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The rhythm of savanna patch dynamics

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Summary

1. Patch dynamics is a new, potentially unifying mechanism for the explanation of tree-grass coexistence in savannas. In this scale-explicit paradigm, savannas consist of patches in which a cyclical succession between woody and grassy dominance proceeds spatially asynchronously. The growing ecological and economic problem of shrub encroachment is a natural transient phase in this cycle.

2. An important step towards understanding patterns at the landscape scale is achieved by investigating mechanisms at a smaller scale. We developed the spatially explicit individual-based simulation model SATCHMO to test the null hypothesis that cyclical succession cannot emerge from a realistic patch scale simulation model of the population dynamics of savanna woody species.

3. We calculated the partial temporal autocorrelation coefficient for 100 simulated time series of shrub cover over 500 years for time lags of up to 200 years to establish the existence and duration of successional cycles. We found a significant positive autocorrelation indicating the existence of cycles with a typical duration of about 33 years.

4. The shrub size frequency distributions over the course of a cycle showed shifts from dominance of small shrub sizes towards larger sizes during the increasing phase of a cycle and the reverse in the declining phase. This supports the three phase explanation as follows: (i) an initial phase when spatially and temporally overlapping favourable conditions lead to mass recruitment of shrubs; (ii) a build-up phase when the shrub cohort grows; and (iii) a break-down phase when increased competition due to crowding and unfavourable conditions lead to the break-down of the shrub cohort. The frequency distribution of shrub age at death over 10 simulations was also in agreement with this explanation.

5. We investigated the relationship between shrub cover, annual precipitation and time-lagged shrub cover to identify the driver of the cyclical successions. More than 90% of the variation in shrub cover was explained by shrub cover of the previous year, precipitation, and their interaction.

6. With the demonstration of precipitation-driven cyclical succession at the patch scale, we show that the mechanistic, temporal component of patch dynamics can be used to explain tree-grass coexistence in semi-arid savannas.

Key-words: *Acacia mellifera*, cyclical succession, individual-based simulation model, patch scale, scale, shrub encroachment, size-frequency distributions, temporal autocorrelation, tree-grass coexistence

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Introduction

Scale is a fundamental conceptual problem in ecology because different processes occur at different scales and are linked to patterns at other (mostly greater) scales (Levin 1992). For a general understanding, ecological theories and empirical studies should therefore not be restricted to one scale. Patch dynamics is a useful

framework to capture ecosystem dynamics spanning several scales of observation. In patch dynamics, it is assumed that the landscape consists of distinct patches of variable size. In every patch, the same cyclical succession proceeds. The successional states may be of variable duration and occur spatially asynchronously. The proportion of each state will be approximately constant at the landscape scale. Hence, at large scales, an equilibrium can persist, although at small scales, non-equilibrium dynamics prevail (Levin 1992). Since Watt's (1947) first account of patch dynamic ecological systems, patch dynamic modelling frameworks have been developed (Wu & Levin 1997; Levin *et al.* 2001) and the patch dynamics paradigm has been applied to a multitude of terrestrial ecosystems, including forests (Remmert 1991), intertidal communities (Levin & Paine 1974; Paine & Levin 1981), grasslands (Coffin & Lauenroth 1990), and also to aquatic ecosystems (Steele 1978).

However, the first empirical attempts to explain tree-grass coexistence in savannas with patch dynamics have been made only recently (Gillson 2004; Wiegand *et al.* 2005; Wiegand *et al.* 2006). Prior to these studies, mostly scale-free theories were proposed to explain tree-grass coexistence in savannas (but for an early exception see Coughenour & Ellis 1993). The first and still prominent explanation is the two-layer hypothesis, based on a rooting depth niche separation between trees and grasses (Walter 1971). However, evidence for this hypothesis to date is equivocal. For example, tree-grass coexistence has been shown on soils too shallow for rooting depth differentiation (Wiegand *et al.* 2005). Other hypotheses include a storage effect of reproductive potential of woody species over unfavourable periods (Higgins *et al.* 2000), disturbances such as fire acting as a buffer to retain both grasses and trees in the system (Scholes & Archer 1997; Jeltsch *et al.* 1998b; Jeltsch *et al.* 2000), or spatially heterogeneous locations that are favourable for either grass or tree establishment (Jeltsch *et al.* 1998a). All mechanisms proposed to date are restricted to certain environmental conditions; a unifying mechanism is lacking. Patch dynamics has the potential to provide this unifying mechanism because it acknowledges the importance of scale and is general enough to allow the integration of most of the mechanisms suggested. In a patch dynamic savanna, patches cycle between grassy and woody dominance, leading to tree-grass coexistence at the landscape scale. Hence, the patch dynamics framework integrates the spatial-heterogeneities explanation by Jeltsch *et al.* (1998a). Other hypotheses such as the disturbance explanation (Scholes & Archer 1997; Jeltsch *et al.* 1998b; Jeltsch *et al.* 2000) or the storage effect (Higgins *et al.* 2000) could be integrated as drivers of the successional cycles.

Understanding savannas as patch dynamic systems would also have implications for management issues. In a patch dynamic savanna, the worldwide ecological and economic problem of shrub encroachment, i.e. the increase in density of woody species often unpalatable

to livestock (Smit *et al.* 1996; Ward 2005), may only constitute part of a natural phase during the successional cycle at the patch-scale. This phase starts with mass recruitment of shrubs in years with favourable rainfall and is followed by shrub cohort build-up, leading to an encroached patch. In the patch dynamics paradigm, shrub encroachment may be enhanced by overgrazing, as suggested by empirical evidence (Skarpe 1990b, 1990a; Perkins & Thomas 1993), but would be a potentially inherent natural and transient phenomenon. However, the synchronous occurrence of shrub encroachment at the landscape scale cannot be explained by patch-dynamics.

In order to test the validity of patch dynamics as an explanation of tree-grass coexistence in savannas, a simulation model is an appropriate tool because it can capture the large scales involved more easily than empirical studies (Levin 1992; but see Gillson 2004 for a palaeoecological study spanning different scales). The patch dynamics hypothesis is based on two different spatial scales, the patch scale and the landscape scale, and ultimately requires investigations at both scales. In this study, we focus on the patch scale because an understanding of patterns at larger scales is promoted by investigating mechanisms at the smaller scale (Wu & Loucks 1995). Results from the present study may then feed into a large-scale study arranging patches into a landscape mosaic (e.g. Schwinning & Parsons 1996a,b). To obtain small-scale understanding, the spatially explicit individual-based patch scale simulation model SATCHMO was developed (see also Meyer *et al.*, in press). Patch dynamics implies cyclical succession at the patch scale. Thus, in the present study, our first aim is to test the null hypothesis that cyclical succession cannot emerge from an ecologically realistic patch scale simulation model of the population dynamics of savanna woody species. If cyclical succession does emerge from SATCHMO, the second aim of this study is to provide a mechanistic explanation for the cycles and to identify the driving factors of the cyclical succession. The four classic savanna key factors (fire, herbivory, nutrients and water; Frost *et al.* 1986; Sankaran *et al.* 2004) are potential candidates for disturbance events driving successional cycles in arid ecosystems. The potential contribution of pulsed resources (nutrients and water) to cyclical successions in arid ecosystems may be particularly important but has not yet been well studied (Chesson *et al.* 2004). Globally, savannas receiving less than 650 mm of mean annual precipitation exhibit a significant relationship between the pulsed resource precipitation and maximum shrub cover (Sankaran *et al.* 2005). Hence, the most promising candidate for driving semi-arid savanna dynamics is precipitation. Herbivory and fire become more dominant in savannas with a mean annual precipitation of more than 650 mm, but these savannas are not covered by SATCHMO. With SATCHMO, we attempt to identify the most relevant driver(s) of cyclical successions in semi-arid savannas.

Methods

The results presented here are based on the spatially explicit, individual-based patch size simulation model SATCHMO, which is described in detail in Meyer *et al.* (in press). In the following, only model features relevant to the present study are summarized. For model details, default parameter values, validation and sensitivity analysis refer to Meyer *et al.* (in press).

STUDY AREA

SATCHMO is based on field data that were collected in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28°35', E 24°29'), 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 to March). The multi-stemmed blackthorn (*Acacia mellifera* (Vahl) Benth) is the dominant woody species in the study area.

MODEL STRUCTURE AND SCALES

The basic objects in SATCHMO are a shrub, a grass tussock, and the root of a shrub. Until the age of 1 year, shrubs and grasses are referred to as seedlings, thereafter as established shrubs and grass tussocks. Shrubs were modelled following the characteristics of the dominant species in the area, *A. mellifera*. Above ground, shrubs and grasses older than 1 year are represented by a circle corresponding to the canopy diameter of the individual. To appreciate the predominant importance of soil moisture mediating plant interactions in semi arid savannas, we modelled shrub roots spatially explicitly in two dimensions. The shrub root system is represented by eight horizontal roots that initially stretch from the shrub rooting point into the cardinal and intermediate directions. Roots are surrounded by an uptake zone whose width approximates the length of side roots responsible for water uptake. Grass tussocks serve as interspecific competitors for the shrubs. Grass roots were not modelled spatially explicitly because grass was not the focus of the model and because information on root lengths or growth rates of savanna grass species is scarce. Instead, water uptake occurs in a circular uptake zone around the grass canopy.

SATCHMO is based on a two-dimensional grid with 512 × 512 cells comprising one patch in the patch dynamics paradigm. The spatial resolution is 10 cm and the spatial extent of the grid corresponds to 51.2 m, which is justified by field observations of annual root length increments and diameters of encroached shrub patches, respectively (K. Meyer, unpublished data). 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 dynamics.

Table 1. Stochastic and deterministic model processes*

Model processes
<i>Environmental stochasticity</i>
Precipitation
Fire
<i>Demographic stochasticity</i>
Shrub seedling germination
Shrub vegetative reproduction
Shrub mortality
Grass germination
Grass mortality
<i>Spatial stochasticity</i>
Location of dispersed shrub seeds
Shrub root growth
<i>Deterministic processes depending on a stochastic process</i> †
Soil moisture (precipitation)
Shrub canopy growth (precipitation)
<i>Deterministic processes</i>
Grass growth

*For a flow diagram of the model processes, refer to Meyer *et al.* (in press).

†The respective stochastic process is given in parentheses.

INITIALIZATION

Initially, one reproductively mature shrub is located in the centre of the grid supplemented by 10 randomly arranged grass tussocks with initial values of shrub and grass characteristics such as canopy diameter or height corresponding to average field data values. Thus, all cells that are not covered by the canopy or roots of the initial shrub or by the canopies of the 10 grass tussocks are empty. Model evaluation started after 300 years of pre-simulation to exclude an influence of initial conditions (Meyer *et al.*, in press).

ENVIRONMENTAL PARAMETERS

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, among the possible environmental variables, we do not explicitly take nutrient dynamics and grazing into account (although grazing is implicitly included in the field data underlying SATCHMO, i.e. the field data were collected at sites with natural grazing intensities). Nutrient dynamics are coupled to soil moisture dynamics (Scholes & Archer 1997), supporting our decision not to consider these two factors separately. We model fire with less detail, and focus on a detailed characterization of precipitation and soil moisture in SATCHMO. A daily precipitation value is calculated for the model grid according to a stochastic algorithm for South-African rainfall based on local long-term weather data (Zucchini *et al.* 1992; see Table 1 for a list of stochastic and deterministic processes in SATCHMO). Fire is characterized by its frequency, with a maximum of one

fire per year and a field data-based default value of 0.006 year^{-1} (yielding on average three fires in the analysed period of 500 years; Meyer *et al.*, in press). In the sensitivity analysis of SATCHMO (Meyer *et al.*, in press), we explored fire frequencies of up to 0.06 corresponding to an average fire-return interval of 17 years. The occurrence of a fire leads to increased mortalities in established shrubs and especially in shrub seedlings. Shrub growth, grass mortality and grass growth are not modified by fire due to compensation for biomass losses through regrowth until the end of the season (Donaldson 1967; Noy-Meir 1995; Van de Vijver *et al.* 1999). Hence, the potential drivers of shrub population dynamics covered explicitly by the model are the extrinsic factors (or disturbances), precipitation and fire, and the intrinsic factor, population demography.

SOIL MOISTURE

Soil moisture, as the basic currency of the model, mediates competition, growth, and some aspects of mortality and reproduction. Soil moisture is calculated independently for each grid cell from the overall precipitation value to account for the influence of roots or canopies on water budgets. Based on Rodriguez-Iturbe *et al.* (1999), temporal relative soil moisture dynamics are obtained by subtracting water lost through vegetation interception, evapotranspiration, and leakage to lower soil layers from total daily precipitation, and then by dividing the remaining amount of water by soil porosity and soil depth (for details see Meyer *et al.*, in press). We modelled a soil depth of 70 cm based on data from *A. mellifera* root excavations (D. Ward, unpublished data). Surface runoff is not included because a flat area is modelled where inflow and outflow balance.

SHRUB REPRODUCTION

In all demographic rates, stochasticity is included (Table 1). Seed production occurs in all mature shrubs if a certain threshold of local total cumulative soil moisture between September and November is exceeded. The threshold is estimated from local weather data (Meyer *et al.*, in press). Based on an empirical relationship, maturity is reached with a height of 104 cm and the number of seeds per reproducing shrub is size dependent (number of seeds = $22.98 \text{ height (cm)} - 2380$; Meyer *et al.*, in press). Seed dispersal distance includes aggregated short distance dispersal within the canopy of the mother shrub (60% of the seeds), twice the canopy radius (35%), and random long distance dispersal in the whole grid (5%, Meyer *et al.*, in press). To account for intraspecific competition, only one seedling per cell (100 cm^2) is allowed. Toroidal edge correction is applied when seed location would be outside the grid borders, i.e. seeds re-enter the grid on the opposite side. Germination of shrub seedlings is contingent on soil moisture reaching a cell-specific cumulative soil moisture

threshold during a certain number of successive days, which were determined from local weather data. The field data based germination rate is 0.19 per year (Meyer *et al.*, in press).

SHRUB MORTALITY

The basic seedling mortality depends on the soil moisture in the cell where the seedling is located according to the experimentally derived relationship *basic seedling mortality* = $75.95 \times 10^6 \text{ }^{-\text{soil moisture}}$ (in year^{-1} , Meyer *et al.*, in press). Seedlings that survive this basic seedling mortality are then subjected to a natural browsing mortality (0.95) to account for the strong influence of herbivory on vulnerable seedlings. If a fire occurs in the simulated year, a seedling that has survived the previous mortality risks can die from fire mortality (0.65). Mortality of established shrubs occurs on the basis of negative growth, through fire (0.09; Meyer *et al.*, 2005), and droughts (0.05). A drought year is defined as a year with less than the long-term mean annual precipitation (377 mm) reduced by one standard deviation (174 mm). Drought mortality also includes mortality due to browsing because browsing of *A. mellifera* usually occurs in dry periods. During estimation of these mortalities in the field, we made sure that no resprouting tissues were present at least 1 year after death.

GRASS REPRODUCTION AND MORTALITY

The grass module is based on literature data that were adapted to our field site conditions via the mean annual precipitation. We focus here on perennials. When the reproduction soil moisture threshold is reached, a fixed density of new grass tussocks (2.35 m^{-2} ; O'Connor 1994) is distributed randomly over the whole grid. The reproduction soil moisture threshold follows the same conditions as the germination moisture threshold of shrubs. Grass seedling mortality (0.28; O'Connor 1994) applies to all new grass tussocks, whereas grass tussock mortality (0.47; O'Connor & Everson 1998) is applied to all tussocks older than 1 year.

SHRUB GROWTH

To model the growth of their first 2 years, new shrub seedlings (age 0 and 1) are deterministically initialized with eight roots with a width of one cell (representing a root width of up to 10 cm) and alternate cardinal and intermediate original growing direction. Roots are surrounded by an uptake zone with a width of two cells (corresponding to 20 cm) as a proxy for fine roots where water uptake occurs. The initial canopy diameter is determined from an empirical relationship between root length and shrub size (Meyer *et al.* 2005). For all shrubs older than 1 year, individual water uptake is calculated by distributing the absolute soil moisture (in mm) in each cell at equal parts to all shrubs and grasses whose uptake zones cover the cell.

Whether the amount of water taken up by a shrub is converted into growth increment is specified by the growth probability (0.55; Meyer *et al.*, in press). The length of the growth increment is determined following the rationale that the resources taken up (represented by moisture) have to be used for maintenance of the plant body (canopy diameter), reproduction (seed number), and above- and below-ground growth (growth increment). 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 Meyer *et al.*, in press, for a detailed account of the fitting procedure and coefficients). Negative growth increments lead to adult shrub mortality (Meyer *et al.*, in press).

Growth of individual roots proceeds by a weighted random walk where the greatest probability for the next growth step is assigned to the cell closest to the original growing direction (Meyer *et al.*, in press). Before a cell can be occupied by a root, overlap of the prospective uptake zone with other shrub uptake zones is checked. In case of overlap, the root belonging to the shrub with the smaller canopy diameter stops growing (asymmetric competition). If competition does not lead to the growth stop of the root, it occupies the chosen cell. We apply toroidal edge correction if root growth exceeds the borders of the grid. For every shrub, age is updated after the end of all growth steps.

GRASS GROWTH

Grass canopy diameter growth is deterministically set to 5 cm per year (O'Connor & Everson 1998) because no field data are available on individual growth increment length and its relation to soil moisture or tussock size (Table 1). Grass age and the uptake zone of the grass are updated corresponding to canopy growth.

SIMULATION EXPERIMENTS

We ran 100 simulations with default parameter values to obtain 100 independent time series of shrub cover with a length of 500 years each. We calculated partial Pearson's autocorrelation coefficients of shrub cover separately for each of these 100 simulations for time lags 1–200 to determine the existence and period of the successional cycles of shrub cover (see also Venables & Ripley 2003). If there is no overall trend in shrub cover, significantly positive autocorrelation indicates recurrence of a similar shrub cover with this time lag, i.e. cyclical behaviour. In general, we defined an autocorrelation as significantly positive (negative), for a certain time lag, if $\geq 95\%$ of the simulated time series showed a positive (negative) autocorrelation coefficient for that respective time lag. We allowed for small variations in the frequency of years favourable for shrub cohort build-up and breakdown by assessing a moving window of 3 years width along the time lags. Significance of positive autocorrelation was achieved if

the window at a certain time lag contained at least one positive autocorrelation coefficient in at least 95% of the simulations. In the following, a particular moving window of time lags will be referenced only by its central time lag to simplify the presentation.

To be able to compare the period of cyclical successions with shrub age at death, we determined the frequency distributions and the average, median and maximum age at death for all shrubs occurring in 10 simulations (yielding more than 900 000 individual shrubs). To further assess the hypothesis of mass recruitment and subsequent shrub cohort build-up and breakdown, we also assembled frequency distributions of shrub canopy diameters from 3 years sampled from a typical shrub cover cycle during a simulation with default parameter values. The three sample points represent a valley ('initiation phase'), an increasing phase ('build-up' phase), and a declining phase ('break-down' phase) of the cycle.

We investigated the relationship between annual precipitation, shrub cover and lagged shrub cover from 100 simulations with a simple linear model because the assumptions of normally distributed errors and homogeneous variance were not violated. We included lagged shrub cover to account for temporal autocorrelation. We included shrub cover with time lags of up to 7 years because cross-correlation between annual precipitation and shrub cover had revealed significant autocorrelation at time lags of up to 7 years. After model simplification, the minimum adequate model for the prediction of current shrub cover included only the explanatory variables shrub cover lagged by one year, mean precipitation without any time lag, and their interaction. For the presentation of precipitation and simulated shrub cover over time, shrub cover was smoothed with robust locally weighted regression with a smoother span of 10 years (LOWESS algorithm, Cleveland 1981). All statistical analyses were carried out with the software package R.

Results

Visual inspection indicates that shrub cover was cycling over time with considerable variation in the local maxima and minima without any long-term trend (Fig. 1). In most cases, the rise of shrub cover values was slow whereas the slope of decreasing shrub cover was steep (Fig. 1). Statistical evidence for cyclical changes is provided by significantly positive autocorrelation in shrub cover over time at the time lags 2 and 33 years. Negative autocorrelation was significant at 15 time lags ranging from 3 to 189 years.

Frequency distributions of shrub age at death were bimodal (Fig. 2). The first mode corresponded to high mortality of young shrubs (up to 5 years). We assumed that these young shrubs did not contribute noticeably to the overall cover of a plot because seedling canopies are very small (about 2 cm²) and very frequently overlap with their parent tree. Hence, for comparison with the

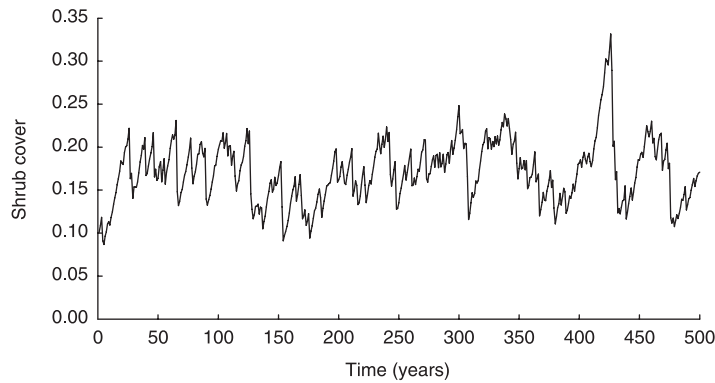


Fig. 1. An example simulation run of shrub cover dynamics over time. Shrub cover was measured as the proportion of cells in the model grid (extent: 512×512 cells representing 51.2×51.2 m in reality) covered by the canopy of one or more shrubs.

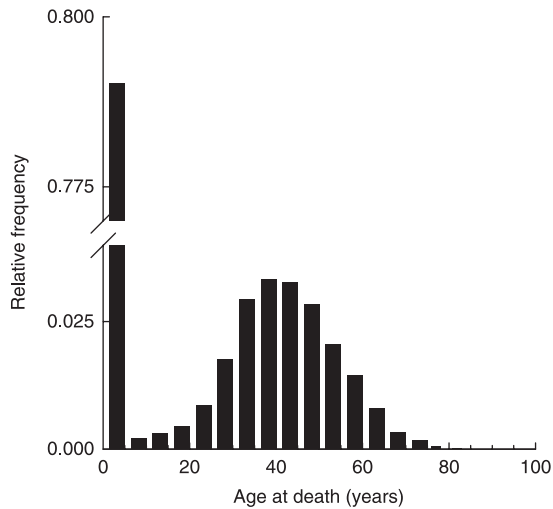


Fig. 2. Distribution of relative frequencies of age at death of all shrubs that survived their first year in 10 simulations over 500 years. The class width is 5 years.

period of cycles of shrub cover, we calculated mean, median and maximum shrub age at death of shrubs older than 5 years. The average and median shrub age at death were 40.5 and 40 years, respectively, which approximately matched the values of the second window of significantly positive time lags. Maximum age at death over all simulations and shrubs was 103 years.

With increasing shrub cover, size-frequency distributions of the simulated shrubs shifted from dominance of small shrubs to dominance of larger shrubs (Fig. 3a,b). In the falling phase of a shrub cover cycle, the relative frequency of larger shrubs decreased and smaller shrubs dominated again (Fig. 3c).

Decreasing annual precipitation coincided with decreasing shrub cover, especially during drought years (when precipitation falls below the dashed drought line in Fig. 4). The minimum adequate model for the prediction of current shrub cover by mean precipitation of the current year, shrub cover lagged by 1 year, and their

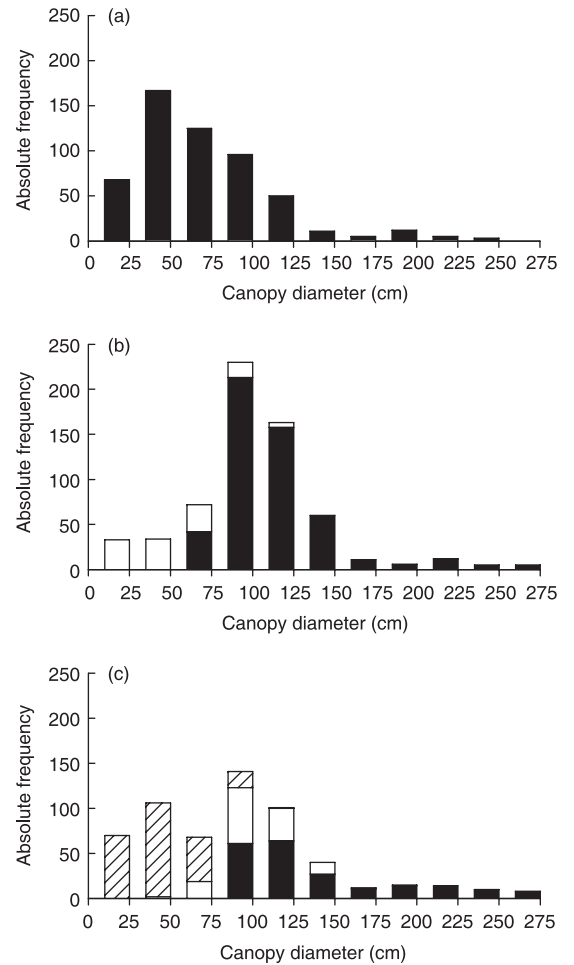


Fig. 3. Absolute frequencies of canopy diameters of all simulated shrubs in three simulation years chosen from one exemplary cycle representing the initiation phase (a), the build-up phase (b), and the break-down phase (c). In this example, 16 years have passed from (a) to (b) and from (b) to (c). Shrubs with a canopy diameter of less than 6.2 cm are seedlings in their first year and were excluded from the size-frequency analysis because they have not yet competed for soil moisture (see also smallest size class in Fig. 2). Solid bars represent the shrub cohort present in year A, empty bars all shrubs present in year B, but not in A, and hatched bars all shrubs present in year C that were not part of the previous shrub cohorts.

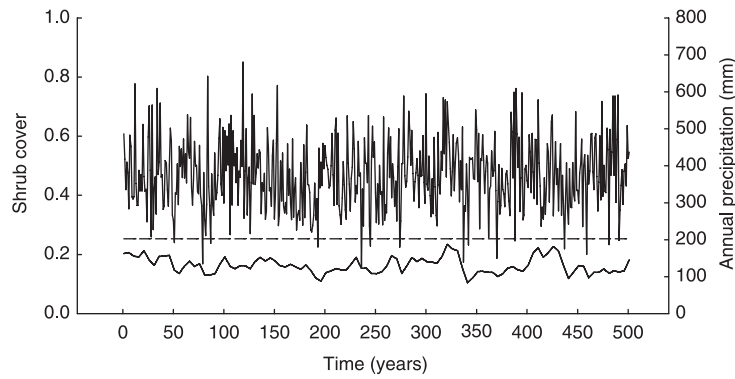


Fig. 4. Annual precipitation (top solid line) and smoothed shrub cover (bottom solid line) over time simulated with default parameter values. Shrub cover was smoothed with robust locally weighted regression with a smoother span of 10 years (LOWESS algorithm, Cleveland 1981). In SATCHMO, additional drought mortalities apply if annual precipitation falls under the drought threshold (dashed line).

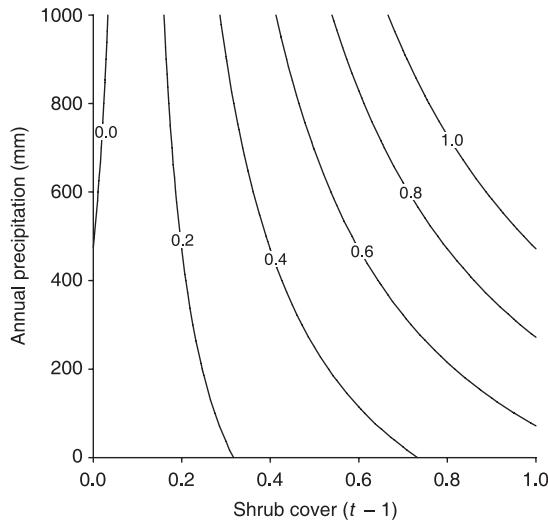


Fig. 5. Relationship between shrub cover at time step t (contour labels), annual precipitation, and shrub cover at time step $t - 1$ predicted by a linear multiple regression model based on 100 simulations over 500 years ($r^2 = 0.92$). For low shrub covers ($t - 1$), the contour lines are almost vertical, showing that annual precipitation has little influence on shrub cover in the subsequent year. In plots with high shrub cover ($t - 1$), shrub cover in the subsequent year is more dependent on annual precipitation because the contour lines are less vertical. Regression equation: $\text{Shrub cover } (t) = 0.0472 - 0.0001 \times \text{annual precipitation} + 0.4811 \times \text{shrub cover } (t - 1) + 0.0011 \times \text{annual precipitation} * \text{shrub cover } (t - 1)$. All coefficients were significant at $P < 0.001$.

interaction ($r^2 = 0.92$), showed that current cover was positively related to rainfall and to shrub cover in the previous year (Fig. 5). The greater the cover in the previous year, the steeper was the slope of the positive relationship between rainfall and cover of the current year (Fig. 5).

Discussion

In the present study, based on the SATCHMO savanna model, we provided evidence that shrub cover can vary cyclically in a semi-arid savanna with low levels of fire

and no explicit consideration of herbivory and nutrient dynamics. These model results are relevant to real-world savannas because SATCHMO has been successfully validated with field and literature data not used to construct the model (Meyer *et al.*, in press). Moreover, there was no in-built cyclicality in SATCHMO because the simulations were initiated with only one single shrub in the middle of the model grid, and from this starting point, the whole cyclic pattern built up. Even precipitation as the most probable driver of the cycles does not show the same cycles as the shrub cover cycles (compare *precipitation* and *shrub cover* in Fig. 4). Note that we define cyclical succession as a cycle between woody and grassy dominance. Hence, shrubs do not necessarily have to go extinct at any point during a cycle.

We propose the following mechanistic explanation for the simulated shrub cover cycles. (i) In years of locally overlapping favourable environmental conditions, mass germination of shrub seedlings occurred (initiation phase). This is also consistent with empirical findings from an arid savanna gradient in Namibia (Wiegand *et al.* 2005, 2006). (ii) Subsequently, the shrub cohort grew simultaneously as long as environmental conditions did not become too unfavourable (build-up phase). Competition was intensifying. If additional favourable years occurred during this phase, additional mass germination events followed by build-up of additional shrub cohorts may have contributed to increasing competitive pressure. (iii) If a year with unfavourable environmental conditions coincided with high shrub cover, the shrub cohorts catastrophically ‘broke down’ (breakdown phase). The more unfavourable the environmental conditions were, the more likely was a shrub cohort breakdown, even at lower shrub cover. In this phase, large shrubs were more likely to be affected by mortality because their resource needs were greater.

The results of the present study support this three-phase explanation of the shrub cover cycles. Overall, it is intriguing how well the mean age at death of the simulated shrubs (40 years) and the duration of the cycles (33 years) matched. Hence, a typical shrub will germinate at the beginning of a cycle and die at the end

of a cycle. Specifically, the age-at-death distributions show that the first 5 years present a serious bottleneck in the life of a shrub (Fig. 2). This is in agreement with many other studies that identify the seedling establishment stage as the most limiting stage in the life history of (savanna) woody plants (e.g. Grubb 1977; Chesson *et al.* 2004; Sankaran *et al.* 2004). It can be assumed that locally overlapping favourable conditions for reproduction and early survival will temporarily widen the bottleneck and may lead to mass recruitment of woody species (= initiation phase).

Simultaneous growth in the build-up phase is supported by the shift of the mode in the size-frequency distributions towards greater sizes in this phase (Fig. 3b). The series of size-frequency distributions assembled from simulations agrees very well with the one postulated by Wiegand *et al.* (2005) for a patch dynamic savanna. The slow increase of shrub cover compared with its steep decline during the cycles emerging from simulations provides evidence for additional shrub cohorts joining in during the build-up phase. This supports the findings of Wiegand *et al.* (2004) that not all recruitment has to be mass recruitment to allow long-term survival of trees. Rather, continuous recruitment is of major importance for maintaining and stabilizing shrub cover cycles.

The steep decline points to a simultaneous breakdown of the shrub cohorts that constitute the build-up phase. In the breakdown phase, size-frequency distributions were biased towards smaller shrubs (Fig. 3c). This indicates that larger shrubs are affected more strongly by mortality. In conclusion, we can reject the null hypothesis that cyclical succession cannot emerge from a realistic patch scale simulation model of the population dynamics of savanna woody species.

We suggest water availability as driver of the cycles, because more than 90% of the variation in shrub cover was explained by lagged shrub cover and annual precipitation. Apart from the expected dependency of shrub cover on shrub cover in the previous year, the only other important effect in the model was water availability. Individual water uptake translates into growth increment and therefore accounts for the difference in shrub size (which is related to shrub cover) between two years.

The influence of precipitation on shrub cover was stronger the greater was the shrub cover in the previous year (Fig. 5). From the size-frequency distributions, we can derive that increases in shrub cover were primarily due to growth and only secondarily due to increased densities. Thus, larger shrubs were more susceptible to changes in precipitation than small shrubs. The underlying mechanism may be increased competition for water in dense populations of large shrubs where root system overlaps are common. Overlap of shrub root systems increased during the build-up phase of shrub cycles, which, in turn, increased the overall moisture requirements so that too little precipitation was a major factor in triggering the breakdown phase. Apart

from mediating competitive exclusion, precipitation falling below the drought threshold also contributed to breakdown by inducing additional drought mortalities in established shrubs.

The importance of water availability for shrub cover is supported by the sensitivity analysis of SATCHMO (Meyer *et al.*, in press). This sensitivity analysis included 27 model parameters covering fire, moisture and population demography and yielded only eight parameters to which shrub cover was significantly sensitive. Six out of these eight sensitive parameters were related to soil moisture. Sankaran *et al.* (2005) also show that in arid and semi-arid savannas with mean annual precipitation below 650 mm, precipitation is the single most important factor determining the upper boundary of shrub cover for a given site. In other demographic bottleneck models, years with favourable rainfall also lead to shrub encroachment (i.e. the peak of a successional cycle) in arid savannas (Sankaran *et al.* 2004). This phenomenon is mostly linked to even-aged stands of woody plants (Sankaran *et al.* 2004), which is consistent with the three-phase explanation presented here.

Precipitation can be seen as an extrinsic driver of the cyclical succession whose interference is needed at several points within the cycle: favourable rainfall conditions trigger the initiation phase and particularly unfavourable rainfall conditions start the breakdown phase. However, precipitation interacts with intrinsic factors such as population demography because the more densely the population grows the greater is the intraspecific competition for moisture and the smaller is the rainfall threshold for the induction of the breakdown phase.

The importance of precipitation on the local scale as shown in this study does not support the common notion that local to landscape scale patterns are more often determined by local disturbances such as fire whereas climatic variables are primarily responsible for global scale vegetation patterns (Wu & Loucks 1995). In moist savannas, fire and herbivory may replace precipitation as the driver of successional cycles (Jeltsch *et al.* 2000; Sankaran *et al.* 2005). However, in semi-arid savannas, fire does not have a major influence on shrub cover cycles. This was also supported by the sensitivity analysis of SATCHMO, where fire frequency was not among the significant variables to which shrub cover was sensitive (Meyer *et al.*, in press).

The consequence of our results for low input management of encroached arid and semi-arid savannas is patience – a natural breakdown phase with little woody cover will follow an encroached phase. However, this is not true if competition intensity is decreased through overgrazing. Thinning by cutting individual shrubs (Smit 2004) may help as long as competition remains strong enough to ensure a breakdown under unfavourable precipitation conditions. Prescribed fires are unlikely to diminish shrub encroachment in arid savannas because shrub cover

was not sensitive to fire frequency in the model. In the light of cycle durations of about 30 years, admittedly, waiting is not a motivating management option. In a patch dynamic setting, large scale spatial rotation systems of grazing areas could overcome these problems so long as grazing intensities do not exceed the threshold to overgrazing (the definition of overgrazing itself dependent on local rangeland conditions and farming knowledge).

In conclusion, we have shown cyclical succession for a semi-arid savanna patch and have provided a three-phase mechanistic explanation of shrub cover cycles driven by precipitation and shrub demography. The next step will be to complement this temporal aspect of patch dynamics with its spatial counterpart by scaling-up to the landscape scale (cf. Schwinning & Parsons 1996a,b). The smaller the spatial or temporal scale, the greater is the variability and non-equilibrium dynamics dominate (Wu & Loucks 1995). There are two possibilities to obtain an equilibrium view, which both increase the scale of observation: averaging over time and/or space or redefining the equilibrium as some bounded range (*sensu* Wu & Loucks 1995). Here, the bounded range could be represented as maximum and minimum shrub cover over all simulations, i.e. 0.05 and 0.35, respectively. While averaging over time is relatively simple for the results shown in this study, averaging over space first necessitates the scaling-up to the landscape scale. A landscape-scale model of semi-arid savanna dynamics should consist of patches as they were set up in SATCHMO. If the spatial resolution corresponds to the grid size in SATCHMO (about 50 m), the temporal resolution should correspond to the significant time lag in the temporal autocorrelation analysis, i.e. about 30 years. This temporal resolution corresponds to the 'break points' in scale-dependent spatial pattern analyses that aim at identifying domains of scale (e.g. Milne 1988; Wiens & Milne 1989; Wiens 1989). Once the landscape-scale model is built, the results from SATCHMO can be used partly for parameterization and partly for validation of the large-scale model (see also Ludwig & Walters 1985). Finally, we will be able to investigate the conditions that constrain the applicability of the patch dynamics mechanism for the explanation of both spatial and temporal savanna dynamics. However, with the establishment of the temporal component of patch dynamics for arid savannas through the results from SATCHMO, a major step towards this end is made.

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