Linking a population model with an ecosystem model:
Assessing the impact of land use and climate change on savanna shrub cover dynamics

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ABSTRACT

In semiarid savannas of Southern Africa current land use practices and climate change may lead to substantial changes of vegetation structure in the near future, however uncertainty remains about the potential consequences and the magnitude of change. In this paper we study the impact of climate change, cattle grazing, and wood cutting on shrub cover dynamics in savannas of the southern Kalahari. We use an established savanna ecosystem model to simulate landscape dynamics in terms of rainfall, fire and distribution of the dominant tree Acacia erioloba. We then incorporate these data into a spatial population model of the common, fleshy-fruited shrub Grewia flava and investigate shrub cover dynamics for a period of 100 years. Depending on the intensity of commercial wood cutting practices tree removal of A. erioloba led to a strong decline of the G. flava population, as shrub recruitment is concentrated in tree sub-canopies due to bird-mediated seed dispersal. Under climate change shrub cover slightly decreased with decreasing precipitation and was unchanged with increase in precipitation variability. Contrarily, grazing by cattle strongly increased shrub cover and facilitated shrub encroachment because of cattle-induced distribution of G. flava seeds into the matrix vegetation. Knowledge of the latter process is particularly important because shrub invasion is a major concern for conservation and savanna rangeland management as a result of its adverse effects on livestock carrying capacity and biodiversity.

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which in turn affects mortality and establishment of trees and shrubs.

Within recent decades human-induced impacts such as grazing by livestock, harvest of A. erioloba wood, and climate change have resulted in substantial changes of savanna vegetation structure. However, large uncertainty remains how these changes develop in the near future. For example, wood clearing practices were initially established in order to restore grazing potential for savanna rangelands. At this, A. erioloba wood was rather a by-product and used for domestic purposes only. However, recently the commercial harvest for charcoal and firewood has become increasingly relevant (Milton et al., 2003), where, as opposite to the first practice, mostly large, solitary trees are removed. This change in vegetation structure may imply a negative impact on biodiversity as large trees are crucial for many plant and animal species in Southern African savannas (Tews et al., 2004a). Secondly, climate change will most likely lead to shifts in the amount as well as in the variability of prevalent precipitation patterns (Mason and Joubert, 1997). This may imply major consequences for woody plants, as water availability is the most important environmental parameter governing crucial life history processes (Schlos and Archer, 1997). Thirdly, grazing by livestock has been proposed as a major threat for the typical vegetation structure of southern Kalahari savannas. Overgrazing by livestock reduces grass biomass and increases water availability for woody plants, resulting in shrub encroachment (see e.g. Jeltsch et al., 1997). For both rangeland and conservation management shrub encroachment is of major concern, as it reduces livestock carrying capacity and regional biodiversity due to the homogenization of savanna vegetation structure (Milton and Dean, 1995; Meuk et al., 2002).

In this study we investigate how shrub cover dynamics in the southern Kalahari may respond to three potential scenarios for the coming decades: (1) wood cutting, (2) climate change, and (3) overgrazing. Here, a process-based understanding of future development for these scenarios needs a dynamic ecosystem approach. Complex interactions of trees, shrubs and grasses in this ecological system prohibit isolated approaches looking at dynamics of single life forms. Therefore, we apply an existing savanna model (see Jeltsch et al., 1996, 1997, 1998, 1999). It is subdivided into a grid comprising 10,000 cells each 25 m² in area. Ecological processes take place within individual cells and with a temporal resolution of 1 year. In the savanna model, those ecological processes are considered that are crucial to the dominant life forms of trees, shrubs and grasses, i.e. rainfall and moisture availability, grass fires, and grazing intensity (e.g., grazing removal). The population structure, density and distribution of A. erioloba trees are mainly determined by the establishment of seedlings and the growth and mortality of trees (Jeltsch et al., 1996). Tree establishment is influenced by the annual soil moisture status and small scale heterogeneities which function as establishment hotspots. Tree growth is mainly driven by soil moisture, tree mortality mainly by fire. The status of available soil moisture is calculated on the basis of rainfall data produced by a rainfall simulator (Zucchini et al., 1992; Jeltsch et al., 1999). Based on these rainfall data, the moisture status generated by the savanna model was classified as either ‘poor’, ‘moderate’ or ‘good’ and subsequently implemented into SGM. Inter-annual distribution of these types approximated 15% for ‘poor’, 72% for ‘moderate’ and 13% for ‘good’ years. Similar classifications have been applied in other studies, e.g. in a spatial simulation model of Acacia nodosa in the Negev Desert (Wiegand et al., 1999). As G. flava shrubs are mostly confined to tree microsites
and tree microsite density strongly determines *G. flava* population size, we used the same initial tree density of 30 trees ha$^{-1}$ for each environmental scenario.

### 2.2. SGM model description

Based on empirical data from the vicinity of Kimberley (see Schurr, 2001), the population model SGM iteratively simulated *G. flava* shrub population dynamics in annual time steps for a period of 100 years. An initial population of 150 shrubs ha$^{-1}$ was distributed on the savanna model grid with 90% of the initial population distributed in tree cells. In each time step, SGM simulated important life history stages, and key ecological processes of the *G. flava* population dynamics. Model validation was based on aerial photographic analysis of long-term changes in Owenia cover for a study plot in the vicinity of Kimberley (see Tews et al., 2004b). For a better understanding of the internal processes we will briefly describe the SGM modules, growth (a), fruit production (b), seed dispersal (c), emergence (d), mortality (e) and density regulation (f). A detailed description of SGM is published by Tews et al. (2004b).

Further studies conducted with SGM and additional information on the simulation model is published elsewhere (Tews and Jeltsch, 2004; Tews et al., 2004a).

#### 2.2.1 Growth

Annual growth, i.e. increase in canopy cover of each individual, was modelled by means of four size classes: seedlings, small, medium-sized and large shrubs. Based on empirical data, each size class was assigned a mean canopy cover (i.e. 0.4 m² for small shrubs, 3.7 m² for medium-sized shrubs and 12.5 m² for large shrubs). An individual may reach the next size class with a certain probability after it has gained a certain amount of growth years ('growth years' are accumulated in years with 'moderate' or 'good' soil moisture status; no growth occurs in 'poor' years). For example, when a small shrub has accumulated five growth years it may attain the next size class with a probability of 20%. For medium-sized shrubs this refers to 20 years and 10% transition probability.

#### 2.2.2 Fruit production

Fruit production was based on mean crop size of *G. flava* size classes. The total amount of fruits may vary depending on the annual moisture type and the individual size class. In general, mean crop size of large shrubs was much higher than that of small- and medium-sized plants resulting in an L-shaped distribution of the reproductive output (Schurr, 2001).

#### 2.2.3 Seed dispersal

Dispersal was represented by two parameters: probability of a fruit (each fruit contains two seeds) removed from a shrub and deposited in a randomly chosen matrix cell, $P_{\text{matrix}}$, and $P_{\text{micro}}$, the same probability for a tree cell. The standard value of $P_{\text{matrix}}$ was 0.01 and represented occasional dispersal through, e.g. small mammals (for modified $P_{\text{matrix}}$ values under cattle grazing see section 'environmental scenarios'). $P_{\text{micro}}$ represents bird-mediated dispersal of fruits and was uniform randomly distributed between 1% and 5% in years with 'good' moisture status, 2.5% and 7.5% in 'moderate' years and 5% and 10% in 'poor' years. Based on estimates from empirical data, this was a reasonable approach as the proportion of fruits removed is most likely to be higher in years of lower fruit set.

#### 2.2.4 Emergence

Emergence of *G. flava* seeds was similar for both cell types, however it varied inter-annually between 1% and 2% for the 'moderate' and 2% and 4% for the 'good' moisture status (no emergence occurred in years with 'poor' moisture status). After emergence seeds automatically transform to the size class 'seedlings'. In the following year those seedlings that have survived potential fire and drought mortality events transform to the size class 'small shrubs'.

#### 2.2.5 Mortality

Mortality was distinguished between fire and drought mortality. Drought mortality for adult individuals was restricted to 'poor' moisture years with a probability of 3% (see Tews et al., 2004b). For individuals in the seedling stage drought mortality was higher: 50% and 90% in 'average' and 'poor' years, respectively. The occurrence of a fire was generated by the savanna model with intervals ranging from 4 to 7 years similar to observed fire frequencies from comparable savanna ecosystems (Van Wilgen et al., 2000). Fire mortality is generally low, due to *G. flava*’s high resprouting capability after fire (Sturpe, 1980; Gandar, 1982). However, the impact of fire varied spatially and demographically. For example, if a fire occurred a seedling in the matrix vegetation had a 95% chance of being killed, compared with 4% for adult shrubs which largely resprouted in the following year (see Tews et al., 2004b). For tree cells, fire mortality probability was 0% for adults and 75% for seedlings. These model assumptions are realistic, as grass fuel accumulation and fire severity beneath trees is less than in tree inter-spaces (see e.g. Jeltsch et al., 1996). Furthermore, if a fire occurred, canopy cover for each shrub individual in the following year was reduced by 50% for individuals in tree cells and uniform randomly distributed between 50% and 100% for individuals in matrix cells.

#### 2.2.6 Density regulation

For the carrying capacity in each cell, we used a simple causal approach that considered cell-based shrub cover. We estimated a carrying capacity $C$ of 75%, i.e. 75% of the actual cell size (see also results for 50% and 100% carrying capacity, Fig. 4 and results). If shrub cover exceeded $C$, individuals in the cell died. This was simulated annually by removing the smallest individuals first, i.e. in descending order of size class, until shrub cover $<C$.

#### 2.3. Linking the savanna and SGM model

In order to create a dynamic environment for the population dynamics of *G. flava* we used the parameters annual moisture type, fire, and the decadal cell coordinates of tree cells of the savanna model as model input for SGM. Prior to each time step of SGM, the annual moisture and fire status were updated, based on the output of the savanna model. Every 10 years we then updated the spatial cell coordinates of *A. erioloba* trees. The spatio-temporal dynamics of trees were governed by internal processes of the savanna model. For example, high fire fre-
generally the smaller (and probably less economically viable) for 16% of ranches that produced firewood for sale. These were cates that Camelthorn wood removal averaged 82 kg/ha/year rate grazing and overgrazing. Therefore, we modified key 2.4.3. Cattle grazing deereased annual precipitation of 10% (IPCC, 2001), and (b) an scenarios lead to a decrease in potential recruitment sites for 2.4. Environmental scenarios. 2.4.1. Wood cutting. A recent unpublished survey of 100 ranches (Table 1) indicates that Camelthorn wood removal averaged 82 kg/ha/year for 16% of ranches that produced firewood for sale. These were generally the smaller (and probably less economically viable) ranches. On 71% of ranches a small amount of Camelthorn wood (0.33 kg/ha/year) was used by the farmers and their workers for heating and cooking; 13% of ranchers made no use of the wood. Camelthorn wood was utilized only when acci- dently killed in chemical control operations targeting other woody plant encroachers (Milton et al., 2001). Based on these data and mean values for wood density and volume of Acasia trees, we tested for moderate and severe intensities of firewood harvest rates. In the savanna model this was equivalent to an annual tree removal rate of 0.01 trees/ha for moderate and 0.1 trees/ha for severe wood cutting, respectively. Both scenarios lead to a decrease in potential recruitment sites for G. flava. 2.4.2. Climate change. In terms of climate change, we applied two different scenar- ios that are currently proposed for the coming decades: (a) a decreased annual precipitation of 10% (IPCC, 2001), and (b) an increased inter-annual variation of precipitation by 10%, i.e. a higher frequency and magnitude of extreme rainfall events (e.g. Kast and Brown, 1992; Gordon et al., 1992; Mason and Joubert, 1997). For a decreased annual precipitation projection we increased the probability of moisture type 'poor' by 10% at the cost of 'average' years. For an increase in the inter-annual variation in precipitation we increased the probability of mois- ture type 'good' and 'poor' by 10% at the cost of 'average' years. 2.4.3. Cattle grazing. Land use in the form of cattle grazing was classified into mod- erate grazing and overgrazing. Therefore, we modified key parameters in both the savanna model and SGM (note, for the climate change and wood cutting scenario we only mod- ified savanna model parameters, i.e. rain and tree mortality). For moderate grazing we implemented an annual removal of 20% grass cover in the savanna model (for details of the grass sub-module see Jeltsch et al., 1996). Additionally, we increased P\text{matrix}, i.e. the probability of seed dispersal into the matrix vegetation, from 0.01% in the SGM standard parameter set to 1%. For the overgrazing scenario we increased annual grass removal to 40% and P\text{matrix} to 10%. Based on empirical data (Schurr, 2001) and simulation results (Tews et al., 2004b), we assumed that the modified values of P\text{matrix} are realistic. For example, for a cattle pasture with a moderate stocking rate of 18 ha per livestock unit the annual proportion of interspace m² reached by G. flava seeds (via cattle dung deposition) was 11.1% compared to 0.2% in the absence of cattle (see Schurr, 2001). With roughly 38 000 fruits/ha produced in a year with a ‘good’ soil moisture status for this area (see Schurr, 2001), a P\text{matrix} value of 1% would result in a proportion of 7.6% of interspace m² reached by G. flava seeds. 3. Results. Based on the standard parameter set of the savanna model and the population model SGM, we assessed the impact of three realistic land use and climate change scenarios on shrub cover dynamics of G. flava in the southern Kalahari. Besides shrub cover, we used shrub density and cell cover as model output. Cell cover, i.e. the proportion of grid cells occupied by at least one individual, gives a good estimate of recruit- ment potential because once a shrub has left the seedling stage mortality rates are low. The previously calibrated stan- dard parameter set of SGM (see Tews and Jeltsch, 2004, Tews et al., 2004a, 2004b, 2004c) generated stable population dynamics for a period of 100 years, i.e. average recruitment success was more or less equivalent to the number of individuals killed in fires or droughts (see Fig. 1). Significant recruitment events mostly occurred in years with a ‘good’ moisture status without fire (see for example year 81 in Fig. 1). After a fire shrub cover strongly decreased, however, due to the excellent resprouting capability of G. flava, it reached the pre-fire value in the fol- lowing year. 3.1. Wood cutting. We tested for two intensities of wood cutting: moderate (0.01 trees/ha) and severe (0.1 trees/ha) removal quantities. For the latter scenarios, average tree density after 100 years resulted in 85% and 12% of the initial tree density, respec-
Fig. 1 – SGM and savanna model output for the default parameter set with stable population dynamics for a 100 year time period. Tree density, moisture status and fire are generated by the savanna ecosystem model. Model output of SGM is given as shrub density, cell cover (solid line) and shrub cover (dashed line) in the lower graph. Note, that major recruitment events of *G. flava* take place in ‘good’ rainfall years without fire. In post-fire years, shrub cover decreases abruptly, however *G. flava* resprouts quickly in the year after.

Consequently, the reduction in potential recruitment sites for *G. flava* led to a strong population decline in the severe wood cutting scenario (Fig. 2). Particularly, cell cover, i.e. the proportion of cells occupied by *G. flava* individuals, strongly decreased from 10% in year 1 to 3.5% in year 100 (Fig. 3). Even though the total amount of shrub cover after 100 years was slightly lower than the initial value, it was less affected than cell cover. Whereas the severe wood cutting scenario showed a strongly negative impact on the *G. flava* population (see also Fig. 2), the moderate scenario did not (Fig. 3). Here, cell cover decreases from 13.6% to 12%, while shrub cover was not affected at all (see Fig. 3).

### 3.2. Climate change

In terms of climate change we tested for a 10% increase in the probability of ‘poor’ moisture years (equivalent to a 10% decrease in precipitation) and a 10% increase in the probability of ‘poor’ and ‘good’ years (equivalent to a 10% increase in the inter-annual variation in precipitation). Even though tree densities were more or less constant over the simulation period, population dynamics of *G. flava* showed a slightly negative response under decreased precipitation (see Fig. 3). For precipitation decrease we found a mean cell cover decline from 15.1% to 12.9% and decrease in shrub cover from 3.9% to 3.4% over the course of 100 years (see Fig. 3). However, the latter result is obscured as shrub cover increased to 5.5% in year 25 and then decreased again. This is most likely due to the fact that, even though recruitment was completely lacking (see decrease in cell cover), individuals grew and reached the next size class unless they were not killed by fire or drought. For an increase in extreme rainfall years we found no impact on *G. flava* canopy cover and recruitment dynamics: shrub and cell cover values after 100 years were similar to the starting conditions (Fig. 3).

### 3.3. Cattle grazing

The cattle grazing scenarios showed a completely different result. While wood cutting and climate change had none or a negative impact on shrub cover dynamics we found a positive effect for two different intensities of cattle grazing. For the latter two scenarios we modified the standard parameter set of the savanna model by increasing the annual rate of grass removal and increasing cattle-induced matrix dispersal of *G. flava* seeds in the SGM model. The first modification benefits trees in two ways. Firstly, the reduced grass fuel reduces the fire probability and thus the tree and shrub
Fig. 2 – Typical simulation runs of spatial distributions of trees and shrubs for three environmental scenarios (location of trees and shrubs is given in black and grey, respectively). The savanna model generates fire frequencies, precipitation pattern and the spatial distribution of A. erioloba trees which are subsequently incorporated into the shrub population model. Results of three scenarios after 100 years are shown: severe wood cutting, climate change (decrease in mean precipitation by 10%) and moderate grazing by cattle. Wood cutting led to a decrease in tree and shrub population, climate change mainly decreased the shrub population whereas overgrazing by cattle resulted in a strong increase in shrub cover.

Seedling mortality. Average fire frequency was 6.3 years for overgrazing, 4.9 years for the moderate grazing scenario and 4.2 for the standard version of the model and covered the range known for similar savanna types (see Jeltsch et al., 1996, 1998; Van Wilgen et al., 2000). Secondly, grass competition for soil water is reduced thereby influencing seedling conditions (see Jeltsch et al., 1998). Compared to the initial tree density, average tree density after 100 years increased with moderate grazing and overgrazing by 12% and 18.4%, respectively. The second modification concerns increase in matrix seed dispersal probability due to cattle (1% and 10% for the moderate grazing and overgrazing scenario, respectively), which facilitated the establishment of seedlings in the open grassland vegetation.

Cattle grazing resulted in a severe increase in shrub and cell cover within 100 years (Fig. 3). For example, the overgrazing scenario led to an increase to 60% shrub cover after 100 years. The proportion of cells occupied by shrubs was even more affected: cell cover reached nearly 100% after 50 years.
Fig. 3 – Results of the simulation experiments for six environmental scenarios. Average shrub cover (dashed line) and cell cover (solid line) are means of 50 simulation runs with error bars showing standard deviations.

Fig. 4 – Mean shrub cover after 100 years plotted against an increase in the probability of matrix seed dispersal for 20% and 40% of annual grass removal, respectively. The solid line indicates a shrub carrying capacity $C$ of 100% (i.e., maximum shrub cover in each cell equals cell size), $C$ values of 75% and 50% are represented by long and short dashed lines, respectively. Each parameter combination was replicated by 50 simulation runs.
of overgrazing (Fig. 3). This serious impact of cattle grazing was less severe under moderate intensities. Here, average shrub cover reached 12.6% after 100 time steps. We hypothesized that the intensity of shrub encroachment was strongly associated with \( P_{\text{m}} \) and the character of the cell-based carrying capacity \( C \). Therefore, we varied both parameters for both the moderate grazing and overgrazing savanna model output (equivalent to 20% and 40% annual grass removal, respectively) and compared average shrub cover after a simulation period of 100 years (see Fig. 4). We found that shrub encroachment severity was primarily governed by \( P_{\text{m}} \) and secondary by \( C \). However, there was no linear relationship between an increase of \( P_{\text{m}} \) and the resulting shrub cover, as indicated by a threshold between 1% and 5% with a shrub cover increase from 12.6% to 59.7% for the standard \( C \) value of 75%. Variation in the shrub carrying capacity \( C \) was primarily effective above a \( P_{\text{m}} \) value of 5%. For a 10% probability of removal into the matrix (similar to the standard parameter set for overgrazing) mean shrub cover rates ranged between 53.6% for \( C = 50\% \), 61.7% for \( C = 75\% \) and 84.6% for \( C = 100\% \). Whereas matrix seed dispersal was the dominant factor governing the severity of shrub encroachment, the annual rate of grass removal showed only a weak impact (compare both charts in Fig. 4).

4. Discussion

The study presented here is the first approach linking potential future impacts of climate change and land use on savanna rangelands with dynamic ecosystem and population models. Based on our simulation results we have demonstrated that land use practices and potential changes in precipitation patterns may affect population dynamics and shrub cover dynamics of \( G. \) flava. Changes in woody plant/grass ratios are a key factor in the southern Kalahari savanna ecosystems, as they determine the carrying capacity for livestock farming (e.g. Jeltsch et al., 1997; Hudak, 1999) and biodiversity. Generally, it is a difficult task to evaluate possible impacts of land use and climate change for two reasons: firstly, empirical studies usually cover only a few years, secondly different woody species are involved in the shrub encroachment process with population dynamics that do not respond independently from each other. However, the dynamic modelling approach used in our study tried to bridge these gaps by using a shrub species that (1) dominates the southern Kalahari shrub vegetation, (2) has been studied empirically and (3) by applying a well-established ecosystem model that generates realistic landscape conditions for the population dynamics of \( G. \) flava. In the following we will discuss the results of the environmental scenarios that have been suggested for the coming decades.

4.1. Effect of wood cutting

In some areas of the southern Kalahari commercial harvest of firewood and charcoal has resulted in the disappearance of the typical ‘parkland’ aspect provided by \( A. \) erioloba (Anderson and Anderson, 2001; Milton et al., 2001). This change in vegetation structure may imply a negative impact on biodiversity because large trees are crucial for many plant and animal species in South African savannas (Tews et al., 2004c). Due to bird-mediated seed dispersal \( G. \) flava is a typical example of a plant that highly depends on trees as a recruitment site. The simulation results showed that if tree densities were strongly reduced, \( G. \) flava population decline followed immediately, i.e. matrix dispersal under natural conditions may be too low to allow long-term persistence (see Fig. 3). Where tree microsites were strongly reduced, \( G. \) flava seeds were mostly dispersed into sub-canopies of other parent plants, i.e. no additional rejuvenation sites could be colonized. Moreover, if a tree was removed adult shrubs experienced higher fire mortality rates in the open in contrast to tree sub-canopy sites with a scarce grass layer.

This mechanism also accounts for other plants and animals in the southern Kalahari as \( A. \) erioloba trees function as a crucial structural component of the savanna vegetation (Tews et al., 2004c). For example, tree microsites are often the only recruitment sites for other fleshy-fruited plants (Dean et al., 1999). \( A. \) erioloba trees also provide shade for ungulates resting in the sub-canopy of adult trees (Milton and Dean, 1995), nests for arboreal rodents (Eccard and Meyer, 2001) or perches and nesting sites for raptors (MacLean, 1970) and other birds. Additionally, we believe that if \( G. \) flava densities locally decrease this would imply cascade effects for other species that in turn depend on e.g. its fruits as food source.

4.2. Effect of climate change

In our study we applied two major climate change scenarios: a 10% decrease in annual precipitation and a 10% increase in inter-annual variation of precipitation. For the latter scenario we found no significant impact on \( G. \) flava population dynamics within the SCM time frame (Fig. 3). Thus, we propose that the predicted increase in inter-annual variability on timescales of decades will have a low impact upon shrub cover dynamics of \( G. \) flava. However, this may differ for populations on rangelands with high cattle grazing; an earlier model version showed that increase in rainfall variability can increase shrub encroachment if additional seed dispersal by cattle into the matrix is considered (Tews et al., 2004b).

For a 10% increase in the probability of occurrence of the ‘poor’ moisture type, equivalent to a precipitation decrease, we found a slight reduction in \( G. \) flava shrub cover (Fig. 3). Although the negative impact was relatively weak compared to the other scenarios, the population response in terms of a mere increase of 1.5% in the probability of ‘poor’ years should be noteworthy, since \( G. \) flava is believed to be highly adapted to this dry environment (Schurr, 2001) (see also low drought mortality probability of 4%). However, an increase in mortality events in drought years mostly affects \( G. \) flava in the critical seedling stage, i.e. even though large, deep-rooted shrubs may persist, the population slowly declines as a result of a demographic bottleneck in the seedling stage. The climate change scenarios, as applied in this study, exemplify only one approach to study the effects of future modifications in rainfall. Further investigations are necessary, since climate change related rainfall patterns may differ within the southern Kalahari and, moreover, new climatological predictions may emerge in the near future.
4.3. Effect of cattle grazing

Cattle grazing strongly increased shrub cover (see Fig. 3). This general process has also been observed in other semi-arid grasslands (Brown and Archer, 1998; Krupa et al., 1998). For example, Hudak and Wessman (2001) reported a 30% increase in woody plant cover between 1955 and 1996 for the Madikwe Game Reserve, South Africa as a result of cattle grazing. The study of Roques et al. (2001) revealed that shrub cover on communal land with subsistence cattle and goat farming increased from 3% to over 40% within 50 years. The latter authors suggested that high grazing pressure was a key determinant of shrub encroachment through the removal of grass fuel and the concomitant reduction in fire frequency.

Compared to empirical studies on G. flava, our simulation results can be considered realistic (see e.g. Skarpe, 1990). For example, for an overgrazed area in the eastern Kalahari sandveld with a mean stocking rate of 11 ha/LSU since 1980, Mphinyane (2001) reported 340 plants per hectare at the actual borehole and 207 individuals at 600 m distance. Less than 50 plants/ha occurred at a distance of 2.4 km. With a mean canopy cover of 3.7%, for medium-sized individuals (see Tews et al., 2004b) we can calculate 12.6%, 7.6% and 1.8% shrub cover for the sample points after 20 years, respectively (for comparison see also methods, Section 2.4.3). Due to the fact that cattle diets show significant browse fractions with an annual mean of 20% (Fritz et al., 1996), it is not surprising that cattle distribute seeds via their dung. Moreover, there is empirical evidence that the proportion of browse in cattle diet is highest during the late wet season – the time when fruits of G. flava are ripe and available for dispersal (Molesle, 1998).

Generally, the observed pattern of shrub encroachment was facilitated by two major processes. Firstly, fire frequency in the savanna model was reduced via an increase in the annual rate of grass removal which in turn increased tree density and reduced G. flava seedling mortality. Secondly, since seedling distribution is usually restricted to tree microsites, cattle enhanced dispersal of G. flava seeds into the matrix vegetation. Here, we found that modifications of the \( P_{\text{seeds}} \) value strongly varied the rate of shrub encroachment (Fig. 4). For an increase in \( P_{\text{seeds}} \) we observed a threshold behavior between 1% and 5% probability of matrix dispersal for both applied rates of grass removal. Within this range, a saturation effect seemed to occur: i.e. the amount of dispersed seeds was large enough to invade all grid cells within 100 years and reach maximum shrub cover as defined by the carrying capacity \( C \). Surprisingly, the intensity of shrub encroachment was only slightly different between the 20% and 40% annual grass removal scenarios (Fig. 4). An increase from 4.4 to 6.3 years fire return interval therefore seemed to provide to significant gain in terms of juvenile establishment. Most likely, fire critically effects establishment only if return intervals are too short to allow for recruitment beyond the critical seedling stage. Moreover, once shrub individuals left the demographic bottleneck at the seedling stage fire mortality is low, and thus grass consumption by cattle affecting the frequency of fires did not alter the intensity of shrub encroachment effectively. Grass removal by cattle also increased the water availability, however, Grewia establishment in the matrix is strongly limited by dispersal and thus a slight increase in available soil moisture and reduction in drought frequency did not show large effects.

Additionally, two critical aspects of the probability of matrix seed dispersal and the carrying capacity \( C \) should be discussed here. In the course of time shrub cover and population density increase, i.e. the total amount of available fruits increases, too. Thus, a constant probability of matrix dispersal resulted in an increase in the total number of dispersed seeds proportional to the number of available seeds per year. Assuming a constant stocking rate for the simulation period the question emerges whether the number of distributed seeds may increase (proportional to fruit crop size), even though stocking rates are constant. The latter may apply if cattle increase their proportional browsing diet when grass biomass becomes sparse and shrubs cover a larger proportion of the rangeland. Besides these aspects, there are uncertainties in terms of the SGM model assumption for the carrying capacity \( C \). From an ecological point of view, the carrying capacity represents competition on soil moisture between G. flava, A. erioloba and other neighboring plants. Yet, it is important to denote that our definition of these classes of density regulation are artificial and may be subject to spatial and temporal variability.

4.4. Conclusions and outlook

With the results presented here, we want to emphasize that even if one should derive general trends of shrub cover dynamics, rather than absolute predictions for the coming decades. Our novel approach linking an ecosystem model with a population model showed that population dynamics of G. flava are balanced by the availability of recruitment sites, rainfall patterns, fire frequencies, and release mechanisms of directed seed dispersal. All contributing factors usually co-occur in a dynamic interplay. In terms of the predicted environmental scenarios for the southern Kalahari this means that climate change will most likely co-occur with local wood cutting and cattle grazing. Eventually, this may lead to dynamics where increase in shrub cover (e.g. through overgrazing) is in balance with mechanisms that lead to decrease in shrub cover (e.g. through precipitation decrease) and thus result in a more or less resilient state of the savanna system. In other words, ‘natural’ savannas are characterized by a suite of mechanisms which make them persist despite of natural changes in rainfall, herbivory and/or fire and therefore these mechanisms may be able to buffer – to a certain degree – changes caused by land use and global change. However, we should be aware that the intensity of current land use practices in the southern Kalahari is beyond this threshold and land use forms such as fire wood removal and cattle farming have to change from purely commercial to sustainable economic principles in order to facilitate ecosystem resilience. Further research is needed in order to assess the overall consequences of this dynamic inter-play of land use, climate change and savanna ecosystem dynamics. As shown in this study, we believe that coupled, spatial simulation models of population and ecosystem dynamics may provide a powerful tool to achieve this goal.
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