nutrient dynamics and grazing into account and model fire with less detail.

A daily precipitation value is calculated for the model grid according to the Zucchini-algorithm for South-African rainfall (Zucchini et al., 1992). The parameterization of this algorithm is based on weather data from Kimberley, the closest weather station to the field sites.

In semi-arid savannas, fire is of minor importance compared to moister savannas because there is insufficient grass biomass present to fuel frequent and intense fires (Bond and Van Wilgen, 1996; Higgins et al., 2000). Hence, in SATCHMO, fire is characterized by its average (0.006 year^{-1}) and maximum (1 year^{-1}) frequency (Table 1). The standard value of fire frequency is derived from a space-for-time substitution: at the study site of 22,000 ha in total, during the last three years, only one fire was observed affecting 400 ha (Meyer et al., 2005), giving a fire frequency of 0.006 year^{-1} for the whole area. The occurrence of a fire leads to increased mortalities in established shrubs and especially in shrub seedlings. Shrub growth is not impaired by fire because *A. mellifera* can compensate for losses by regrowth from the stem bases (Donaldson, 1967). Grass mortality and growth are not modified by the occurrence of a fire because grasses will have compensated for biomass losses until the end of the vegetation period (Noy-Meir, 1995; Van de Vijver et al., 1999).

Grazing and browsing are not modelled explicitly (e.g. via stocking densities) because the field data underlying SATCHMO were collected in areas with grazing intensities corresponding to natural conditions (E. Tegg, farm manager, personal communication) so that grazing effects are implicitly included in the parameterization of SATCHMO. On the other hand, overgrazing scenarios are not included because the focus of SATCHMO is on the investigation of natural drivers of shrub encroachment.

2.2.6. *Submodels*

2.2.6.1. *Soil moisture.* From precipitation, soil moisture is calculated independently for each grid cell, because local soil moisture can differ in the presence of roots or canopies which influence soil moisture availability through interception and the amount of moisture left after water uptake. Soil moisture is the basic currency of the model mediating competition, growth, and some aspects of mortality and reproduction. Temporal soil moisture dynamics is modelled as

$$\frac{\Delta s(t)}{\Delta t} = \frac{R(t)}{nZ} - \frac{D(t)}{nZ} - \frac{E(s(t), t)}{nZ} - \frac{L(s(t), t)}{nZ} \quad (1)$$

where $s(t)$ is the relative moisture content of a cell, t the time step (daily), n the soil porosity, Z the depth of active soil or rooting depth, $R(t)$ the amount of incoming rain, $D(t)$ the amount of incoming rain lost through interception by canopy cover, evapotranspiration $E(s(t), t)$ the amount of water lost through transpiration of plants and evaporation of bare ground, and $L(s(t), t)$ is leakage to deeper soil layers (Table 1). Surface runoff is not included because the field data were collected in a reasonably flat area so that it can be assumed that inflow and outflow balance each other. The algorithm for the calculation of soil moisture for a specific cell with residual soil moisture from the previous day $s(t-1)$ follows roughly Rodriguez-Iturbe et al. (1999, see Appendix A).

2.2.6.2. Shrub reproduction. Shrubs can reproduce vegetatively and sexually. Sexual reproduction involves seed production, seed dispersal, germination, and seedling mortality. Seed production and germination can be initiated only after certain cumulative soil moisture thresholds are exceeded (Table 1). For seed production, this threshold is defined by the total cumulative soil moisture between September and November. For parameterization of SATCHMO, the seed production threshold was determined conservatively from regional weather data from 2004 when seed production was observed at the study site (contrarily to 2003 when no seed production occurred and cumulative moisture was much smaller). The number of seeds per shrub depends on its size and is determined from the empirical relationship

$$\text{Number of seeds} = 22.98 \times \text{height (cm)} - 2380 \tag{2}$$

which also defines the minimum height for seed production (104 cm, $r^2 = 0.72$, D. Ward, unpublished data). Every shrub taller than 104 cm can produce seeds.

Seed dispersal includes aggregated short-distance dispersal and random long-distance dispersal. Based on seed-dispersal distances assembled from two shrubs in the study area, 60% of the seeds of a shrub are randomly distributed within its canopy radius, another 35% are randomly distributed within the radius and twice the radius, and the remaining 5% are pooled for all seed-producing shrubs and then randomly distributed in the whole grid to account for long-distance dispersal. This also is close to an exponential decline (Okubo and Levin, 1989; Witkowski and Garner, 2000). To include intraspecific competition, only one seed per cell ($100\,\text{cm}^2$) is allowed. Assuming that the number of seeds leaving the grid will be balanced by the number of seeds entering the grid, we applied toroidal edge correction.

Germination of shrub seedlings occurs only if the cumulative soil moisture of a certain number of successive days exceeds the germination threshold (Table 1). The germination soil moisture threshold and the number of days were determined from the closest rain flush prior to the germination event observed at the study site in January 2005. Whether the moisture threshold is reached may vary from cell to cell. If the threshold is exceeded, seeds germinate according to the germination probability determined in an experiment at the field site in 2005. In this experiment, *A. mellifera* seeds were sown in fourteen 2 m × 2 m plots at a density of 400 seeds per plot. Half of the plots were cut to simulate heavy grazing, the other half was left uncut as controls. The plots were watered every two to three days to field capacity. Germination rate was 0.19, and we did not find significant differences between cut and uncut plots ($t = -0.33$, d.f. = 1, $p = 0.37$). Germination does not depend on temperature because temperature is not a limiting factor at the field site in summer when germination occurs.

Although genetic analyses indicate that vegetative reproduction may occur in *A. mellifera* (B. Nxele, unpublished results), we did not find any evidence for rhizome resprouting during root excavations of close neighbours (Meyer et al., 2005). To account for this in SATCHMO, vegetative and sexual reproductions are mutually exclusive within one year and the probability of vegetative reproduction and the numbers of resprouts are very low (Table 1). If vegetative reproduction occurs, the respective number of resprouts is randomly distributed within the root system radius of the individual.

2.2.6.3. Shrub seedling mortality. The basic seedling mortality depends on the soil moisture in the cell where the seedling is located following the equation:

$$\text{Seedling mortality} = m^{(-\text{soil moisture})} \tag{3}$$

where m is the seedling mortality coefficient which was determined from the germination experiment described above. After one year, no seedling had died of the 3041 seeds that germinated in the experiment which was watered to field capacity (0.442). Conservatively assuming that the next seedling would have died, we determined m from the empirical relationship

$$\frac{1}{3042} = m^{(-0.442)}. \tag{4}$$

To account for the strong influence of herbivory on vulnerable seedlings, we included an additional natural browsing mortality (Table 1). If a fire occurs, seedlings are affected by an extra fire mortality (Table 1).

2.2.6.4. Shrub mortality. The basic annual shrub mortality (Table 1) is not modelled explicitly but included into the growth submodel so that the mortality emerging from negative regrowth does not exceed the empirically found mortality (see Section 2.2.6.7). The size–frequency distributions of dead and alive shrubs did not differ significantly (Wilcoxon's signed rank test, $p = 0.06$, but note the small sample size of dead shrubs $n = 3$), so that basic shrub mortality was not modelled size dependent. Additional mortality occurs through fire and droughts (Table 1). A drought year is defined as a year with less than the long-term mean annual precipitation minus one standard deviation. Drought mortality also includes mortality due to browsing because browsing of *A. mellifera* usually occurs in dry periods. If a shrub dies, the shrub and its roots and uptake zone are removed from the simulation.

2.2.6.5. Grass reproduction. Grass population dynamics is modelled with less detail than shrub population dynamics because grass was not in the focus of the model and data on individual grass tufts are scarce. The parameterization of the grass submodels in SATCHMO relies entirely on literature data which was adapted to our field site conditions via the long-term annual mean precipitation. We assume that only perennial grasses are present. We do not differentiate between sexual and vegetative reproduction because grasses with stoloniferous or rhizomatous growth do not necessarily produce fewer seeds than grasses that have no vegetative reproduction (O'Connor, 1992). When the reproduction soil moisture threshold is reached, a fixed density of new grass tufts is distributed randomly over the whole grid (Table 1). This reproduction soil moisture threshold is equal to the germination moisture threshold of shrubs (see above).

2.2.6.6. *Grass mortality.* Grass seedling mortality applies to all new grass tufts whereas grass tuft mortality is applied to all tufts older than one year (Table 1). We do not include an extra fire mortality because tiller losses due to fire are compensated until the end of the growing season (Silva and Raventos, 1999).

2.2.6.7. *Shrub growth.* To model the growth of their first two years, new shrub seedlings (age 0 and 1) are deterministically initialized with eight roots starting in the eight cells surrounding the seedling's centre (*xy*-location) and further occupying every second cell in the second row around the seedling's centre. Thereby, the eight roots alternately are assigned an originally cardinal or intermediate growth direction. It follows that the initial maximum root system radius of all seedlings is twice the diagonal length of a cell, i.e. 28.28 cm for a cell size of 10 cm. Resulting from the empirical relationship between root length and canopy diameter (0.5-quantile in Fig. 3a in Meyer et al., 2005), the initial canopy diameter of seedlings deterministically is set to 6.23 cm giving an initial height of 12.43 cm.

For all shrubs older than one year, individual water uptake is calculated by iterating over all cells in the grid and distributing the absolute soil moisture (in mm) in each cell at equal parts to all shrubs and grasses whose uptake zone covers the cell. We assume that plants cannot extract all soil moisture from a cell due to physical reasons, so that only a specified proportion of the soil moisture is distributed (*relative water uptake* in Table 1).

Whether the total amount of water taken up by a shrub is translated into regrowth is specified by the regrowth probability (Table 1). The regrowth probability was estimated from the average proportion of regrowing shrubs at the field site in two consecutive years ($n = 282$ shrubs). Whether a shrub produced regrowth in the second year did not depend on whether it had produced regrowth in the first year (Spearman's rank correlation, $\rho = 0.28$).

If a shrub does produce regrowth, regrowth length is determined following the rationale that the resources taken up have to be used for maintenance of the plant body, reproduction, and above- and belowground growth. We use moisture as a proxy for resources, canopy diameter as a proxy for maintenance, seed number as a proxy for reproductive effort, and regrowth length as a proxy for growth. Based on approximations from field data, we fitted linear models with square-root transformed moisture for seed-producing shrubs and for shrubs without seed production (see Appendix B for a detailed account of the fitting procedure).

We fitted the following models with square-root transformed moisture and shoot regrowth as an offset to ensure a realistic shoot regrowth range (corresponding to Eqs. (B2) and (B3)):

1. For seed-producing shrubs:

$$\text{Root growth} = 4.22 \times \text{shoot growth} + 0.0, \tag{5}$$

$$\text{Shoot growth} = \frac{\begin{array}{c}\text{moisture}^{0.5} - 2.49 \times \text{canopy diameter}\\ +0.17 \times \text{seeds} + 358.60 + 0.20 \times 0.0\end{array}}{1.0 - 0.20 \times 4.22}. \tag{6}$$

2. For shrubs that have not produced seeds:

$$\text{Root growth} = 4.54 \times \text{shoot growth} + 0.0, \tag{7}$$

$$\text{Shoot growth} = \frac{\begin{array}{c}\text{moisture}^{0.5} - 0.01 \times \text{canopy diameter}\\ -0.44 + 0.18 \times 0.0\end{array}}{1.0 - 0.18 \times 4.54}. \tag{8}$$

In the model, established shrubs die when they have negative regrowth. However, to account for the competitive effects that were not included into the moisture calculations and to ensure that the emergent mortality of established shrubs matches the empirically determined mortality, only those shrubs die that have a shoot growth of less than 0 minus a certain buffer. The buffer is determined separately for seed-producers and non-seed-producers by recalculating the shoot growth of the empirical data set with Eqs. (6) and (8) and arranging shrubs with negative regrowth values in descending order. The value of the buffer is equal to the *x*th lowest absolute regrowth value of the ordered shrubs where *x* is the empirical basic mortality of established shrubs multiplied with the number of shrubs with negative regrowth. Through this procedure, the line of zero regrowth is lowered by the value of the buffer, so that the actual regrowth length is obtained from the sum of the regrowth calculated with Eq. (6) or (8) and the buffer.

For shoot growth, twice the actual regrowth length is added to the canopy diameter of the shrub (because empirically determined regrowth refers to canopy radius) and, multiplied with the constant 0.659 to reproduce the empirical canopy–height relationship (K. Meyer, unpublished data), to the height of the shrub. We do not model aboveground competition explicitly because in semi-arid savannas, belowground competition for water is of much greater importance than aboveground competition for light (Wilson, 1988; Scholes and Archer, 1997; Vila, 1997).

Root regrowth proceeds cell by cell in an iteration over all roots of a shrub nested within an iteration over all shrubs whose order is randomized. At the end of each growth step, the remaining regrowth length L is updated for every root by subtracting the distance covered (one side or diagonal length of a cell, see below). The iteration excludes roots that have stopped to grow or that have a remaining regrowth length of 0. To be able to process root growth even if the remaining regrowth length is less than one cell, we apply a probabilistic procedure based on the ratio r of the remaining regrowth length and cell size. The probability for a root to be admitted to another growth step is proportional to r. Both the side length of a cell S and the diagonal length of a cell D have to be included in r, because root growth can proceed in cardinal or intermediate direction (see below), i.e. $r(L) = 0.5((L/D) + (L/S))$. For every root, $r(L)$ is calculated. If $0 < r \leq 1$, root growth proceeds for another step with probability r. If another growth step does not occur, the remaining regrowth length is set to 0. Otherwise, the next cell to grow into can be determined.

The most distant cell of the root has the choice between three cells for its next growth step depending on its original growth direction (cardinal or intermediate). These are the three closest cells to the original growing direction if we imagine the most distant cell of the root to be the starting cell of the root (see A, B, and C in Fig. 1). The cell among the three cells of choice which has the shortest linear distance to the original growing direction (A in Fig. 1) has *line probability* (Table 1) to be grown into. The other two cells have a probability of $(b/(b+c))(1-\textit{line probability})$ and $(c/(b+c))(1-\textit{line probability})$, respectively, with b and c representing the respective perpendicular distance of the cell to the original growing direction in units of cells.

Before a chosen cell can be occupied by a root, the prospective uptake zone around the chosen cell is searched for the existence of uptake zones of competing roots. In case of an overlap of two uptake zones, one of seven mutually exclusive competition scenarios applies:

1. Both roots stop to grow (and are assumed to turn vertically downwards as observed at the field site).
2. Both roots stop to grow and the respective opposite roots compensate for the remaining root growth length.
3. One randomly selected root stops to grow (and turns downwards).
4. The randomly selected root stops to grow and its opposite root compensates.
5. Asymmetric competition: the root belonging to the shrub with the smaller canopy diameter stops to grow (and turns downwards).
6. Asymmetric competition: the root belonging to the shrub with the smaller canopy diameter stops to grow and the opposite root compensates.
7. Nothing happens; complete overlap of uptake zones is allowed (which was observed several times during root excavations at the field site).

If competition does not lead to the growth stop of the root, it occupies the chosen cell and its remaining regrowth length is reduced according to the direction of growth (growth in cardinal direction covers less distance than growth in intermediate directions). We apply toroidal edge correction if root growth exceeds the borders of the grid. For every shrub, maximum root system radius and age are updated after the end of all growth steps.

2.2.6.8. Grass growth. Grass canopy diameter growth is deterministically set to 5 cm/year (Table 1) because no field data are available on individual regrowth length and its relation to soil moisture or tuft size. Grass age and the uptake zone of the grass are updated corresponding to canopy growth.

2.3. Model calibration and validation

For calibration and validation of SATCHMO, the model was run 10 times with the default parameterization (Table 1). We calculated the standard error of the average shrub cover over time of 10 simulations. We use shrub cover as the main output variable because it is directly related to shrub encroachment. However, when we use shrub cover in the following, the result applies to shrub population sizes as well because shrub cover and population size are strongly correlated (Pearson's correlation coefficient: 0.99).

We determined the maximum and minimum shrub cover of 10 simulations to compare it with literature values (Sankaran et al., 2005). For model calibration, the simulated and observed average annual shoot regrowth lengths were compared with t-tests. The simulated regrowth length was determined as the slope of the linear relationship between canopy diameter and age of all shrubs older than one year within 500 years. The observed regrowth length was obtained from averaging over all regrowth length measurements of 282 shrubs in 2004 and 2005 including non-regrowing shrubs with a zero. For model validation, emergent properties of SATCHMO such as average population sizes, maximum canopy diameter, and shrub thicket diameter were compared with the respective field data. Population sizes were compared with t-tests. Simulated population size in the model grid (50 m × 50 m) includes only shrubs older than one year and was averaged over 500 years. Observed population size was averaged over ten 10 m × 10 m plots and twenty 15 m × 15 m plots and converted to model grid dimensions. The maximum canopy diameter and the size–frequency distributions of all shrubs occurring during 10 runs of 500 simulation years and of 461 observed shrubs in 2004 and 2005 were visually compared. For the simulation year with the maximum canopy diameter, we determined the diameter of the simulated shrub thickets via the spatial distribution of their canopies based on a Neyman–Scott clustering process for the top left 15 m × 15 m corner of the model grid (for details see Appendix C). Following the same procedure, we determined the observed shrub thicket diameters for twenty 15 m × 15 m field plots and compared the averaged values with t-tests. All t-tests were applied with Welch-correction to account for unequal variances. All statistical analyses were carried out with the software package R.

2.4. Sensitivity analysis

We applied the global sensitivity analysis method Latin Hypercube sampling to save processing time while covering as much parameter space as possible (McKay et al., 1979). We included 27 parameters in the analysis and chose the ranges and distributions for the sampling procedure according to best knowledge or field data distributions if available (Table 1). For each parameter, 11 values covering the whole range of the parameter were specified and reordered randomly generating 10 input parameter sets. This procedure was replicated three times. The model was run 10 times for each set of parameters. In six cases, the model was run less than 10 times due to processing power constraints, i.e. 3, 1, 5, 3, 8, and 6 times. Additionally, two simulation runs were excluded from the analysis because the shrub population went extinct within the first 300 years of pre-simulation. The resulting shrub cover and population sizes were averaged over time and over the simulation runs. After a successful check of normality and independence of errors, two linear regression models were applied with shrub cover and population size, respectively, as response variables and the 27 parameters as explanatory variables. During regression model simplification, the least significant parameters were excluded stepwise from the analysis until the model contained only significant parameters ($p < 0.05$). To obtain a measure for the relative importance of the remaining parameters with respect to shrub cover and population sizes, the standardized regression coefficients were calculated as the absolute ratio of the coefficient and the corresponding standard error.

3. Results

3.1. Model validation

The standard error of the average shrub cover and of the average population size over 10 runs is very low (cover, mean ± S.E.: 16.80 ± 0.14%; population size, mean ± S.E.: 794 ± 9). Simulated maximum and minimum cover of 31.11 and 6.51% agree well with maximum and minimum cover of 38.58 and 0% predicted for a mean annual precipitation of 377 mm by the relationship found by Sankaran et al. (2005). Average annual shoot regrowth length, average population size, and average thicket diameter are not significantly different for simulated and observed shrubs (Table 2). The observed maximum canopy diameter of 560 cm is very closely reached by the simulated maximum canopy diameter of 550 cm (run 8 in Table 2). Visual comparison of the simulated and observed size–frequency distributions of canopy diameters reveals fairly good agreement (Fig. 4).

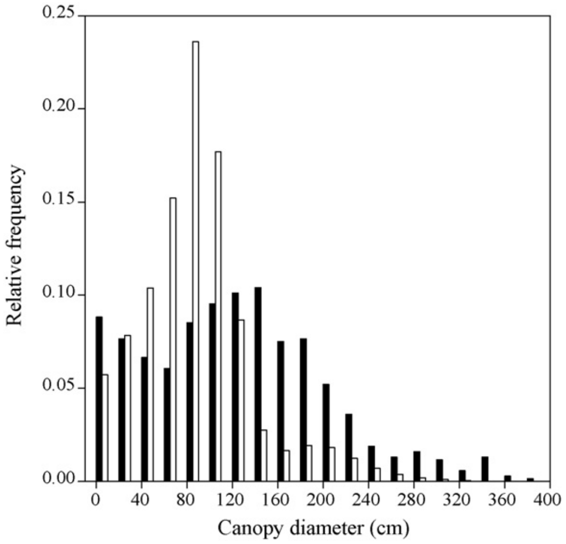

Fig. 4 – Distribution of relative frequencies of the canopy diameter of 461 observed shrubs (solid bars) and all simulated shrubs occurring during 10 runs of 500 simulation years (open bars). The representation of the distribution is truncated at 400 cm because relative frequencies would not have been visible (total remaining frequencies: observed −0.0014, simulated −0.00003).

3.2. Sensitivity analysis

The number and identity of significant parameters in the minimum adequate model of the sensitivity analysis results was

Table 2 – Simulated (1–10) and observed (Obs.) average annual regrowth length, population size, maximum canopy diameter, and shrub thicket diameter

	Annual regrowth length (cm)	Population size	Maximum canopy diameter (cm)	Year	Thicket diameter (cm)
1	3.07	537	434	300	182.4
2	3.08	509	457	310	268.4
3	3.06	531	445	302	192.4
4	3.01	528	455	730	175.2
5	3.10	519	402	410	124
6	3.06	558	481	385	164.4
7	3.10	527	387	380	200.8
8	3.09	513	550	655	124
9	2.94	524	416	610	174.4
10	3.08	522	398	340	207.2
Obs.	3.38	584	560	2004	178.4
t	1.656	−0.586	–	–	−0.055
d.f.	284.235	29.114	–	–	21.455
p	0.10	0.56	–	–	0.96

Simulations are based on the default parameterization and were run 10 times. Simulated average *annual regrowth length* was determined as the slope of the linear relationship between canopy diameter and age of all shrubs older than 1 year within 500 years. The observed regrowth length was obtained from averaging over all regrowth length measurements of 282 shrubs in 2004 and 2005 including non-regrowing shrubs. Simulated *population size* in the model grid (50 m × 50 m) includes only shrubs older than 1 year and was averaged over 500 years. Observed population size was averaged over ten 10 m × 10 m plots and twenty 15 m × 15 m plots and converted to model grid dimensions. *Maximum canopy diameter* was determined from 500 years of simulation, and from 2 years of observation of 461 shrubs. *Year* gives the year when the maximum canopy diameter occurred. For this year, the shrub *thicket diameter* was determined as 2σ based on a Neyman–Scott clustering process (for details see Appendix C) for the top left 15 m × 15 m corner of the model grid and for twenty 15 m × 15 m field plots (here, the average is shown). Observed and simulated average values were compared with *t*-tests with Welch-correction for unequal variances (t—test statistic, d.f.—degrees of freedom, *p*—*p*-value).

similar for the response variables shrub cover (9 out of 27 parameters sensitive) and population size (11 sensitive parameters). In both cases, most of the demographic parameters such as mortality of established shrubs and shrub germination rate were eliminated from the final model, as well as environmental variables such as fire frequency and soil porosity (Table 1). For shrub cover, the cumulative seed moisture threshold was the most important parameter, followed by soil depth, browsing mortality of seedlings, grass mortality, interception of shrub canopies, germination moisture of grasses, relative water uptake, mean rainfall, and soil field capacity (Table 1). With the exception of mean rainfall, the same parameters were retained in the population size analysis, albeit in a different order and supplemented by the parameters critical soil moisture of shrubs, maximum evapotranspiration, and seedling mortality coefficient (Table 1). Population size is by far most sensitive to browsing mortality of seedlings (Table 1).

4. Discussion

The spatially explicit, individual-based simulation model SATCHMO was built to investigate the small-scale conditions leading to cyclical successions within savanna patches. The successful validation of emergent properties of SATCHMO such as maximum canopy diameter, population size, and shrub thicket diameter shows that SATCHMO is suitable for studying the small-scale shrub cover and population size dynamics in a semi-arid savanna. The agreement between model and data collected at the field site is enhanced by successful comparisons of minimum and maximum shrub cover from simulations with the respective values derived from the empirical relationship found by Sankaran et al. (2005) in their comprehensive study of more than 800 data points from African savannas. For a savanna with more rain than at our field site (675 mm versus 377 mm mean annual rainfall), the maximum equilibrium shrub cover (40%, Roques et al., 2001) was also slightly higher than the maximum cover in our simulated semi-arid savanna patch (31%). Hence, SATCHMO can be used to generate realistic conclusions for semi-arid savannas in general (as long as the model assumptions hold for the site of application) which are not restricted to the shrub population and cover dynamics at our specific field site. Specifically, SATCHMO can be used to mechanistically explore the ecological processes that produce the patterns found in semi-arid savannas, such as the relationships discovered by Sankaran et al. (2005). The hypothesis that one such mechanism may be patch-dynamics can be tested with SATCHMO by searching for positive autocorrelation in the simulated shrub cover time series.

The sensitivity analysis of SATCHMO quantitatively confirms the common view that soil moisture is the most important parameter affecting shrub cover dynamics in semi-arid savannas (Sankaran et al., 2005). Still, it is surprising that almost none of the demographical parameters such as shrub germination probability or shrub mortality is of importance for shrub cover dynamics, leading to the conclusion that demographic bottlenecks inherent to the population (as described by Sankaran et al., 2004) do not matter as much as external factors. With respect to model structure, this can be explained by soil moisture being the key driver of processes in SATCHMO. While shrub and grass growth, competition, mortality, and reproduction depend on soil moisture, there is only a weak indirect feedback of these processes to soil moisture (e.g. via uptake zones depleting the available water in the cells they cover and by canopies intercepting precipitation). Thus, without sufficient soil moisture, shrub growth, and reproduction are impaired and mortality increased, generating high sensitivities of shrub cover and population sizes to soil moisture parameters. This is particularly apparent when focussing on the most sensitive parameter with respect to shrub cover: the cumulative moisture threshold for seed production is invoked early in the annual cycle of population dynamics and its high sensitivity points to the importance of seed production conditions—without seeds no adult shrubs can grow. This is in agreement with the patch-dynamics concept where years of overlapping local rainfall events may create the necessary conditions for mass recruitment and subsequent expansion of whole shrub cohorts leading to the naturally encroached phase of the successional cycle (Wiegand et al., 2006). The only sensitive parameter related to shrub demography is browsing mortality of shrub seedlings. Analogous to the soil moisture parameters, seedling mortality occurs early in the life cycle and therefore creates the conditions subsequent demographic processes such as growth rely on.

However, the majority of the sensitive parameters are not well studied, e.g. browsing mortality of seedlings or relative water uptake (see *Accuracy* in Table 1). In the light of increasing shrub encroachment, it would be valuable to invest more effort into the empirical study of these parameters in the future because these parameters are of major importance for the determination of shrub cover. Management will be efficient if centered on sensitive parameters that are easy to manipulate. If management aims at reducing shrub encroachment, continuous action would be required in a patch-dynamic savanna because cyclical succession has to be stopped at the desired shrub density and further succession has to be prevented. Moreover, the sensitive parameters identified in the present study are not easy to manipulate, because holding the cycle in the phase dominated by grass would require reducing soil moisture parameters. The only exception may be browsing mortality of seedlings which could be raised with a reasonable effort. In particular, following our results, fire management may not be efficient in arid and semi-arid savannas because fire frequency was one of the first parameters eliminated from the regression model during model simplification. This agrees with the common notion that fire does not play an important role in arid savannas where precipitation is not sufficient to allow for enough grass biomass to fuel frequent and intense fires (Bond and Van Wilgen, 1996; Higgins et al., 2000; Bond et al., 2003).

Sankaran et al. (2004) split savanna models into two families: competition-based models and demographic-bottleneck models. Competition-based models concentrate on spatial or temporal concentration of intraspecific versus interspecific competition and mostly ignore life-stage dependency of competition although there is evidence for it (Scholes and Archer, 1997; House et al., 2003). On the other hand, most demographic-bottleneck models do not include competitive interactions explicitly or only semi-quantitatively (Sankaran et al., 2004). Hence, for a better understanding of savanna dynamics, Sankaran et al. (2004) advocate new savanna modelling approaches taking demographic bottlenecks and competitive interactions at each life stage of a shrub explicitly into account. This claim is based on the rationale that coexistence may be reached if intra-life form competition is stronger during periods favourable for that life form and inter-life form competition otherwise (Chesson and Huntly, 1997; Chesson, 2000). Following Sankaran et al.'s (2004) suggestion, we constructed SATCHMO as a demographic-bottleneck model that explicitly includes different competition scenarios between shrub roots as well as competition for water in cells that are covered by the uptake zones of more than one individual grass or shrub. Competition is life-stage dependent because small shrub seedlings have much smaller uptake zones than established shrubs and also than most grass tufts. This results in strong competition when a seed is dispersed to a location completely covered by a larger uptake zone of another individual. As the soil moisture taken up within the uptake zones is translated quantitatively into regrowth length, competition is included quantitatively as it was called for by Sankaran et al. (2004). During periods favourable for shrubs, shrub densities and uptake zones expand, leading to greater probabilities of intra-life form contact and subsequent intra-life form competition. Hence, SATCHMO unifies the competition-based approaches with the demographic-bottleneck ideas by placing a strong focus on spatially explicit belowground interactions.

In the future, further applications of SATCHMO may include the explicit investigation of patch-dynamics by the identification of cycles in shrub cover dynamics over time and their relationship to annual precipitation and other savanna determinants (cf. Meyer et al., in press). SATCHMO is also well suited to comparing the consequences of different belowground competition scenarios for savanna dynamics in general and shrub encroachment in particular at a great level of detail which would be much more time-consuming in the field. This could be supported by the analysis of the spatial patterns of long-term chronosequences of model shrubs and grasses. Patterns emerging under the competition scenarios (i.e. symmetric/asymmetric, with/without compensation, no competition at all) can be tested for agreement with field patterns. Only those scenarios that result in equivalent patterns may have acted in nature. This way one could screen the competition scenarios for fulfilling the hypothesis that the long-term impact of competition leads to less aggregated spatial shrub patterns (Wolf, 2005). As in any other model application, it should be warranted that the application area is consistent with the model assumptions in future SATCHMO applications.

Among the strengths of SATCHMO is the explicit and detailed simulation of belowground growth and competition matching the recognized importance of belowground interactions in savannas (Scholes and Archer, 1997). SATCHMO is based on a solid field data foundation and has been successfully validated with independent field data for a semi-arid savanna. SATCHMO operates on large temporal scales allowing the evaluation of long-term spatially explicit savanna woody species dynamics.

Admittedly, the great level of spatial and temporal detail comes at a cost because the processing of certain scenarios can be quite computing-power-intensive. Fortunately, the small standard errors justify a reduced number of simulations, although more replications are of course always desirable as they increase the power of the conclusions. Another drawback of the model is its small spatial scale which serves the current purpose of investigations but should be expanded to the landscape scale to be able to ultimately test the predictions of the patch-dynamics concept and its integrative power. To keep SATCHMO as simple as possible in spite of the high level of detail desired, some aspects of reality were not included that were unnecessary to fulfil the current purpose of SATCHMO. If the model purpose was expanded to focus more on grass population dynamics and, given the availability of the relevant field data, it could be reasonable to also include an explicit feedback of soil moisture on grass growth and explicit competition scenarios between grasses and shrubs. Possible extensions to belowground growth and interactions could be active root foraging behaviour according to moisture gradients in the root neighbourhood and the implementation of facilitative interactions or mixed competition scenarios. In mixed competition scenarios, the type of competitive interaction could depend on the actual conditions, e.g. root overlap without consequences prevails in years with high precipitation and asymmetric competition with strong territoriality (=wide uptake zones) in drought years.

Additionally, SATCHMO can be easily extended to include an overgrazing scenario to test the relative importance of natural drivers of shrub encroachment and overgrazing. In future model extensions, the impact of insect herbivores and burrowing animals can also be considered as can differences in grazer preferences for various grass species. To increase reality of the model, shrub objects with the characteristics of other important savanna woody species may be added to investigate tree–tree interactions and their positive and negative feedbacks influencing overall woody species densities and encroachment. Management or encroachment restoration scenarios can easily be included and tested with SATCHMO by evaluation of the consequences for long-term shrub dynamics, e.g. Smit's (2004) hypothesis that thinning of woody species to low densities of large individuals will prevent shrub encroachment most effectively. After a scaling-up procedure, generalized results on patch transition frequencies and duration of transitional states (woody, grassy, bare ground) from SATCHMO can be used to parameterize a patch-dynamic landscape-scale model. If the landscape-scale population dynamics and spatial patterns of woody species correspond to those derived from aerial photographs from corresponding semi-arid savannas, the patch-dynamics concept has the potential to be one integrative mechanism explaining tree-grass coexistence and shrub encroachment in savannas.

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Appendix A

Algorithm for the calculation of soil moisture for a specific cell with residual soil moisture from the previous day $s(t-1)$ based on Rodriguez-Iturbe et al. (1999):

1. Given rainfall $R(t)$, calculate soil moisture $s'(t)$ including interception $D(t)$, but not yet considering evapotranspiration and leakage:

$$\begin{array}{ll} \text{If } R(t) > 0 & s'(t) = s(t-1) + \dfrac{R(t)}{nZ} - \dfrac{D(t)}{nZ} \\ \text{Else} & s'(t) = s(t-1) \end{array}$$

2. Calculate evapotranspiration $E(s'(t), t)$ taking critical soil moisture s_c and maximum evapotranspiration $E_{\max}$ into account where s_c defines the threshold when plants begin closing their stomata:

$$\begin{array}{ll} \text{If } s'(t) \geq s_c & E(s'(t), t) = E_{\max} \\ \text{Else} & E(s'(t), t) = \left(\dfrac{E_{\max}}{s_c}\right) s'(t) \end{array}$$

3. Calculate leakage $L(s(t), t)$ including soil field capacity s_{fc}:

$$\begin{array}{ll} \text{If } s'(t) > s_{fc} & L(s(t), t) = s'(t) - s_{fc} \\ \text{Else} & L(s(t), t) = 0 \end{array}$$

4. Update soil moisture:

$$s(t) = \frac{s'(t) - E(s'(t), t)}{nZ - L(s(t), t)}.$$

Appendix B

Fitting procedure for the relationship between moisture and regrowth based on approximations from field data:

With

$$\text{Moisture} = a \times \text{shoot growth} + b \times \text{canopy diameter} + c \times \text{seeds} + d \times \text{root growth} + e, \tag{B1}$$

$$\text{Root growth} = f \times \text{shoot growth} + g, \tag{B2}$$

$$\text{Shoot growth} = \frac{\text{moisture}^{-0.5} - b \times \text{canopy diameter} - c \times \text{seeds} - e - d \times g}{a + d \times f}, \tag{B3}$$

where a to g are regression coefficients which were estimated from field data. Unfortunately, there was no data set available encompassing values for all these variables at the same time, and for soil moisture, no direct measurements were accessible. However, approximations were possible based on the field data that were available. The largest available data set comprised canopy diameter, height, and shoot regrowth length (but not seed number and root regrowth length) for 590 *A. mellifera* shrubs in 2004 and 2005.

To obtain an estimate of seed number, we calculated the number of seeds for all heights in the data set from Eq. (2). For an estimate of root regrowth length, we assumed that the relation of root regrowth length to root length is the same as the relation of shoot regrowth length to canopy radius. From quantile regressions, we know that canopy diameter is significantly related to maximum root length (Meyer et al., 2005). Hence, we estimated root length as a random value between the 0.5- and the 0.9-regression quantile at the given canopy diameter in the data set. With root length, shoot regrowth length, and canopy radius, we estimated root regrowth for the data set.

To determine the moisture uptake of the shrubs of the data set, the area of the uptake zone of the shrubs was calculated as the sum of eight rectangles. The area of each rectangle was calculated as the product of the root length of the shrub and the width of its uptake zone. Thereby, we assume that the eight roots of a shrub had all the same lengths and had followed their original direction without deviations. The total area of the uptake zone of a shrub was partitioned into the part under bare ground and the part under the shrub canopy.

An absolute annual soil moisture value (in mm) was calculated from the Kimberley weather data for bare ground and shrub canopy-covered ground for 2004 and 2005, respectively. Absolute annual moisture uptake per shrub (in mm^3) was estimated as absolute annual moisture uptake multiplied with the uptake zone areas under bare ground and under the shrub canopy. In this estimation, possible moisture losses due to competitive uptake zone overlap are not included.

Appendix C

Patch size was determined with canopy diameters and *xy*-coordinates of all shrubs in combination with a univariate Neyman–Scott cluster process (Diggle, 1983). A Neyman–Scott cluster process is constituted by randomly distributed "parent" points and "offspring" points with a bivariate normal distribution relative to the location of the parent. For the Neyman–Scott process, Ripley's *K*-function and the pair-correlation function $g(h)$ (Stoyan and Stoyan, 1994) are

$$K(h, \sigma, \rho) = \pi h^2 + \frac{1 - e^{(-h^2/4\sigma^2)}}{\rho}$$

and

$$g(h, \sigma, \rho) = 1 + \frac{e^{(-h^2/4\sigma^2)}}{4\pi\sigma^2\rho},$$

where h is the scale investigated, ρ the intensity of the parent process (i.e. number of points per area), and σ^2 is the variance of the distance between each offspring and the parent (Diggle, 1983). A certain number of points, l, was randomly distributed within the borders of each canopy circle where l is given by the area of the canopy circle divided by a square area with the fifth smallest canopy diameter in the plot as side length. The overall canopy point pattern was then fitted to a Neyman–Scott process in which the cluster diameter corresponded to the size of the patch and was approximated as 4σ.

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