

FROM INDIVIDUAL SCALE TO POPULATION AND COMMUNITY SCALE: MODELING DYNAMICS OF THE SEMI-ARID GRASSLANDS OF SOUTH AFRICA

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1. INTRODUCTION

Understanding how processes and factors at lower hierarchical scales determine the dynamics of ecological systems at higher scales is a major challenge in ecology (Levin 1992). For example, dynamics of rangelands are highly complex and characterized by the interaction of factors and processes at different spatial and temporal scales. A number of factors that impact the fate of individual plants are restricted to the immediate neighborhood of the plants (i.e., water availability, competition, or facilitation), but seed dispersal, the rainfall pattern, or grazing management usually operate at larger scales. Also, one of the major concerns in semiarid rangelands, desertification, is a phenomenon that becomes evident and visible at larger temporal and spatial scales. Grazing by domestic herbivores has been identified as the one of the major agents of desertification (Walker et al. 1981, Soriano & Movia 1986, Schlesinger *et al.* 1990, Dean & Macdonald 1994, Milton *et al.* 1994). However, grazing is a small-scale process that operates at the scale of individual plants. Grazing alters the resource status of individual plants, their water status, nutrient balance, and relative growth rates and can cause dramatic changes in e.g., species composition, cover, primary production (Oesterheld & McNaughton 2000), and nutrient balance (McNaughton et al. 1989) of semiarid rangelands. Therefore, integrating processes and factors from the scales of individual plants, populations, communities and systems is required if the dynamic nature of rangelands in response to several driving forces is to be understood.

Although demographic processes at the individual plant scale (e.g., establishment, competition, mortality, growth) are responsible for community level changes in grassland composition and state, most research has been devoted to investigate community level responses to climate and grazing (i.e., system approach). An example is dynamics of the semi-arid grasslands in South Africa. In this system, the community scale responses in e.g., species composition, basal cover, water use efficiency (WUE), diversity, and primary production to climate and grazing are well documented (e.g., Snyman & Fouché 1991; Snyman 1998, 1999, 2000; O'Connor *et al.* 2001). However, knowledge on the underlying demographic processes of the grassland is sparse and little research has been dedicated to investigate recruitment, growth, and mortality of individual grass tufts (i.e., demographic approach). In this article, we present an individual-based, spatially explicit simulation model describing the dynamics of semi-arid grasslands in South Africa. The general aim of the model is to understand the dynamics and demography of grassland in good compositional state. More specifically, we aim to identify the key processes and factors at the individual plant scale that produce the known long-term community scale responses in basal cover, species composition, and primary production to climate. We use the model to test our knowledge and hypotheses on demographic processes in the grassland and produce specific hypothesis that can be tested with further field trials.

2. METHODS

2.1 The strategy of the model

The grassland model integrates our data and hypotheses on the functioning of grassland dynamics on the scale of individual plants. The basic idea of this bottom-up approach is to incorporate knowledge and hypotheses in form of mechanistic rules into a computer simulation model (Wiegand *et al.* 1995, Wiegand *et al.* 1999). In order to investigate grassland dynamics, the model simulates the fate and the interactions of individual plants within the plant community. By using long-term climatic data and management scenarios, the model extrapolates the behavior of individual plants at small spatial and temporal scales to long-term vegetation dynamics. Because of their high structural realism, the output of individual-based models can directly be compared to field data. Prerequisite for this is that the spatial and temporal scales of the model output and the field data match, and that the model includes mechanisms that are potentially able to

generate data that correspond to the field data. Additionally, the simulation model needs to consider the management, the external driving forces (i.e., rainfall pattern), and the initial condition that constrained the dynamics of the system on the scales of interest.

Our simulations experiments resemble closely the experimental and climatic conditions during a long-term field experiment that was conducted between 1977 and 1996 at the farm Sydenham of the University of the Free State (Snyman & Fouché 1991; Snyman & Fouché 1993; Snyman 1998; O'Connor *et al.* 2001). The long-term experiment followed the fate of grassland plots in three typical compositional states (good, moderate, poor condition) over a total of 19 years. In this article, however, we study only grassland dynamics of grassland in the good compositional state. We formulate a number of alternative hypotheses on processes and factors on the individual scale (i.e., on germination, establishment, growth, vitality, competition, fragmentation, moisture availability, and mortality of grass tufts) and compare the simulated model output with data that were collected during the long-term experiment. For comparison with the model output, we use 19-year data on population scale changes of species composition and basal cover in response to climate, as well as data on establishment, drought mortality, and size distribution of tufts collected during selected years. These data describe different characteristic features of grassland dynamics with respect to the aim of our model (hereafter-called patterns) at scales higher than the individual scale. It is important to note that these data are not included in the model, but are the high-scale synergetic outcome of the interaction of the individual-scale processes with the weather and management (Wiegand *et al.* 2003a). We use a formalized method to analyze the correspondence between simulated and observed patterns (see Wiegand *et al.* 2003a, b) and accept only model variants that reproduce all observed patterns simultaneously. Because the available data on grassland dynamics describe different characteristic features of the grassland, it is by far non-trivial to reproduce all of them simultaneously (e.g., Kendall *et al.* 1999; Reynolds & Ford 1999; Wiegand *et al.* 2003a, b). This assures that a model variant that fulfils all observed patterns simultaneously captures indeed characteristic aspects of the grassland demographics. On the other hand, a model variant that is not able to reproduce one or more characteristic dynamic features of grassland dynamics is deficient and needs improvement in its process structure.

2.2 Study site and data collection

The long-term experiment was conducted at the farm Sydenham of the University of the Free State in the vicinity of Bloemfontein, South Africa (29°06'S, 26°67'E; altitude 1350m). Additional data were collected in Bloemfontein (28°50'S; 26°15'E, altitude 1350m), and in Glen (28°57'S; 25°20'E, altitude 1304m), some 30 km northeast of Bloemfontein. The study sites are situated in the semiarid summer rainfall region (annual average 560 mm) of South Africa within *Themeda triandra* – *Cymbopogon plurinodis* grassland (Acocks 1953) (plant nomenclature follows Arnold and De Wet 1993). The soil [Shorrock Series (Hutton Form) (Macvicar *et al.* 1977)] is representative of the sandy loams of the Free State on which most of the semiarid grassland is situated. Rain falls almost exclusively during summer (October to April), with an average of 78 days of precipitation per year. Mean maximum monthly temperatures range from 17°C in July to 33°C in January, but extremes of 41°C in January and 28°C in July have been recorded. On average, frost occurs 119 days per year (Schulze 1979). The grassveld is typically tall (0.75 to 2m), and appears relatively uniform at a coarser scale (Tainton 1999). The majority of the grasses are perennial and basal cover (6% to 15%) is typically clumped at a finer scale. The arid and semiarid areas have already undergone serious degradation, and bare areas are common.

The population-level data on basal cover, species composition, and phytomass production were collected during a long-term experiment from 1977 to 1996 (Snyman & Fouché 1991; O'Connor *et al.* 2001) at Sydenham experimental farm. Prior to the 1977–1978 growing season three typical compositional states (good, moderate, poor condition) were created to reflect closely the distinct composition and basal cover that could arise as a result of different grazing histories of this grassland (Mostert 1958; Van den Berg *et al.* 1975). In this article, we focus on the data collected for good condition grassland that was dominated by the perennial bunchgrass *Themeda triandra* and co-dominated by perennial bunchgrasses of *Eragrostis* species. The aboveground phytomass production of each experimental unit was harvested to a height of 30 mm, the effective stubble height, after the end of the growing season following the first frost. Details on the experimental design are given in Snyman and Fouché (1991) and O'Connor *et al.* (2001). Tuft mortality data after the severe 1982/83 - 1983/84 drought was measured at Sydenham farm, but at a different experiment (Snyman & van Rensburg 1990), which had a similar design as the long-term experiment. Data on germination and seedling survival were collected during the 2000/01 and 2001/02 seasons at Bloemfontein, and the data on spacing of seedlings and adults, and size of individual tufts were collected in April 2000 at the Glen study site.

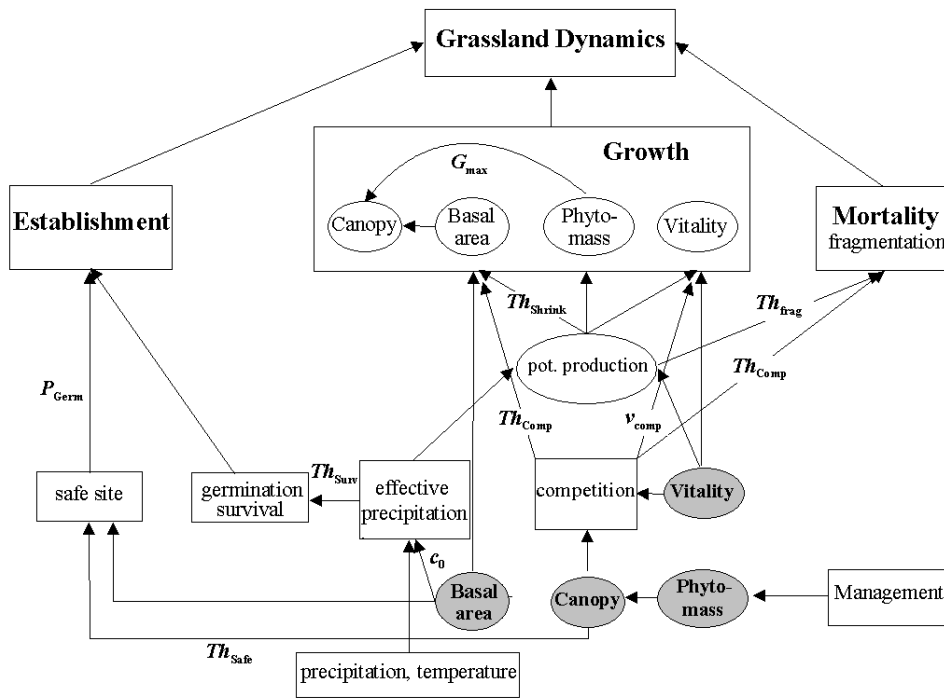


Figure 1. Overview over the grassland model. The grey ellipses are the state variables characterizing single grass tufts, and the white boxes show the processes that change the state variables. Arrows indicate mechanistic relations, and corresponding model parameters are shown beside the arrow.

2.3 The grassland model

The model simulates grassland dynamics in a 10 m × 10 m area of a homogeneous sward of grassland in good compositional state. This grassland is dominated by two functional groups (O'Connor *et al.* 2001), a dominant group of climax species (*Themeda triandra*, *Digitaria eriantha*, *Digitaria argyrograpta*, *Panicum stapfianum*, *Setaria flabellata*), and a second group formed by subclimax species (*Eragrostis curvula*, *E. chloromelas*, *E. lehmanniana*, *E. obtusa*, and *Triraphis andropogonoides*). Our model follows only the dynamics of plants of the dominant functional group, plants of the other functional group are considered as fixed environment (e.g., Wiegand *et al.* 1995). Plants of the subclimax group do not grow, not die, and do not reproduce, but they occupy space, and exert competition. Note that we do not aim here to describe changes among compositional states (i.e., degradation) neither to apply the model at different sites. Therefore, we assume that soil conditions and amount of organic material remain approximately constant and that soil and nutrient loss does not occur. Fire, another possible factor that influences dynamics of the semiarid grasslands, was not included in the experiment and is neglected in the current version of the model.

The state variables of individual grass tufts are location, basal radius, canopy radius, green phytomass, and tuft vitality *vit* (fig. 1). The model rules represent our current knowledge and hypotheses on grassland demographics. With these rules, we attempt to describe the key factors and processes of the dynamics of the semiarid grassland in good compositional state during the long-term experiment, i.e., (1) competition, (2) effective precipitation, (3) growth, (4) mortality and fragmentation of tufts, (5) safe sites, (6) germination and seedling survival, and (7) management (fig. 1). In the following, we give a short overview over the model rules and define the model parameters with which we alter the assumed importance of the different processes. For example, a parameter value of zero means that the corresponding process is removed from the model.

2.3.1 Vitality of tufts and phytomass production.+

The variable vitality (*vit*) is a measure of the condition of the plant due to past weather conditions and competition. It represents the potential of the tuft to grow and to produce phytomass in response to precipitation (fig. 1). Monthly phytomass production is a linear function of monthly precipitation weighted by two factors, vitality and a temperature index that scales mean monthly temperature to values between 0 and 1 (table 1B). The temperature index reflects physiological constraints of the C₄ grasses that have high temperature optima for photosynthesis (Ehleringer and Bjorkman 1977) and describes the growing season, i.e., it prevents high phytomass production during the cold season. Vitality describes a carry-over effect from past weather conditions (see table 1B) and acts as weighting factor that amplifies (after wet periods) or reduces (after dry periods) phytomass production (Oesterheld *et al.* 2001). Strong competition (i.e., the tuft is totally dominated by competition, see *competition* below) decreases the vitality of a grass tuft with decrement v_{comp} . By setting $v_{comp} = 0$, we can remove the influence of competition on vitality and thus vitality depends only on effective precipitation (see fig. 1). The parameter c that describes the time-scale of the memory of

vitality (see table 1B) was directly determined from the data on phytomass production (Thorsten Wiegand, unpublished analysis).

2.3.2 Competition

Competition is based on a circular zone of influence with area ZOI that represents the area from which the plant potentially can draw resources or perform competition to other plants. We identify the zone of influence with the canopy area, thus assuming that the area where grasses perform competition is predominantly defined by their canopy area (shade, space), and not by e.g., root extension. Over its own zone of influence, a given tuft exerts competition with a strength per unit area that is calculated as the product of vitality (vit) and a species-specific competitive strength (P_s). Consequently, the total competitive power of a tuft is $own = vit \times P_s \times ZOI$. To determine the degree of competition suffered by a given tuft we sum up the total competitive power of all tufts (including that of the focal tuft) exerted over the zone of influence of the focal tuft ($= all$). The fraction own/all is a measure of the competition suffered by the focal tuft. For $own/all = 1$, the zone of influence of the tuft is not overlapped by that of other tufts, and consequently the tuft does not suffer competition. We describe the effect of competition on growth of basal area and on mortality with a final competition index f_{comp} that is a function of the fraction own/all and a threshold Th_{comp} . For $own/all \leq Th_{comp}$, we define $f_{comp} = 0$ (i.e., the tuft is totally dominated by competition), for $own/all = 1$ we define $Th_{comp} = 1$ (no competition), and for $Th_{comp} < own/all < 1$ (intermediate levels of competition) we interpolate linearly. If $Th_{comp} = 0$, we model size symmetry in competition (Schwinning & Weiner 1998), i.e., the impact of competition is proportional to the competitive power of a tuft relative to its competitor. For $Th_{comp} > 0$ we model asymmetric competition where tufts that are more powerful grow relatively more than weaker competitors do. We hypothesize that strong competition reduces vitality. If a tuft that is totally dominated by competition, we reduce its vitality with decrement v_{comp} .

2.3.3 Effective precipitation.

Surface runoff in areas with low basal cover reduces local water availability and infiltration. As a consequence, tufts with high degree of bare areas in their neighborhood suffer localized droughts even during periods of reasonable rainfall. To calculate the effective precipitation for a given tuft, we determine the mean basal cover in the 20 cm neighborhood of the basal area of this tuft ($= cover$) and compare it to a parameter c_0 that gives the threshold basal cover above which no water is lost due to runoff. For $cover \geq c_0$, no runoff occurs and effective precipitation is given through the rainfall data. Otherwise, rainfall is reduced by multiplication with the factor $c_0/cover$. We can remove the process runoff by setting $c_0 = 0$. Effective precipitation influences directly potential production (table 1B), germination and seedlings survival, and via potential production growth of basal area, vitality, phytomass production, and mortality (fig. 1).

2.3.4 Growth

The module "Growth" (fig. 1) includes aboveground phytomass production (see *Vitality of tufts and phytomass production* above), and changes in the basal and canopy areas of tufts (i.e., growth and shrinking). The basal areas of different tufts are not allowed to overlap, while the canopy areas may overlap (this causes competition). Monthly growth of basal area depends multiplicatively on effective production (the product of effective rainfall, the temperature index and vitality; table 1B), the competition index f_{comp} , and a size factor f_{size} . The size factor equals one for small tufts and decreases to zero at the maximum basal radius R_B^{max} (see table 1B). Thus, a tuft grows more if rainfall, temperature, and vitality are higher, and runoff, competition, and its size are smaller. Growth of basal area is scaled by a parameter G_{max} that gives the maximal monthly growth increment. For $G_{max} = 0$ no growth occurs. Stress due to prolonged droughts or heavy competition may result in shrinking of the basal area if the tuft did not grow in basal area and if it is weak (i.e., its vitality is smaller than a threshold Th_{Shrink}). The magnitude of shrinking depends on the vitality of the tuft and on parameter Th_{Shrink} . For $Th_{Shrink} = 0$, no shrinking occurs.

The canopy radius of a tuft depends deterministically on its basal radius and on the phytomass it holds. If the tuft is totally defoliated, the canopy radius is identical with the basal radius. In the other extreme, if the tuft holds the maximum aboveground phytomass per basal cover, the canopy radius is the maximal radius that corresponds to its basal radius. For cases of partial re-growth after defoliation, we interpolate with a linear function.

Table 1. Variables, parameters, patterns, and important model equations.

A) Properties and variable of individual tufts		Symbol
Species		
Coordinates of plant center		
Basal radius		R_B
Canopy radius		R_C
Green phytomass		B_g
Vitality at month m		$vit(m)$
B) Other important variables and equations		Symbol or equation
Precipitation at month m		$R(m)$
Temperature index at month m		$T(m)$
Effective rainfall $R_{eff}(m)$ at month t for $cover < c_0$		$R_{eff}(m) = R(m) \times cover/c_0$
Recursive definition of vitality [†] , with $c = 0.95$ for climax grasses		$vit(m+1) = vit(m) \times c + R_{eff}(m) \times (1 - c)$
Potential production		$R_{eff}(m) \times T(m) \times vit(m)$
Competition index f_{comp} for $own/all \geq Th_{Comp}$		$f_{comp} = (own/all - Th_{Comp})/(1 - Th_{Comp})$
Size factor f_{size}		$f_{size} = G_{max}(1 - R_B/R_B^{max})$
Phytomass production at month m		$R_{eff}(m) \times T(m) \times vit(m)$
Mortality index, accumulated from September to month m		$\sum_t R_{eff}(t) \times T(t) \times vit(t) \times f_{comp}$
Growth of basal radius at month m		$R_{eff}(m) \times T(m) \times vit(m) \times f_{comp} \times f_{size}$
C) Model parameters		Symbol
Max. growth increment of basal radius [cm] at average month		G_{max}
Percentage basal cover above which no run-off occurs		c_0
Vitality threshold for shrinking of basal area		Th_{Shrink}
Competition threshold for not growing		Th_{Comp}
Vitality decrement due to competition		v_{comp}
Mortality index threshold for fragmentation		Th_{frag}
Threshold monthly rain for survival [mm]		Th_{Surv}
Probability to germinate in a safe site		P_{Germ}
Competition threshold for safe sites		Th_{safe}
D) Pattern	Community scale data	Criterion for pattern fulfillment
1	19-year time series of basal cover (figure 2A)	Statistical permutation criterion
2	19-year time series of species composition (figure 2A)	Statistical permutation criterion
3	Fraction dead tufts during the 1982 – 1994 drought ($mort_{82-84}$)	$mort_{82-84} \in (0.37, 0.57)$
4	Number of recruits per m^2 in 2001 (rec_{01})	$rec_{01} \in (0.8, 2.4)$
5	Size-class distribution of tufts collected in April 2000	Statistical permutation criterion

[†] Vitality decreases additionally if the tuft is totally dominated by competition (see rule “competition“)

2.3.5 Fragmentation and mortality

Large tufts of the perennial climax and subclimax grasses do not die directly. Instead, the basal area shrinks or fragments into smaller units, which are then prone to mortality. Fragmentation of the basal area occurs during periods of stress, i.e., due to severe defoliation, strong competition or during prolonged droughts. We apply fragmentation and mortality at the end of the cold and dry season in August, but use a mortality index that sums up the stress of the tuft during the past year. This mortality index sums up, month by month, the product of effective precipitation, vitality, and the competition factor (see table 1B). Thus, the risk of fragmentation or mortality increases with increasing runoff, lower rainfall and vitality, and higher competition. Mortality or fragmentation occurs if the mortality index is below a threshold Th_{frag} . The probability of fragmentation is zero if the mortality index equals Th_{frag} , and one if the mortality index equals zero. In between, we interpolate linearly. For $Th_{frag} = 0$ no mortality and fragmentation occurs.

2.3.6 Safe sites

Safe sites are cells that are not too far away from the canopy of an established plant to benefit from facilitation, while competition from established plants is not too strong. Our field data shows that the furthest seedling of *T. triandra* was 11 cm away from the canopy of an established plant; the closest seedling was found 10 cm inside the canopy. In the model, the distance of a safe site to the next canopy has to be smaller than 11 cm, and the total competitive power in the immediate neighborhood of the safe site must be smaller than a threshold Th_{save} .

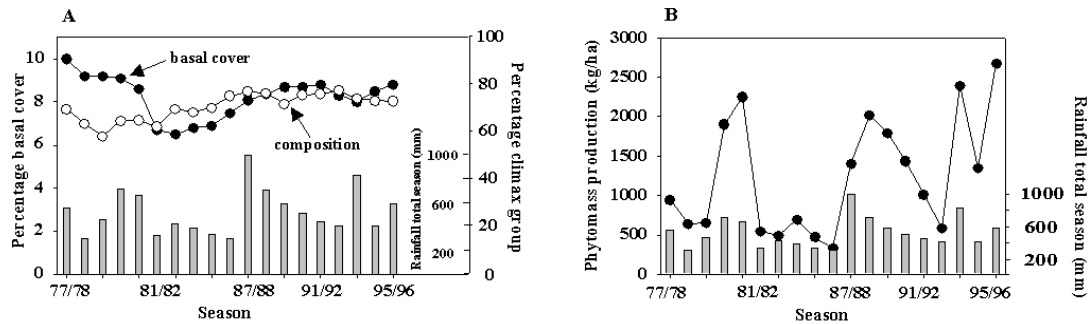


Figure 2. Community scale data for the grassland in good compositional state, collected during the long-term experiment. (A) Percentage basal cover (closed circles), species composition (percentage plants of climax functional group), and seasonal precipitation (bars). (B) Phytomass production (closed circles), and seasonal precipitation (bars).

2.3.7 Germination and seedling survival

Because we model grassland in good compositional state, we assume that seed availability is not a limiting factor and do not explicitly model seed production and dispersal. However, water availability during the growing season (October to March) limits germination and seedling survival, and the conditions for a safe site must be met. Germination occurs at month m in a given safe site with a probability P_{Germ} if enough water is availability for germination [i.e., $R_{\text{eff}}(m) > 30$ mm], and if enough water is availability for survival in subsequent months [$R_{\text{eff}}(m+1) > Th_{\text{Surv}}$, and $R_{\text{eff}}(m+2) > Th_{\text{Surv}}$]. The threshold Th_{Surv} is a model parameter.

2.3.8 Management and initial condition

The initial condition of the long-term experiment consisted in a grassland in good compositional state. We use an initial condition typical for grassland in good compositional state that approximated the size distribution of basal radius and canopy radius data collected in the field, and the data on species composition from initiation of the long-term experiment. To mimic the field experiment where above ground biomass was clipped at the end of the growing season to simulate grazing, we harvest in the model all phytomass at the end of the growing season.

3. RESULTS

We run our model with a total of 63194 model parameterizations that were a systematic sample of the parameter space spanned by the nine parameters shown in table 1C. Parameter ranges were conservatively wide and included values that removed the process from the model (in most cases the value zero). Our model simulated the time period from January 1977 to May 2002. Model stochasticity was relatively small because the model plot was large enough to buffer local fluctuations in plant density, and because we used for all simulations the same precipitation data. Therefore, performance of replicate simulations with the same model parameterization was not necessary. The model predictions for each model simulation were compared to the corresponding data from the long-term experiment or other sources. We used five different known features of grassland dynamics (= patterns, table 1D) to compare with the simulated data: (1) the 19-year time series of the basal cover (figure 2A), (2) the 19-year time series of the percentage species composition of the climax functional group (figure 2A), (3) data on tuft mortality during the severe 1982 – 1994 drought (i.e., the percentage of dead tufts in 1984 must be between 37% and 57%), (4) data on recruitment collected in 2001 (i.e., the number of recruits per m^2 must be between 0.8 and 2.4 recruits), and (5) data on the size-class distribution of tufts of the climax functional group collected in April 2000 (i.e., the percentage of tufts with basal diameter < 6 cm must be between 27% and 49%). The data on phytomass production were used to directly calibrate the rule on phytomass production. To measure the match between simulated and observed time series data (pattern 1 and 2) we used the sum of squares of the two time series. Based on statistical permutation tests that consider the uncertainty of the pattern data we defined a fulfilment interval of the sum of squares. Within the fulfilment interval observed and simulated time series are not significantly different. The acceptance interval for the patterns “percentage dead tufts after the drought” [$mort_{82-84} \in (0.37, 0.57)$] and “number of surviving recruits per m^2 ” [$rec_{01} \in (0.8, 2.4)$] was provided (conservatively wide) by researchers familiar with the species. The acceptance interval for the pattern “percentage of tufts with basal diameter < 6 cm” was based on a statistical permutation test using the observed size-class distribution of

basal diameters. Thus, we used binary interval error measures (i.e., there are only two options: the pattern is fulfilled or the pattern is not fulfilled; Reynolds & Ford 1999) to decide whether or not the model reproduces the observed data. This approach has the advantage that we can easily handle several patterns simultaneously. It is exactly the model's simultaneous performance on the different patterns that needs to be observed in order to obtain a better understanding of model performance and to locate deficiency sources. A total of $n = 395$ ($= 0.065\%$) model parameterizations yielded model grassland dynamics that reproduced all five observed features of the grassland. In all other cases, one or more features were not fulfilled and the resulting dynamics was not in accordance with our data. The 395 remaining model parameterizations represent our current knowledge (and uncertainty) of grassland demographics.

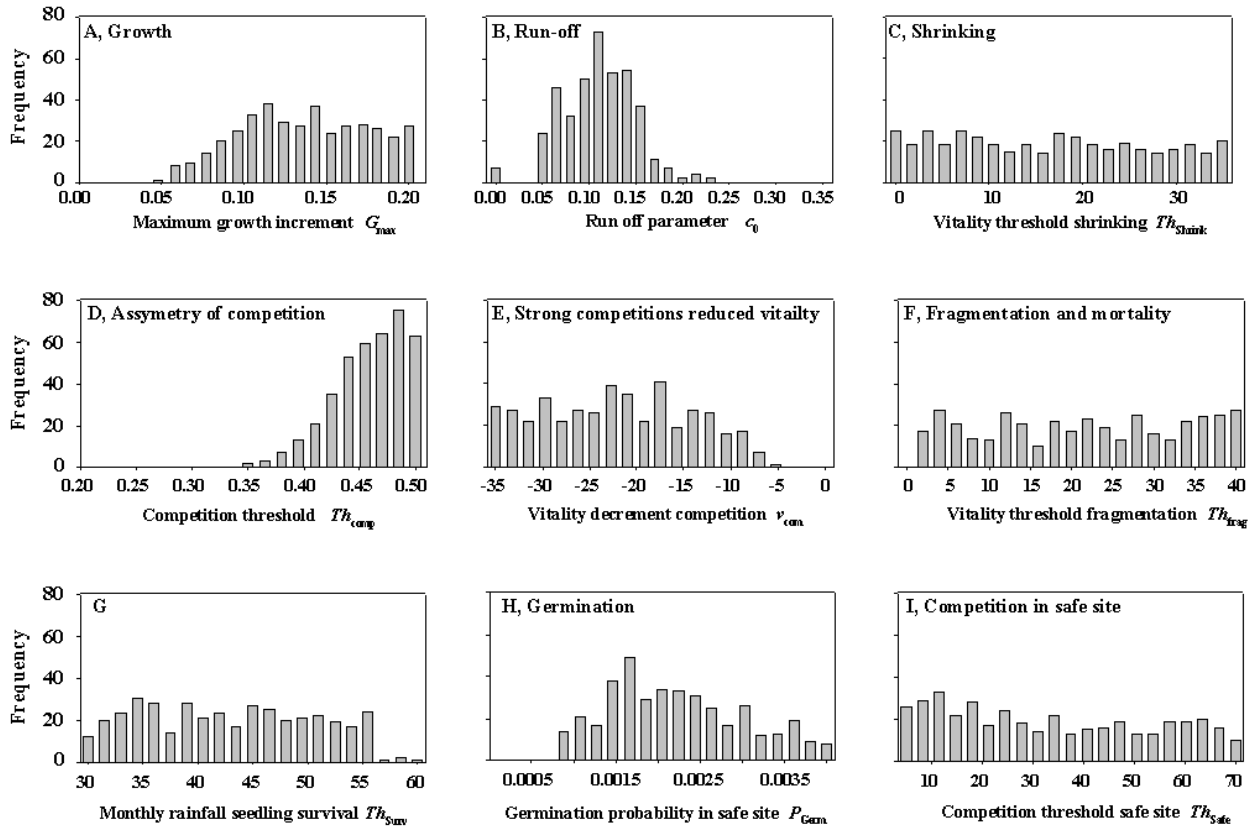


Figure 3. Frequency distribution of the parameters under complete fulfillment of all five grassland features The frequency distributions were calculated from the $n = 395$ parameterizations, out of a total of 63194 model parameterizations, which satisfy features (1), (2), (3), (4), and (5).

The frequency distribution of a parameter, taken from the 395 model parameterizations dynamics that reproduced all five observed patterns simultaneously, is a simple indicative tool to decide whether or not a process is a key demographic processes of grassland dynamics. If the frequency distribution at zero is very low, the model variant without this process was not able to reproduce one or more observed grassland features and the process is a key process. In turn, if the frequency distribution is approximately constant or “high enough at zero” the process is not necessary to produce the observed grassland features.

3.1 Growth.

As expected, growth of tufts is a key process of grassland dynamics (figure 3A). For very low growth increments, the model does not reproduce the mortality and recruitment data but we find model variants that produce overall stable grassland dynamics with little fluctuation in basal cover and species composition that fulfill patterns (1), (2) and (6). In these cases, mortality was low, tufts did not grow much, and very little recruitment occurred; the existing tufts simply remained. However, these dynamics, which might be possible if tufts regenerate vegetatively by building new tillers, contradicted our data on drought mortality and recruitment.

3.2 Runoff

We found that a model variant that did not consider loss of water in areas with low basal cover (i.e., $c_0 = 0$) was able to reproduce all patterns simultaneously, but at $c_0 \approx 0.1$ there was a clear peak in the number of model parameterizations with complete fulfillment (figure 3B). Thus, including run-off in our model enhanced its performance (i.e., with run-off there are more parameterizations with complete fulfillment), but run-off is not necessary for simultaneous pattern fulfillment. Interestingly, the biological interpretation of the maximum at $c_0 = 0.1$ is that no (local) run-off occurred if the basal cover in the 20 cm neighborhood of a tuft was above 10%. This result accords well with the results of experiments in $2 \times 15\text{m}$ run-off plots that showed that little long-term runoff occurred in grassland in good compositional state, and no run-off above an overall basal cover of some 10% (Snyman and Fouché 1991). Because larger gaps occur infrequently in grassland in good compositional state we did not need this process to reproduce the dynamical features of grassland in good compositional state. However, for the moderate or poor compositional states, which are characterized by lower basal cover [6.4% and 2.9%, respectively (O'Connor *et al.* 2001)], we anticipate that simulating run-off would be more important.

3.3 Shrinking of weak tufts

Figure 3C shows that shrinking of weak tufts was not necessary to reproduce all five patterns simultaneously. Consequently, shrinking is no key process. However, shrinking of underutilized tufts is known to be an important process at the semiarid grasslands, but it was not important during the conditions of the long-term experiment because tufts were not underutilized during the experiment: above ground biomass was clipped at the end of the growing season to simulate grazing.

3.4 Assymmetric competition

Figure 3D shows that asymmetric competition (i.e., $Th_{\text{comp}} > 0.35$) was necessary to simultaneously fulfill all five patterns of the grassland in good compositional state. Tufts that did not grow because of too much competition suffered a reduction in vitality (with decrement v_{comp}), which increased the risk of mortality and fragmentation. Thus, competition introduced a density dependent regulation in basal cover, either by preventing tufts to grow too large, or by increasing the probability of fragmentation and mortality. Several model variants with parameter values $Th_{\text{comp}} < 0.35$ were able to fulfill the patterns (2), (3), (4), and (5), but they yielded too high values of the basal cover and very high tuft densities (> 11 tufts per m^2) during seasons characterized by high recruitment. This violated pattern (1). Thus, model variants that do not consider a strong impact of competition on growth are not able to produce a sufficient level density dependent regulation necessary to obtain realistic basal cover and tuft densities during and after years of high recruitment.

3.5 Competition decreases vitality

Figure 3E shows that a decrease in vitality of tufts that suffer strong competition (i.e., $v_{\text{comp}} < -5$) was necessary for simultaneous fulfillment of all patterns. Model parameterizations with too small decrements (i.e., $v_{\text{comp}} > -5$) yielded unrealistically low tuft mortality during the 1982-84 drought. Note that the vitality directly influences tuft mortality (Fig. 1).

3.6 Fragmentation and mortality of weak tufts.

Clearly, one would assume that mortality and fragmentation of weak large tufts (i.e., $Th_{\text{frag}} > 0$) would be a key process of grassland dynamics. Our results showed a threshold behavior, model variants without mortality (i.e., $Th_{\text{frag}} = 0$, figure 3F) were not able to reproduce all patterns simultaneously, however, even small values of the parameter Th_{frag} yielded complete pattern fulfillment, and increasing value of Th_{frag} did not increase the number of parameterizations with complete pattern fulfillment. Parameter values $Th_{\text{frag}} > 0$ were necessary for reproduction of the time series of basal cover (pattern 1) and drought mortality (pattern 3). Tufts typically became weak after a prolonged period of drought, or through high competition.

3.7 Seedling survival and precipitation.

Figure 3G shows that complete fulfillment of all five patterns is possible if the monthly precipitation thresholds Th_{Surv} for seedling survival ranges between 30 mm and 56 mm. Higher water requirements (i.e., $Th_{\text{Surv}} > 56$) yielded very few years with recruitment and contradicted our data.

3.8 Germination.

Recruitment is a key process of grassland dynamics. Consequently, very low values of the germination probability (i.e., $P_{\text{Germ}} < 0.0007$) yield a grassland dynamics with too little recruitment in 2001 (figure 3H).

3.9 Competition for safe sites

Figure 3I shows that limiting competition in safe sites is not necessary for simultaneous fulfillment of the five grassland features, but there is a slight tendency for better fulfillment (i.e., there are more model parameterizations with complete pattern fulfillment) if less competition is tolerated (i.e. smaller values of Th_{save}).

4. DISCUSSION

The model presented in this article summarizes knowledge and hypotheses on key processes and factors of the dynamics of the semiarid grasslands in South Africa on the scale of individual tufts. The model simulates processes at the individual scale, but produces outputs on the community scale. These predictions arise as the outcome of interaction of the individual-scale processes with the climatic data and the management scenario (i.e., harvesting of phytomass at the end of the growing season). We compared the model output at the community scale with corresponding field data. Each field data set (= pattern) describes an important feature of grassland dynamics, and we used quantitative criteria to define fulfillment the patterns. Fulfillment of all patterns together defines a minimal requirement for (quantitatively) reasonable model dynamics.

Our first important model result is that there are indeed model variants that produce model predictions which are in accordance with the minimal requirements. Thus, our model describes important features of grassland dynamics correctly. Simultaneous fulfillment of different features of grassland dynamics, such as 19-year development in basal cover, a correct size class distribution, a correct level of drought mortality, or a correct level of recruitment is highly non-trivial and cannot be obtained with arbitrary model structures (Kendall *et al.* 1999; Wiegand *et al.* 2003a, c). Thus, our claim for simultaneous pattern fulfillment is a very strong test for our model. However, one may argue that one can always find a model that is able to reproduce an observed pattern, provided that one adds enough parameters in the model. Such a critique may hold true for “blind” statistical fits and descriptive regression models that do not rely on information on the underlying biological processes (an example is conventional statistical time series analysis). In contrast, our approach is a process-oriented approach that uses biological information on patterns and processes rather than arbitrary functions for fitting (Wiegand *et al.* 2003a).

The evaluation of different hypotheses on model processes yielded clear results. As expected for a demographic model, one would define growth, mortality, and recruitment *a priori* as key-processes of grassland demography. Therefore, it is not surprising that our results show that they are indeed key processes (see figure 3 A, F, H). However, we found that some model variants with little or no recruitment, growth, fragmentation, and mortality did nevertheless fulfill pattern 1 (the time series of basal cover), pattern 2 (composition), and pattern 5 (tuft sizes). The resulting dynamics corresponds to a case where large grass tufts persist unchanged over long periods, and where tufts would mostly regenerate vegetatively by building new tillers. However, these dynamics, although plausible, are not in accordance with our drought mortality and recruitment data. This result outlines the importance of using multiple patterns; the more criteria the model fulfills, the lower is the probability that “wrong” processes is producing the “right” patterns. This does not mean, however, that one should use indiscriminately all data as patterns that were ever collected about the system under study. Formulation of criteria and selection of patterns must be oriented towards the aim of the model and the scales of interest. We do not want a model that can reproduce everything, but a model that is best suited to answer our scientific question in relation to the available data. Additionally, one has to bear in mind that patterns describing similar features of the system will be correlated (i.e., they do not provide extra information, Wiegand *et al.* 2003c) and that the patterns bear internally uncertainties that have to be considered when defining pattern fulfillment (Wiegand *et al.* 2003a).

We found that asymmetric competition and a vitality loss due to strong competition are key-processes of our grassland’s dynamics (figure 3D, E). Model variants that did not contain asymmetric competition produced too weak density dependent regulation during and after years with high recruitment. As a consequence, basal cover and tuft densities were unrealistically high during these years. Model variants that did not contain vitality loss due to strong competition yielded too low drought mortality. Interestingly, we found that the processes runoff and shrinking of weak tufts were not needed to reproduce the five features of grassland dynamics. This result points to an important point we have to remember when interpreting our results. The current version of the model describes only a limited range of grassland dynamics and reproduced the conditions and management during the long-term experiment: we considered only grassland in good compositional state, and we did not include grazing which is a key-factor of grassland dynamics that can trigger transitions to other compositional states. We also did not include changes in the soil of degraded areas. As explained above (in sections “Results: “runoff”, and “shrinking of weak tufts”), runoff and shrinking will probably become important if we leave the domain of our current model version and include degradation and grazing.

The discussion of the last paragraph raises the question what we gain with a model that consciously ignores grazing, soil degradation (and fire), all of them processes which are evidently all important in the semiarid grassland of South Africa. The answer to this doubt is the same as the response to the question why one would performs a field experiment under controlled conditions (which do in general not include all possible conditions). In such experiments, one or more

factors are excluded by the experimental design because investigation of all factors simultaneously would be too complicated. For the same reason we started with a simpler model for a limited set of conditions. In forthcoming modeling efforts we will include, further processes (e.g., grazing, soil degradation, fire) into this minimal model, and compare the behavior of the modified model to community level data that involve transitions to different compositional states. Such iterative steps of model modification and testing with independent high-level data are a promising strategy to handle the inherent complexity of grassland dynamics. An initial model that includes all known or hypothesized processes and factors would be too complex to analyze, even with advanced methods such as the pattern-oriented modeling strategy (Grimm *et al.* 1996; Wiegand *et al.* 2003a, c). In the past, the use of individual-based and spatially explicit simulation models has been heavily criticized because of high data requirements, problems associated with parameter estimation and possible magnifications of parameter errors. It was also argued that these models are often unnecessarily complex and arbitrary in the inclusion of detail, and lack the rigorosity of analytical approaches (Kareiva *et al.* 1997; Beissinger and Westphal 1998; Wiegand *et al.* 2003c).

In addition to the results presented here, our model can produce a number of further predictions (i.e., the recruitment and mortality rates during each simulation year). Because of the high structural realism of our individual-based model we can test these model predictions with specific field trials. This will provide new data for further model validation and for increasing our understanding on grassland demographics and dynamics.

Our approach provides a link among scales and integrates data from different hierarchical levels. We used data and natural history knowledge on the scale of individual tufts for model construction, and we calibrated the model with data on the community scale. In this, our model facilitated the combination of information from different scales into a single framework. It also provided means for studying the consequences of rules formulated on lower hierarchical levels for the dynamics at higher hierarchical levels. Because processes on the individual scale produce ultimately phenomena on the community scale, and because of the mismatch between relevant spatial and temporal scales and the experimentally feasible scales, it is difficult to analyze the link among scales of grassland dynamics with purely experimental or descriptive approaches.

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