

Simulation models for semi-arid rangelands of Southern Africa

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Abstract

In semi-arid regions, the effects of grazing or sparing management on natural communities of long-lived plants generally take decades to become evident. Event driven dynamic behaviour, unpredictable and low rainfall and complicated interactions between species make it difficult to gather sufficient understanding of vegetation dynamics to be able to develop guidelines for sustainable management. Simulation models that consider the essential processes that determine vegetation dynamics offer scope for quantitatively exploring long-term vegetation dynamics of arid and semi-arid rangelands. In this paper we review three models that were aimed to provide an understanding of the vegetation dynamics and management of different typical vegetation types in South Africa; including the Karoo shrubland, the shrub-grassland of the southern Kalahari, and pure semi-arid grasslands.

Additional index words: semi-arid grasslands, Kalahari, Karoo, shrubland, vegetation dynamics

Introduction

Degradation and desertification is one of the most urgent threats to arid and semi-arid plant communities where rainfall is low and unpredictable. On all continents, utilisation by domestic livestock has resulted in changes in plant species composition that reduce carrying capacity for these animals (Dean & Macdonald 1994; Friedel 1991; Friedel *et al.* 1990; Schlesinger *et al.* 1990). For example, an increase of unpalatable species, or shrub encroachment is reducing the carrying capacity of the Karoo shrublands, the Kalahari and other semi-arid grasslands in Southern Africa. Because such vegetation changes are relatively slow processes, and because animals are stocked at low densities in these areas, field experiments for determining stocking rates that avoid degradation under various rainfall scenarios are almost impossible to replicate. On the other hand, degradation may be rapid, but recovery is slow because plant growth is rain-limited and denudation reduces rainfall effectiveness (Milton *et al.* 1994). To avoid degradation and desertification it will be necessary to develop management strategies that sustain production and landuse options. However, because of the inherent complexity of the dynamic behaviour of such plant communities and because of the mismatch between time scales for observation and typical scales of vegetation change (Scholes 1990, Wiegand *et al.* 1996) it is difficult to assess the long-term effects of management.

In practice, rangeland management is necessarily based on an intuitive model (Westoby *et al.* 1989). Each farmer or land manager has a clear idea (i.e. a model) about the functioning of *his* system. This model is a philosophic system of concepts, generalisations or assumptions rather than a qualitative model and is used to predict how the system reacts in response to climate, disturbance, and management. The understanding that a farmer or manager has of the ecosystem, is the basis for defining the management strategy. Clearly, this understanding depends on the current knowledge and on the experience of the particular farmer or manager,

and on the time they could observe the system – a time span which usually does not exceed 20 or 30 years. Consequently, not having long-term experience in face of rare and unpredictable driving events that may occur only a few times in a century, may lead to an inappropriate conceptual model which would facilitate non-sustainable management decisions. Walker (1993) stated that "undesirable changes in rangelands have mostly been brought about by applying the wrong ecological model(s) of rangeland dynamics". Therefore, an understanding of the long-term dynamics of arid or semi-arid plant communities is indispensable for developing strategies for sustainable management (Wilson 1984).

Simulation models

Computer simulation models are able to link current knowledge about the processes that drive vegetation dynamics and facilitate a systematic investigation of the interactions between all relevant factors and their logical consequences. Also, simulation modelling is a tool found powerful for conducting controlled experimental manipulation for a large number of environmental conditions and over long time spans. Different modelling approaches have recently been used to investigate vegetation dynamics in semi-arid systems (e.g., Sharpe *et al.* 1985; Archer 1989; Coffin & Lauenroth 1990; Lauenroth *et al.* 1993). A class of spatially explicit models, the grid-based simulation models, has proved valuable for dealing with problems on large temporal scales, and where complex interactions depend on coincidences in time and space (Thiéry 1995; Wiegand *et al.* 1995; Jeltsch *et al.* 1996, 1997a, b). Grid-based models, characteristically subdivide a modelled area by a grid of spatial subunits, so-called "cells". Each cell is characterised by its location and by one or more discrete ecological states. These may change in the course of time due to the influence of neighbouring cells, the previous state of the cell itself and to external factors as climate, disturbance or management actions. The size of these spatial subunits is determined by the initial question to be addressed by the model. It is characteristically based on typical biological scales of the modelled system, e.g., the size of individual plants, characteristic distances for seed dispersal or typical types of plant interactions (Jeltsch & Wissel 1994; Wiegand *et al.* 1995; Jeltsch *et al.* 1996). In a recent grid-based model on vegetation dynamics of a Karoo shrubland, for example, the grid cell size is oriented towards individual shrubs because the modelled area is characterised by isolated shrubs or by small, mixed-species clumps of shrubs interspersed with bare ground (Wiegand *et al.* 1995). However, if plant life forms of distinctively different sizes are to be modelled (e.g. a mixture of grass and shrubs or trees), or if individuals are difficult to recognise (e.g. in grassland) it is often necessary to base the model on plant assemblages instead of individuals (Jeltsch *et al.* 1996; Jeltsch *et al.* 1997a, b; Weber & Jeltsch 1997; Stephan *et al.* 1997).

Grid-based models focus on the crucial processes and mechanisms that drive vegetation dynamics. Although there is usually little long-term field data available on the full dynamics of semi-arid plant communities, rainfall-dependent life-history attributes (e.g. growth, seed production, germination, recruitment and mortality factors) as well as information on seed dispersal, interactions between individual species, water availability, and disturbance processes are relatively easy to observe on shorter time-scales. The basic idea of this grid-based, bottom-up approach is to incorporate such short-term knowledge in form of rules into a computer simulation model. In order to investigate vegetation dynamics, the model simulates the fate and the interactions of individual plants (or plant assemblages) within the plant community. By using long-term climatic data and plausible management scenarios, the model extrapolates from the known short-term behaviour of individual plants (or plant assemblages) to long-term vegetation dynamics. An important advantage of grid-based simulation models is the inclusion of the necessary biological information for the modelled processes in the form of rules rather than mathematical equations. Especially in more complex problems this allows

Table 1. Summary and comparison of the three models

	Karoo model	Kalahari model	grassland model
Aim of the model	Understanding of long-term dynamics, identifying key-processes of vegetation change	Identifying time-scales and dynamics of vegetation change, impact of grazing	Identifying key processes (e.g. abiotic habitat-dependent and grazing processes, management) of vegetation change
study sites	Plans shrubland on Tierberg site, Prince Albert	Southern Kalahari	Semi-arid grasslands, main study sites in Glen, Senekal, and Reitz
time step	annual, but in submodel SEED consideration of monthly rainfall	annual, but rainfall considered on a daily basis	weekly, but water balance calculated on a daily basis
simulation time o. temporal extension	centuries	decades	decades to centuries
size of spatial subunits	33cm × 33cm, site of one adult plant	5m × 5m, maximum scale of direct shrub-grass interaction	30cm × 30cm, maximum space covered by a mature grass tuft
grid size	56 x 78 grid cells	100 x 200 grid cells	100 x 100 grid cells
vegetation, life-forms	5 dominant perennial shrubs species	life forms: shrubs, perennial grasses and herbs, annuals	5 perennial and annual grasses representing ecological response groups
contents of grid-cells	bare ground, one adult plant, various seeds or seedlings	bare ground, dominating life-form, or combination of life-forms	bare ground, several seedlings, up to two adult tufts, or combinations
impact of herbivores	sheep grazing, reduction of seed production of palatable plants	cattle grazing and trampling, spatially explicit reduction of herbaceous biomass, variable stocking rates	cattle grazing, spatially explicit, species and size dependent reduction of biomass
fire	-	grass fire causing risk of shrub mortality	grass fire
plant available moisture	Phenomenological description via gap sizes for establishment	top and subsoil layers, moisture uptake of local vegetation	moisture uptake per tuft depending on soil and meteorological conditions
local dynamics	cyclic succession between "coloniser" and "successor" species	competition between life forms	patch formation
long-term dynamics	event-driven behaviour	threshold dynamics	

the direct inclusion of expert knowledge that is not necessarily restricted to hard data [for this rule-based approach see also Jeltsch & Wissel (1994), Wiegand *et al.* (1995) and Jeltsch *et al.* (1996, 1997a, b)].

In this paper we present three grid-based models for typical semi-arid biomes of Southern Africa (pure shrubland, mixed shrub-grassland, pure grassland) that were aimed to provide an understanding of the long-term vegetation dynamics and to support management.

The models

The rule-sets of all three models are hierarchical in design. On the highest level, the rules cover the essential processes recruitment, growth and mortality. Depending on the appropriate grid size chosen, the possible states of the cells, and on the characteristics of the system modelled, these basic processes are specified in one or two more levels. The level of detail of the

basic processes depends on the climatic data, local water availability, the management scenario (e.g. grazing pressure), and disturbance regimes (e.g. fire). Table 1 summarises and compares the three models in terms of model aim, time-step, cell size, ecological state of cells, organisation of vegetation, representation and impact of herbivores, etc..

The Karoo shrubland model

The aim of the Karoo model is to attain an understanding of the long-term dynamics of a the shrub community, to identify key processes of vegetation change, and to calculate probabilities and timespans for transitions between different vegetation states. The model is based on field-investigations for a typical semi-arid ecosystem at the Tierberg Karoo Research Centre (TKRC) 33° 10' S, 22° 17' E in the southern Karoo, South Africa. Detailed information about inter-annual variation in rainfall, and on rainfall-dependent plant attributes, is included in the model. Five shrub species dominate the plains' vegetation at TKRC. These are *Brownanthus ciliatus* (Mesembryanthemaceae), *Ruschia spinosa* (Mesembryanthemaceae), *Galenia fruticosa* (Aizoaceae), *Osteospermum sinuatum* (Asteraceae), and *Pteronia pallens* (Asteraceae).

The plains' shrubland is characterised by isolated shrubs or by small, mixed-species clumps of shrubs interspersed with bare ground. Therefore, an individual-based approach is chosen and the space is divided into a grid of cells which represent sites of mature plants (Wiegand *et al.* 1995). The five dominant shrub species differ in their life-history attributes and in palability to domestic sheep. Less common species were considered in the model only as occupiers of space, and termed "fixed plants". Their life-histories are not considered, and they remain at fixed densities throughout simulated time, their only function being to prevent colonisation of cells by pioneers.

The five dominant species can be divided into two functional groups. Seedlings of "coloniser species" (*B. ciliatus*, *G. fruticosa* and *R. spinosa*) need large gaps in open vegetation to establish while seedlings of "successor species" (*P. pallens* and *O. sinuatum*) establish in shaded sites under the canopy of coloniser plants. The local dynamic (succession) within a cell is given by the sequences ("empty" → "coloniser plant" → "successor plant" → "empty") or ("empty" → "coloniser plant" → "empty"). For a given cell, the pathway followed and the duration (in time steps) of each state, is determined by the variables which characterise the state of a cell (e.g. open or species, size, age, number of seeds and seedlings), and the rule-set which determines how these variables change in the course of time depending upon the states of neighbouring cells, and on the external factors rainfall and management (e.g. grazing, clearing of unpalatable plants).

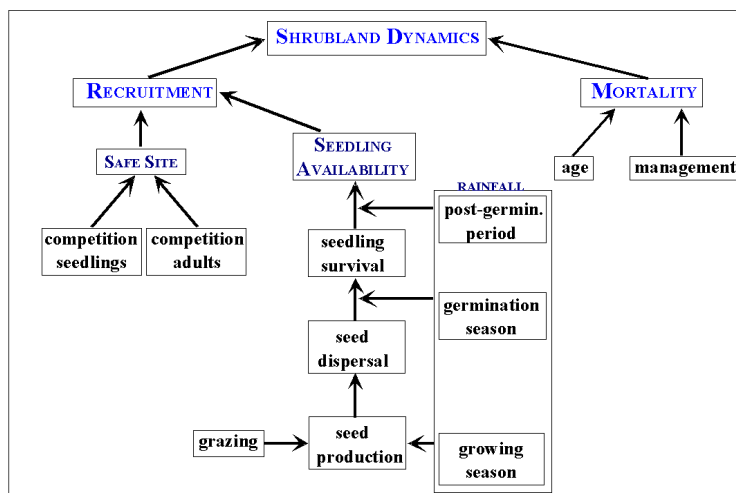


Figure 1: Process-chart of the Karoo model showing the model structure and the factors modelled. Each box represents one (or more) rules which are specified for the five dominant shrub species modelled.

The rule set specifies seed production, germination, seedling survival, seed dispersal, safe sites, competitive interactions, establishment, growth and mortality for the modelled plant species (Figure 1). Detailed descriptions of the rule set are given in Wiegand *et al.* (1995), Wiegand & Milton (1996), and Wiegand *et al.* (1997). Although the output for the spatial and temporal simulations is in annual time-steps, processes such as seed production, germination and survival depend on rainfall seasonality. For this purpose a sub-model (SEED) internally calculates on a monthly basis the total number of seeds produced and dispersed, as well as germinating and surviving, and sums these values for one year (*seedling availability*, Figure 1). The cell dynamics for a single iteration (one year) then proceeds by determining effects of neighbouring plants (*competition adults*, Figure 1) and competition on seedling survival (*competition seedlings*, Figure 1), and deleting all dispersed, non-surviving seeds other than those in the short-lived seed bank of *G. fruticosa* and *R. spinosa*. Considerable mortality occurs only during the seedling stage and when plants have reached their maximal age (*mortality*, Figure 1). The annual iteration is concluded once weather, time and management effects on plant size, reproductive maturity and survival have been considered.

The Kalahari shrub-grassland model

The example of a grid-based shrub-grass simulation model is oriented towards the vegetation dynamics of the southern Kalahari (26°S, 20°E - 27°S, 24°E). A more general version of this model investigates questions of long-term tree-grass coexistence in semi-arid savannas (Jeltsch *et al.* 1996) whereas the applied version discussed here focuses on the problem of shrub encroachment under the impact of cattle grazing (Jeltsch *et al.* 1997a, b; Weber & Jeltsch 1997). The main aims of the latter model are the identification of timescales and dynamics of vegetation changes and the investigation of the impact of small scale spatial variability of grazing utilization for vegetation dynamics in this semi-arid rangeland. In contrast to the Karoo shrubland model, this example is investigating the vegetation dynamics of more than one life form – a grass-shrub mix. Therefore an individual-based approach is not well adapted, and instead plant assemblages are considered. Only the dominating life forms in each grid cell are modelled, distinguishing cells dominated by shrubs, perennial grasses and herbs, annuals and combinations of these. The dynamic of single stemmed Kalahari trees takes place on larger timescales and is discussed elsewhere (Jeltsch *et al.* 1996). The model subdivides an area of 50 ha into 20.000 grid cells of a size of 5 m × 5 m. This size corresponds with observed maximum scales of direct shrub-grass interaction (Jeltsch *et al.* 1997a, b).

On the basis of these grid cells and a one year timestep different submodels are distinguished, simulating moisture availability in a top and sub soil layer, vegetation dynamics and biomass production, grazing by cattle, and grassfires (Figure 2).

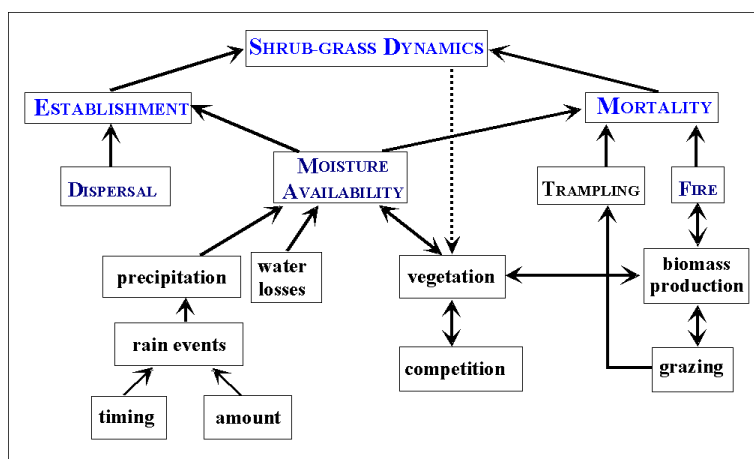


Figure 2: Process-chart of the Kalahari model showing the model structure and the processes modelled.

In each grid cell the actual soil *moisture availability* is calculated on the basis of the annual *precipitation* (resulting from single *rain events*), *water losses* (e.g. evaporation and runoff) and moisture uptake by the local *vegetation*. The moisture levels and the vegetation cover determine the annual *grass biomass production* in the modelled area which is the basis for both cattle *grazing* and *grass fire* fuel. The submodel *grazing* simulates the spatially explicit reduction of herbaceous biomass by cattle and the corresponding trampling effects. Varying spatial grazing behaviour of cattle is simulated by modifying the rules for choosing individual patches (i.e. grid cells) for grazing (Weber & Jeltsch 1997). The grazing and trampling pressure on the herbaceous component in a grid cell eventually influences the potential biomass production and the local occurrence of the herbaceous vegetation. Finally, in the submodel *grass fire*, the amount of remaining grass fuel determines whether grass fires occur in the modelled area with a certain probability. Grass fires are modelled to cause a small mortality risk for shrubs and to modify the potential biomass production.

The grassland model

Rangeland condition is commonly assessed by the ecological interpretation of vegetation and soil properties and expressed on grazing and condition or degradation gradients. Threshold values and benchmark sites are often identified on the constructed gradients which serve as a directive for the management of the rangeland (Bosch 1989; Bosch & Janse van Rensburg 1987; Bosch & Gauch 1991; Bosch & Kellner 1991; Bosch *et al.* 1987; Friedel 1991; Gibson & Bosch 1996; Kellner & Bosch 1992; Jordaan 1997; Martens *et al.* 1990). The condition of the vegetation community is primarily related to the ecological status (succession stage, botanical composition, cover and density), its productivity, nutritive value and palatability of the species as well as the adaptation to habitat changes (Snyman & Fouche 1993).

In the proposed semi-arid grassland model an attempt is made to understand the interactions between vegetation, habitat and management to determine the ecological dynamics and biomass production of certain swards. To achieve this goal it is important to combine information of the demography, population dynamics, competitive abilities, and physiological response of individualistic species to soil and climatic properties as well as to management (e.g. fire and grazing). The latter is necessary to gain an insight into the processes influencing the species' spatial and temporal changes on an ecosystem level (Henning & Kellner 1994; O'Connor 1994, 1995; Schakleton 1991).

A specific homogenous sward in the semi-arid grassland which is characterized by a certain soil type, topographical unit, climatic zone (i.e. annual mean rainfall of 550 - 650 mm) and grazing system is chosen in the construction of this particular model. Range condition changes are determined by the species compositional change of certain ecological response groups on grazing or degradation gradients, i.e. types of Increaser and Decreaser species (Bosch & Janse van Rensburg 1987; Jordaan 1997; Kellner 1994; Janse van Rensburg & Bosch 1987; Vorster 1982). The dominant species representing the different ecological response groups for this model are the following: Increaser I - *Cymbopogon plurinoidis*, Increaser II - *Eragrostis curvula*, Increaser III - *Aristida congesta* and Decreaser species - *Themeda triandra*.

In contrast to other models where mainly individual species are used as basis to calculate the biomass production of a particular sward (Fouche 1984, 1992), the interaction of a number of dominant species in combination (type of Increaser and Decreaser species) is used in this model to simulate rangeland dynamics and to determine biomass production over a short or long-term.

Important characteristics of grid-based models are the spatial and temporal extent and resolution such as time steps and cell size. A cell size of 0.3 m × 0.3 m is chosen which corresponds to the space covered by one mature grass tuft, several seedlings, or a combination of

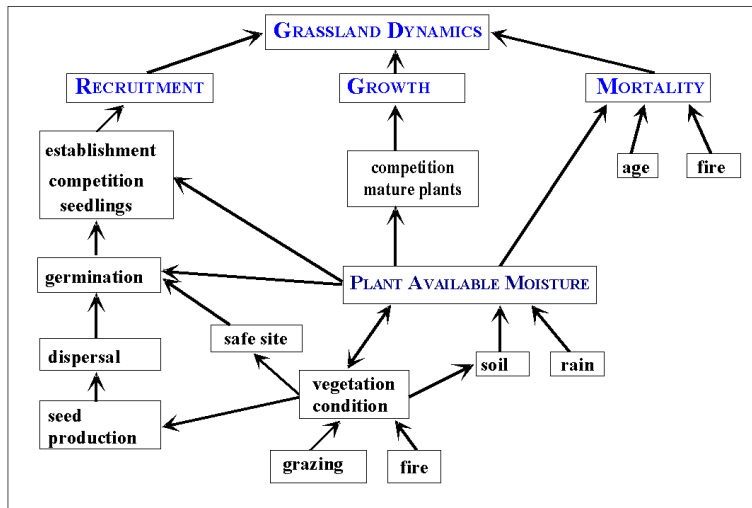


Figure 3: Process-chart of the grassland model showing the model structure and the processes modelled. Each box represents one (or more rules) which are specified for the five functional groups modelled.

both. The state of a cell can range from bare ground, mixtures of seedlings of different status groups to completely covered by one species of a specific ecological response group. Weekly time steps are considered to simulate species response characteristics for short (10 years) to long-term (e.g. 100-200 years) intervals.

The processes that determine the interactions between vegetation, habitat and management are indicated by a set of rules as shown by the process-chart in Figure 3. The main demographic aspects influencing the dynamics and biomass production of the semi-arid grassland include the recruitment, growth and mortality of individualistic species (Figure 3). Factors that influence the recruitment are the production, dispersal, viability and germination of seeds, the survival of seedlings in a safe site as well as the competitive ability of a certain grass species (O'Connor 1993, 1994; O'Connor & Pickett 1992; O'Connor & Roux 1995). The most important factor for growth is *plant available moisture* which depends on rainfall (amount and frequency), season and temperature (evapotranspiration) as well as on site- and soil properties (e.g. soil water balance, infiltration rate, run off) (Snyman 1988, 1989, 1997; Snyman & Fouche 1991; Snyman & Opperman 1983; Snyman & Janse van Rensburg 1987; Snyman *et al.* 1985). Species-specific water uptake from the soil by the plant would depend on the size and growth stage of the plant in a cell and it's neighboring cells within the grid. Mortality of adult plants is mostly age dependent, but may also be due to water stress (submodel *plant available moisture*) or influenced by management aspects such as grazing and fire frequencies and intensities (Danckwerts & Stuart-Hill 1988; Everson & Everson 1987; Snyman & Janse van Rensburg 1990; Trollope 1996). Reproduction starts with the submodel *seed production* which is applied in an appropriate season. The amount of rain in the preceding weeks and the size, condition and growth of the plant (*vegetation condition*) will determine the amount of seeds produced and dispersed. The dispersed seeds can germinate in a safe site (i.e. empty cell) given an initiation event, e.g. an amount of moisture above a certain threshold and temperature (submodel *plant available moisture*) (Adams 1996). In the following 6 weeks only those seedlings which had a competitive advantage for moisture uptake will establish and grow into mature plants (submodel *establishment*) (O'Connor 1997).

However, the process-chart also makes explicit some of the mechanisms leading to degradation which have a major influence on the dynamics and biomass production. Continued grazing reduces the height of palatable plants (submodel *grazing*) which will eventually cause a deterioration in their condition (*vegetation condition*) and consequently reduce seed production. In case of heavy grazing over longer periods the plants may become small or die, leading to patches of bare ground (open cells). If no immediate recolonization takes place in the open

cell(s) the rate of erosion will increase (submodel *soil*). Changes in the soil properties, however, will influence the soil water content, e.g. higher evaporation, increased run off and decreased infiltration appears on these bare patches (submodel *plant available moisture*). This will negatively influence the establishment of plants in such degraded cells, leading to an even higher rate of erosion, which will result in subsequent decreases in the range conditional state. The important question arising at this stage is to what extent this retrogressive process can be reversed. With this model it would be possible to identify and understand the biotic and abiotic key-factors and -processes that will lead to the change in the vegetation, and to calculate the probabilities and timescales of crossing certain thresholds on a condition or degradation gradient. The results could facilitate the understanding of the semi-arid grassland and help to make more correct management decisions for the long term.

Results

In the following we give a short overview about typical results that can be obtained with this type of simulation models. Extensive descriptions of the analysis of the Karoo and Kalahari model can be found in Wiegand *et al.* (1995); Jeltsch *et al.* (1996); Wiegand & Milton (1996a); Jeltsch *et al.* (1997a, b); Wiegand *et al.* (1997); Weber & Jeltsch (1997). No results for the semi-arid grassland model are given, as this model is still in a construction phase.

The Karoo shrubland model

Simulation results show that relative densities of component species in the Karoo shrubland do not reach a state of equilibrium (Figure 4). Instead, an episodic, event-driven behaviour occurs, with quasi-stable periods interrupted by sudden, discontinuous changes in species composition. Sudden increases in density of coloniser species occur when rain events suitable for germination and recruitment follow long periods with rainfall not favourable for recruitment. Failure of plant populations to replace natural mortality during these prolonged periods lead to a decrease in the density of established plants, and consequently, to an increase in the size and abundance of gaps that serve as safe establishment sites for colonisers. The coincidence of rainfall conditions suitable for reproduction and availability of safe recruitment sites is such a rare event that large recruitment events are likely to occur only 2-5 times per century in these semi-arid shrublands (Figure 5).

Because of the stochastic and unreliable rainfall (which results in unpredictable driving events) the future development of the plant community can be described only probabilistically. To deal with this problem Wiegand & Milton (1996a) conducted subseries of 100 simulation runs. They used for each run a different sequence of rainfall data, but all rainfall data had the same monthly mean and variance as the original rainfall data. To be able to categorize and compare the vegetation state they introduced a grazing potential index that sums up the densities of all species weighted with their sheep utilization index (*B. ciliatus*: 0.063, *G. fruticosa*: 0.588, *O. sinuatum*: 1.0, *P. pallens*: 0.0, *R. spinosa*: 0.185) (Milton & Dean 1993; Wiegand & Milton 1996a).

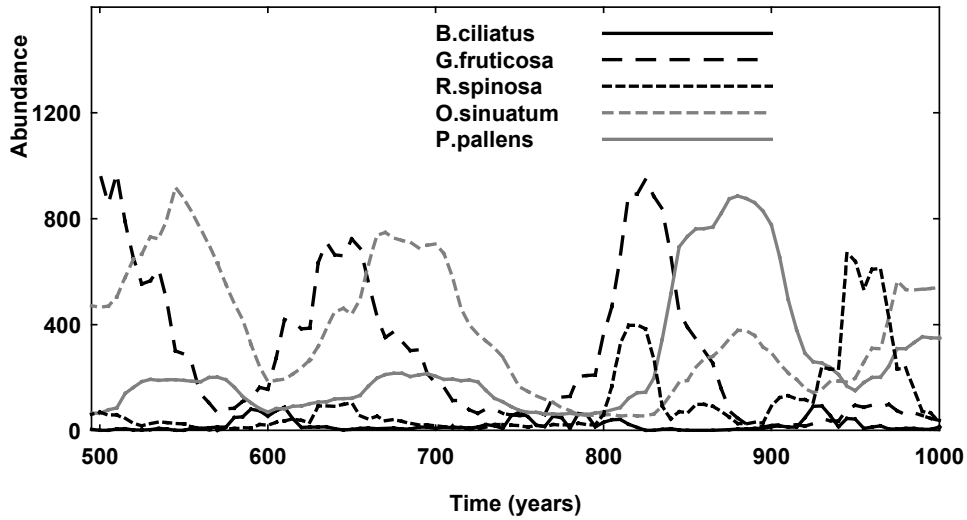


Figure 4: Timeseries showing the mean abundance of the five species between simulation years 500 and 1000.

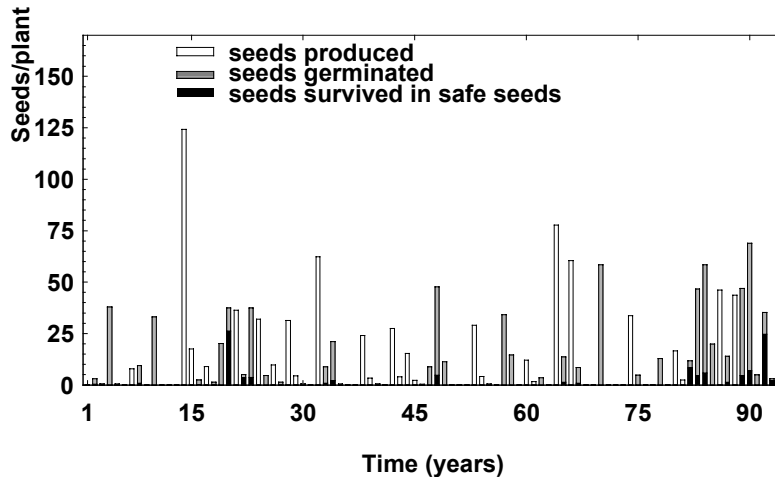


Figure 5: Seed production, germination and number of seedlings which would survive in safe sites of the species *R. spinosa* calculated with the submodel (SEED) over the 93 years of the Prince Albert rainfall scenario.

Simulation results show that little improvement in rangeland condition is likely during a period of 60 years. After 60 years resting there is a high probability that the overgrazed rangeland will remain in an overgrazed condition or even deteriorate, and only a small probability that there will be a substantial improvement in its condition (Wiegand & Milton 1996a). Even such active management as (simulated) clearing of unpalatable shrubs, did not guarantee a recovery of degraded shrubland within 60 years. Simulating overgrazing of rangeland in good conditions showed that the rangeland remains (on the mean) 20 years after the initiation of heavy grazing in good condition (Figure 6). Thereafter the mean range condition declines almost linearly and after 50 years the probable range of the grazing potential varies from degraded to good. After 70 years of this treatment, the mean range condition has declined to that of an overgrazed rangeland (Figure 6).

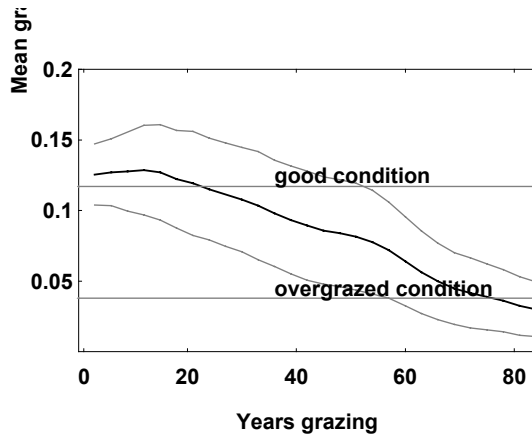


Fig. 5. The temporal development of the mean grazing potential and its standard deviation for a rangeland initially in good condition under heavy, continuous grazing. 100 simulation runs were performed, each using a different sequence of rainfall data (with the same monthly mean and variance as the original rainfall data).

The Kalahari shrub-grassland model

Results of the simulation experiments indicate that the shrub-grass dynamics depend on the quantity and sequence of rainfall (Jeltsch *et al.* 1997a, b). Simulated cattle grazing leads to bush encroachment under a wide range of rainfall scenarios (i.e. 220 mm - 385 mm mean annual precipitation), once grazing pressure exceeds a threshold determined by long-term mean annual rainfall (Figure 7). However, the stocking rate threshold for shrub encroachment is clearer under mesic than xeric climatic scenarios. This is because either competition from the herbaceous layer or rain may limit the establishment of woody plants. In relatively mesic scenarios, where shrub encroachment is limited mainly by grass competition, the grazing of grasses beyond a certain threshold leads deterministically to an increase in shrub cover. However, under xeric climates, where rainfall is lower and more stochastic, the rate of shrub encroachment, in response to a given intensity of grazing, becomes less predictable. In addition, stocking rate threshold levels and rates of shrub encroachment are sensitive to small scale local variability of grazing pressure. For more homogenous grazing regimes threshold levels of shrub encroachment shift towards higher grazing pressure whereas a high local grazing variability leads to a high risk of shrub encroachment already at a lower overall grazing pressure (Weber & Jeltsch 1997).

Comparing the stocking rate thresholds produced by the model simulations with stocking rates of the southern Kalahari currently recommended by pasture scientists (here: potential carrying capacity) it becomes obvious that these recommendations underestimate the risk of shrub encroachment on timescales that exceed the experience of individual farmers or land managers (Jeltsch *et al.* 1997b). The recommended stocking rates are unlikely to lead to shrub encroachment within ten or twenty years but they have a high probability of bringing about shrub encroachment within a century (Figure 8).

Discussion

Within the last 10 years it has been increasingly recognised (Harrington *et al.* 1984; Smith 1988; Westoby *et al.* 1989; Friedel 1991; Walker 1993; Milton & Hoffman 1994) that arid- and semi-arid rangelands often exhibit complex nonequilibrium dynamics where complicated non-linear processes (Westoby *et al.* 1989) and stochastic event-driven behaviour (Walker 1993) are involved. The complex interactions between climate, grazing and the plant life-history attributes, and the mismatch between observation times (years) and time scales of vegetation change (centuries) make it difficult to understand the dynamics of semi-arid or arid rangelands. But even the availability of long-term records would have limited predictive value much because of the high inherent stochasticity of these systems.

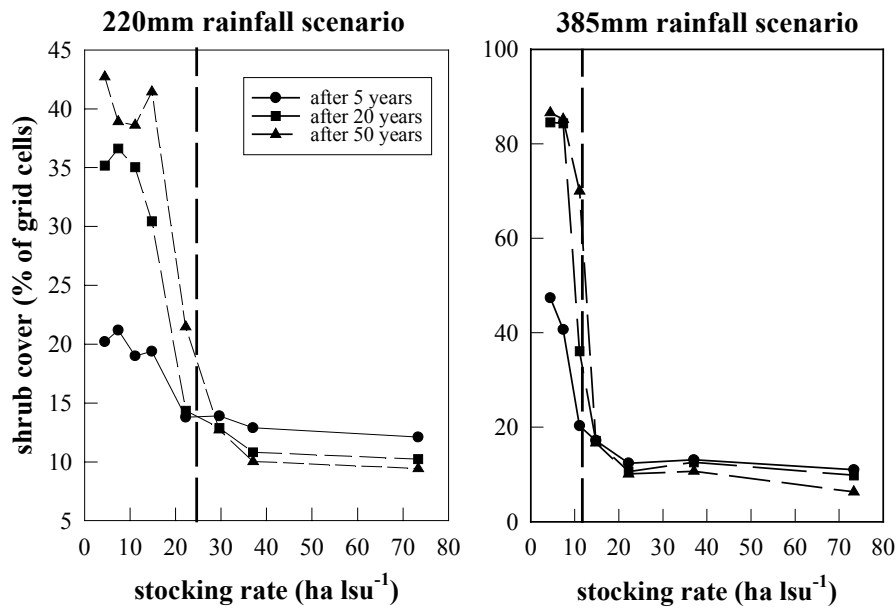


Figure 6: Comparison of simulation results of shrub cover versus stocking rate after 5, 20, and 50 years of grazing at a low and a high rainfall site. The dotted line gives the potential carrying capacity for the two sites (after Fourie et al. 1985).

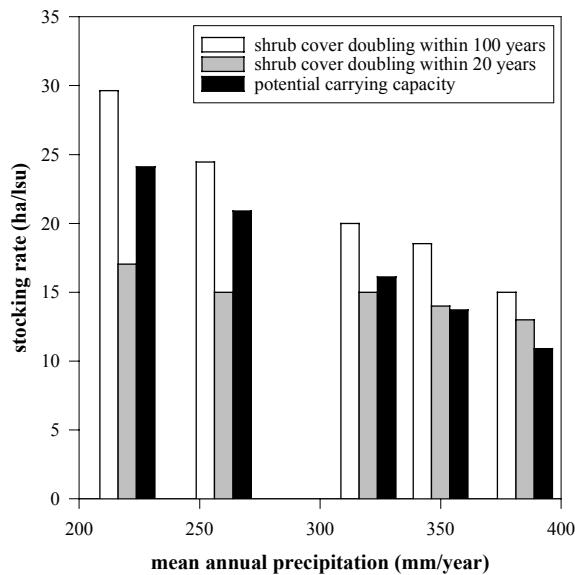


Figure 7: The potential carrying capacity (after Fourie et al. 1985) for five modelled sites with different mean annual precipitation compared with simulation results of these sites. Stocking rates within the range of the white (grey) columns show, on average, a doubling of shrub cover within 100 years (20 years) or less.

One way of dealing with these problems is to use advanced modelling techniques that focus on the processes essential for rangeland dynamics on individual (or plant assemblage) level, and which are able to extrapolate short-term knowledge on recruitment, growth, and mortality

to long term rangeland dynamics. In this paper we have presented three grid-based models that are based on detailed (short-term) knowledge about the life history of the dominant species of three typical semi-arid biomes of South Africa. We showed that this type of modelling can help to gather an understanding of the dynamics of arid or semi-arid rangelands, and that modelling can deliver a significant contribution to its management. First, a detailed book-keeping (Wiegand *et al.* 1995) of all processes that are relevant for the temporal and spatial dynamics and the grid-based modelling technique forced us to structure the knowledge available into a logical framework. The transformation of the rule-set into a qualitative simulation model and the comparison of the model output with the field situation is a strong test of the self-consistency of the rules (and knowledge). At this stage the model can be used to detect gaps in knowledge available and to guide future field work. The logical framework of the model gives each process a certain importance which is not always obvious without the model. For example, the results of the Karoo model presented in Figure 5 are basically a new arrangement of knowledge already available and simply accessible without using the model. But within the logical structure of the model this submodel becomes central to understanding the effect and the importance of the rainfall events. Second, computer simulation models facilitate the performance of replicated simulation experiments over long time frames that are impossible to perform in the field. For example, by adapting their savanna model to several specific sites Jeltsch *et al.* (1997b) found that stocking rates recommended for the southern Kalahari underestimate the risk of shrub encroachment on timescales that exceed the experience of individual farmers or land managers (Jeltsch *et al.* 1997b). Also, the performance of replicate simulation runs using the full range of rainfall scenarios (that are constrained by the characteristics of the original rainfall data) overcomes the problem of stochastic and unpredictable rainfall and facilitates a calculation of probabilities for vegetation change under specific management scenarios.

However, because every model is an abstraction, one has to make sure that the essential processes have been captured, that the parameter estimation was good enough, and that the model is close to ecosystem performance. This is a difficult task, especially with these long-term "uncheckable" models. The authors tried to build confidence in their models by checking whether the models were able to reproduce simple observed pattern (e.g. coexistence or relative abundances of the five dominant shrub species at the Tierberg study site, or piosphere-formation around artificial waterholes in the southern Kalahari) and by performing a sensitivity analysis of the model rules and parameters.

Kalahari shrub-grassland model—. The shrub-grass model was successful in qualitatively and even quantitatively reproducing the process of "piosphere"-formation (i.e., distinct vegetation zones) around artificial waterholes in the southern Kalahari (Jeltsch *et al.* 1997a). The realistic pattern formation occurred as a synergistic consequence of the grazing gradient and the modeled local vegetation dynamics. The agreement of these results with empirical findings confirm that the parameters and processes of the model mirror reality satisfactorily.

Karoo shrubland model—. The authors varied and tested the rules and parameters implemented into the model within their probable ranges to find out if all essential processes were captured and how sensitive the model output depended on variations of rules and parameters. Generally, the model output was insensitive among most parameters and rules. Only seed production (Wiegand & Milton 1996b), the rainfall pattern (Wiegand *et al.* 1995), and disturbances (Wiegand *et al.* 1997) could alter the event-driven dynamics of the model qualitatively. Using the Prince Albert rainfall data they found a broad range in the (seed production) parameter space where all five species could coexist over long timespans within the episodic and event-driven dynamic state (Wiegand & Milton 1996b). To calibrate the parameter values for seed production the authors assumed that seed production parameter should facilitate coexis-

tence of all five species over long timespans and they compared the plant densities observed on the study site with the simulation output after simulating community dynamics with 92 years of original rainfall data from Prince Albert.

In semi-arid grassland management gradient analysis is used to monitor changes in range condition and production systems due to species composition changes. Long-term experiments are used to assess the response of the ecological response groups (within a certain condition = status group composition) to single parameter such as grazing pressure, soil condition, or climate. This descriptive model is a good tool for classifying and categorizing, but it cannot provide an understanding of the ecological processes in total. To understand the processes that cause species compositional changes and subsequent changes in the production and conditional state of the sward it is important to consider all possible parameters (i.e. autecology of species, climate, habitat and management) in conjunction to each other and not only one parameter in isolation (e.g. only soil condition or soil moisture regimes or the recruitment potential of a particular species). In this respect, grid-based models can play an integrative role by bringing together the already existing pieces of knowledge from the different experiments and disciplines.

Grid-based models are also able to extrapolate local short-term information to long temporal and spatial scales. This ability, however, critically depends on the quality of the local information available. In most cases data were not collected especially for the requirements of grid-based models and therefore quite often information essential (from the point of view of the model) is missing or unsure. At this stage bookkeeping can be used to detect gaps in knowledge and to guide future field work. Nevertheless, it would be more fruitful to combine initially empirical studies with modelling. An iterative interaction between field work and modelling can help to find the most important parameter to measure in the field, and successively increase the predictive power of the model. Such a combined approach between modelling and specific data collection would reduce costs, but increase the scientific output and the confidence into the model. However, modelling is still not an integral part in the training of ecologist or the design of long-term experiments.

A further focus of semi-arid rangeland models is the explicit inclusion of economic aspects (e.g. Stephan *et al.* 1997). Rule-based simulation models can easily incorporate economic constraints into their rule-set and perform cost-benefit calculations or risk analysis of possible management options.

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