Long-term dynamics of a semiarid grass steppe under stochastic climate and different grazing regimes: A simulation analysis

J.M. Paruelo [a,*], S. Pütz [b], G. Weber [b], M. Bertiller [c], R.A. Golluscio [a], M.R. Aguiar [a], T. Wiegand [b]

[a] *Laboratorio de Análisis Regional y Teledetección, IFEVA—Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Avenue San Martín 4453, C1417DSE Buenos Aires, Argentina*
[b] *Department of Ecological Modelling, UFZ Centre for Environmental Research Leipzig-Halle, Permoserstr. 15, D-04318 Leipzig, Germany*
[c] *CENPAT—CONICET, Boulevard Brown s/n, U9120ACV Puerto Madryn, Argentina*

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ABSTRACT

We built a grid-based spatial explicit stochastic model that simulates grazing events and basic processes like seedling establishment, growth or mortality of the dominant species in the grass steppes of Patagonia. After evaluating the model with field data, we performed simulation experiments aimed to explore the interaction of precipitation and grazing regimes on vegetation dynamics. Grazing generated a reduction in tussock density which results in a decline in aboveground net primary production (ANPP). Both response variables presented a non-linear behavior including high temporal variability and delay effects, which may prolong for decades. There was a clear threshold in the response of the variables to stock density, though changes become evident only when a highly selective grazing scenario was used. Under high stock density conditions, precipitation use efficiency (PUE) was 82% lower than the values for non-grazed runs. The inter-annual variability of precipitation was more important than the grazing regime in explaining differences in tussock density. Simulation results highlight important issues regarding rangeland management: grazing regime might be as important as stocking density as a degradation agent, temporal lags might obscure degradation processes for decades, the definition of monitoring variables need to consider their response time constants.

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1. Introduction

Desertification has been identified as one of the major environmental problems that arid and semiarid systems face (Dregne, 2002). Although climatic and geologic forces may promote desertification (Hartley and Chong, 2002; Hillel and Rosenzweig, 2002; Oba et al., 2001) at ecological time scales, grazing by domestic herbivores has been identified as one of the major agents (Ares et al., 2003; Manzano et al., 2000; Soriano and Movia, 1986). Grazing promotes changes at different levels and on different components of the system (Briske and Richards, 1995). It alters the physiology of individual plants, modifying their water status, nutrient balance, and relative growth rates. Selective grazing modifies both directly and indirectly the interactions among the different components of biotic community and plays a key role in changing the structure of the plant community. Grazing is a complex process that involves a large number of individual processes: selection of a forage item at the species and individual plant level, herbivory in itself, trampling, etc. (Parsons and Dumont,

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* Corresponding author. Tel.: +54 11 4524 8070x8109.
 E-mail address: paruelo@agro.uba.ar (J.M. Paruelo).

2003). The impact of grazing at the organism, population, and community level scale up to the ecosystem, promoting changes in primary production (Oesterheld et al., 1999), resource use efficiency (O'Connor et al., 2001), species composition (Altesor et al., 1998; León and Aguiar, 1985), or nutrient balance (McNaughton, 1990).

Due to the relatively recent introduction of livestock (the beginning of the XXth century), degradation (reduction in plant cover, plant functional type replacement, decreasing primary and secondary production) started not far ago and it is currently taking place in Patagonia, an extensive arid and semiarid area in southern South America. Livestock raising is extremely extensive in Patagonia, sheep flocks stay in the field all year round in paddocks often of thousands of hectares and they are exposed to extreme weather conditions (Golluscio et al., 1998a; Paruelo et al., 1998). Flocks behave as "semi-natural" populations, i.e., populations with limited human intervention (Texeira and Paruelo, 2006). Ecologists started to recognize signs of degradation in the Patagonian steppes in the 1950s (Boelcke, 1957; Soriano, 1956b). The grass steppes, dominated by *Festuca pallescens*, experienced the highest changes in plant cover and physiognomy (Aguiar and Sala, 1998; Bertiller and Bisigato, 1998). Vegetation changes due to grazing by domestic herbivores lead to a steadily reduction of *F. pallescens* cover and, latter on, to shrub encroachment (Bertiller et al., 1995; León and Aguiar, 1985). The reduction in the amount of senescent material in grazed *Festuca* tussocks starts a positive feedback between successive grazing events: the lowest the amount of dead material, the highest the number of defoliation events. *Festuca* standing dead biomass is not consumed by sheep, and may last in the tussock for several years (Jobbagy and Sala, 2000; Soriano et al., 1976). Green biomass located in tussocks with a high proportion of standing dead biomass is protected from defoliation, due to the spine-like character of the standing dead material. Tussock structure affects then the selection of a grazing site at the spatial scale of a single-tussock. Due to the selective defoliation regime, grazing pressure is not homogeneously distributed over the tussock population in a grazed area. Livestock grazes on only a fraction of the total resource, maintaining distinct tussock populations side by side: heavily grazed tussocks with low fractions of standing dead, and almost ungrazed tussocks with high fractions of standing dead material. As a consequence, predictions of livestock impacts based on mean utilization intensity given by consumed over produced biomass are inappropriate, since such approaches ignore the differential impact of grazing on the preferred tussocks. We hypothesize that the impact of livestock at the landscape scale depends on the effect of the selective foraging on the structural heterogeneity of individual tussocks.

How to detect and monitor degradation in arid and semiarid ecosystems? Scientists dealing with this issue face several challenges. First, it is critical to separate out the effects of aridity and degradation. A similar vegetation structure or productivity may be a consequence of the restrictions imposed by water availability (throughout the precipitation level or topographic or soil factors) or, alternatively, the result of a degradation processes. Second, because degradation is a process, its analysis requires either to track changes through time or to have reference (non-degraded) situations. Finally, semiarid rangeland dynamics is characterized by episodic and event-driven behavior that occur in response to rare or extreme events, e.g., triggered by stochastic rainfall (Walker, 1993; Wiegand et al., 1995). As a consequence, the dynamics of many rangelands cannot be conceptualized using equilibrium theory (Walker, 1993) and vegetation change may occur unpredictably over time scales much longer than most long-term studies.

The nature and the scale of the processes involved make the analysis of the degradation extremely difficult from a pure experimental approach. This is especially difficult in arid and semiarid rangelands because rangeland dynamics are determined by complex interactions of biological processes, grazing, climate, and management which operate at different temporal and spatial scales. A new set of models have been developed during the last years aimed to describe community or ecosystem dynamics by simulating the fate of individuals or assemblages of individuals including the essential biological processes (recruitment, mortality, etc.) in the form of empirical relationships ("rules") rather than differential equations (e.g., Coffin and Lauenroth, 1990; Wiegand et al., 1995, 2004a). A clear advantage of these models is that they allow the direct inclusion of expert knowledge (i.e., they are not necessarily restricted to hard data). Although there are few long-term dataset documenting the full dynamics of arid plant communities, attributes of individual plant behavior are relatively easy to observe or measure. The basic idea is therefore to incorporate the short-term knowledge in form of simple empirical equations into a computer simulation model and to extrapolate from the local behavior of individual plants to long-term and landscape-level vegetation dynamics using time series of the external drivers such as rainfall. *F. pallescens* steppes are an ideal system to develop such models because most of the biomass is concentrated in one single species, individual plants form discrete units (tussocks) that can be modeled as individuals, and enough information is available to define the rules and to parameterize the model.

In this article, we sought to understand how the effect of processes operating at the individual level determines the behavior of the systems at the stand level. The connection between the behavior of low and higher levels is a major challenge in ecology (Levin, 1992) and it is critical to develop management schemes at the ecosystem level. We were interested in evaluating the influence of two groups of factors (factors upon subjected to management decision such as utilization intensity and timing of defoliation, and climatic factors) upon variables which can be considered as indicators of the long-term impact of livestock grazing: tussock density, aboveground net primary production (ANPP), and precipitation use efficiency (PUE). To achieve this goal, we built a grid-based spatially explicit simulation model aimed at scaling up from small-scale processes at the tussock level to the dynamics of a homogeneous stand of *F. pallescens* considering external controls such as selective foraging. From simulation experiments, we sought to identify threshold in the response of the *F. pallescens* steppes to changes in the grazing regime and in the temporal variability in precipitation.

The temporal scale of the analysis spans over decades and has a temporal resolution of 1 year. Our study included field measurements aimed to generate data at the same scale than the output variables of the model. The evaluation of the model included an empirical test of its main assumptions, a sensitivity analysis, and the comparison of model outputs

against field data. We performed, finally, a set of simulation experiments to evaluate the response of the system to different climate and grazing scenarios.

2. Methods

2.1. Description of the study area

Our analyses focused on the grass steppes of *F. pallescens* ("coirón blanco") that characterize the Sub Andean district of the Patagonian Phytogeographic Province, a narrow north–south strip between 71°W and 71°30′W (León et al., 1998; Paruelo et al., 2004; Soriano, 1956a) (Fig. 1). They occur in areas receiving between 300 and 600 mm of mean annual precipitation (MAP). Precipitation is concentrated in winter (June, July, and August) and mean temperature is lower than 5 °C (Paruelo et al., 1998). Both the west and east boundaries of the district correspond to a wide ecotone where vegetation physiognomy changes gradually to shrub steppes, toward the east, or to forest, toward the west. The grass steppes have been defined phytosociologically as the "community of *F. pallescens*, *Rhytidosperma picta* and *Lathyrus magellanicus*" (Golluscio et al., 1982). The non-degraded steppes have a mean plant cover of 64% and *F. pallescens* by itself accounted for by 69% of the plant cover. Total grass cover, including other perennial grass species, represents more than 80% of the total plant cover. Overgrazing produces a sharp decline in *F. pallescens* cover, an increase of bare soil patches and, in advanced stages of degradation, the invasion of shrubs (*Mulinum spinosum*) and/or dwarf-shrubs (*Acaena splendens*) (Bertiller et al., 1995; León and Aguiar, 1985). Such structural modifications were associated to changes in water dynamics, net primary production, and herbivore biomass (Aguiar et al., 1996; Golluscio et al., 1998a). A number of field studies analyzed the impact of grazing
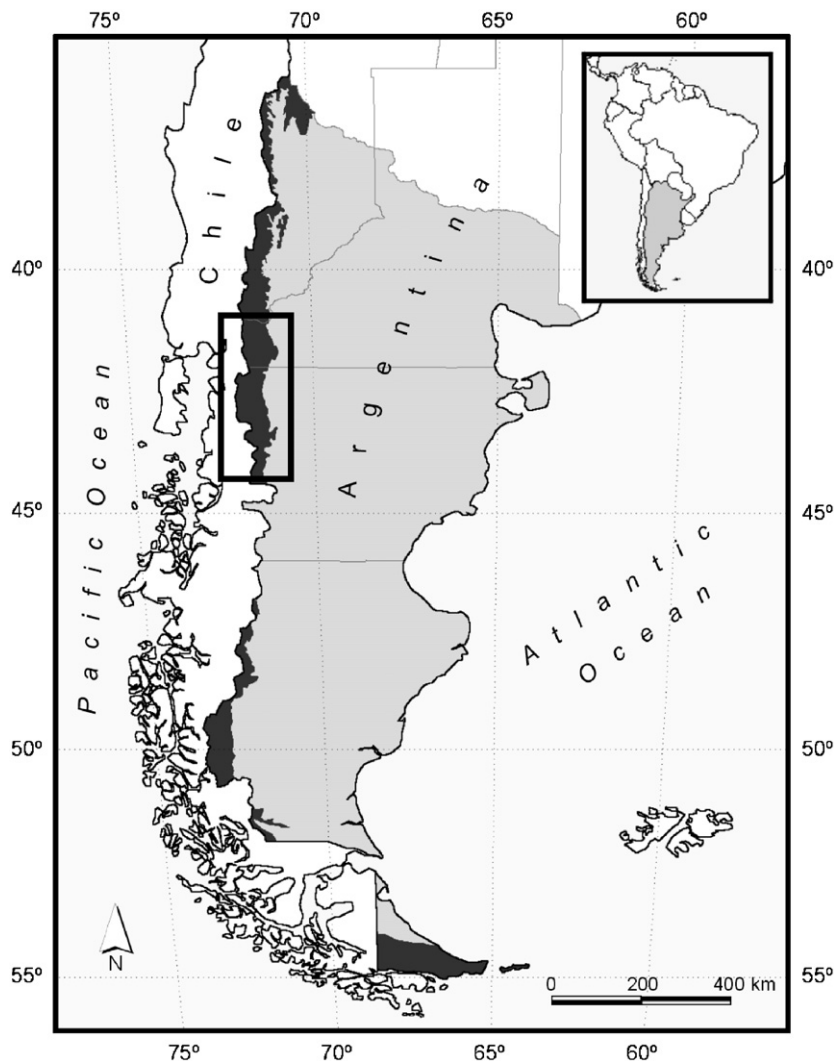

Fig. 1. Map of the study region: the black areas correspond to the *Festuca pallescens* grass steppes (Subandean district). Redrawn from León et al. (1998).

on single processes at the population or ecosystem level (Bertiller, 1992, 1996; Bertiller and Coronato, 1994; Defosse et al., 1990, 1997a, b; Paruelo et al., 2000). The degradation of the vegetation impacts on sheep flocks, affecting their growth rate and generating a steady decline in stocks (Texeira and Paruelo, 2006). Stock densities vary over the region according to the productivity and vegetation physiognomy of the paddocks from 0.4 to 1.6 sheep ha^{-1} (Golluscio et al., 1998a). Paddocks are grazed all year round in most ranches.

2.2. The model

COIRON is a grid-based two-dimensional spatially explicit individual-based simulation model of the population dynamics of *F. pallescens*, including a detailed grazing model mimicking individual grazing decisions of the herbivores (sheep). The model includes ecological processes operating at different levels: the individual grass tussock and the patch level (the whole grid). Because *F. pallescens* is the dominant grass and its dynamics is a key control of the whole community, the model only simulates the dynamics of this species to represent the system at the stand level. Based on the authors experience, *F. pallescens* dynamics may provide a good proxy of the dynamics of the "xerophitic grasses" functional type. We adapted our model description to the scheme presented by Grimm et al. (2006). Their protocol consists of three blocks: overview, design concepts, and details. We present in this section the first two blocks and the details of the model (including the equations and specific rules) are presented in Appendix 1 (electronic version only).

2.2.1. Model overview

2.2.1.1. Purpose. We built an individual-based spatially explicit model (COIRON) to (i) investigate incipient steps of degradation in an semiarid grass steppe dominated by *F. pallescens* (Fig. 2) and (ii) understand the interacting effects of stochastic precipitation and grazing on vegetation at different temporal scales

Our model built on several studies on the effect of grazing on semiarid ecosystems that use "rule-based simulation models" including stochastic rainfall (Beukes et al., 2002; Jeltsch et al., 1997; Weber et al., 1998; Wiegand and Milton,

Fig. 2. General view of the grass steppes of the Subandean district and detail of a *Festuca pallescens* tussock (photo JMP).

1996). Our focus was on individual tussocks of *F. pallescens*, the dominant component of the system. Therefore, we did not include in the model invasive shrubs (*M. spinosum* or *A. splendens*). The goal of the model is to simulate the dynamics of the system in the first stages of degradation, before shrub invasions takes place. Though important, the simulation of shrub dynamics in this system is precluded by the lack of data and empirical studies. We considered, but did not simulate explicitly, the dynamics of scarce but preferred by sheep species of forbs and small mesophytic grasses.

2.2.1.2. Scales. The spatial resolution (cell-size) of the model is equivalent to a fully grown individual tussock (30×30 cm). This is the spatial scale at which most of the plant processes and livestock forage decisions take place. The whole simulated area comprises 128×128 cells covering an area of approximately $1500 \, m^2$, an area similar to the one covered during our field surveys.

The model has an annual time step and the grazing model includes several options to vary forage selectivity at the patch level on an annual time scale; however, seasonal grazing is implicitly considered by modifying the selectivity of herbivores on grass tussocks: winter grazing is less selective than spring and continuous grazing (CG). Summer and autumn grazing has an intermediate selectivity.

2.2.1.3. Structure and state variables. There are three possible states for a cell (Fig. 3). A cell can be empty or occupied by a live or dead tussock. A cell is still considered empty if only seedlings are present. A cell occupied by a live tussock is characterized by two state variables: green biomass (*gb*) and dead biomass (*db*) (Fig. 3). Both fractions appear interspersed in the tussock. Tussock structure (*dfrac*) denotes the fraction of standing dead biomass *db* over total standing biomass *db+gb*. The dead material of the tussock corresponds to senescent biomass accumulated during previous growing seasons (Soriano et al., 1976). As a consequence, *dfrac* reflects pre-grazing event conditions. A tussock is characterized by a discrete level of "vitality" (*vit*) or potential productivity, a property that integrates historical effects of climate and grazing. Vitality or potential productivity depends on the density of tillers and the amount of standing dead material. Both structural characteristics of the tussock will affect its ability to intercept radiation and then its potential primary production. In the model, the dynamics of the state variable is controlled by plant available soil water (*w*) throughout its influence on the input and transference fluxes of matter (production, senescence). On an annual time step, water is the main constrain of productivity (Paruelo et al., 1999, 2000). Dead biomass may last in the tussock for several years (Jobbagy and Sala, 2000; Soriano et al., 1976). Standing green biomass is defoliated, goes senescent, or is carried over to the subsequent year. Standing dead biomass is carried over to the subsequent year or turns into litter. Litter is not considered as a state variable and leaves the system as a consequence of strong winds or photodegradation (Austin and Vivanco, 2006). A list and description of the state variables is presented in Table 1.
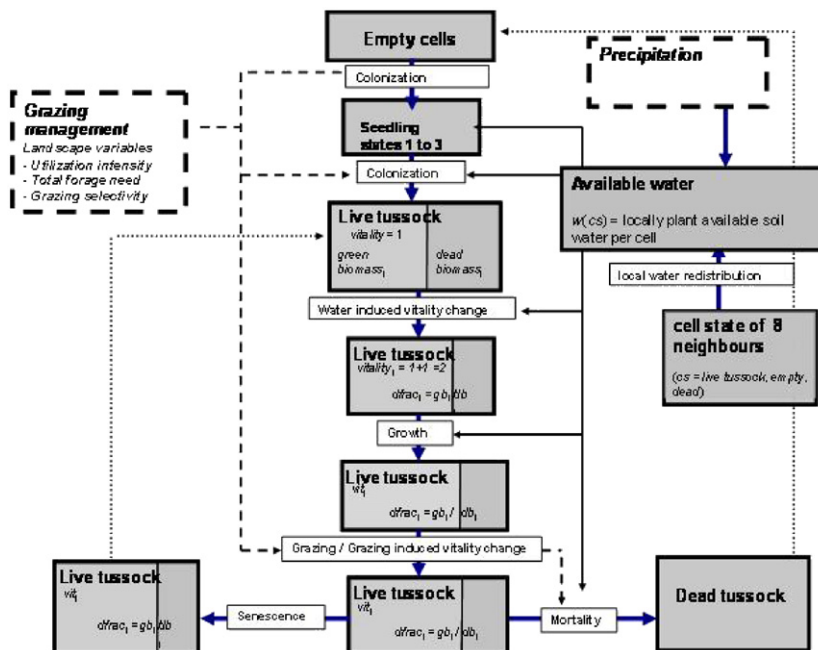

Fig. 3. Diagram of the COIRON model: state variables are presented in shadowed boxes (seedlings are not explicitly modeled). Non-shadowed boxes correspond to the different processes associated to the dynamics of the systems. Internal and external driving factors are represented in italics in dashed line boxes.

Table 1
State variables of the semi arid steppe grazing simulation model COIRON

State variable	Explanation	Unit	Detailed explanation	Set value
Tussock level				
$cs\,(x,y,t)$	*Cell state* of one grid cell at location (x,y) and time t	–	States a grid cell at location (x,y) and time step t can take in: $cs = 0$ for a empty/bare soil cell; $cs = 1$ for a dead tussock; $cs = 2$ for a live tussock	$cs = \{0,1,2\}$
$w_{(cs\ neighbours)}$	Plant available soil water	H_2O/area (mm/cm)	Local plant available soil water after local water redistribution	
vit	*Tussock vitality*	–	Potential productivity of a tussock; vitality accounts for the memory the tussocks' history; if $cs = 2$ then $vit > 0$; $vit = 0$ for dead tussock (tuss., $cs = 1$); $vit = 1$: tuss. with low vitality; $vit = 2$: mean vital tuss., $vit = 3$: tuss. with high vitality; $vit = 4$: tuss. with highest vitality	$vit = \{0,1,2,3,4\}$
$Prod$	ANPP per tussock	gb/cell area year (g DM/0.09 m^2 y)	Annual plant production is modelled as a function of vit and w with Michaelis-Menten kinetics	
gb_i	Green *F. pallescens* tussock biomass	Live biomass/cell area year (g DM/0.09 m^2 y)	Live biomass (expressed in dry matter, DM) of a tussock; it is altered or updated during one time step (year) during following processes $I =$ biomass carry over (Co), production (P), grazing (G) and senescence (S). Only cells in cell state $cs = 2$ (live tussock) contribute to green biomass production	
$db(cs)$	Dead *F. pallescens* tussock biomass	Dead biomass/cell area year (g DM/0.09 m^2 t)	Dead biomass of a tussock, depends from cell state (cs), cell states $cs = 1$ (dead tussock) and $cs = 2$ (live tussock) include dead biomass	
$dfrac_i$	Dead fraction of *F. pallescens* biomass	–	Dead fraction of total biomass of the ith tussock; defines tussock structure	
lc_i	Local defoliation severity	gb_{prod}/cell area year (g DM/0.09 m^2 y)	Local consumption: total removed green biomass per tussock and time step during I defoliation events	
S_i	Seedling of state i	–	Seedling of state I; $I = 0$: emerged from empty cell ($cs = 0$); (1): 1-year-old seedling; (2): 2-year-old seedling; survival of S_2 leads to a fully grown tussock and to transition from $cs = 0 \rightarrow cs = 2$.	$I = \{0,1,2\}$
$Dsmax$	Maximum defoliation severity	–	Maximum relative defoliation severity depends from $dfrac$, calculated once before grazing routine	
$Gprob, gprob_{GR.5}$	Probability of a tussock to be accepted for grazing	–	Depends on M, $dfrac_i$, and season ($GR.5$); $gprob_{GR.5} \in [0,1]$; At default for GR.5 $= 1.0$ continuous grazing (a) it depends only on M and $dfrac_i$	
$Gbmin$	Minimum residual biomass after grazing	gb/cell area year (g DM/0.09 m^2 y)	Minimum residual biomass after grazing is calculated before grazing and depends on $dfrac$ and gb	
Ds	Relative defoliation severity	–	Relative defoliation severity per tussock and time step, ratio of total consumed forage (lc_i) and pre-grazing total biomass gb_P	

Population level			
Population structure			
$Dfrac$	Mean dead biomass fraction	–	Mean dead biomass fraction ($dfrac$) returns the mean $dfrac$ for all single $dfrac_i$ of all live tussocks, per grid and per time step
fT_{dfrac_i}	Tussock distribution over $dfrac$-class i	–	The tussock distribution over $dfrac$ calls I denotes the proportion of tussocks with high or low proportion of dead biomass, and thus indicates how strong forage selection will act on the tussock population; $dfrac$-class $i = 1$ ([0–20%[dead biomass $dfrac$ per tussock), 2 ([20–40%] $dfrac$), 3 ([40–60%] $dfrac$), 4 ([60–80%] $dfrac$), 5 ([80–100%] $dfrac$)
Mean vit	*Mean vitality*	–	Simulated mean vitality is calculated from all live tussocks per grid per time step
Mean vit_{dfrac_i}	Mean vitality $dfrac$-class i	–	Mean vitality $dfrac$-class i gives the distribution of mean vitality for the live tussock population per grid, time step and per $dfrac$-class $i = 1$ ([0–20%[dead biomass $dfrac$ per tussock), 2 ([20–40%] $dfrac$), 3 ([40–60%] $dfrac$), 4 ([60–80%] $dfrac$), 5 ([80–100%] $dfrac$)
Population function			
Mean $prod$	Mean ANPP per tussock	gb/cell area year (g DM/0.09 m^2 y)	Mean *ANPP* per tussock and time step
B_i	Standing green biomass i	Mean B/grid area year (kg DM/ha t)	Landscape level standing green biomass as the sum of all live tussock biomasses ($gb(i)$) is updated during following processes i = biomass carry over (Co), production (P), grazing (G) and senescence (S)
Mean gb_i	Mean green biomass per tussock i	gb_i/cell area year (g DM/0.09 m^2 y)	Mean live biomass (expressed in dry matter, DM) of a tussock; it is altered or updated during one time step (year) during following processes i = biomass carry over (Co), production (P), grazing (G) and senescence (S). Only cells in cell state $cs = 2$ (live tussock) contribute to green biomass production
Patch/landscape level			
Td_S	Tussock density	Tussocks/area (n/m^2)	The simulated tussock density (Td_S) is calculated directly as ratio of all live tussocks/total grid size (~1500 m^2). Due to the resolution of the grid (1 tussock = 0.09 m^2) 100% plant cover are equivalent to a tussock density of 11.1
cov_i	Cover cell state i	%	Relative abundance of different cell states i: F: live *Festuca pallescens* tussocks; D: dead tussocks; E: empty cells; EL: large bare patch cells; ES: cells potentially optimal for recruitment.
Mean PUE	Mean precipitation use efficiency, whole grid	–	Landscape/patch level average precipitation use efficiency, ratio w (all live tussocks)/wG (all cells), i.e., the sum of all plant available soil water for live tussocks/total precipitation input for all cells per time step.
ANPP	Annual net primary production	Sum $prod$/grid area year (kg DM/ha t)	Landscape level annual net primary production, derived from the sum of all tussocks' annual green biomass production ($prod$) per grid and time step.
$max B$	Max green biomass	Max(B_S)/grid area year (kg DM/ha t)	Maximum landscape level standing green biomass during one simulation, derived from yearly B_S.

Table 1 (*continued*)

State variable	Explanation	Unit	Detailed explanation	Set value
AF	Available forage from *F. pallescens*	gb_{prod}/area (kg DM/ha)	Total available forage from *F. pallescens*	
FN	Total forage need	bm/area (kg DM/ha)	Total annual Forage need by livestock	
F	Forage need from *F. pallescens*	gb_{prod}/area (kg DM/ha)	Forage yielded from *F. pallescens*	
M	Theoretical defoliation severity *M*	–	Relative landscape/patch level necessary mean defoliation severity, relative to forage available from *F. pallescens* per time step	
Mreal	Realised mean utilisation severity	–	Relative realised mean *ds* for all tussocks/grid per time step	
C	Consumed forage	gb_P/area (g DM/1500 m^2 t)	Landscape/patch level consumed forage per time step: sum of lc_i for all live tussocks of the whole grid	

Abbreviations are used in the text and the equations of the rule-set. General remark: the basic attribute carrying unit 'live tussock' (cell state $cs = 2$) comprises nearly all biological variables at the tussock level, e.g., $prod(cs, vit, w) = prod(vit, w)$, etc. and is not mentioned in every variable due to redundancy. In analogy to this syntax, the variables related to the plant available soil water $w/w_G/w'(x, y, t)$, which depend on location and time, are written as $w/w_G/w'$ in the rule set. All global variables depend on time step t.

2.2.2. Process overview

2.2.2.1. Water dynamics. Annual rainfall is the same in every cell. A fixed fraction of annual rainfall is transformed into plant available soil water (w), based on observed and simulated values of transpiration/precipitation ratios (Paruelo et al., 2000). We generated a 100-year dataset based on the mean annual rainfall and variability of a typical grass-steppe site (Medialuna, Chubut) using actual data for the period 1931–1998. There is no carry-over of w from one year to another. Locally, w depends on climatic and on neighborhood effects. Neighborhood effects are modeled through soil water status exclusively: (1) gains of soil water in cells occupied by tussock due to lateral influx (due to root absorption) from empty cells in the neighborhood and (2) losses due to lateral efflux to tussocks in the neighborhood. This redistribution of the homogeneous soil water input (precipitation) results in a locally heterogeneous pattern of w. Runoff/runon is not modeled as a flat landscape is assumed.

2.2.2.2. Plant production. Biomass production depends on local "vitality", and on locally available soil water. For production response to soil water—the only resource considered—we assumed a Michaelis-Menten kinetics. Potential productivity (*vitality*) determines the maximum production of the tussock.

2.2.2.3. Colonization. F. pallescencs reproduce exclusively from seeds. Seed production and distribution are not modeled explicitly but seed distribution is considered spatially homogeneous (Bertiller, 1992, 1996; Bertiller and Coronato, 1994). Seedling establishment occurs only in empty cells and depends on locally available soil water w (Defosse et al., 1997a, b) and total grass cover.

2.2.2.4. Grazing induced vitality change. A change in the "vitality" of a tussock will depend on water availability. Deterministic water thresholds will define the transitions between vitality classes. Additionally, increasing defoliation severity will determine a reduction in tussock vitality. Fixed defoliation severity thresholds will determine the transition.

2.2.2.5. Senescence and littering. Litter decomposition proceeds with a fixed annual rate.
    A dead tussock with less than a minimum amount of standing dead biomass is removed and the respective cell is considered empty.

2.2.2.6. Mortality. Mortality occurs only for tussocks in the lowest vitality class and for seedlings. The probability of dying depends on thresholds related to soil water availability and defoliation severity. In the case of seedlings, it has been shown by Bertiller (1996) and Defosse et al. (1997a, b).

2.2.2.7. Grazing pressure. We distinguish two spatial scales for the grazing process: the local or tussock level and the patch or landscape unit level. The last one covers the whole area considered, e.g., a paddock, or a part of a paddock. Grazing pressure or "utilization intensity" is defined as the forage need over the available forage. A fixed total annual forage need *FN* ($kg\,ha^{-1}$) results from a fixed forage need per capita (i.e., 1 kg sheep^{-1} day^{-1}) and a fixed stocking rate (i.e., 1 sheep ha^{-1}). The total amount of available forage *TF* ($kg\,ha^{-1}$) includes available forage from *F. pallescens* (*AF*) and a component of other species, which are consumed with higher priority than *F. pallescens* (i.e., forbs and small grasses), called primary forage (*PF*). We assumed that they contribute with 30% of total forage need, when *F. pallescens* cover is 40% or more, and its contribution is linearly reduced to 5%, when *F. pallescens* cover is 10% or less. The availability of both sources of forage are positively related (León and Aguiar, 1985). As degradation progresses the reduction of small grasses (*R. picta*, *Poa ligularis*, *Bromus pictus*, *Koeleria* sp., etc.) is more pronounced than the decrease in *F. pallescens* cover. To calculate the forage consumed from *F. pallescens*, *PF* is discounted from total forage need *FN*. Landscape level mean utilization intensity *M* for *F. pallescens* then is given as

$$M = \frac{FN - PF}{AF}.$$

2.2.2.8. Grazing process. The grazing process is considered a sequence of local grazing events that continue until the total forage need has been met, available forage reaches a minimum or no suitable cell has been found over several consecutive trials. Due to off take restrictions, green biomass might not be available for grazing, e.g., high proportion of tussocks with high fractions of standing dead (high *dfrac*), allowing only limited defoliation severity. A grazing event consists of the selection of a tussock, and its subsequent defoliation. A tussock is selected by randomly drawing a cell from any position on the grid. If the cell holds a tussock which has not yet been grazed down to its minimum residual green biomass, it is accepted for grazing with probability that depends on the structure of the tussock (*dfrac*) and the mean utilization intensity.
    Under very low utilization intensity (*M* close to 0), grazing probability shows a close to linear decrease with an increasing fraction of standing dead. By increasing utilization intensity *M*, livestock would increasingly accept tussocks with higher fractions of standing dead. The maximum defoliation severity (*dsmax*) a tussock can experience depends on the fraction of standing dead biomass (*dfrac*) and it is calculated only once, prior to the grazing routine. That is, if *dsmax* is not altered during the grazing process.

A tussock that has been accepted for grazing is defoliated with a local defoliation intensity (*lc*). Although initially cells are selected at random, the algorithm ensures that tussocks are not grazed randomly but in a highly selective way since the probability of a tussock being accepted for grazing (*gprob*) depends on its individual composition (*dfrac*) as well as on the overall utilization intensity (*M*). With increasing utilization intensity, the grazing probability of a tussock with a given structure (*dfrac*) increases. In addition maximum defoliation intensity of a grazing event is determined by tussock structure.

2.2.2.9. Grazing regimes. We simulated different grazing regimes based on the seasonality of the defoliation: (a) continuous year round grazing or (b) all forage needed is consumed in spring, (c) summer–fall, or (d) winter. Because the time step of the model is 1 year, grazing seasonality was simulated through its influence on *dfrac* and hence on the probability of a tussock of being grazed (*gprob*). The low availability of forage items of high quality and the relatively softer structure of the tussock when the dead material is wet determines the seasonal changes in selectivity (Paruelo et al., 1993). As a consequence, the highest selectivity occurs in spring or when the paddock is grazed continuously, i.e., the influence of dead fraction is higher than in other seasons.

2.2.3. Design

Parameter values were derived or estimated from the literature, unpublished data and the opinion of experienced local ecologists and range scientists. Further details on the parameters and the specific rules and equations of the model are provided in Appendix 2. This version of the model, then, has been parameterized without indirect calibration using the field data. The structure of the model formalizes and integrates a set of hypotheses on the dynamics of the systems. Such hypotheses have a variable degree of empirical support. To evaluate the model, we tested critical assumptions of the model, we performed a sensitivity analysis varying the level of 14 groups of parameters, and we compared model outputs against field data.

2.3. Model testing

2.3.1. Field studies

We conducted field studies: (a) to compare field data with model outputs and (b) to test three key model assumptions related to the relationship between (1) dead material and grazing pressure, (2) consumption of individual tussocks and the percentage of dead material of the tussock, and (3) the vitality index and the potential productivity of a tussock. We selected 16 grazed paddocks in five private ranches and three exclosures distributed across the Subandean district. We had, then, estimates of six sites, one ungrazed with three replicates (exclosures) and five grazed with a variable number of replicates (one to five paddocks). All paddocks corresponded to intermediate levels of degradation of the steppe according to the floristic criteria defined by León and Aguiar (1985). Extremely degraded paddocks were excluded from the analysis because *F. pallescens* was not longer the dominant species (León and Aguiar, 1985). Reliable estimates of long-term stock densities are very scarce because of the lack of good records at the ranches. Additionally, the effective stock density varied spatially and it is impossible to assess such heterogeneity in large paddocks (more than 2500 ha). In an environmentally (soil, aspect, slope) homogeneous area of each paddock, we randomly placed three 30-m-long transects. On each transect, we measured, every 3 m, the distance to the closest *F. pallescens* tussock. From the average distances of each transect, we derived an estimate of tussock density as (Mateucci and Colma, 1982):

$$\text{Density (tussock m}^{-2}) = [(\text{distance (m)} \times 2)^2]^{-1}.$$

On each of the tussocks, we recorded the following attributes:

- Basal perimeter (cm)
- Height of the vegetative portion (excluding panicles) (cm)
- Proportion of standing dead biomass in the tussock (*dfrac*)
- Defoliation (0, no defoliated; 1, slightly defoliated; 2, intermediately defoliated; and 3, intensely defoliated) (see Golluscio et al., 1998b)
- "Vitality" (0, a dead tussock; 1, low; 2, medium; 3, high vitality; and 4, very high vitality). Such categorical variable represents a qualitative assessment of the potential productivity of the tussock.

We harvested 30% of the tussocks recorded and we determined in the lab the weight (oven dried at 70 °C) of the green and standing dead fractions. For the rest of the tussocks, the standing dead fraction was estimated visually. From the original data, we calculated the *diameter* (cm) and the *total volume of the tussock* ($= \pi \times (diameter/2)^2$ height/3, assuming a coned-shape tussock). Multiplying the total volume times *dfrac*, we obtained the *forage volume.* A subset of the recorded individuals were harvested and used to calculate the *biomass density* of the tussock (g cm^{-3}). The product of the *biomass density* and the *forage volume* generates an estimate of the *green biomass* per tussock. Observations were performed during the growing season (September–April).

On a subset of the sites, we estimated the fraction of the photosynthetically active radiation intercepted (fPAR) by the tussock. Monteith (1981) showed that the product of fPAR and PAR, the intercepted PAR (IPAR) is the main determinant of productivity. Based on this rationale, fPAR is a linear estimator of the potential productivity of the tussock and hence an alternative way to estimate the vitality of the tussock. fPAR was assessed using the Normalized Difference Vegetation Index (NDVI), a spectral index derived from the reflectance in the red and infrared band (NDVI = (IR−R)/(IR+R)). Many studies (i.e., Asrar et al., 1984; Sellers et al., 1992) showed that NDVI is a linear estimator of fPAR, even in the presence of dead material (Di Bella et al., 2004). We measured the reflectance of two or three portions of aproximately $50\,cm^2$ on each tussock and we averaged them. We used a hand-held radiometer SKYE that measured reflectance in 650 nm (red) and 789 nm (near infra-red).

2.3.1.1. Comparison of the field patterns and model outputs. We based the comparison between field data and simulation outputs on three attributes: tussock density (m^{-2}), tussock green biomass ($g\,tussock^{-1}$) and the proportion of standing dead material of the tussock (*dfrac*). Comparisons were performed at similar spatial scales; field and simulated estimates were averages of several plots representing an area of approximately $1500\,m^2$. We generated with the model an estimate of each of the variables every 10 years and we averaged the values for decades 6–10. Simulations were performed for three stocking densities that covered the range observed in the ranches studied (0, 0.9, and $1.5\,sheep\,ha^{-1}$) and for 100 years. The field data were summarized at the level of individual ranches ($n = 6$). Standard errors were calculated over the paddocks analyzed per ranch. In one of the ranches, only one paddock was surveyed. Because of the high spatial variability of the effective stocking density within a paddock, it is difficult to assign a unique value to each particular plot of $1500\,m^2$.

2.3.1.2. Testing model assumptions. We used field data to test three essential assumptions of the model: (1) the amount of dead material decreases as grazing pressure increases, (2) the degree of consumption of individual tussocks and its spatial variability decrease as the percentage of dead material of the tussock (*dfrac*) increases, and (3) the vitality index is a reliable estimator of the potential productivity of a tussock. To test the last assumption, we generated (for the average precipitation conditions of the sampled *F. pallescens* steppes) values of biomass production per tussock using the equation included in the model (see Appendix 1). We estimated tussock production from peak biomass (Sala and Austin, 2000) and from NDVI data. We averaged tussock production for each vitality class ($n = 570$).

2.3.2. Sensitivity analyses

We analyzed the sensitivity of three key output variables of the model (tussock density, green production, and average fraction of dead material per tussock) to changes in the parameter values. We grouped the parameters into 14 classes (Appendix 2, electronic version only) because many of them only may vary simultaneously. Each class was associated to a particular ecological process simulated by the model. Grouping the parameters reduced the numbers of runs and simplified the sensitivity analysis without loosing much information.

We defined a lower (LV) and upper value (UV) for each parameter within a group (Appendix 2, electronic version only). Such definition was based on our best knowledge of the possible variation of the parameters because of the lack of information on the probability distribution of each parameter. Each of the 14 groups of parameter was modified in the same direction in each of the runs. We performed, for the same initial conditions and climate scenario, 2^{14} runs. We investigated the relative main effect (RME) of each parameter class on each of the three output variables (tussock density, green production, and average fraction of dead material per tussock). The RME was calculated as the difference between the sum of the values of the output variable for runs with the LV (−1) and UP (1), divided by the sum of the output variable for the whole set of runs (Paruelo and Sala, 1995).

2.4. Modeling experiments

To understand the dynamics of the system, we designed several modeling experiments that combined five climatic scenarios and 12 management scenarios resulting from combining different grazing seasonalities and stock densities. We represented the behavior of the system from the temporal dynamics of tussock density, the proportion of tussock grazed, the structure of the tussock, and the annual ANPP. We calculated the PUE (mean annual ANPP/MAP) (Le Houérou, 1984) and the precipitation marginal response (PMR) (the slope of the relationship between ANPP and annual precipitation) (Verón et al., 2005). These two variables are particularly sensitive to degradation (Veron et al., 2006). The five climatic scenarios were built on a series of MAP generated from a MAP = 375 mm and a coefficient of variation (CV) = 20%. Such series represented the typical mean and variability of a grass steppe site (Jobbágy et al., 1995). The original data were rearranged in order to generate two scenarios with a higher autocorrelation than the original data, one having a period of 10 years (C10) and the other of 20 years (C20). Two additional scenarios differed in the inter-annual variability. One of them, "high variability", was generated by removing from the series the years with MAP close to the average, and the other, "low variability", by removing extreme years. For the high variability scenario, the CV was 28% and for the low variability scenario the CV was 8%. Every scenario had the same MAP (375 mm). The management scenarios were derived from combining stock densities and grazing seasonality. For three ranches, we collected data on the long-term stocking density of 22 paddocks. The average size of the paddocks was 2571 ha, ranging from 555 to 7443 ha. Mean stocking density was $0.75\,sheep\,ha^{-1}$, ranging from

0.29 to 1.58 sheep ha^{-1} (CV = 48%). Based on the observed data, we defined stocking density scenarios, from 0 up to1.5 sheep ha^{-1}. Only data for 0, 0.9, and 1.5 sheep ha^{-1} are presented. According to the information available for the area on grazing management (Golluscio et al., 1998a), we defined four scenarios of seasonality: continuous, winter, spring, and summer/fall grazing.

3. Results

3.1. Model evaluation

3.1.1. Testing model assumptions using field data

The fraction of standing dead material of a tussock (*dfrac*) differed between grazed and excluded areas ($p < 0.05$) (assumption 1: the amount of dead material decreases as grazing pressure increases) (Appendix 3, electronic version only). In average, more than 50% of a tussock in an excluded area corresponded to standing dead material. Most of the tussocks in excluded areas were concentrated in the 60–80% *dfrac* class while they were concentrated in the 40–60% *dfrac* class in grazed areas (Fig. 4).

Our data support the relationship between sheep preference and plant structure incorporated in the model: the degree of consumption of individual tussocks and its spatial variability decreases as the percentage of dead material of the tussock (*dfrac*) increases (assumption 2) (Appendix 4, electronic version only). The relationship based on the individual tussocks ($n = 480$) showed also a significant negative relationship between the consumption level and *dfrac* ($r = -0.37$, $F = 61$, $p < 0.01$). Dead material estimates corresponded to pre-grazing conditions.

The relative variability of the degree of consumption decreased as the grazing pressure increased (assumption 3) (Appendix 5, electronic version only). At low grazing pressures (low mean degree of consumption), highly defoliated tussocks coexist with not-defoliated plants. As the mean degree of consumption of a patch increases, the proportion of grazed tussock and the intensity of the defoliation of each tussock increase, reducing the variance among tussocks. The model (using the standard parameterization, Appendix 2, electronic version only) was able to simulate the same exponential decline in variability as the proportion of the biomass consumed augmented (Appendix 5, electronic version only). The magnitude of the CV was similar between simulated and field data.

Although they were completely independent, field and model estimates showed a similar relationship between productivity and vitality with a maximum around 25 g $tussock^{-1}$ for vitality class 4 (assumption 3: the vitality index is a reliable estimator of the potential productivity of a tussock) (Fig. 4). NDVI, an independent estimate of light interception and hence carbon gains showed also a positive relationship with tussock vitality (Fig. 4).

3.1.2. Sensitivity analysis

Only six of the 14 groups of parameters have a RME on the output variables higher than 10%. The model was particularly sensitive to those parameters related to water inputs (Fig. 5). The RME of the fraction of the precipitation available for plants (WI_1, parameter group 1) on tussock density was 0.38. The rain factor parameter WI_1 represents the proportion of the incoming water transpired by the vegetation. Our estimates (0.57, Appendix 2, electronic version only) are well supported on the local data provided by the literature (Paruelo et al., 1998, 2000).

Changes in the water redistribution parameters (group 2) had a larger effect on tussock production than on *dfrac* or tussock density. No data were available to support directly the values used, but studies on root lateral spread of Patagonian
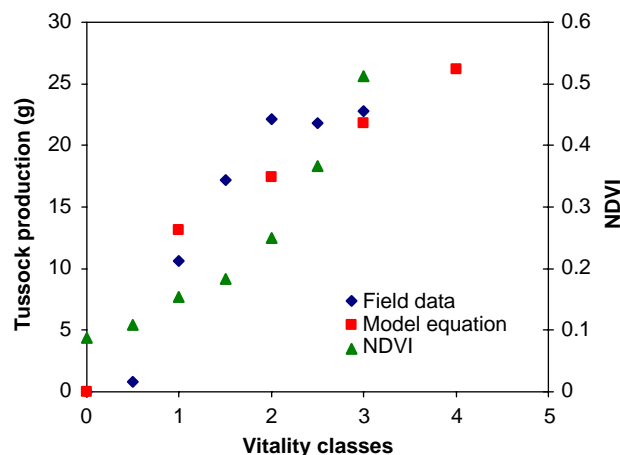

Fig. 4. Average tussock production per vitality class as derived from model equation (squares) and field data (peak biomass, diamonds) ($n = 570$). Triangles represent the NDVI recorded on 216 tussocks. Vitality was assessed visually.
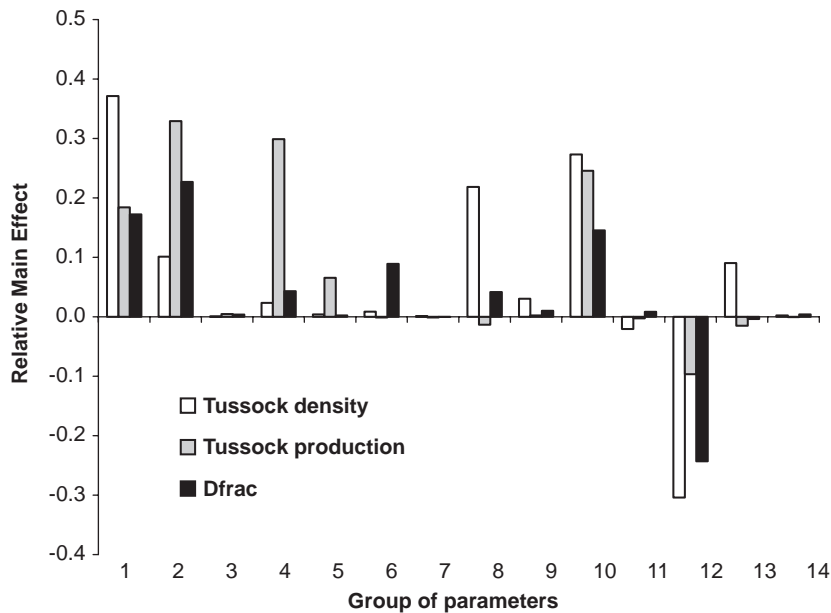
Fig. 5. Relative main effect of 14 groups of parameters (defined in Appendix 2, electronic version only) on three output variables of the model: tussock density, tussock production, and the fraction of dead biomass per tussock (*dfrac*). (1) Fraction of rain available to plants, (2) water loss to neighboring tussocks, (3) water loss due to large bare patch, (4) relationship between ANPP and vitality, (5) Michaelis-Menten constant for production, (6) senescence and littering rate, (7) defoliation parameters, (8) colonization parameters, (9) colonization parameters, (10) soil water controls of vitality, (11) defoliation controls of vitality, (12) water controls of mortality, (13) defoliation controls of mortality, and (14) forage provided by other items.

grasses (Soriano et al., 1987) and experiments on water competition in the steppe (Aguiar et al., 1992) suggest that the values assumed were reasonable.

Plant growth parameters (group 4) had a high effect on tussock production (RME = 0.30) but no substantial influence on the other two output variables. A differential sensitivity of output variables was also evident for the colonization parameters pertaining to group 8. The rate of senescence and littering (group 6) had an important impact only on *dfrac* (RME = 0.10). The group of parameters that include the water thresholds for vitality-class change of a tussock (group 10) had a large effect on tussock density and on tussock production (RME = 0.27 and 0.25, respectively) and a lower but still high impact on *dfrac* (RME = 0.15). The parameters related to the effect of water availability on mortality rate (group 12) had a large impact on the tussock density and *dfrac* (|RME| > 0.23) and a lower but strong impact (|RME| = 0.10) on tussock production. The large influence of this group of parameters was probably associated to the broad range of values used in the analysis. For two of them, the upper value was one-order of magnitude higher than the lowest value and for the remaining two, the upper value was almost twice the lowest value. The influence of the parameters related to the grazing and the colonization routines was relatively minor within the range of values studied (Fig. 5).

3.1.3. Comparison of field patterns and model outputs

The tussock density simulated by the model covered the range defined by the extreme values observed in the field (0.39 and 7.20 tussocks m^{-2}) (Fig. 6a). Tussock green biomass simulated by the model laid within the range of observed average values per ranch (Fig. 6b). The simulated green biomass was slightly lower and less variable than the values measured in the field. The indirect approach used to generate field estimates may be responsible of their high spatial variability. Except for the heavily grazed conditions runs (1.5 sheep ha^{-1}), simulated and observed values of *dfrac* (the proportion of standing dead biomass per tussock) were similar, ranging between 0.30 and 0.60 (Fig. 6c). As we observed in the field, grazing increased the relative abundance of tussock with low *dfrac*.

3.2. Simulation experiments

Long-term simulation of the dynamics of the *F. pallescens* showed that the structural and functional attributes simulated are highly variable in time regardless of the grazing management or the stock density (Fig. 7). Under non-grazing conditions, the 10-year mean tussock density varied between 5 and 9 tussocks m^{-2} (Fig. 7a). Grazing generated a delayed reduction in tussock density (Fig. 7a). After 10 years of grazing, even under the high selectivity regime (continuous grazing), the differences among stock density scenarios were small. There is a clear threshold in the response of variable simulated in between 0.9 and 1.5 sheep ha^{-1}. Such change, though, was evident only when a highly selective grazing scenario was
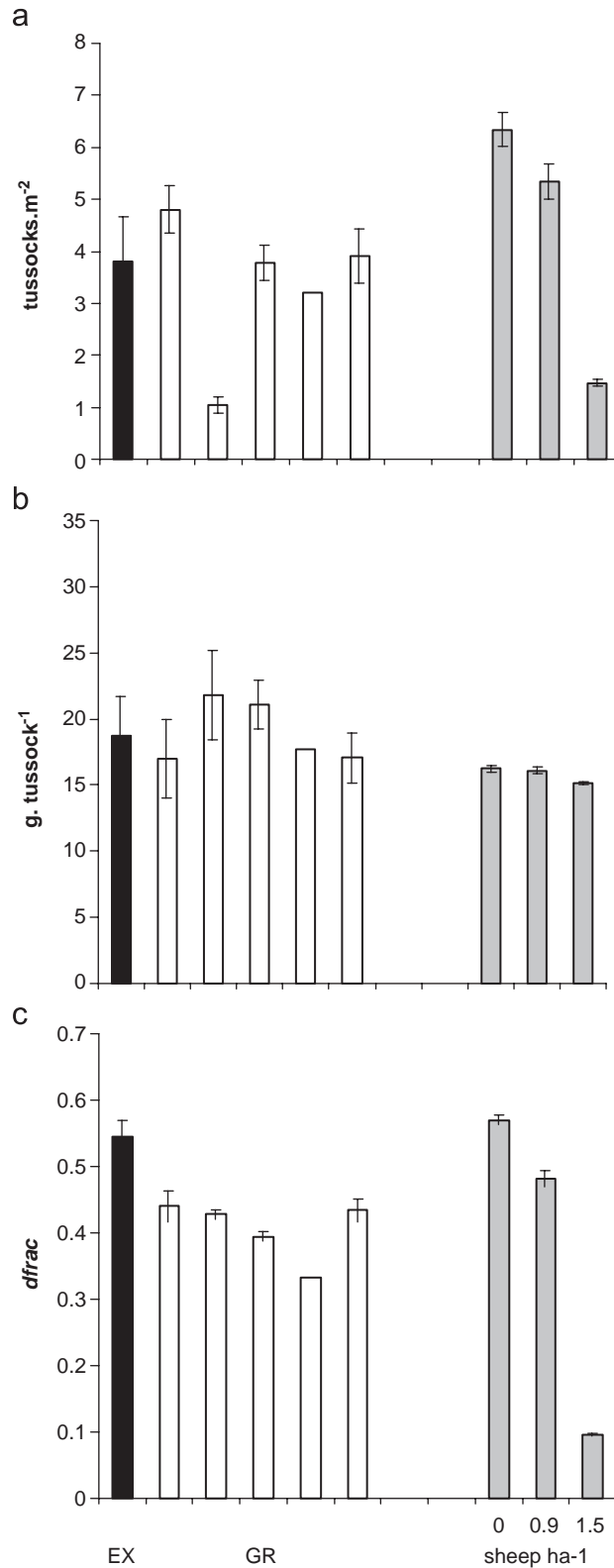
Fig. 6. Averaged values of tussock density, tussock green biomass, and the fraction of dead biomass per tussock in six sites corresponding to private ranches, one ungrazed (EX) (black bar) and the other five grazed (GR) with different stocking densities (white bars), and from model outputs (gray bars) for three stocking densities (0, 0.9, and 1.5 sheep ha^{-1}). The lines on top of the bars correspond to the standard error.
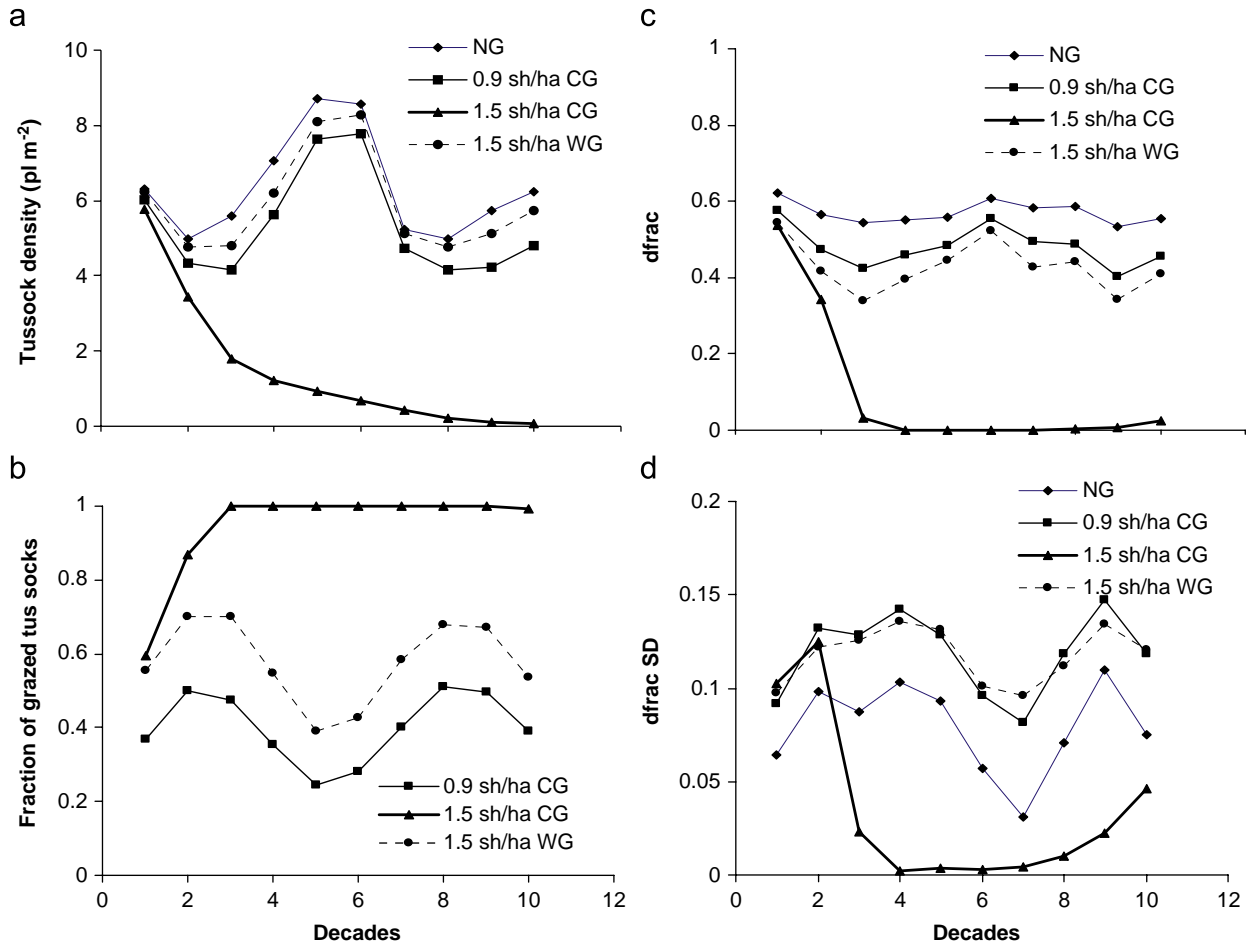
Fig. 7. (a) Ten-year average values of simulated tussock density, (b) fraction of grazed tussock per grid, (c) proportion of dead biomass per tussock (*dfrac*), and (d) standard deviation of *dfrac*. Simulations were performed for the ungrazed (NG) and continuous grazing (CG) conditions, at three different stock densities, 0, 0.9, and 1.5 sheep ha^{-1} and for winter grazing (WG) at 1.5 sheep ha^{-1}. The results reported correspond to the control climate scenario.
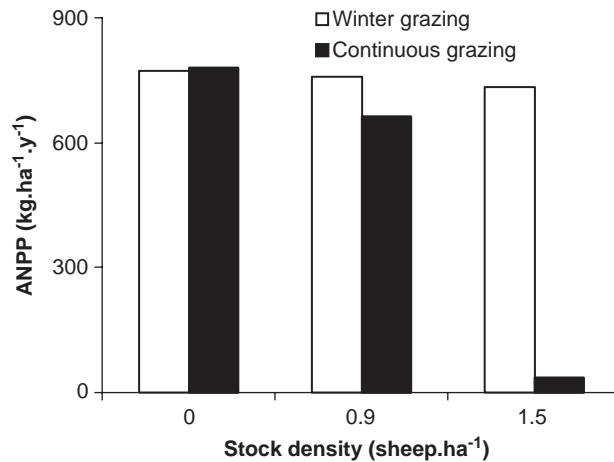

Fig. 8. Average aboveground net primary production (ANPP) for the last decade of the simulation for different stocking densities and grazing systems (continuos vs. winter grazing). The climate scenario was the control.
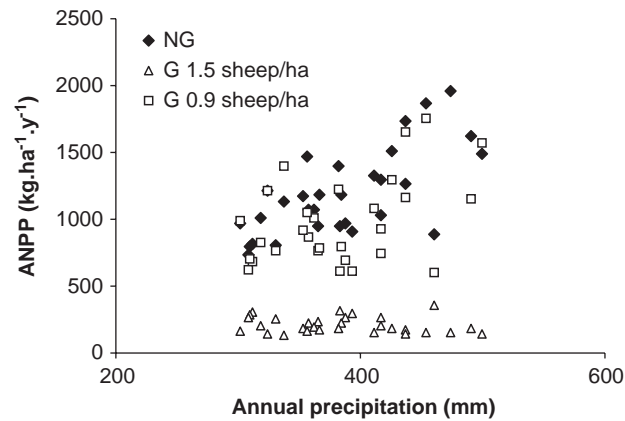
Fig. 9. Simulated aboveground net primary production (ANPP) for different stocking densities (NG: ungrazed, 0.9 and 1.5 sheep ha^{-1}) as a function of current year precipitation.

simulated (continuous grazing). In fact, tussock density is higher for a stock density of 1.5 sheep ha^{-1} under winter grazing (less selective) than for 0.9 sheep ha^{-1} under continuous grazing (more selective). However, under winter grazing more tussocks were grazed (Fig. 7b) and they had a lower *dfrac* (Fig. 7c). The magnitude of the differences in grazed tussocks among grazing scenarios varied through time and can become minimum after a sequence of high precipitation years (decades 6 and 7, Fig. 7a and c). For moderate stocking densities, it ranged between 22% and 44% (Fig. 7c). As grazing pressure increased, up to 100% of the tussocks were grazed. It took, though, 20 years to achieve such proportion of grazed tussock under the more selective scenarios (continuous grazing) (Fig. 7c). Grazing modified the structure of the steppe by reducing the amount of dead material per tussock (*dfrac*) and the spatial variability of this attribute. The proportion of dead biomass per tussock (*dfrac*) was less variable among years than tussock density, ranging from 0.53 to 0.62 (Fig. 7b). The spatial variability of *dfrac* (standard deviation) varied between 0.03 and 0.11 (Fig. 7d). The temporal CV of the average potential productivity (*vitality*) of the tussocks was 11% (data not shown).

The reduction in tussock density by grazing (Fig. 7a) resulted in a decline in ANPP (Fig. 8). For the same range of stocking densities, the decline in ANPP is linear under a low selective grazing regime. Again a threshold is evident for the same range of grazing pressure when a highly selective grazing condition was simulated. Tussock density explained 82% of the inter-annual variability in ANPP. ANPP showed a temporal coefficient of variation of 23% (data not shown) with extremes values of 456 and 1561 kg ha^{-1}. Under non-grazing conditions, the PUE averaged 0.35 g m^{-2} mm^{-1}. Differences in ANPP among grazing regimes become evident only at high stocking densities (>0.9 sheep ha^{-1}). The changes were minimum for winter grazing and maximum for continuous grazing, reflecting changes in selectivity. Under high stock density conditions, PUE was 82% lower than the values for non-grazed runs (0.055 g m^{-2} mm^{-1}). Grazing reduced also the sensitivity of ANPP to inter-annual changes in precipitation (PMR, Verón et al., 2005) (Fig. 9). The slope of the relationship between simulated ANPP and precipitation (PPT) was 0.35 g m^{-2} mm^{-1} for non-grazed conditions and 0.16 g m^{-2} mm^{-1} for the grazed with a stock density of 0.9 sheep ha^{-1}. Stochastic and delayed effects incorporated into the models determined that less than 20% of the inter-annual variability of ANPP was explained by annual precipitation under non-grazing conditions (Fig. 9). The precipitation from the two previous years accounted for a substantial portion of the unexplained variance (an additional 19%, data not shown). For high grazing pressures (1.5 sheep ha^{-1}), the system became insensitive to changes in annual precipitation (Fig. 9).

The variability and autocorrelation of the precipitation data had an important effect on tussock density, and hence on ANPP. The inter-annual variability of precipitation was more important than the grazing regime in explaining differences in tussock density (Fig. 10). Tussock density was higher and less sensitive to the grazing regime under a low-variability scenario (Fig. 10a and b). The autocorrelation of the precipitation data increased the sensitivity of the system to high stock densities under CG (Fig. 10b).

4. Discussion

Long-term dynamic of semiarid systems are often inherently complex because they may exhibit non-equilibrium dynamics where nonlinear processes (Briske et al., 2005; Westoby et al., 1989) and stochastic event-driven behavior (Jeltsch et al., 1999; Walker, 1993; Wiegand et al., 1995) are involved. Our model results confirmed these findings. Moreover, an additional difficulty arises because temporal and spatial scales may not be well separated, but complex interactions occur across scales. For example, degradation due to grazing is a process which operates on the small spatial scale of individual plants and at the small temporal scale of defoliation events, but it becomes visible only at larger, say paddock, scales and at larger time scales of often decades.
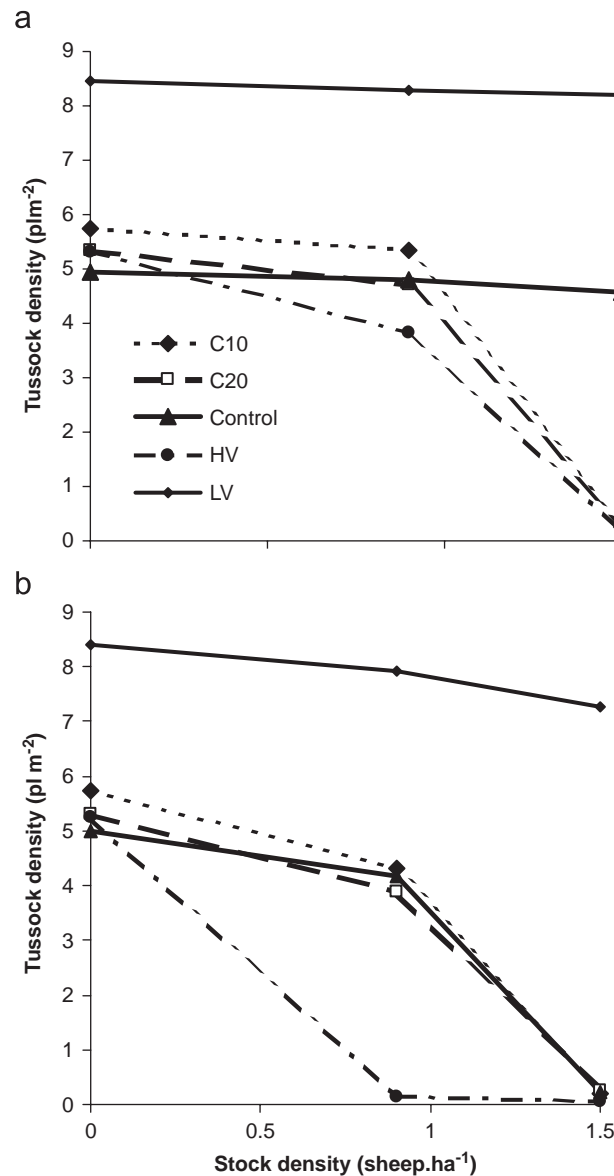
Fig. 10. Simulated tussock density as a function of the stocking density for two grazing systems: (a) winter grazing and (b) continuous grazing for five climate scenarios; control, 10-year-period cycle (C10), 20-year-period cycle (C20), low inter-annual variability (LV).

4.1. The modeling approach

We constructed our model on a spatial scale (i.e., the scale of individual tufts) which facilitates a direct comparison of model outputs with field observations. This had two advantages: first, because the scale of the model was also the scale of observation, we could transform our knowledge directly as rules into the model, and second, we could simulate the same variables we measured in the field.

An additional ingredient of our approach was that we compared the model against multiple field data. While it might be relatively simple to reproduce one feature of a system (e.g., tussock density) with a number of substantially different model versions, the simultaneous agreement with multiple data each describing different key-features of the system is by far non-trivial (e.g., Grimm et al., 2005; Wiegand et al., 2003, 2004a). Because the initial conditions and the variability of the driving forces of the *F. pallescens* system (stock density, grazing seasonality, etc.) are difficult to access and because the simulated structure of the *F. pallescens* steppe was highly variable in time, we performed qualitative model evaluations which are one of few alternatives under such circumstances. The model showed in general good qualitative agreement with field observations. For example, simulated values of tussock density, tussock biomass and *dfrac* for the range of stock

densities, where within the range of field observations (Fig. 6) and the spatial variability of the estimates was similar between simulated and observed data. Interestingly, the relationship between the relative variability among the degree of consumption of individual tussock and the measure of grazing pressure was similar for both simulated and observed data. The changes in tussock density and primary production associated with grazing matched the trends reported in the literature (Aguiar et al., 1996; León and Aguiar, 1985).

A sensitivity analysis provided us a complementary evaluation of the model. Such analysis allowed us to find critical model processes and parameters which deserved further field studies and to assure that the simulated dynamics of the model did not critically depend on the model parameterization. The model showed a moderate sensitivity (less than 40% of RME) to changes in the parameter values within a plausible range (Fig. 5). Such analyses indicated that, given the present structure of the model, the parameters related to water use efficiency and the effect of water on the potential production and mortality of a tussock had the largest influence on the outputs of the model. Field experiments focusing on the influence of water availability on actual and potential productivity at the tussock level and on plant mortality will certainly contribute to improve the model throughout a better definition of the parameters. Such experiments should be based on generating a broad range of water availability using watered plots and rainout shelters (see Yahdjian and Sala, 2002). We found that the behavior of our model was surprisingly stable and even the initial parameter estimates yielded reasonable model behavior. This shows that our model indeed captures "the essence" of the dynamics of the F. pallescens steppe in a robust way.

Despite its ability to reproduce observed field patterns, the model has some limitations. One of them is that it does not consider the dynamics of shrub encroachment described for the area (Bertiller et al., 1995; León and Aguiar, 1985). The model only simulates the early states of degradation by grazing, which can be observed in the field. An additional limitation is the absence of explicit simulation of erosion processes. Erosion alters water redistribution and dynamics, and it also constrains recruitment processes (Defosse et al., 1997a, b). To investigate later stages of degradation, the mechanisms of shrub encroachment and erosion need to be explicitly incorporated into the model. This, however, requires collection of more experimental data to gain a better understanding of these mechanisms.

The temporal variability of the system makes difficult the evaluation of model performance using field data because the initial conditions and the variability of the driving forces of the system (stock density, grazing seasonality, etc.) are difficult to assess. This sets logistic limits to a formal evaluation of the model at the level of the predictions, particularly if it is not possible to reconstruct the management history of the field plots.

4.2. The long-term dynamics of the F. pallescens steppe

The long-term simulations of the dynamics of F. pallescens steppe highlighted some interesting characteristics of the system that are neither obvious nor clear from field observations and/or experiments. One of them is the temporal variability of its structure. Even in the absence of grazing, tussock density varied by a factor of two (Fig. 7). The temporal variability would be associated with an important autocorrelation of the output variables. This autocorrelation generates a "memory" or inertia in the system that may last many years. Memory effects differed among variables: *tussock density > dfrac > fraction of tussock grazed*. Such differences among ecosystem attributes are critical in evaluating the response of the system to management practices. Inertia often characterizes the response of vegetation structure to environmental changes, as reported in studies of several ecosystems at different time. Memory and carryover effects might play an important role in the functioning of semiarid rangelands by buffering inter-annual fluctuations in biomass production between wet and dry years and by amplifying fluctuations if wet or dry sequences of several years take place (Goward and Prince, 1995; Oesterheld et al., 2001; Wiegand et al., 2004b). In the past, such carryover effects have been demonstrated for a few perennial grasslands and shrublands (for example, see Gibbens and Beck, 1988; Jobbagy and Sala, 2000; O'Connor et al., 2001; Oesterheld et al., 2001). Our model goes one step further by identifying differences in memory in the dynamics of some of the variables that determine biomass production at the ecosystem level. Many mechanisms may account for the memory of the system. In this model, a key processes in determining carryover effects is the dynamics of tussock structure. The amount of dead material accumulated and its impact on tussock vitality or potential productivity and on the probability of being grazed play a central role in the ability of an individual tussock of using the available resources. The episodic nature of the events of mortality and recruitment made an important contribution to explain carryover effects.

Assessing the status of a plot based on the density or cover of F. pallescens would be, as a consequence, extremely difficult. The inter-annual variability of tussock density was higher than the spatial variability that grazing management and stock densities may generate (Fig. 7). The most reliable indicator of the impact of grazing was the fraction of dead material of the tussock (dfrac). Grazing treatments start to differ in dfrac earlier than in other variables. Highly selective grazing regimes (spring or continuous grazing) generate a population with almost no standing dead material. Grazing also increases the spatial variability of dfrac within patches.

Experimental data showed that current year precipitation explained a relative low proportion of the inter-annual variability in grassland and shrubland ANPP (Lauenroth and Sala, 1992; Paruelo et al., 1999). Oesterheld et al. (2001) identified the influence of previous year production on current ANPP. Wiegand et al. (2004b) showed that in semiarid grasslands, the memory of the system on previous precipitation might last many years. Simulation results indicate that

even when precipitation is the main driver of ANPP, a relatively small proportion of its variance is explained by current year precipitation (Fig. 9). This is because the memory of the system (see above) determines an important effect of the distribution of "good" and "bad" years on tussock density dynamics and hence on ANPP inter-annual changes (Fig. 10). A change in the variability or in the amplitude of cycles of precipitation levels may have an enormous impact on the system, even under the same MAP. Interestingly, the response of the system to the inter-annual pattern of precipitation variability changes under different management scenarios.

A highly degraded system cannot respond to inter-annual changes in precipitation (Fig. 9). In such conditions, most of the incoming water is lost as deep percolation or runoff. An increase in runoff may generate serious erosion problems in the steppe (Paruelo and Aguiar, 2003). Each of the remaining tussocks will have, though, enough water and consequently the productivity of individual plants will not change dramatically with annual precipitation. As many authors pointed out (Le Houérou, 1984; Prince et al., 1998), a degradation of the system leads to an important reduction of PUE. O'Connor et al. (2001) observed a reduction in PUE in experimental plots as degradation increases in South African grasslands. Such decrease may result from a reduction in tussock density but also from lower PUE per unit of basal cover. The reduction in plant cover determined that the system becomes unresponsive to annual changes in precipitation. The slope of the ANPP–PPT relationship (the PMR) has been proposed as a descriptor of desertification (Paruelo et al., 2005; Veron et al., 2006). Our simulation results showed that long-term grazing reduced significantly not only PUE but also the PMR of ANPP (Fig. 9). Our modeling results support the use of the PUE and PMR as a reliable indicator of degradation in arid and semiarid system. The possibility of monitoring PUE and PMR from remotely sensed (Prince et al., 1998; Veron et al., 2006) data makes this approach particularly appealing.

Stock density reduced tussock density, ANPP, and the fraction of standing dead material of a tussock among simulations (Fig. 6). The total amount of biomass removed decreased the productivity of the steppe because of its impact on tussock potential production ("vitality") and hence on tussock mortality. The magnitude of this change varied for different grazing management layouts. Those that increase the selectivity of grazers generated more differences in tussock density and ANPP between non-grazed and grazed treatments (Fig. 8). The impact of grazing on the production of biomass of the individual tussocks was much more limited. The impact of grazing on ANPP was associated more to a reduction in tussock density than to a decrease in individual production. The response of tussock density and ANPP to stock density and grazing seasonality was nonlinear suggesting the existence of sustainability thresholds. Such kind of response, added to the lag in the response of the system to management practices and to the interactions with climate, turns highly risky the definition of optimum stock densities and grazing systems on the base of "trial and error" approaches.

4.3. Implications for management

The model developed provides an important tool to explore the long-term behavior of the system under different scenarios of grazing management and climate variability. Both range managers and conservation agents may take advantage of this tool. An exploration of scenarios that combine different stock densities and grazing seasonality regimes would provide the basis to analyze the sustainability of different land use alternatives for the steppe both in economic and ecological dimensions. In such a way, the model may become an important aid in assessing desertification risks in the region. Model runs may help also to evaluate in the field the results of specific land use policies by providing an estimate of the probability of detecting changes using different survey variables (ANPP, tussock density, tussock structure, etc.).

Acknowledgments

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2008.07.010.

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