



Simulated shrubland ecosystem dynamics in the semi-arid Karoo, South Africa

T. Wiegand¹ & S. J. Milton²

¹Department of Ecological Modelling UFZ-Centre of Environmental Research, P.O. Box 2, Leipzig, 04301, Germany,

Email: towi@oesa.ufz.de; ²FitzPatrick Institute, University of Cape Town, Rondebosch 7700, South Africa

Abstract

In 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 plant community dynamics to be able to develop guidelines for sustainable management. To gain a better understanding of the main processes and mechanisms involved in vegetation change, we have developed a spatially explicit individual based model that simulates changes in plant communities over long time spans. The specific aim of the model is to identify key processes of vegetation change and to calculate probabilities and timespans for transitions between different vegetation states.

The model shows that the dynamics of the shrub community are typified by episodic and discontinuous changes in species composition with intervening quasi-stable phases lasting some decades. The short-term community dynamics (years to decades) are very sensitive to the sequence of rainfall events. In all simulation experiments the final vegetation state varied by more than 37% after a 60 year simulation period. However, time-scale for changes of the dynamic state of the system are long compared with human lifespans. Simulating resting of an overgrazed part of the shrub community indicated that little improvement in rangeland condition was likely during a period of 60 years. Overgrazing of a rangeland in good initial condition, simulated by reducing seed production in preferred forage plant species, only became obvious 40 or 50 years after the initiation of heavy grazing, and after 70 years the mean vegetation state eventually reached that of an overgrazed rangeland.



1. Introduction

Degradation and desertification is one of the most urgent threats to arid and semiarid 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.^{2,4,5,14} Degradation may be rapid, but recovery is slow because plant growth is rain-limited and denudation reduces rainfall effectiveness.¹⁰ 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^{13,18} it is difficult to assess the long-term effects of management.

In practice, rangeland management is necessarily based on an intuitive model which shows the farmer or manager how his system functions.¹⁷ 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 timespan which does not usually 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 time in a century, may lead to an inappropriate conceptual model which would facilitate non-sustainable management decisions. Walker¹⁶ stated that “undesirable changes in rangelands have mostly been brought about by applying the wrong ecological model(s) of rangeland dynamics”. An understanding of the long-term dynamics of arid or semiarid plant communities is indispensable for developing strategies for sustainable management.

Ecological models offer scope for quantitatively exploring long-term vegetation dynamics of arid and semiarid rangelands. 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.

In the following we present a simulation model^{18,19,20} that is aimed at understanding of the long-term dynamics of a typical shrub community in the semiarid Karoo, South Africa. Our model shows how such an understanding can be used to develop sustainable management strategies, and we contrast them with current rangeland models.

1.1 Rangeland models

The early model of rangeland dynamics, which still forms the basis of much current management¹⁶ is a simple application of Clementsian theory of ecological succession.¹ This model assumes continuous and reversible transitions along a single, monotonic gradient between an overgrazed subclimax and an undisturbed climax state of vegetation and assumes that grazing and interannual variation in rainfall cause vegetation to change in the same direction. Over the past decades this range succession model has been criticised because of its inability to deal with vegetation changes, especially in the arid and semiarid zones.^{4,17} Instead of continuous and reversible transitions semiarid rangelands typically show abrupt, discontinuous and irreversible transitions between discrete states. Changes in the species composition are commonly episodic, occurring in response to rare and extreme events, or particular sequences of events. In between such events, fodder production will vary from year to year in response to variation in rainfall, but the composition of the rangeland remains essentially the same, changing little in response to management.¹⁶

To deal with the complicated dynamics of semiarid and arid ecosystems, some range scientists suggested that these ecosystems could be described in terms of discrete states and inter-state transitions.^{9,16,17} Transitions could be triggered by natural events (rainfall, drought, hail, fire) or by management actions (removal of herbivores, altered intensity or timing of herbivory, addition of fertiliser, burning). Such "state-and-transition" models are valuable tools for describing the structure of the ecosystem, but they provide little information applicable to forecasting and prediction.

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.^{7,8,15,18} 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.^{6,7,18}

Grid-based models based on individual plants¹⁸ focus on the processes and mechanisms that drive community dynamics at individual level. Although there is usually little long-term field data available on the full dynamics of arid plant communities, rainfall-dependent life-history attributes (e.g. growth, seed production, germination, recruitment and mortality factors), seed dispersal and interactions between individual species are relatively easy to observe on shorter time-scales. The basic idea of our bottom-up approach is to incorporate such



420 Ecosystems and Sustainable Development

short-term knowledge in form of rules into the computer simulation model. In order to investigate community dynamics, the model simulates the fate and the interactions of individual plants within the community. In this way the model extrapolates from the behaviour of individual plants to long-term community 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 the direct inclusion of expert knowledge that is not necessarily restricted to hard data.

2. The model

The model presented in this paper is based on field-investigations, for a typical semiarid 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), a mat-forming stem-and-leaf succulent, *Ruschia spinosa* (Mesembryanthemaceae) an evergreen leaf-succulent, and three non-succulent species, namely semi-deciduous *Galenia fruticosa* (Aizoaceae), deciduous *Osteospermum sinuatum* (Asteraceae), and evergreen *Pteronia pallens* (Asteraceae). These shrubs differ in their life-history attributes and in acceptability to domestic sheep. The dominant species do not reproduce vegetatively, *P. pallens* and *O. sinuatum* have no seedbank, and *B. ciliatus*, *G. fruticosa* and *R. spinosa* appear to have a short-lived seedbank.³

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. 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 space is divided into a grid of cells which represent sites of mature plants. The local dynamics (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, and the rule-set which determines how these

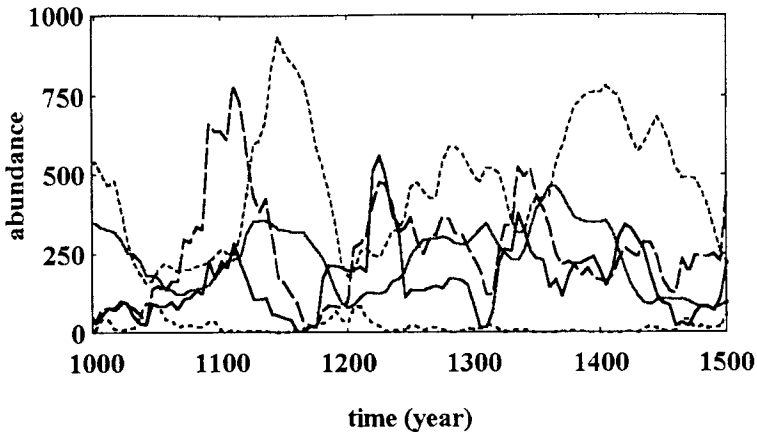


Figure 1: Time series showing the mean abundance of the five species between simulation years 1000 and 1500. Dotted black: *B. ciliatus*, long-short dashed black: *G. fruticosa*, dashed grey: *O. sinuatum*, solid grey: *P. pallens*, solid black: *R. spinosa*.

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).

The rule set specifies seed production, germination, seedling survival, seed dispersal safe sites, competitive interactions, establishment, growth and mortality for modelled plant species. Detailed descriptions of the rule set are given in Wiegand et al.¹⁸ Wiegand & Milton¹⁹ and Wiegand et al.²⁰ 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 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. The cell dynamics for a single iteration (one year) then proceeds by determining effects of neighbouring plants and competition on seedling survival, and deleting all dispersed, non-surviving seeds other than those in the seed bank. The annual iteration is concluded once weather, time and management effects on plant size, reproductive maturity and survival have been considered.

3. Results

3.1. Event-driven dynamics

We used a parameter set for ungrazed vegetation¹⁹ and started simulations with a species composition typical for rangeland in good condition.¹¹ Modelling

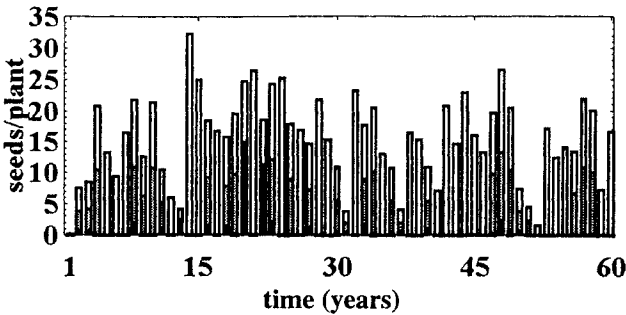


Figure 2: Seed production, germination and number of seedlings which would survive in safe sites of the species *G. fruticosa* calculated with the submodel (SEED) over the first 60 years of the Prince Albert rainfall scenario. Bar shading denotes seeds that fail to germinate (white), seeds that germinate but die (hatched), surviving seedlings (black).

results show that in this case all five species can co-exist for a simulation period of some centuries. However, relative densities of component species do not reach a state of equilibrium (Fig. 1) 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. Large recruitment events occur only if timing and amount of rainfall over the year facilitates seed production, seed germination and post-germination survival of seedlings (Fig. 2), and secondly if safe sites are available to the dispersing seeds. 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 arid shrublands.

3.2. Simulation experiments

The stochastic and unreliable rainfall results in unpredictable driving events. For this reason the future development of the plant community in the next, say 60, years can be described only probabilistically. To deal with this problem we conducted for different scenarios subseries of 100 simulation runs using a different sequence of rainfall data (with the same monthly mean and variance

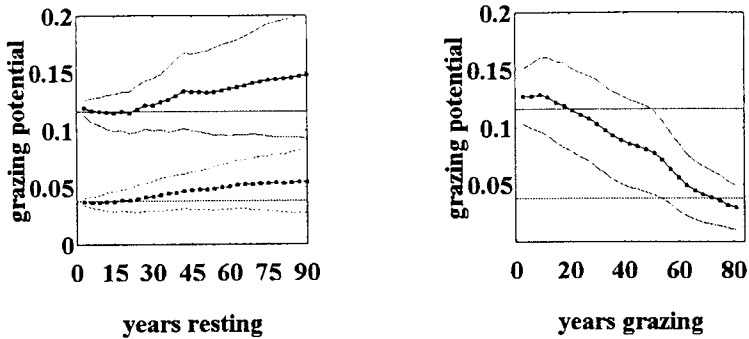


Figure 3. The temporal development of the grazing potential and its mean variation. (a): solid lines: simulation experiment 1, dashed lines: simulation experiment 2; (b): simulation experiment 3. The upper horizontal lines give the value of the grazing potential index of a rangeland in good condition, the lower horizontal lines correspond with an overgrazed rangeland.

as the original rainfall data) for each run.¹⁹ We simulated resting of rangelands in (1) good and (2) in overgrazed initial condition and (3) we conducted a subseries of simulation experiments where we simulated 80 years of heavy, continuous grazing of rangeland in good conditions. The vegetation state was characterised through a grazing potential index P that sums up the densities of all species at the simulation grid weighted with their sheep utilisation index.¹²

Simulation of resting of rangelands in good condition (Fig. 3a) showed that the short-term dynamics (decades) and the development of the grazing potential index P were highly stochastic and sensitive to the rainfall pattern. Depending on the occurrence – or absence – of driving events, the pathway that the plant community follows can vary considerably between simulation runs. Because of the long lifespans of component species and the rare occurrence of big establishment events a single such event can determine the vegetation state of the plant community for many years. Consequently, we found that the grazing potential index P varies greatly between simulation runs (Fig 3a). A direct consequence of this high stochasticity is that the condition of even a good, ungrazed rangeland had a 13% probability of deteriorating after 60 years rest.

In overgrazed rangeland little improvement was likely during a period of 60 years (Fig. 3a). After 60 years resting there is a 54% probability that the overgrazed rangeland will remain in an overgrazed condition or even deteriorate, and only a 7% probability that there will be a substantial improvement in its condition.

To investigate time-scales for vegetation change due to overgrazing we conduct a subseries of simulation experiments¹⁹ where we simulated 80 years



424 Ecosystems and Sustainable Development

of heavy, continuous grazing of rangeland in good conditions. Continuous grazing was modelled by reducing the seed production of palatable species by a certain factor. The results of this simulation experiment (Fig. 3b) show that the rangeland remains (on average) 20 years after the initiation of heavy grazing in good condition. 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.

4. Discussion

4.1. Range succession and state-and-transition model

With our quantitative simulation model we are able to test the two main concepts existing for rangeland ecology, the “range succession model” and the “state-and-transition” model. The results of our model confirm existing doubts about the application of Clementsian ecological succession theory to semiarid ecosystems and support the state-and-transition concept. The plant community at the TKRC showed essential properties described by the state-and-transition concept: (1) Event-driven change, (2) long time scale of changes, (3) demographic inertia and lag-effects, (4) unpredictability of vegetation change and (5) huge variation in fodder production. We identified the rare recruitment-events to be the key processes driving the dynamics of the plant community. Just the occurrence of one big establishment event after a sequence of dry years can drive the dynamics of the plant community towards a completely different direction and can determine the vegetation state of the plant community for many years. Such events are opportunities for management to influence vegetation change in a desirable direction (e.g., maintain a viable population of palatable species within the plant community) which may occur once in ten or twenty years. To recognise these rare opportunities managers should monitor the vegetation and estimate the densities of safe sites for the different species or functional groups of the rangeland to assess if a large recruitment event may be possible.

4.2. Specific lessons for the Karoo shrubland

However, by simulating time scales of vegetation change of a typical Karoo shrubland we were able to go much further than it would be possible with the conceptual “state-and-transition” model. We found that time scales of vegetation change in this plant community are generally much longer than human lifespans. Demographic inertia and the rare occurrence of establishment opportunities are responsible for this property. Overgrazing of a rangeland in good condition takes (on average) at least 70 years to become evident, and during the first 20 years no significant changes are likely to occur. Rehabilitation after



withdrawal of sheep may take much longer than degradation and may be almost impossible within economic time-scales. For that reason management should be long-term management. Of course, this requires a good memory for the history (detailed record-keeping) of the rangeland and knowledge about the age-structure of the plant community.

The unpredictability of the events and a uncertainty and lack of precise knowledge make management necessarily risk-based¹⁶. Both, “bad periods” and “good periods” are innate to the system. “Bad periods” and “good periods” are evenly distributed over centuries, but not over the short term (decades) which is the economic time scale of the farmer. Even resting of rangeland does not guarantee an improvement in carrying capacity. Thus, managing semiarid rangeland always involves a considerable risk and flexibility to respond rapidly to an driving event is needed (“event-management”).

However, being able to recognise the significant events is the key to successful rangeland management. With the help of our simulation model we could uncover the coincidence of rainfall conditions suitable for reproduction and availability of safe recruitment sites being the particular sequence of events that drive the dynamics of this plant community.

Our modelling exercise demonstrates that each system has very specific characteristic that have to be considered by developing sustainable management strategies. We cannot hope to obtain a general model or recipe that can be applied universally for guiding sustainable management. Rather we need concepts or tools that can help to gather a sufficient system understanding in every concrete case.

References

1. Clements, F.E. Plant succession: an analysis of the development of vegetation. *Carnegie Institute Publication* 1916, 242:1-512, Washington DC, USA.
2. Dean, W.R.J. & Macdonald, I.A.W. Historical changes in stocking rates of domestic livestock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. *Journal of Arid Environments*, 1994, 26:281-298.
3. Esler, K.J. Vegetation patterns and plant reproductive processes. Ph.D. thesis, University of Cape Town, South Africa, 1993.
4. Friedel, M.H. Range condition assessment and the concepts of thresholds: A view point. *Journal of Range Management*, 1991, 44:422-426.
5. Friedel, M.H., Foran, D. B. & Stafford Smith D. M. Where creeks run dry or ten feet high: pastoral management in arid Australia. *Proceedings of the Ecological Society of Australia*, 1990, 16: 185-194



426 Ecosystems and Sustainable Development

6. Jeltsch, F., & Wissel, C. Modelling dieback phenomena in natural forests. *Ecological Modelling*, 1994, 75/76:111-121.
7. Jeltsch, F., Milton, S.J., Dean, W.R.J. & van Rooyen, N. Tree spacing and coexistence in semi-arid savannas. *Journal of Ecology* 1996, 84:583-595.
8. Jeltsch, F., Milton, S.J., Dean, W.R.J. & van Rooyen, N. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* 1997, 8:177-189
9. Milton, S.J. & Hoffman M.T. The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. *African Journal of Range and Forage Science* 1994, 11:18-26.
10. Milton, S. J., Dean, W. R. J., du Plessis, M. A. & Siegfried, W. R. A conceptual model of arid rangeland degradation - the escalating cost of declining productivity. *BioScience* 1994, 44: 70-76.
11. Milton, S. J. & Dean W.R.J. Seed production in rangelands of the southern Karoo. *South African Journal of Science* 1990, 86: 231-233.
12. Milton, S. J. & Dean W.R.J. Selection of seeds by harvester ants (*Messor capensis*) in relation to condition of arid rangeland. *Journal of Arid Environments*. 1993, 24: 63-74.
13. Scholes, R. J. Change in nature and the nature of change: interactions between terrestrial ecosystems and the atmosphere. *South African Journal of Science* 1990 86: 350-354
14. Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A. & Whitford, W. G. Biological feedbacks in global desertification. *Science* 1990, 247: 1043-1048.
15. Thiéry, J.M., D'Herbés J.M. & Valentin C. A model simulating the genesis of banded vegetation patterns in Niger. *Journal of Ecology*, 1995, 83:497-507.
16. Walker, B.H. Rangeland ecology: Understanding and managing change. *Ambio*, 1993, 22: 80-87.
17. Westoby, M., Walker, B.H. & Noy-Meir, I. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 1989, 42: 266-274.
18. Wiegand, T., Milton S.J. & Wissel, C. A simulation model for a shrub-ecosystem in the semi-arid Karoo, South Africa. *Ecology*, 1995, 76: 2205-2221.
19. Wiegand, T. & Milton, S.J. Vegetation change in semiarid communities, simulating probabilities and time scales. *Vegetatio* 1996, 125:169-183.
20. Wiegand, T., Dean, W. R. J. & Milton, S. J. Simulated plant population responses to small scale disturbances in semi-arid shrublands. *Journal of Vegetation Science* 1997, 8:163-176.