

Modelled effects of grazing strategies on native grass production, animal intake and growth in Brahman steers

Walter Svinurai¹ , Abubeker Hassen^{1*} , Eyob Tesfamariam²  and Abel Ramoelo³ 

¹ Department of Animal and Wildlife Sciences, University of Pretoria, Pretoria, South Africa

² Department of Plant and Soil Sciences, University of Pretoria, Pretoria, South Africa

³ Department of Geography, Geoinformatics and Meteorology, University of Pretoria, Pretoria, South Africa

*Correspondence: abubeker.hassen@up.ac.za

Inadequate information about the long-term effects of grazing strategies on native grass production and animal growth poses limitations to sustainable management of beef cattle. A 20-year simulation study was conducted using the Sustainable Grazing Systems model to analyse implications of different stocking rates (SRs) and simple rotational grazing systems (SRGSs) for rangeland-based Brahman steers. Simulations included three SRGSs (two, three and four paddocks per herd) and four SRs that were compared for their effects on grass production, dry matter intake (DMI) and live weight gain (LWG). Stocking rates included a recommended SR of 10 ha livestock unit (LU)⁻¹, 30% high (7 ha LU⁻¹) and, 50% and 100% low (15 and 20 ha LU⁻¹), respectively, SR. Overall, there were no observable differences in the long-term response of grass production and DMI to all treatments for SRGS and SR. In addition, effects of SRGSs on animal production were almost similar across treatments in short and long timeframes, but differential responses of LWG to SRs were more pronounced regardless of time. These findings provide a useful criterion for choosing effective SRs to achieve sustained grass and animal production with lowest risk.

Keywords: animal production, grazing system, stocking rate, sustainability

Introduction

Despite their importance to economic development, extensive beef production systems in semi-arid rangelands of southern Africa have evolved from highly variable climatic conditions (Walker et al. 1981). Management of these rangelands is difficult as decisions must be adapted to large variation of seasonal climate and persistent droughts. In the past fifty years, grazing experiments led to advances in grazing management concepts aimed to enhance the decision-making skills of ranch managers (Stuth and Maraschin 2000). However, experiments have limited scope to represent the huge variation in climate and environment in rangelands and have often provided inconclusive results about the viability of grazing strategies across locations (Briske et al. 2008). Moreover, there are disagreements between experimental and experiential knowledge about the effects of grazing systems and stocking rates (SRs) on forage and animal production (Teague et al. 2013). Recently, research emphasis has shifted to the overriding interactive influence of climate variation and SRs on forage production and cattle weight gains (Reeves et al. 2013, 2014). For research to be valuable to managers, there is need for embracing a systems analysis approach that enables recommendations to be made at grazing management unit level based on long-term, landscape-level changes.

Whole farm system models give quantitative description of interactions of components in rangeland systems, some of which have opposing effects and are too complex to be analysed by the human mind (Rickert et al. 2000).

Simulation models provide state variables of the soil–plant–animal system that enable the analysis of the long-term growth patterns of grass and cattle relative to climate conditions (Doran-Browne et al. 2014; Fang et al. 2014). In southern African savanna rangelands, previous efforts in modelling the impacts of grazing strategies have been limited to deterministic and stochastic approaches (Illius et al. 1998; Richardson et al. 2000), mostly applied on a short-term basis (Kazembe 2010). These types of models, however, are founded on animal component models that do not accurately predict body composition, due to lack of detailed and accurate experimental data (McNamara et al. 2016). However, fat and protein deposition are influential variables for predicting nutrient requirements for growth in animals of different breeds (Tedeschi 2019). Given that mechanistic models contain default parameters for body composition that are adjustable across genotypes, they offer model users opportunities to adequately represent metabolism and growth dynamics in regions with limited measured data. Thus, extending the use of mechanistic models to long-term impact assessments of grazing strategies will assist ranch managers in making strategic decisions.

Process-based models (PBMs) are a subset of mechanistic models that explicitly integrate different levels of biological organisation to understand the behaviour of grazing systems and to compare the productivity and sustainability impacts of management practices (Tedeschi

2019). The models have many built-in management options that enable detailed simulation and impact analysis of management actions. Stocking rate and adequate resting are key management factors that influence animal production under simple rotational grazing systems (SRGSs) in extensive rangelands of southern Africa (van de Pol and Jordaan 2008). Stocking rate causes variability in herbaceous vegetation community and production and animal weight gains (Derner et al. 2008), with the grazing effects varying by location, climate and timing and period of grazing (Teague et al. 2008). Interactions between the biophysical and management factors are complicated and difficult to quantify or comprehend yet they are important in decision-making. Therefore, there is need for broadening experimental knowledge by using PBMs that effectively incorporate soil, plant, and animal inputs to explicitly represent the complex interactions in rangelands and improve management planning.

Process-based models have been widely applied to assess the influence of rotational grazing systems and SRs on rangeland and cattle production in the wet and dry regions of North America (Fang et al. 2014) and northern Australia (Doran-Browne et al. 2014), respectively, but rarely in southern African rangelands. Nevertheless, the current SRs for Zimbabwean rangelands are still based on archaic recommendations for agroecological regions (Vincent and Thomas 1960). Considering the increase in dry years and decrease in wet years that occurred in the region after the 1970s' global climate shift (Gaughan et al. 2016), there is possibility that the seasonal dynamics of grass production and livestock carrying capacities changed too. This emphasises the need for re-evaluating the current grazing strategies under changing grazing pressures to prevent degradation of herbaceous vegetation. Process-based models provide useful information needed to improve ranch managers' skills for selecting effective long-term SRs that avoid deterioration of herbage condition (O'Reagain et al. 2014). The models are capable of resolving the proper combination of rotational grazing systems and SRs, thus enabling ranch managers to choose grazing strategies that maintain plant vigour, composition and productivity (Teague et al. 2013). In this study, the animal module of the Sustainable Grazing Systems (SGS) model was parametrised and used in the whole model to test the hypothesis that change of SRGSs and SRs from those recommended for the northern Limpopo river basin does not affect grass production, intake and growth of Brahman weaner steers.

Materials and methods

Description of the modelled beef production system

The study area comprised 1 139.13 km² at the Nuanesti ranch (21°25'12" S, 30°43'48" E) at an altitude of 480 meters above sea level, directly north of the Limpopo river basin in the southern Lowveld of Zimbabwe. The region has comparative advantages for commercial beef production (Mavedzenge et al. 2006) and commercial beef systems are based exclusively on exotic breeds, with the Brahman genotype and its crossbreeds making 60 to 70% of the total commercial herd (Norval 2016). The climate of the study

area is semi-arid subtropical with strongly seasonal wet summers, and long cool dry winters. Long-term mean annual rainfall is 460 mm. Mean annual temperature is 25 °C. The soils are predominantly dark brown, shallow chromic luvisol of medium texture that are formed from mafic-gneiss parent material. At landscape scale, the vegetation is dominated by moderately tall *Colophospermum mopane* tree stands that cover most of the area. This canopy supports a medium understory of palatable perennial suit of tufted grasses, mostly monospecific stands of *Urochloa mosambicensis* and *Panicum maximum* under shade. Some patches of sparse tree-shrub layer of *Combretum* and *Grewia* spp. that are associated with short, unpalatable grass species, such as *Eragrotis* spp. and *Aristida* spp., are visible (Farrell 1968). At plant community level, three vegetation types namely; closed woody life forms, closed to open tree/shrubs, and open herbaceous vegetation dominate the study area. Given its large spatial coverage, the ranch presents a complicated land use system that requires high level of management for viability of large herd sizes.

The ranch operates an extensive 'breed and sell' beef production system with a capacity of 10 000 cattle. The 'breed and sell' beef production system involves two intermeshed systems, that is, a breeding system for herd replacement and a system for producing calves for sale. The paddocks range in size from 350 to 1 500 ha with an average size of 500 ha. Depending on size, each paddock has up to three water points that are sited strategically to achieve even use of forage resources. Each herd is managed in a grazing management unit comprising of two, three or four paddocks. Cows are bred between December and March and are culled based on their performance records. Supplementation with protein-rich supplements is done in some dry seasons when necessary. Calves (i.e. progeny <120 kg) are weaned at seven months of age, reared on the veld until they reach 18 months, at which time they are either upgraded to one-year old steers and heifers or sold. Animal productivity is very high and up to 100 kg per head per year post-weaning weight gain can be achieved.

The animal growth modelling tool

Overview of the SGS animal module

The SGS animal module was developed by Johnson et al. (2012) with the intention of integrating it with the pasture module into a whole-system biophysical model. The whole-system model is meant to simulate animal growth and its response to pasture, forage, concentrate and mixed ration when supplied as combined feed (Johnson 2016). The animal module was developed to simulate intake in cattle and sheep in relation to feed composition of crude protein (CP), neutral detergent fibre (NDF) and neutral detergent solubles, animal weight and pasture quality and availability. The intake is then converted into metabolisable energy (ME), which is used for metabolic processes of growth, maintenance, lactation, and pregnancy in the simulation, thus affecting these processes directly. Energy dynamics in the animal's body depend on the balance between ME intake and the ME requirement for a class and breed of animal. Growth and energy dynamics are simulated in response to energy available in the body, which include

water, protein and fat (Johnson et al. 2012). The module simulates animal growth by partitioning metabolisable energy intake into maintenance and growth or pregnancy, lactation and nitrogen dynamics, which were recently included in the model by Johnson et al. (2016). Animal protein content determines the state of metabolism and its growth is simulated as a function of protein weight. The potential protein growth is deduced as the difference between protein synthesis and degradation. Fat growth is modelled as a secondary process related to protein growth and maximum potential fat fraction of body weight. Normal growth occurs if the energy intake is enough for potential protein growth and associated fat growth. The model contains default parameters for energy that have been defined for energy densities and efficiencies of synthesis for protein and fat, and efficiencies of fat catabolism and protein degradation.

Animal and feed management parameters

The SGS animal module has many parameters for growth and reproduction that were not available at the mechanistic level required for all cattle classes found at the ranch and, thus the animal module was parameterised for steer calves only. The parameter values were prescribed using published literature, whereas default values were maintained where information was not available (see Table 1). A Gompertz coefficient of 2.6% per day for initial specific growth rate of empty body weight (EBW) protein content in Brahman cattle was used (Miguel et al. 2012). The fat growth coefficient of 0.03 kg fat per kg protein per day set in the model as the maximum daily fat deposition as a fraction of EBW protein content was also used for cattle (Johnson et al. 2012). The protein and fat content of body weight gain and expected body fat content at a given weight depend on rate of daily weight gain (National Research Council 2000). Parameters for body fat content were adjusted to represent an average daily gain (ADG) of 1 kg for medium-frame beef cattle.

The feed management parameters of the SGS were adjusted on the basis that the high dietary CP in *C. mopane*-dominated savannas, persist long into the dry season and could be responsible for maintaining animal weight during the dry season (Hooimeijer et al. 2005). Thus, the composition of forage supplement in the SGS model was set to represent the annual average nutritive value of browsable leaves of three woody species dominant in the study area namely, *C. mopane*, *C. apiculatum* and *G. flavescens*. The annual average CP content of the browse in the Limpopo river basin have been observed to be 12.5, 13.5, 13.2 and 12.2% by Kos et al. (2012),

Codron et al. (2007), Lukhele and van Ryssen (2002), and Hooimeijer et al. (2005), respectively. An average value of 12.8% CP was thus used. Studies conducted by Lukhele and Ryssen (2003) and Codron et al. (2007) show that NDF content of the browse range from 35.2 to 38.4%. An average NDF content of 36.8% was set for the browse supplement in the model and this value was used to calculate the NDF digestibility from *in vitro* DM digestibility, using the formula of Hoffman et al. (2001). The maximum forage dry matter intake (DMI) was set at 2.2% of mature body weight, since the grass in Sweetveld is palatable and highly digestible. The CP%, NDF% and NDF digestibility values of concentrate were set at 12, 20 and 60%, respectively, based on nutrient requirements for steers growing on tropical native pasture (Sibanda 1998).

Preliminary model simulations were run to test whether animal production can be sustained with grass only, grass and forage supplement or grass supplemented with forage and concentrate. These simulations revealed that cattle under a grass-based diet persistently lost weight over time, while adding concentrate to grass and forage in the animal diet provided marginal growth benefits (see Figure 1). Therefore, feed management parameters for grass supplemented with browse foliage were used in all simulations for evaluating grazing management impacts.

Model calibration and evaluation

The overall structure and performance of the SGS model in simulating observed grass aboveground biomass at the study area have been evaluated in different contexts (Svinurai et al. 2021). Model parameters for soil and plant were modified using values obtained from soil surveys previously conducted at the ranch (CSRI 2007). Plant canopy structure and growth parameters for key grass species were obtained from published literature. To calibrate the model, the model was run using daily climate inputs until modelled grass biomass was similar to peak-season biomass measured during the 2016–2017 season, and Normalised Difference Vegetation Index calculated from pixels corresponding to sampled plots. The SGS model represented measured grass biomass moderately well at reasonable overall prediction error ($R^2 = 0.57$; RMSE, 820 kg DM ha⁻¹), and predictions were also significantly correlated with remotely sensed grass biomass ($R^2 = 0.46$; RMSE, 981 kg DM ha⁻¹). Model evaluation was performed by comparing modelled with long-term remotely sensed grass biomass estimated from peak-season, cloud-free Landsat images. These

Table 1: Animal weight, body composition and growth parameters used for Brahman weaner steers

Animal parameter (units)	Default value	Weaner steer	Reference
Birth weight (kg)	50	32	Pico et al. (2004)
*Normal mature weight (kg)	600	431	Schoeman (1996)
Fat at normal mature weight (%)	30	25.6	National Research Council (2000)
Fat at maximum mature weight (%)	45	28.5	National Research Council (2000)
Gompertz coefficient: initial protein specific growth rate during growth (% d ⁻¹)	1.2	2.6	Miguel et al. (2012)

*Body weight of bulls at approximately 430 days of age

comparisons were significantly correlated ($R^2 \geq 0.63$; $p < 0.05$), but as expected, the SGS model underestimated remotely sensed biomass. A global sensitivity analysis was also performed to ascertain the extent of parameter adjustments on model output behaviour relative to biomass production patterns known for grasses native to the study area. The model calibration and evaluation results were presented to more than fifty experts in range science and animal production at the 54th Annual Conference of the Grassland Society of Southern Africa, with mostly positive feedback. Observed data for daily DMI and live weight were not available for Nuanetsi ranch. Thus a technical evaluation was done to assess whether model responses were reasonable relative to published information for extensively managed medium-frame beef cattle in the region.

Evaluation of grass and animal responses to grazing strategies

Ecological considerations for managing semi-arid rangelands of southern Africa depict that grazing strategies should be designed with a view to maintain or improve the grazing resource by fixed moderate, but persistent level of stocking (Danckwerts et al. 1993). This is achieved by controlling the period of stay and absence of grazing to enable productive perennial grasses to grow at desired quality (van de Pol and Jordaan 2008). Based on these propositions, two facets of grazing management were analysed. Firstly, the impacts of SRGS were analysed followed by evaluation of the sustainability of SRs widely recognised for the region. In Sweetveld, Barnes (1979) reported that use of three paddocks or less per herd provide the basis for maintaining or improving the grazing resource, whereas Danckwerts and Daines (1981) recommended use of two paddocks (alternate stocking), three or four paddocks per herd. High herbaceous biomass production in semi-arid rangelands is enhanced by short period of stay and long periods of absence by cattle (Kazembe 2010). As a result, the effects of periods of stay of 5, 10, 15 and 20 days, respectively, were tested by running the model for each period of stay and SRGS. The most bearable period of stay for each SRGS was used to compare the impacts of the three SRGSs. The most sustainable SRGS was then considered for the assessment of SRs.

A preliminary review of SR recommendations for the region suggest SRs of 1 livestock unit (LU): 9.6 and 1 LU: 10 ha for cattle grazing for Nuanetsi cattle ranch (Walker 1976) and Buffalo Range ranch (Taylor and Walker 1978), respectively. The SR of 1 LU: 10 ha was thus considered as the recommended rate for the ranch. Regional recommendations of SRs for the semi-arid rangelands of southern Zimbabwe vary widely from 1 LU: 12 to 20 ha (Vincent and Thomas 1960) to 1 LU: 6 to 12 or more ha (Barnes 1979). To represent the wide variation in SRs for region, the recommended SR was increased to 1 LU: 7 ha and lowered to 15 and 20 ha LU⁻¹. The impacts of four SRs on the sustainability of herbaceous plant and animal production were analysed. The number of weaner steers required to match each of the SRs was determined using the formula $LU = 450^{0.75}/W^{0.75}$, where W is the average weight of an animal; and LU, livestock unit. The LU, also known

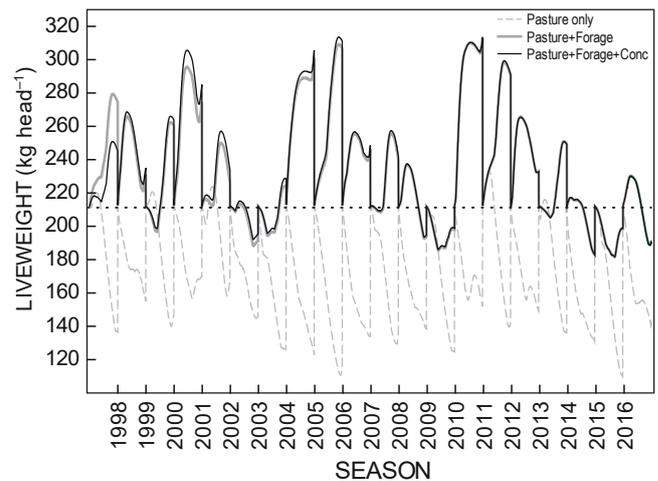


Figure 1: Live weight of weaner steers weaned in July (even numbered years) and January (odd numbered years) under three feed management practices. The dotted line represents the weaning weight of calves

as an animal unit, is defined as medium-frame beef steer with a live weight of 450 kg, which gains 0.5 kg d⁻¹ on grass pasture, with a digestible energy of 55% (Meissner 1983). The animal unit requires 75 MJ ME d⁻¹.

Model simulation runs

The SGS pasture model has up to 100 paddocks that can be modelled individually in different soil types, soil nutrient conditions, pasture species and stock management practices. It was recognised that rangeland condition and species composition could have changed over the past 30 years, due to impacts of grazing strategies. However, modelling those changes was beyond the scope of the study. Thus, the model was applied to a typical grazing management unit in the mid-slope land type, which was widely spread across the study area, with monospecific stands of *U. mosambicensis*. Simulation experiments were performed between July 1988 and June 2017 in individual paddocks to examine grass production and animal production response to separate treatments of three SRGSs and four SRs. The grazing management units were constituted by two, three or four paddocks per herd in the grazing system simulation experiment, whereas a three paddock per herd system was used for the SR simulation experiment. The area of paddocks modelled was set at 500 ha representing the average size of paddocks at the study site.

Daily climate data namely solar radiation (Wm⁻²), rainfall (mm) and minimum and maximum temperature (°C) for Nuanetsi ranch obtained from *in situ* and geo-spatial data were used as inputs. The starting weight for Brahman weaners, that is 205-day weight at approximately seven months, was set at 212 kg (Pico et al. 2004), whereas normal mature weight of Brahman cattle was set at 431 kg (Schoeman 1996). The weaner steers were brought into the paddocks in July and January in even- and odd-numbered years, respectively to represent the recommended weaning periods in the region. The weaners were managed on a

fixed-time rotation basis in three four-month phases and were removed after one year. Twenty repeated annual assessments of grass production, intake and animal growth were performed for each treatment in two, three or four replicate paddocks to produce 40, 60 and 80 site-by-year observations corresponding to the three SRGSs. At the beginning of each simulation run, coordinates and elevation of the central point of each paddock were entered in the model to enable adjustment for environmental conditions at that paddock. Output from the first 10 years of each simulation were discarded as this period was regarded for allowing model parameters to stabilise to levels that are typical of the real system. Daily model outputs produced in each paddock were averaged to come up with weighted grass production (kg DM ha⁻¹), dry matter intake (kg head⁻¹ d⁻¹) and live weight (kg head⁻¹) for each grazing management unit.

Analysis of model outputs

The behaviour of model outputs from simulation runs for three SRGSs and four SRs were separately analysed over a 20-year period. Graphical analysis of time series was done to detect long-term differences in response of grass and animal to grazing management practices. The median, minimum, and maximum values of grass and animal production were derived from box-and-whisker plots to determine the short-term responses in selected dry and wet seasons. The dryness or wetness of seasons was characterised using the standardised precipitation index (SPI) of McKee et al. (1993). The SPI identified mild drought seasons in 1998, 2006, 2011 and 2012 and a moderate drought in 2005. The box-and-whisker plots were used to describe the central tendency of variables for the selected seasons. The variability in the values of variables was represented in this plot by the 25th and 75th percentiles, the larger box in the box-and-whisker plot, whereas the minimum and maximum values of the variable were represented by the 'whiskers' in the plot. Relative difference in grass production, animal intake and final live weight between simulated outputs of grazing management options were also calculated.

Results

Overall, there were no observable differences found in the long-term response of grass production and DMI to all treatments for SRGS and SR. In addition, simple rotational grazing effects on animal production were almost similar across treatments in both short and long terms, but differential responses of LWG to SRs were more pronounced across timeframes. Weaners stocked at the recommended SR grew persistently at high rate, reaching a final LW of 234 kg over one year, but animal productivity was adversely affected in the long-term. Increasing the recommended SR by 30% resulted in reduced LW of weaners in the short term whereas 50% lower SR achieved sustained high animal intake and growth.

Effects of stocking rates on plant and animal responses

The effects of four SRs on grass production, DMI and final LW are presented in Figure 2. Descriptive statistics of

grass production modelled between 1998 and 2017 show that grass yield averaged approximately the same (2 524 to 2 586 kg DM ha⁻¹) across the four SRs, ranging from 990 to 3 700 kg DM ha⁻¹ (see Figure 3a). The coefficient of variation in grass production ranged from 23% for high SR (7 ha LU⁻¹) to 27% for SRs of 15 and 20 ha LU⁻¹ over the 20 years. The DMI of weaners was approximately similar among the four SRs with an average of 5 kg head⁻¹ d⁻¹ and ranging between 3.8 and 7.3 kg head⁻¹ d⁻¹. Mean final LW of weaners stocked at 7 ha LU⁻¹ varied by 9 kg from the final LW of weaners (234 kg) stocked at the recommended or lower SRs. The minimum LW of weaners ranged from 179 kg in 20 ha LU⁻¹ to 183 kg in 7 ha LU⁻¹ (Figure 2c). Maximum final LW of 345 kg head⁻¹ for weaners stocked at the recommended rate was 32 kg more than maximum final LW of weaners stocked at 15 ha LU⁻¹ over the 20-year period. Despite the high LWG response, the pasture stocked at the recommended rate only supported a sustained DMI and LW during the first 13 years, after which animal productivity was adversely affected (Figure 2). Increasing SR by 30% from the recommended rate resulted in reduced DMI and LWG of weaners over four to five years seasonal cycles (Figures 2b and 2c). Grass from paddocks stocked at 50 to 100% lower SRs than the recommended rate persistently supported animal intake and growth over the 20 years (Figures 2b and 2c) though there were no justifiable animal responses for increasing the SR beyond 50%.

Differences in model outputs of grass and animal production among the four SR treatments were also pronounced during mild and moderate drought seasons. For example, during the mild drought season of 1998, DMI and LW of cattle stocked at 15 ha LU⁻¹ exceeded that of cattle stocked at the recommended SR by 1 kg head⁻¹ d⁻¹ and 45 kg head⁻¹, respectively, despite having grass production that is 14% (300 kg DM ha⁻¹) less (Figure 3). During the moderate drought season of 2005, the final LW was almost similar between weaners stocked at recommended rate and 50% low SR though grass production from paddocks stocked at recommended rate was 66% higher. The greatest loss in DMI and LW between a 30% high SR and the recommended rate was observed in subsequent below-normal rain seasons. For example, in 2006 and 2007, the DMI of weaners stocked at the recommended rate fell by 1.1 and 0.7 kg head⁻¹ d⁻¹, whereas the final LW was 81.7 and 35.6 kg head⁻¹ lower, respectively (Figure 3).

Effects of simple rotational grazing systems on plant and animal responses

Grass aboveground biomass production modelled between 1998 and 2017 show that biomass averaged approximately the same (2 515 to 2 560 kg DM ha⁻¹) across the three SRGSs, ranging from 1 000 to 3 600 kg DM ha⁻¹ (see Figure 4a). The lowest coefficient of variation in grass production of 23% was observed in the alternate stocking system, whereas the three and four paddock systems had the highest CV of 27% over the 20 years. Alternate stocking showed a consistently opposing trend in grass production relative to the three and four paddocks per herd systems. The DMI of weaners did not vary widely among

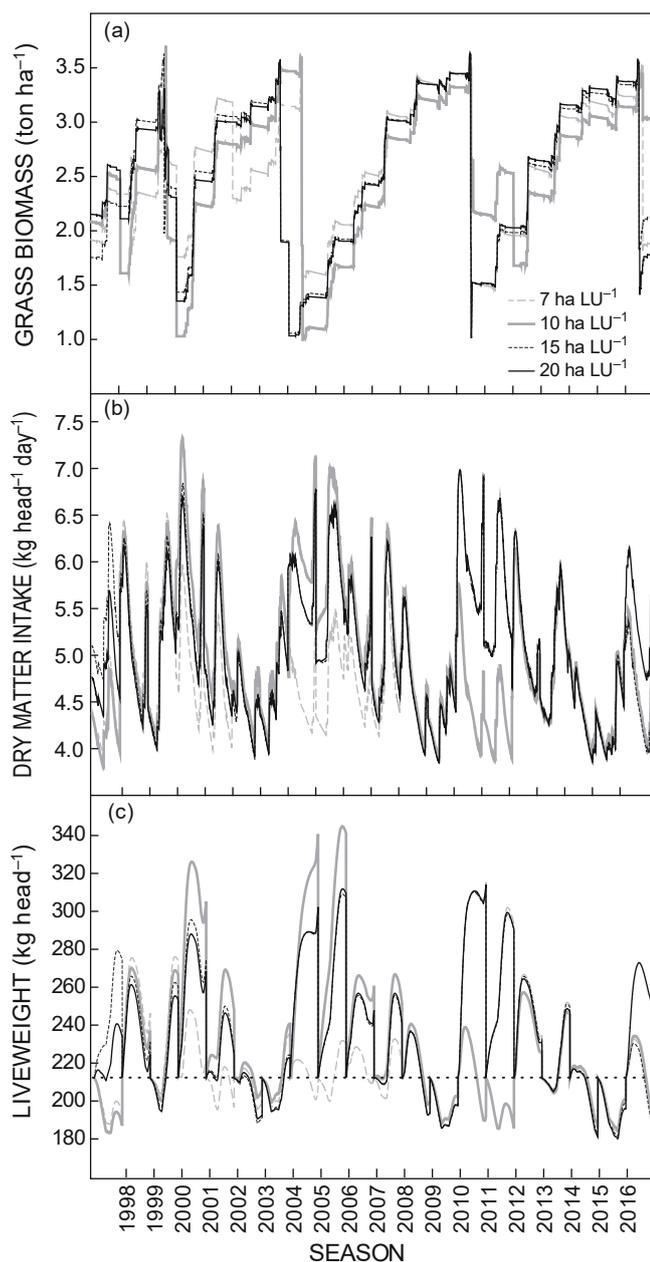


Figure 2: Model outputs of (a) grass biomass, (b) dry matter intake and (c) live weight of weaner steers weaned in July (even numbered years) and January (odd numbered years) under three paddock systems. The dotted line in (c) represents the weaning weight of calves

the three SRGSs. It ranged between 3.8 and 7 kg head⁻¹ d⁻¹ and averaged at 5 kg head⁻¹ d⁻¹. In addition, the mean LW of weaners was almost similar (231 to 234 kg) across the three SRGSs. The minimum loss of LW of weaners of 180 kg was the same across the three SRGSs evaluated (Figure 4c). Maximum final LW of weaners of 331 kg head⁻¹ was obtained under alternate stocking, however, exceeded the LW of weaners in the recommended grazing system by 17 kg over the 20-year period. Dry matter intake and LWG of weaners in the alternate stocking system declined drastically after 13 years (Figures 4b and 4c).

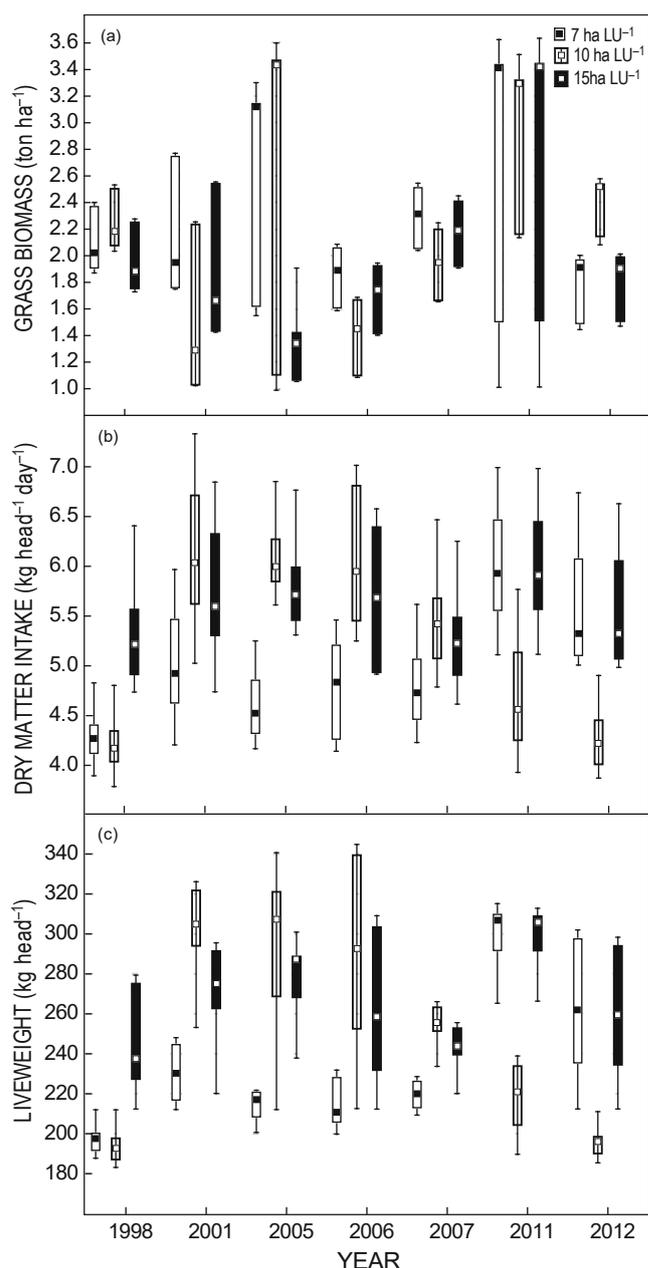


Figure 3: Box-and-whisker plot of (a) grass biomass (b) dry matter intake and (c) live weight of weaner steers stocked at three stocking rates for selected years. The smallest box in the box-and-whisker plot represent median values

The most noticeable differences in grass and animal productivity among the three SRGSs were observed during mild and moderate drought seasons. Despite 14% (300 kg DM ha⁻¹) more herbage yield than the three paddocks per herd system during the mild drought of 1998, LWG of weaners in the alternate stocking system was 20.4 kg lower. During the moderately dry season of 2005, final LW of weaners was almost similar between the alternate stocking and the three and four paddock per herd systems though herbage yield was 66% higher in the alternate stocking system. The greatest loss in DMI and LW was

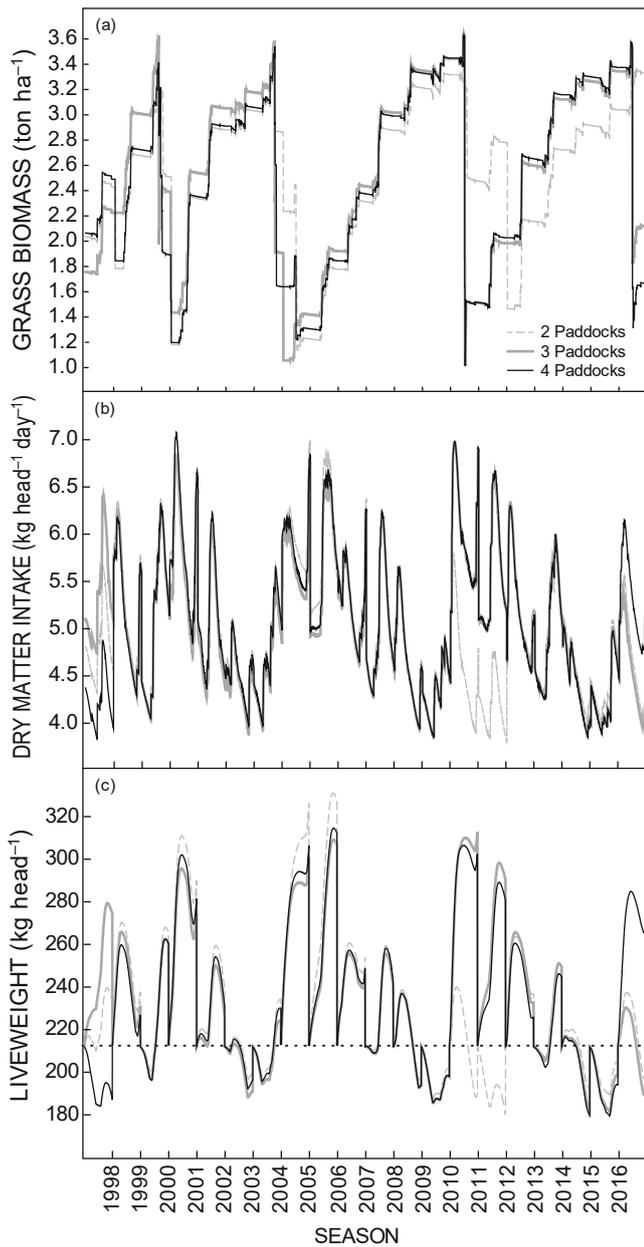


Figure 4: Model outputs of (a) grass biomass, (b) dry matter intake and (c) live weight of weaner steers weaned in July (even numbered years) and January (odd numbered years) under three paddock systems. The dotted line in (c) represents the weaning weight of calves

observed succeeding mildly dry seasons. For example, in 2011 and 2012, the DMI of weaners in the alternate stocking system fell by 1.4 and 1.2 kg head⁻¹ d⁻¹, whereas the final LW was 85.1 and 65.4 kg lower, respectively (Figure 5).

Discussion

This study has demonstrated the effect of SRGSs and SRs on plant and animal responses. Overall findings showed that there are no observable differences in herbage

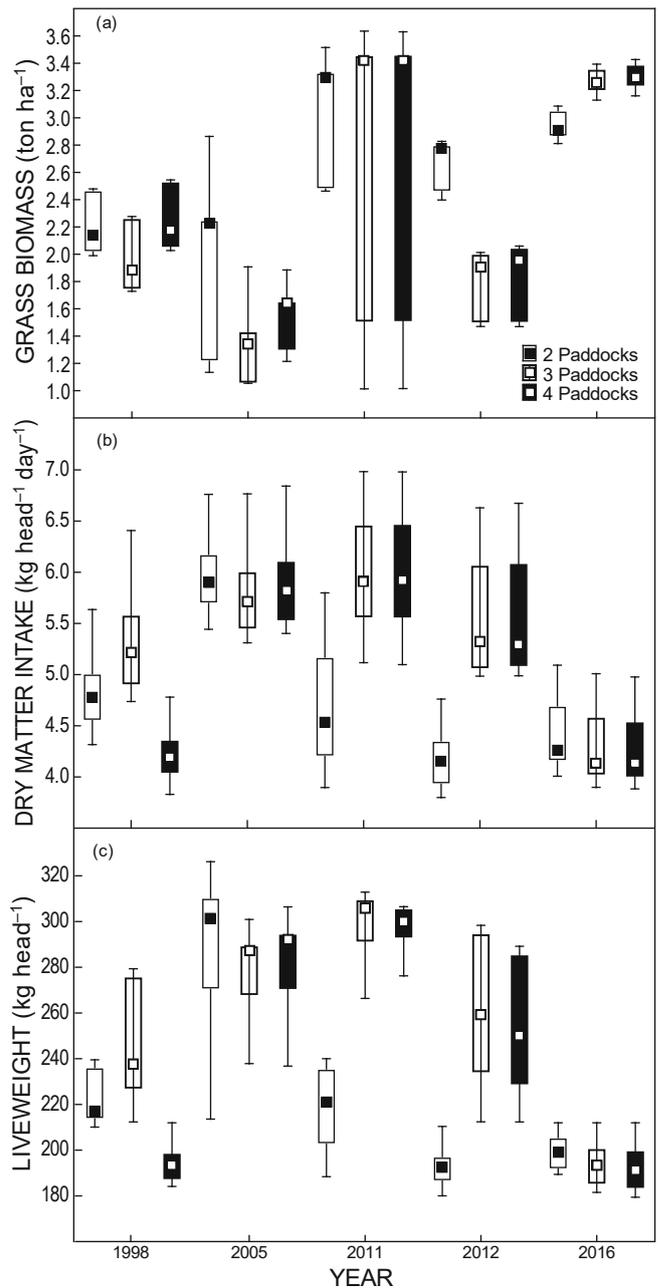


Figure 5: Box-and-whisker plot of (a) grass biomass, (b) dry matter intake and (c) live weight of weaner steers stocked in three multi-paddock grazing systems for selected years. The smallest box in the box-and-whisker plot represent median values

production and DMI response to all treatments for SRGS and SRs. In addition, SRGSs displayed approximately similar effects on animal production across treatments, but differential responses of LWG to SRs were more pronounced. Increasing the recommended SR resulted in reduced DMI and LWG of weaners in the short term, whereas persistently high animal intake and growth occurred in the long term under reduced SR. These results illustrate the potential of PBMs in providing direction for selecting the appropriate SR that achieves a continuous

grass and animal production with minimum risk in the long term. Generally, the findings suggest that ranch managers should put more management emphasis on SRs over SRGSs, since proper SRs enable maximised cattle productivity over time.

Effects of stocking rate on plant and animal responses

The findings reveal that, irrespective of the SR, there were no observable differences in grass production. This implies that the periods of stay and absence of grazing tested were within the levels of stocking that maintain the grazing resource in pauci-paddock systems (van de Pol and Jordaan 2008). There have been mixed views about the grass biomass responses to further increases in SRs from the recommended rate in tropical rangelands. In agreement with our findings, considerable number of studies have shown that increasing SR from the recommended rate does not show distinguished differences on grass production in multi-paddock rotational systems in nutrient-poor rangelands of south western Zimbabwe (Denny and Barnes 1977; Gammon 1978; Barnes and Denny 1991). Also, modest SR increase above the recommended rate posed little adverse effects on native pasture condition or individual animal performance in tropical Australian savannas in a modelling study (Scanlan et al. 2013).

However, some studies observed that LW gain in individual animals decrease as SR increases across stocking intensities in a semi-arid Lowveld of southern Africa (Hatch and Tainton 1995). Decline in pasture condition was also realised when SR was increased above the long-term carrying capacity in simulations across nine regions (Scanlan et al. 2011). These inconsistencies in observed grass responses reveal that the extent to which SRs can be increased without reducing grass production is not clear. The response may differ with intensity of stock rotation and period of absence (van de Pol and Jordaan 2008) or paddock size (Teague et al. 2013). Illius et al. (2000) noted that grass responses to various SRs differ across climate regions and locations, due to differences in soil nutrient status. Assessment of the subsequent effects of high SRs on DMI and LWG could enable a better understanding of the biophysical impacts.

The findings showed that increasing SR from the prescribed rate reduces animal intake and production, a widely recognised opinion. Similarly, Hatch and Tainton (1997) observed that individual steer weights decreased with increasing SR in tropical southern African savanna. In northern Australian rangelands, very high SRs led to reduction in LWG per hectare (Scanlan et al. 2013). The reduction in animal performance at high SR shown in this study can be attributed to reduction in grass availability per animal. Stocking rates higher than the recommended rates often result in reduced plant vigour and productivity, due to reduced root energy reserves necessary for quick regrowth (Peddie et al. 1995). Considering that increasing the prescribed SR by 30% resulted in reduced DMI and LWG of weaners in the short-term, stocking cattle above the reference SR is very risky in the study area. However, other field studies showed that steer production per hectare increased with increasing SRs. In southwestern Zimbabwe, Barnes and Denny (1991) observed that a SR twice the

recommended regional average sustained steer weight gains per hectare for 5 years without causing adverse effects on rangeland condition. Their grazing experiment was conducted in small paddocks (<50 ha) over short to medium timeframes (5–11 years). Such field studies do not represent all the actual conditions in rangelands where large paddocks up to 1 500 ha are grazed over many decades (Teague et al. 2013). These findings illustrate that, animal production responses to high SRs are difficult to compare across grazing systems and may differ with paddock size and unit of observation. As such, the extent to which SRs can be increased to sustain grass production and attain optimum animal production over long timeframes tends to be location-specific. This emphasises the importance for location-specific assessments of different SRs on cattle productivity.

Effects of simple rotational grazing systems on plant and animal responses

Strategies of using two to four paddocks per herd at a SR 50% lower than the recommended rate enabled pastures to recover periodically throughout the growing season and sustained steer production over time. Similar findings were obtained for a high intensive grazing system in the mesic regions of central Zimbabwe (Denny et al. 1974). These simple, low management-intensive rotational grazing systems can allow one-third of the grazing management unit to be utilised, while resting the remainder and enabling adequate growing season recovery in each paddock every two to four years (van de Pol and Jordaan 2008). This creates forage reserve that can be carried over to the next season to reduce forage deficits associated with climate variability. As with other studies for varying SRs, some studies have illustrated that responses of grass production are the same irrespective of grazing system (Heitschmidt et al. 1987; Barnes and Denny 1991). Using a modelling approach, Noy-Meir (1976) found little effect of moderate rotation with few paddocks and short grazing cycles on plant productivity in arid rangelands. As expected, increasing the number of paddocks from 2 to 4 per herd resulted in increased DMI and LWG. The findings concur with those from a simulated high intensity system in which a linear increase in cattle growth when paddocks per herd were increased (Kazembe 2010). The benefit of increasing the number of paddocks per herd is that it enables range managers to control grazing resources, but time and management inputs also increase.

Overall, this modelling study contributes to previous experimental knowledge (Barnes and Denny 1991) and modelling studies (Richardson et al. 2000; Kazembe 2010) for semi-arid rangelands of southern Africa by assessing the long-term effects of SRGSs and SRs on grass and animal production. The whole-farm mechanistic model and its results do not focus on explicit assessment of the model, but demonstrate the potential utility of a real-time animal modelling system for impact analysis of management actions. The current model application approach combined data and assumptions to answer 'what if' questions (Thornley and Johnson 2000). Given that the assumptions produced reasonable results, the consequences of the scenarios analysed are worthy further research. However,

the consequences of varying SRGSs and SR on grass and animal production may not be as complete as in reality. This highlights the importance of understanding the limitations of the current modelling approach.

Firstly, the use of a well-managed ranch precludes proper understanding of the impacts under varied management of both SR and number of paddocks. The size and spatial and temporal variability of paddocks influence the grass and animal production responses (Barnes et al. 2008), but these cannot be simulated by the SGS model in its current state. Secondly, measures of CP%, NDF% and NDF digestibility do not represent the real quality of woody species, which often contain secondary metabolites that potentially reduce digestibility and daily intake rate (e.g. Feng et al. 2008). The omission of these compounds in grazers' diets can significantly overestimate nitrogen (CP) availability (e.g. De Gabriel et al. 2009). Lastly, inclusion of an explicit tree/shrub growth module in the SGS model could enable a more realistic representation of the biophysical processes occurring in savanna rangelands. Trees and shrubs pose negative, neutral, and positive effects on grass production and biomass allocation with the effects varying by tree age, size, and density. All these areas could be developed in the SGS model to improve the model's capacity to represent real conditions in tropical southern African savannas.

Conclusions

The whole SGS model produced reasonable illustrations about the effects of varying SRs and SRGSs on Brahman weaner steers grazing natural pasture. Overall, there were no observable differences found in response of grass production and DMI to all treatments for SRGSs and SRs. In addition, effects of SRGSs on animal production were almost similar across treatments, but differential responses of LWG to SRs were more pronounced in short and long timeframes. Weaners stocked at the recommended SR grew persistently at a high rate, but animal productivity was adversely affected in the long term. Increasing the recommended SR by 30% resulted in reduced LWG of weaners in the short term whereas 50% lower SR achieved sustained high animal growth over time. The findings illustrate the potential of PBMs in providing direction for selecting the appropriate SR that achieves continued grass and animal production with minimum risk in the long term.

Acknowledgments — The Department of Research and Innovation Support of the University of Pretoria provided the postgraduate research bursary to this research programme and its contribution much appreciated. The National Research Foundation of South Africa is also acknowledged for in part funding of the research. Management personnel at Nuanetsi cattle ranch are hereby thanked for allowing us to conduct this study at their property. This work was supported by the National Research Foundation of South Africa (Grant No. 95734).

ORCIDs

Walter Svinurai: <https://orcid.org/0000-0002-9583-0052>
 Abubeker Hassen: <https://orcid.org/0000-0002-8240-3414>
 Eyob Tesfamariam: <https://orcid.org/0000-0003-0724-9864>
 Abel Ramoelo: <https://orcid.org/0000-0002-9917-9754>

References

- Barnes DL. 1979. Cattle ranching in the semi-arid savannas of East and Southern Africa. In: Walker BH (Ed.), *Management of semi-arid ecosystems*. Amsterdam: Elsevier Scientific Publishing Company. pp 9–54. <https://doi.org/10.1016/B978-0-444-41759-6.50006-2>.
- Barnes DL, Denny RP. 1991. A comparison of continuous and rotational grazing on veld at two stocking rates. *Journal of the Grassland Society of Southern Africa* 8: 168–173. <https://doi.org/10.1080/02566702.1991.9648285>.
- Barnes MK, Norton BE, Maeno M, Malechek JC. 2008. Paddock size and stocking density affect spatial heterogeneity of grazing. *Rangeland Ecology and Management* 61: 380–388. <https://doi.org/10.2111/06-155.1>.
- Briske DD, Derner JD, Brown JR, Fuhlendorf SD, Teague WR, Havstad KM, Gillen RL, Ash AJ, Willms WD. 2008. Rotational grazing on rangelands: reconciliation of perception and experimental evidence. *Rangeland Ecology and Management* 61: 3–17. <https://doi.org/10.2111/06-159R.1>.
- Codron D, Lee-thorp JA, Sponheimer M, Codron J. 2007. Nutritional content of savanna plant foods: implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research* 53: 100–111. <https://doi.org/10.1007/s10344-006-0071-1>.
- CSRI (Chemistry and Soil Research Institute). 2007. Soils of the proposed Lapache irrigation project. CSRI Report No: A689 prepared for the Department of Research and Specialist Services. Ministry of Agriculture, Mechanisation, and Irrigation Development, Zimbabwe.
- Danckwerts JE, Daines T. 1981. Animal production off grassveld. *Proceedings of the Annual Congress of the Grassland Society of Southern Africa* 16: 19–22.
- Danckwerts JE, O'reagain PJ, O'connor TG. 1993. Range management in a changing environment: a southern African perspective. *The Rangeland Journal* 15: 133–144. <https://doi.org/10.1071/RJ9930133>.
- DeGabriel J, Moore B, Foley W, Johnson C. 2009. The effects of plant defensive chemistry on nutrient availability predict reproductive success in a mammal. *Ecology* 90: 711–719. <https://doi.org/10.1890/08-0940.1>.
- Denny RP, Barnes DL. 1977. Trials of multi-paddock grazing systems on veld. III. A comparison of six grazing procedures at two stocking rates. *Rhodesia Journal of Agricultural Research* 15: 129–143.
- Denny RP, Barnes DL, Franklin MF. 1974. Some effects of varying the duration, frequency and intensity of grazing on the growth of steers on veld. *Proceedings of the Annual Congress of the Grassland Society of Southern Africa* 9: 133–137. <https://doi.org/10.1080/00725560.1974.9648732>.
- Derner JD, Hart RH, Smith MA, Waggoner JW. 2008. Long-term cattle gain responses to stocking rate and grazing systems in northern mixed-grass prairie. *Livestock Science* 117: 60–69. <https://doi.org/10.1016/j.livsci.2007.11.011>.
- Doran-Browne NA, Bray SG, Johnson IR, O'Reagain PJ, Eckard RJ. 2014. Northern Australian pasture and beef systems. 2. Validation and use of the Sustainable Grazing Systems (SGS) whole-farm biophysical model. *Animal Production Science* 54: 1995–2002. <https://doi.org/10.1071/AN14569>.
- Fang QX, Andales AA, Derner JD, Ahuja LR, Ma L, Bartling PNS, Reeves JL, Qi Z. 2014. Modeling weather and stocking rate effects on forage and steer production in northern mixed-grass prairie. *Agricultural Systems* 129: 103–114. <https://doi.org/10.1016/j.agsy.2014.05.011>.
- Farrell JAK. 1968. Preliminary notes on the vegetation of the lower Sabi-Lundi basin, Rhodesia. *Kirkia* 6: 223–248.

- Feng Z, Liu R, DeAngelis DL. 2008. Plant-herbivore interactions mediated by plant toxicity. *Theoretical Population Biology* 73: 449–459. <https://doi.org/10.1016/j.tpb.2007.12.004>.
- Gammon DM. 1978. A review of experiments comparing systems of grazing management on natural pastures. *Proceedings of the Annual Congress of the Grassland Society of Southern Africa* 13: 75–82. <https://doi.org/10.1080/00725560.1978.9648838>.
- Gaughan AE, Staub CG, Hoell A, Weaver A, Waylen PR. 2016. Inter- and Intra-annual precipitation variability and associated relationships to ENSO and the IOD in southern Africa. *International Journal of Climatology* 36: 1643–1656. <https://doi.org/10.1002/joc.4448>.
- Hatch GP, Tainton NM. 1995. The influence of stocking rate, range condition and rainfall on residual herbage mass in the semiarid savanna of KwaZulu-Natal. *African Journal of Range & Forage Science* 12: 76–80. <https://doi.org/10.1080/10220119.1995.9647868>.
- Hatch GP, Tainton NM. 1997. The influence of stocking rate, range condition and rainfall on seasonal beef production patterns in the semi-arid savanna of KwaZulu-Natal. *South African Journal of Animal Science* 27: 50–54.
- Heitschmidt RK, Dowhower SL, Walker JW. 1987. 14- vs. 42-Paddock rotational grazing aboveground biomass dynamics, forage production, and harvest efficiency. *Journal of Range Management* 40: 216–223. <https://doi.org/10.2307/3899082>.
- Hoffman P, Shaver RD, Combs DK, Combs DK, Undersander DJ, Bauman LM, Seeger TK. 2003. Using NDF digestibility of forages. *Focus on Forage* 3: 1–3.
- Hooimeijer JF, Jansen FA, De Boer WF, Wessels D, van der Waal C, De Jong CB, Otto ND, Knoop L. 2005. The diet of kudus in a mopane dominated area, South Africa. *Koedoe* 48: 93–102. <https://doi.org/10.4102/koedoe.v48i2.96>.
- Illius AW, Derry JF, Gordon IJ. 1998. Evaluation of strategies for tracking climatic variation in semi-arid grazing systems. *Agricultural Systems* 57: 381–398. [https://doi.org/10.1016/S0308-521X\(98\)00025-0](https://doi.org/10.1016/S0308-521X(98)00025-0).
- Illius AW, Gordon IJ, Derry JF, Magadzire Z, Mukungurutse E. 2000. Environmental variability and productivity of semi-arid grazing systems. Final Technical Report DFID Livestock Production Programme. Scotland, UK.
- Johnson I. 2016. DairyMod and the SGS pasture model: a mathematical description of the biophysical model structure. IMJ Consultants, Dorrigo, New South Wales, Australia. http://imj.com.au/wp-content/uploads/2016/05/DM_SGS_documentation.pdf. [Accessed 4 January 2017].
- Johnson IR, France J, Cullen BR. 2016. A model of milk production in lactating dairy cows in relation to energy and nitrogen dynamics. *Journal of Dairy Science* 99: 1605–1618. <https://doi.org/10.3168/jds.2015-10068>.
- Johnson IR, France J, Thornley JHM, Bell MJ, Eckard RJ. 2012. A generic model of growth, energy metabolism, and body composition for cattle and sheep. *Journal of Animal Science* 90: 4741–4751. <https://doi.org/10.2527/jas.2011-5053>.
- Kazembe JA. 2010. Modelling the influence of rainfall variability and different grazing systems on the spatiotemporal dynamics and productivity of semi-arid rangelands. PhD thesis, University of Cape Town, South Africa.
- Kos M, Hoetmer AJ, Pretorius Y, De Boer WF, De Knecht H, Grant CC, Kohi E, Page B, Peel M, Slotow R, et al. 2012. Seasonal diet changes in elephant and impala in mopane woodland. *European Journal of Wildlife Research*. 58: 279–287. <https://doi.org/10.1007/s10344-011-0575-1>.
- Lukhele MS, van Ryssen JBJ. 2003. The chemical composition and potential nutritive value of the foliage of four subtropical tree species in southern Africa for ruminants. *South African Journal of Animal Science* 33: 132–141. <https://doi.org/10.4314/sajas.v33i2.3767>.
- Mavedzenge BZ, Mahenehene J, Murimbarimba F, Scoones I, Wolmer W. 2006. Changes in the livestock sector in Zimbabwe following land reform: the case of Masvingo province. Brighton, UK.
- McKee TB, Doesken NJ, Kleist J. 1993. The relationship of drought frequency and duration to time scales. In: *8th Conference on Applied Climatology*, American Meteorological Society. pp 179–184.
- McNamara JP, Hanigan MD, White RR. 2016. Invited review: Experimental design, data reporting, and sharing in support of animal systems modeling research. *Journal of Dairy Science* 99: 9355–9371. <https://doi.org/10.3168/jds.2015-10303>.
- Meissner HH, Hofmeyr HS, Van Rensburg WJJ, Pienaar JP. 1983. Classification of livestock for realistic prediction of substitution values in terms of a biologically defined Large Stock Unit. Technical Communication No. 175. Pretoria: Department of Agriculture.
- Miguel JA, Melendez SJ, Asenjo B, Bonilla LM, Ciria J. 2012. Growth modeling of castrated Brahman males raised in tropical conditions and born in different seasons. *Ciencia e Investigación Agraria* 39: 279–288. <https://doi.org/10.4067/S0718-16202012000200004>.
- NRC (National Research Council). 2000. Nutrient requirements of beef cattle. (Seventh Revised Edition). Washington DC: National Academy Press.
- Norval J. 2016. The Brahman remains king in Zimbabwe. In: *BSSA (Brahman Breeders Society of Southern Africa)*. Supplement 1 of 7. Cape Town: Brahman in southern Africa. pp 40–42.
- Noy-Meir I. 1976. Rotational grazing in a continuously growing pasture. A simple model. *Agricultural Systems* 1: 87–112.
- O'Reagain P, Scanlan J, Hunt L, Cowley R, Walsh D. 2014. Sustainable grazing management for temporal and spatial variability in north Australian rangelands – A synthesis of the latest evidence and recommendations. *The Rangeland Journal* 36: 223–232. <https://doi.org/10.1071/RJ13110>.
- Peddie GM, Tainton NM, Hardy MB. 1995. The effect of past grazing intensity on the vigour of *Themeda triandra* and *Tristachya leucothrix*. *African Journal of Range & Forage Science* 12: 111–115. <https://doi.org/10.1080/10220119.1995.9647877>.
- Pico BA, Nester F, Van Wyk JB. 2004. Genetic parameters for growth traits in South African Brahman cattle. *South African Journal of Animal Science* 34: 44–46. <https://doi.org/10.4314/sajas.v34i6.3827>.
- Reeves JL, Derner JD, Sanderson MA, Hendrickson JR, Kronberg SL, Petersen MK, Vermeire LT. 2014. Seasonal weather influences on yearling beef steer production in C₃-dominated Northern Great Plains rangeland. *Agriculture, Ecosystems & Environment* 183: 110–117. <https://doi.org/10.1016/j.agee.2013.10.030>.
- Reeves JL, Derner JD, Sanderson MA, Petersen MK, Vermeire LT, Hendrickson JR, Kronberg SL. 2013. Temperature and precipitation affect steer weight gains differentially by stocking rate in northern mixed-grass prairie. *Rangeland Ecology and Management* 66: 438–444. <https://doi.org/10.2111/REM-D-12-00157.1>.
- Richardson FD, Hahn BD, Schoeman SJ. 2000. Modelling nutrient utilization by livestock grazing semiarid rangeland. In: *McNamara JP, France J, Beever DE (Eds), Modelling Nutrient Utilization*. Oxon: CAB International. pp 263–280. <https://doi.org/10.1079/9780851994499.0263>.
- Rickert KG, Stuth JW, McKeon GM. 2000. Modelling pasture and animal production. In: 't Mannetje L, Jones RM (Eds), *Field and Laboratory Methods for Grassland and Animal Production Research*. London: CAB International. pp 29–66. <https://doi.org/10.1079/9780851993515.0029>.
- Scanlan J, MacLeod N, Pahl L, Whish G, Cowley R, Mclvor J. 2011. Grazing management options for improving profitability and sustainability. 2. Modelling to predict biological and financial outcomes. In: *Proceedings of the Northern Beef Research Update Conference*. Darwin. pp 47–52.

- Scanlan JC, Macleod ND, O'Reagain PJ. 2013. Scaling results up from a plot and paddock scale to a property - A case study from a long-term grazing experiment in northern Australia. *The Rangeland Journal* 35: 193–200. <https://doi.org/10.1071/RJ12084>.
- Schoeman SJ. 1996. Characterization of beef cattle breeds by virtue of their performances in the National Beef Cattle Performance and Progeny Testing Scheme. *South African Journal of Animal Science* 26: 15–19.
- Sibanda S. 1998. Supplementary feeding of beef cattle. In: *Beef Production Manual*, Commercial Farmers Union, Harare, Zimbabwe. 15 pages
- Stuth J, Maraschin GE. 2000. Sustainable management of pasture and rangelands. In: Lemaire G, Hodgson J, de Moraes A, Nabinger C, de F Carvalho PC (Eds), *Grassland ecophysiology and grazing ecology*. Oxon: CABI Publishing. pp 339–354. <https://doi.org/10.1079/9780851994529.0339>.
- Svinurai W, Hassen A, Tesfamariam E, Ramoelo A, Cullen B. 2020. Calibration and evaluation of the Sustainable Grazing Systems pasture model for predicting native grass aboveground biomass in southern Africa. *African Journal of Range and Forage Science*. <https://doi.org/10.2989/10220119.2021.1875501>.
- Taylor RD, Walker BH. 1978. Comparisons of vegetation use and herbivore biomass on a Rhodesian game and cattle ranch. *Journal of Applied Ecology* 15: 565–581. <https://doi.org/10.2307/2402611>.
- Teague R, Provenza F, Kreuter U, Steffens T, Barnes M. 2013. Multi-paddock grazing on rangelands: why the perceptual dichotomy between research results and rancher experience? *Journal of Environmental Management* 128: 699–717.
- Teague R, Provenza F, Norton B, Steffens T. 2008. Benefits of multi-paddock grazing management on range- lands: limitations of experimental grazing research and knowledge gaps. In: Schroder HG (Ed.), *Grasslands: Ecology, Management and Restoration*. New York: Nova Science. pp 41–80. <https://doi.org/10.1016/j.jenvman.2013.05.064>.
- Tedeschi LO. 2019. Future of data analytics in nutrition: mathematical modeling in ruminant nutrition: approaches and paradigms, extant models, and thoughts for upcoming predictive analytics. *Journal of Animal Science* 97: 1921–1944. <https://doi.org/10.1093/jas/skz092>.
- Thornley JHM, Johnson IR (Eds). 2000. *Plant and crop modelling: a mathematical approach to plant and crop physiology*. Caldwell: The Blackburn Press.
- van de Pol R, Jordaan JJ. 2008. The fodder bank system: its current place in veld management. *Grassroots: Newsletter of the Grassland Society of Southern Africa* 8: 36–44.
- Vincent V, Thomas RG. 1961. An agro-ecological survey of Southern Rhodesia: Part I agro-ecological survey. Salisbury (now Harare): Government Printers.
- Walker BH. 1976. Utilisation of marginal lands in Rhodesia. *Rhodesian Science News* 9: 191–195.
- Walker BH, Ludwig D, Holling CS, Peterman RM. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* 69: 473–498. <https://doi.org/10.2307/2259679>.