Long-Term Impact of Grazing on Vegetation under Stochastic Climate:
A Cross-Scale Simulation Study

Ph.D. Thesis

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Typical view of the *Festuca pallescens* steppe in North-West Patagonia (Argentine) at Estancia Tecka (Foto: Sandro Pütz).

That is what we meant by science.

That both question and answer

are tied up with uncertainty,

and that they are painful.

But that there is no way around them.

And that you hide nothing;

instead,

everything is brought out into the open.

(Peter Høeg, Borderliners)

Table of Contents

Index of Tables

Index of Figures

ABSTRACT

The separation of the relative contributions of anthropogenic factors and stochastic natural factors is of particular importance for long-term sustainable management of semi-natural ecosystems. Due to the long inherent time-scales of vegetation change and a lack of long-term monitoring data, the separation of the effects of the two basic factors affecting vegetation in semi-arid ecosystems, i.e., grazing and highly variable rainfall has not been possible empirically and was not explicitly addressed by modelling studies. The general aim of this PhD is to provide an understanding of the small-scale processes involved in degradation. More specifically, I present an individual- and rule-based stochastic and spatially-explicit simulation model to investigate the effect of grazing under stochastic rainfall on the perennial tussock grass *Festuca pallescens* and to separate the causal effects on *F. pallescens* dynamics. One essential characteristic of the simulation model is that both exogenous drivers – grazing and precipitation – act on each demographic process of each individual grass tussock. This property of the model will finally facilitate the separation of the relative effects of both drivers for each simulated time step on *F. pallescens* dynamics.

To respond to its aim, the model needs to include a number of detailed factors affecting the *Festuca* population dynamics under grazing. This is reflected in an intermediate complexity with some thirty model parameters. Due to the lack of field data most of these parameters could not be estimated directly. To calibrate the simulation model I followed the indirect multi-criterial pattern-oriented approach, which was developed by Wiegand et al. (2003). Within this PhD thesis I further developed this approach, using a step wise and cross calibration. I showed that the medium complex *Festuca* model with 30 free parameters can be calibrated with a small field data set to produce behaviour in accordance with field observations. An extensive sensitivity analysis showed the novel result that lateral local water redistribution has a relevant impact on the behaviour of the dynamics of the grazed ecosystem. It further revealed that the model system is highly sensitive against the senescence and the littering rate. Both parameters compete with the herbivores for green biomass.

After model calibration (or with the expert parameterisation) I performed various simulation experiments to investigate the behaviour of the system and to investigate the effect of grazing on vegetation under stochastic rainfall. I found that the *Festuca* steppe shows an event-driven behaviour which is modified by grazing gradually as well as qualitatively. The vegetation cover showed threshold behaviour under the grazing gradient which is also reflected by the recovery times of the grazed system. I found that the beginning of vegetation decrease depends on both climatic and biological uncertainty. I proposed a method for determining risk levels for degradation and for the determination of long-term sustainable stocking rates. I analysed temporal autocorrelations of essential variables of *F. pallescens* to show how memory effects influence its complex vegetation dynamics. Finally I separated the relative effects of grazing and precipitation on vegetation for specific precipitation time-series. This elucidated the link between the short-term interaction of grazing and precipitation and the observed long-term grazing threshold. The presented simulation model improves the understanding of the effect of small-scale biological processes on patterns emerging at larger scales as e.g. the landscape scale.

This PhD-thesis contributes significant new insights into the interaction of grazing and stochastic precipitation in semi-arid systems and provides instruments to estimate degradation risk considering biological and climatic uncertainty. Furthermore the presented indirect multi-criterial pattern-oriented calibration method helps to bridge the gap between theoretical and empirical ecology as it enables us to gain strong confidence into simulation models even if we dispose only over scarce evidence from empirics. This aspect leads not only to a better understanding of ecosystems which are endangered by land use and strongly affected by stochastic environmental processes, but is also of general interest for simulation models facing a high degree of uncertainty because this method allows to tie the model closely to the data, i.e. ensuring a biologically reasonable behaviour and parameter values.

1 INTRODUCTION: MOTIVATION FOR THE STUDY

1.1 GENERAL INTRODUCTION

The loss of perennial vegetation and soil in arid and semi-arid regions is considered as one of the main ecological threats facing the world (Schlesinger et al. 1990, Pickup 1996, Scheffer et al. 2001, Dregne 2002). This phenomenon occurs at a planetary scale, affecting more than 70% of the area in Africa, Asia and the Americas and more than 50% in Australia (Cardy 1994). It threats one third of the earth's surface, adding up to an area of over 4 billion hectares and affecting one fifth of the world's population. The effects can be locally observed, for example, in many areas of Asia, the Sahel, Latin America, throughout North America or along the Mediterranean.

There are two different processes involved in the loss of vegetation and soil in drylands: Desertification and Degradation. The concept of desertification is used in a wide range of situations and contexts, and, probably due to the widespread use of the term, its definition has been controversial and vague (Schlesinger 1990, Reynolds and Stafford-Smith 2002). 'Desertification' refers to different natural processes leading to the expansion of deserts, including climatic change and gradual changes of summer radiation on earth (Schlesinger 1990, Scheffer et al. 2001). These processes can be also indirectly influenced by human actions. 'Degradation' is the long-term and potentially permanent loss of vegetation cover and soil which is directly induced by humans and often related to grazing (Pickup 1996). Degradation may also provoke the reduction of animal productivity in rangelands. Therefore, an understanding of mechanisms that lead to man-induced degradation by overgrazing is essential for developing a sustainable land management and for avoiding further loss of productive soil. The general aim of the presented PhD-Thesis is to provide an understanding of the small-scale processes involved in degradation. I will use a bottom-up approach and investigate the general questions based on a specific system, the *Festuca pallescens* steppe in semi-arid North-West Patagonia (Argentine). In the next section I provide background information and motivate important specific objectives of my thesis. The structure of the thesis and the specific aims of the different chapters are given at the end of this chapter.

1.2 BACKGROUND, STUDY SYSTEM, SPECIFIC AIMS, METHODS, AND CHALLENGES

Understanding the interaction of precipitation and climate. — Debates related with degradation in semi-arid and arid regions have mostly focused on animal productivity (Ellis and Swift 1988, Ellis 1994, Illius and O'Connor 1999, Illius and O'Connor 2000). Although the problem of degradation is known since decades, the details of the processes which are involved are poorly understood. It is often postulated, and generally accepted that the interaction between grazing and the stochastic variability in rainfall in semi-arid regions can cause discontinuous shifts in vegetation (Schlesinger 1990, O'Connor 1994, Pickup 1996, Fuhlendorf and Smeins 1997, Stafford Smith and McKeon 1998, Illius and O'Connor 2000, Teague et al. 2004). Although conceptually tempting, it is widely unknown how this interaction works in detail, and only recently some simulation studies have investigated the effect of white environmental noise on semi-arid vegetation within ecological and management relevant time-frames (e.g., Wiegand and Milton 1996; Jeltsch et al. 1996, Jeltsch et al. 1997). White environmental noise is defined as a stochastic varying external driving factor – like annual precipitation – which shows no temporal autocorrelation.

The effect of stochastic environmental variation on population dynamics is an important issue in theoretical ecology (Levins 1969, Lewontin and Cohen 1969, May 1973, Chesson 1978, Wissel 1989) and in conservation biology in relation with the risk of (meta)population extinction (Lande and Orzack 1988, Lande 1993, Beissinger and McCullough 2002, Lande et al. 2003, Drake and Lodge

2004). Approaches in theoretical ecology were mostly concerned with equilibrium probability distributions under stochastic environmental conditions, whereas conservation studies have focused on the extinction risk of small populations at longer time scale. However, a more systematic investigation of the effect of environmental fluctuations on semi-arid vegetation has yet not been undertaken. An extensive analysis of the interaction between highly variable rainfall and grazing is necessary to provide an understanding of the degradation process on a short management relevant time-scale. This is a central theme of this thesis.

Equilibrium- and non-equilibrium dynamics. — Possibly due to scarce knowledge about the mechanism of degradation, a controversy about the type of dynamics shown by semi-arid and arid systems has arisen in the last years (Ellis and Swift 1988, Ellis 1994, Illius and O'Connor 1999, Illius and O'Connor 2000, Briske et al. 2003). Ellis and Swift (1988) postulated that livestock does not exert on the long-term a strong negative impact on semi-arid and arid vegetation with high variable rainfall, whereas Illius and O'Connor (1999/2000) argued that grazing has a negative effect on vegetation. This controversy is strongly linked to the notion that vegetation in arid and semi-arid regions shows non-equilibrium dynamics, due to the importance of precipitation and water availability (Noy-Meir 1973, Walker et al. 1981, Westoby et al. 1989). The basic aim of this thesis is to investigate the equilibrium dynamics of a specific semi-arid system in detail and how the dynamics are affected by grazing.

Approaches to sustainable management. — The present thesis has also a strong applied focus. I will try to develop a criterion which helps to find long-term sustainable management of the ecosystem under study. The question how degradation and desertification could be faced is up to date an unresolved issue and 'there is an urgent need for new, interdisciplinary approaches for addressing this global problem' (Reynolds and Stafford Smith 2002).

Pattern oriented and individual based spatially explicit modelling. — Due to the highly variable rainfall, the strong dependence of vegetation on rainfall, cross-scale interactions, the long time-scales of vegetation change, and the lack of empirical long-term studies on vegetation dynamics (Briske et al. 2003), it is nearly impossible to perform an integrated study of semi-arid systems without a simulation model. Therefore, I use a simulation model to answer the questions stated above. It simulates the grazing impact of herbivores on a dominant tussock grass species in a temperate semi-arid steppe. The model includes also highly variable inter-annual stochastic precipitation. This simulation model will help assessing the short-term effects on vegetation of the interaction between grazing and highly variable rainfall, and the long-term effects of this interaction.

I use a rule and individual based, spatially explicit simulation model and the pattern oriented modelling approach. Both concepts were introduced successfully into ecology during the last decade (Grimm 1994, Uchmanski and Grimm 1995, Wiegand et al. 1995, Grimm et al. 1996, Jeltsch et al. 1996; Grimm 1999, Jeltsch et al. 1999, Grimm 2002, Wiegand et al. 2003, Grimm and Railsback 2005, Grimm et al. 2005). The individual-based approach allows for an optimal up-scaling from grazing effects which act on the individual tuft level to a landscape level where degradation becomes visible. The pattern oriented approach (Grimm 1994, Grimm et al. 1996; Wiegand et al. 2003) allows for an optimal adaptation of the simulation model to the question and the data. In situations of scarce data the pattern oriented approach allows to use the available field data as a reference to calibrate the simulation models and to infer biological processes which operate at lower hierarchical levels than the provided field data (Wiegand et al. 2004a/b).

Modelling grazing systems. — Several studies using rule based simulation models have investigated the effect of grazing on semi-arid ecosystems under stochastic rainfall (Jeltsch et al. 1996, Wiegand and Milton 1996, Jeltsch et al. 1997, Stephan et al. 1998, Weber et al. 1998, Weber et al. 2000, Weber and Jeltsch 2000, Beukes et al. 2002). This approach has proven to be feasible and useful. However, no simulation study has yet combined a biologically plausible (and not only

theoretical) grazing model with the effect of stochastic rainfall on the demographic processes of individual plants. The simulation model presented here works at the individual level where individual plants of the tussock grass *Festuca pallescens* represents the smallest unit. In consequence the simulation model operates on a small spatial scale.

The ecosystem under study. — The *Festuca pallescens* steppe is a cold temperate, semi-arid steppe in North-West Patagonia (Argentine) influenced by a highly variable rainfall. The tussock grass species *F. pallescens* is the dominant species in this steppe and accounts for ca. two-third of the vegetation cover and approx. 50-90% of biomass production (Defossé et al. 1997a). This ecosystem is endangered due to the long-term continuous grazing. The *F. pallescens* steppe is an especially suitable study system because its structure and productivity is mainly determined by one species which allows, in a first approximation, to abstract the ecosystem for the question of this thesis as a one species system. Of central importance for the feasibility of this modelling study is a large body of empirical studies which enables to generate specific and well-founded hypotheses about the rules of population dynamics of *F. pallescens* and the character of the grazing impact on it.

Methodological challenge I: High complexity versus scarce field data. — Grazing systems are complex systems (Parsons and Dumont 2003). This is mainly due to the fact that grazing may create heterogeneity at several hierarchical scales, e.g. at the population, the community, and the landscape scale (Golluscio et al. 1998, Parsons and Dumont 2003). My model includes the main drivers 'grazing' and 'highly variable rainfall' into the demographic processes of *F. pallescens*. This makes the model mechanistically rich, and requires inclusion of a large number of independent parameters. But as often the case in ecology, empirical data is limited. In the *F. pallescens* steppe and other semi-arid systems this can be attributed mostly to the effort required for extensive long-term studies which are needed observing the inherent complex dynamics (Wiegand et al. 1995; Wiegand and Milton 1996). Despite the high number of studies on *F. pallescens*, many important processes and parameters remain unknown.

Inverse pattern oriented modelling. — Therefore a sophisticated approach was necessary to nevertheless determine uncertain parameters and processes of the model with the available data. The pattern-oriented modelling approach (Grimm 1994, Grimm et al. 1996; Wiegand et al. 2003) enabled me to adapt my model optimally to my questions and data. For pattern-oriented models a sophisticated calibration method, which might be called 'inverse pattern oriented modelling', can be applied. This method reveals characteristics of unknown demographic processes from a multi-criterial calibration of all parameters at an instant and allows finding model versions which describe the data best. The basic idea of this indirect method is to perform systematic model simulations over the entire plausible parameter space and to compare several observed and simulated patterns, rejecting model parameterisations (or model variants) which do not generate important observed patterns. If a simpler model variant does not reproduce one (or several essential pattern), it has to be replaced by a model with a more adequate structure, whereas alternative model variants that do not improve pattern fulfilment can be rejected. This method was conceptualized in Wiegand et al. (2003) and implemented in Wiegand et al. 1998, Wiegand et al. 2004a) for models with moderate complexity of a dozen unknown or uncertain model parameters. I applied and further developed this methodology for a medium complex model with some 30 independent parameters and scarce field data. A sensitivity analysis of all accepted and thus potentially biologically realistic parameterisations provided new insights on the functioning of the *Festuca* steppe. This new understandings of the fundamental biological processes of a semi-arid steppe might be tested in the field in a further investigation step.

Challenge II: Up-scaling. — Understanding how the effect of individual processes at lower levels determines the behavior of an ecosystem is a major challenge in ecology (Levin 1992) and it is critical to device management schemes capable to operate at the ecosystem level. The presented

simulation model provides an up-scaling of the grazing (which impacts individual tussock) to the patch level (ca. 1500 m²). Finally I will discuss if the results of my model can be up-scaled to the landscape level. A further challenge of the up-scaling process will be to integrate and combine the results of the small-scale grazing impact on vegetation patches with the factors influencing grazing decisions of sheep on the paddock and the landscape scale (Rietkerk et al. 2002). To conceptualise the up-scaling procedure, I will discuss the results of this thesis with respect to its value for such an approach.

1.3 STRUCTURE OF THE THESIS

The general aim of the presented PhD-Thesis is to provide an understanding of the small-scale processes involved in degradation. More specifically, I investigate the long-term impact of grazing in a semi-arid *F. pallescens* steppe under stochastic climate. The presented thesis is structured in four main chapters. The single chapters are already submitted (Chapter 3) or planned to be submitted to international journals. The structure of four chapters follows directly from the logical sequence of challenges to be solved.

I took over the first implemented version of the presented simulation model from Dr. Gerhard Weber. After I took over the first implemented version, I revised the complete rule set, and together with the cooperation partner Dr. Jose M. Paruelo we modified or newly included the following rules (see Appendix I): Rule I.12, I.13, I.17, and I.26. As I took over the simulation model there was no routine implemented to simulate specific scenarios or repetitions. There existed nor any result neither any analyses which were performed with the presented simulation model before I took over this project. The rule set was no yet documented, or any experiment was designed or conceptualised before I took over the project.

The presented results in Chapters 2, Chapter 4, and Chapter 5 are completely the results of my own efforts and work. My contributions to Chapter 3, which was already submitted for publication, are indicated in section 2.7. The field data used during Chapter 3 and Chapter 4 were provided by Dr. Jose M. Paruelo.

Chapter 2 is dedicated to the presentation of the simulation model. I present the philosophy of the simulation approach, the biological background and the translation of the biological data into model rules. I use the standard model parameterisation to investigate basic properties of the model such as the emerging *F. pallescens* demographic behaviour and the type of vegetation dynamics. (The standard model parameterisation was derived in Chapter 3 by field experts without calibration.) Key questions of this chapter are: (1) what type of vegetation dynamics shows the *Festuca* steppe in terms of equilibrium vs. non-equilibrium dynamics? (2) does grazing alter the type of dynamics found for the assumed 'natural dynamics' without grazing? and (3) what is the effect of stochastic rainfall on the demographic processes or compositional state of *F. pallescens*, and how are they modified by grazing?

Chapter 3 tests basic assumptions of the simulation model with field data, the output of the model, produced by the standard model parameterisation, is compared with available field data, and a first global sensitivity analysis of the model is performed. Chapter 3 has a special status within the thesis because it presents to a certain extend the model development done previous to my thesis. However, this chapter does not portray the model as it was when I took over the project. I revised the model rules substantially and all analyses were based on the current model rules. Since this manuscript is already submitted I decided to include it as a separate chapter. Therefore some overlap exists between introduction, model rules and discussion of Chapter 3 and the rest of my thesis.

Chapter 4 presents an exhaustive inverse pattern-oriented model calibration under limited empirical data, as well as a global sensitivity analysis of the investigated parameters. This is a great methodological challenge since the medium complex model contains some 30 uncertain or unknown

parameters. The main aims of this chapter are: (1) to calibrate and validate the simulation model presented in Chapter 2 and Chapter 3 by means of a multi-criterial, hierarchical indirect pattern oriented approach based on limited empirical data (calibration and validation), (2) to analyse the relative importance of the independent parameters and processes with respect to the key variables of the *Festuca* steppe (sensitivity analysis), and (3) to discuss the biological and ecological implications for the *Festuca* steppe and the general implications which result out of the sensitivity analysis.

Finally, in Chapter 5 the accepted model parameterisations are used to investigate several applied questions concerning the degradation process of the *F. pallescens* steppe. I investigate the interaction of grazing with precipitation, and ask if the history of the stand plays a role within the grazing process. Key issues of this chapter are: (1) the impact of grazing on tussock density under stochastic climate and the remaining parameter uncertainty, analysed for different time scales, different types of forage selection and different grazing regimes, (2) development of a criterion for long-term sustainable grazing management under stochastic climate conditions which considers the remaining parameter uncertainty, (3) the temporal autocorrelation between the precipitation time series and the former state of the vegetation on key variables of the *Festuca pallescens* dynamics, and (4) how the interaction between grazing and stochastic climate affects the dynamics of *F. pallescens*.

In the final discussion in Chapter 6 I come back to the challenge to up-scale the model to larger landscapes in discussing the relevant results of Chapter 5.

2 SIMULATION OF VEGETATION DYNAMICS UNDER GRAZING AND STOCHASTIC CLIMATE

2.1 INTRODUCTION

In Chapter 2 I present the detailed biological background, the basic philosophy of the modelling approach, the rule-set and an analysis of the basic dynamics of the simulation model which investigates the grazing impact of herbivores on the dominant tussock grass species *Festuca pallescens* in a temperate semi-arid steppe in Northwest Patagonia (Argentine). The main focus of this work is how grazing affects the dominant species due to an interaction with the highly variable interannual stochastic precipitation. The background and motivation for this study is the worldwide desertification and degradation of semi-arid and arid regions (Schlesinger et al. 1990, Pickup 1996, Scheffer et al. 2001, see Chapter 1).

The basic philosophy of the modelling approach. — I use an individual based modelling approach (see Chapter 1), which integrates the two most important external driving forces – stochastic rainfall and grazing – into the essential demographic process of individual plants. This approach may allow separating short-term effects, which might be due to stochastic climate, from long-term effects, which might be due to grazing (Pickup 1996). The separation of natural and anthropogenic effects is especially difficult in semi-arid systems with stochastic environmental factors (Pickup 1996). Several studies have been carried out addressing the effect of grazing on semi-arid ecosystems, using rule based simulation models including stochastic rainfall (Jeltsch et al. 1996, Wiegand and Milton 1996, Jeltsch et al. 1997, Stephan et al. 1998, Weber et al. 1998, Weber et al. 2000, Weber and Jeltsch 2000, Beukes et al. 2002, see Chapter 1). Additionally a series of simulation models exists, which are mostly so-called process based models, emphasizing the physical details of different processes related to water dynamics, plant production or grazing (Riedo et al. 2000, Laio et al. 2001a, Laio et al. 2001b, Mitchell and Csillag 2001, Parsons et al. 2001, Pierson et al. 2001, Porporato et al. 2001, Schulte 2003, Schulte et al. 2003, Janssen et al. 2004). All these models include theoretical grazing models, with different degree of realism.

The rule based simulation model presented here includes a grazing model, which moves one step further towards a biologically realistic grazing model that mimics the interaction between the herbivore and the actual state of the individual grass tussocks. Additionally, the model integrates the joined effects of the grazing process and of the stochastic, highly variable rainfall on the essential biological processes, e. g. seedling recruitment, plant growth, and tussock mortality. Finally my approach includes space, which is essential for grazing (Parsons and Dumont 2003). This new approach for investigating grazing systems promises to yield new insights on grazing systems and to contribute to an improvement of management.

Chapter 2 presents in the first place the biological background and the rule set, and specifies how the model includes the main drivers stochastic rainfall and grazing into the essential biological processes for *F. pallescens*, the dominant species within the *Festuca* steppe. Together with the presentation of the modelling concept, I will investigate the basic dynamics of the simulation model, i.e., the model behaviour with and without grazing and the behaviour of the demographic processes, in- and excluding grazing, and finally I will describe the basic effect of the highly variable rainfall on the demographic processes.

Type of dynamics: equilibrium or non-equilibrium? — If the basic dynamics of the modelled system shows equilibrium- or non-equilibrium behaviour is decisive to understand the dynamics of a semi-arid system (Wiegand et al. 1995). As introduced in Chapter 1, there is an ongoing debate about the negative effects of grazing in non-equilibrium systems. One of the aims of this study is to contribute to a further elucidation of this ongoing debate, but this is only possible after testing the

basic model behaviour. Wiegand et al. (1995) found during simulation of the demographic behaviour of a semi-arid shrub steppe in the Karoo in Southern Africa, that the system showed highly event-driven behaviour for recruitment and mortality and thus clear non-equilibrium behaviour. I will test within this chapter, if the *Festuca pallescens* steppe shows similar demographic behaviour as the Karoo shrub steppe and if and how such dynamics are altered by grazing.

Questions. — Chapter 2 describes the philosophy of the modelling approach, the biological background of the study system, the rule-set, and simulation experiments to answer the following basic questions:

- What type of vegetation dynamics shows the *Festuca* steppe in terms of equilibrium vs. non-equilibrium dynamics?
- Does grazing alter the type of dynamics found for the assumed 'natural dynamics' without grazing?
- What is the effect of stochastic rainfall on the demographic processes or compositional state of *F. pallescens*, and how are they modified by grazing?

2.2 MATERIAL AND METHODS

2.2.1 General description of the study area

The *Festuca pallescens* grass steppe is one of the most important grasslands of Patagonia with regard to productivity and forage value (Defossé et al. 1997a). It is one of the arid and semi-arid ecosystems of Patagonia, which occupy the majority of the Patagonian region of Argentina. The *Festuca* steppe occurs in the North-West of Patagonia within the province of Chubut as a narrow belt only few kilometres east of the Andes, ranging from 43°25' S to 46° 15' S and continues at 51° 05' S near the Andes, widens towards the Southeast and reaches the Atlantic Ocean. The *Festuca* steppe has been classified as the Sub-Andean Floristic District of the Patagonian Phytogeographic Province (Soriano 1956a, Cabrera 1976)).

Vegetation. — The dominant species is *Festuca pallescens* (St. Yves) Parodi, which produces 50-90% of the above-ground biomass (Soriano 1956a, Ares et al. 1990, Defossé et al. 1990, Aguiar et al. 1996). *F. pallescens* is a perennial grass, growing in tussocks and reproducing strictly from seeds (Soriano 1956b, Bertiller 1992). The community is defined in phytosociological terms as the 'community of *F. pallescens*, *Rhytidosperma picta* and *Lathyrus magellanicus*' (Golluscio et al. 1982). The community has a mean total vegetation cover of 64%. *F. pallescens* itself has a mean cover of 44% or 69% relative to the total vegetation cover. The community is species rich and its biodiversity reaches ca. 60 species including 2 exotic species (León et al. 1998). One sample in the field, covering ca. 500 m², may lead to 34 species at average. The number of endemic species is high (León et al. 1998). Regarded from the viewpoint of biodiversity there is no doubt that this community is worth being preserved.

Climate. — The meteorological reference site for our study is Media Luna Ranch (45° 36' S, 71° 25' W), approx. 700 m above sea level. The precipitation data used in this simulation model is taken as a reference from the meteorological data of this site. This area is representative for the Sub-Andean Floristic District (Defossé et al. 1990, Bertiller and Coronato 1994). At this site *F. pallescens* comprises approx. 45% of the total vegetation cover. The soils have a uniform, coarse texture, are well drained and accumulate organic material at the surface down to 30 cm (A.M Beeskow int. report 1987 in Defossé et al. 1997a). Winters are cold and wet; summers warm and dry including a mid-summer drought (Defossé et al. 1990). The mean annual temperature is 4.7° C and the mean precipitation 374 mm/year, with 67% of the precipitation occurring in winter and early spring. There is no frost-free period and strong westerly winds blow continuously throughout the year. The community occurs at a

lower precipitation limit of 300 mm and is limited to the East by the Patagonian shrub-grass steppe (León et al. 1998). In the West *Nothofagus* forests mark the boundary of the *F. pallescens* steppes. The upper precipitation limit for the *Festuca* steppe is approximately the 500 mm y^{-1} isohyet (Ares et al. 1990).

Grazing history. — It is assumed, that the Patagonian arid and semi-arid ecosystems evolved under a very low grazing pressure, which few native herbivores exerted on the native vegetation (Soriano 1983). Since the introduction of sheep around the end of the 19th century these ecosystems have been subjected to disturbances mainly caused by sheep grazing (Soriano 1956a, Soriano 1983, Ares et al. 1990). In many areas, grazing has reduced the vegetation cover and facilitated the development of bare soil patches where wind and water remove litter, plant propagules and in some instances the upper layer of the soil (Soriano 1956a, Ares et al. 1990). The bare soil areas are more vulnerable to wind and water caused erosion, and they are exposed to higher degrees of frost heaving (Defossé et al. 1997a). *F. pallescens* is considered one of the most valuable grasses native to Patagonia (Parodi 1953).

Despite qualitative observations of a negative grazing impact on *F. pallescens* have been made, a quantitative understanding of the grazing impact on the long-term development of the native vegetation has not been achieved. It is discussed that the combined effects of long-term grazing and wind and water erosion have created relatively large bare patches between *Festuca* tussocks (Defossé 1997a). Grazing pressure is the major form of this disturbance on *F. pallescens* and may account for its reduction (Soriano 1956b, Abadie 1967 in Defossé et al. 1997b, Léon and Aguiar 1985, Ares et al. 1990).

2.2.2 Available knowledge about processes

In the following the empirical evidence about the *Festuca* grass steppe will be summarized and I will describe how a it is used for model development. The summary of the empirical evidence follows the order of implemented processes.

Water inputs. — I use the Media Luna Ranch as meteorological reference. The long-term mean precipitation is 374 mm/year (Defossé et al. 1997a). The coefficient of variation (CV) for a precipitation sequence during 1975-1997 is CV = 17.4% (data provided by Family Ayling, owner of the Media Luna Ranch, one missing year). As the precipitation time series available for the Media Luna Ranch was too short for the time frame of the simulation model, we used a precipitation time series from Leleque Ranch during 1931-1998 (provided by J. Paruelo, mean precipitation 459 mm, CV = 25.9%) and transformed the nearby Leleque Ranch precipitation data to a mean annual precipitation (MAP) of 375 mm / year, a CV of 20% and a range of annual precipitation with values from 211 mm to 561 mm). The precipitation time series from the Leleque Ranch has a similar CV as the CV of the Media Luna Ranch and the temporal autocorrelation shows a similar pattern as that from Media Luna Ranch, and has no significant temporal autocorrelation as the Media Luna Ranch data, too. As the simulation model requires at least a precipitation time series of 100 years, the series was completed randomly and independently out of the first 68 available precipitation data points. Autocorrelation of the precipitation time series used for simulations within years was not significant. Only the time lag = 3 shows a trend to a negative autocorrelation for the transformed precipitation data (autocor. = -0.29, p = 0.077 (determined after Box & Ljung Q-statistics, StatSoft, Inc. (2004)). As the precipitation data lack a significant autocorrelation, I assume an independence of interannual precipitation.

In addition to the annual precipitation, it is essential to estimate the proportion of precipitation that will be available to plants for transpiration. Paruelo et al. (2000) estimated the range of precipitation use efficiencies (PUE = transpiration per year / precipitation per year, equivalent to *mean*

PUE in the simulation model, compare Tab. 2.2) for semi arid ecosystems in Patagonia over a precipitation gradient ranging from 150 to 600 mm mean annual precipitation, using the water balance model DINAQUA (Paruelo and Sala 1995). For annual precipitation they found values between 200 and 600 mm and PUE values between 0.1 and 0.7 with an overall mean of 0.38 respectively. The mean estimation is used as a guideline for the parameter estimation of PUE in the simulation model. The variability of PUE decreased with increasing annual precipitation (Paruelo et al. 2000). The soil moisture content is higher during winter and early spring with a steady decline during summer and a recharge in fall (Defossé et al. 1997a). The summer drought, I interpret in the way that no soil water from the previous growing season is available for plants with shallow roots (i.e. grasses) in the following growing season.

Water redistribution. — Defossé et al. (1997b) show that in the 0-5 cm soil layer soil water content next to tussocks is higher than in the interspace between tussocks. This result shows that emerging seeds are favoured nearby the tussocks in comparison to the interspaces. This finding is interpreted as an effect of the local water redistribution, which is performed by the roots of adult grass tussocks which extend laterally to the bare soil neighbourhood in early spring. It can also be regarded as a reduction of evaporation in the neighbourhood of tussocks in comparison to the interspaces. On the other hand Defossé et al. (1997b) show, that adult *F. pallescens* tussocks exert competition against neighbouring emerged *Festuca* seedlings which are at least older than 4 months, contain at least 5 leaves up to one tiller, and start to use water from the 5-20 cm deep soil layer. This soil layer is mainly used by adult *Festuca* tussocks (Defossé et al. 1997b). Abadie (1967) in Defossé et al. (1997b) found that after several years of grazing exclusion, *F. pallescens* tussocks increase in size, whereas little or no seedling establishment of *F. pallescens* occurred. The competition adult tussocks exert against neighbouring *Festuca* seedlings is interpreted as a local water redistribution during summer where adult tussock gain additionally plant available soil water from their neighbourhood.

Both observations will be indirectly included into the simulation model in the form of a local water redistribution rule, which will affect seedling dynamics in the neighbourhood of adult *Festuca* tussocks negatively (see eqn. I.3, **Appendix I**). The second possible spatial effect concerning the small-scale water redistribution is discussed by Bertiller and Coronato (1994). They propose that larger bare patches show negative effects, which might enhance the loss of *Festuca* seeds. A normal sized bare patch between two *Festuca* tussocks can be estimated with 40 cm diameter (Defossé et al. 1997b). Ares et al. (1990) discuss that a reduction of the *Festuca* cover is followed by aeolian soil erosion. Both hypotheses will be tested by the inclusion of a second local water redistribution rule, which increases water loss in large bare patches and thus indirectly considers erosion and leads to negative effects on seedling survival.

Water induced vitality change. — How soil water influences individual plants is a complex process. A consistent quantitative theory about the impact of soil water stress on grasses seems yet not to exist. Drought obviously has negative effects on individual plants and has been studied since decades (see references in Novoplansky and Goldberg 2001). It can be expected, that both shoot and root biomass are negatively affected by drought (Briske 1991 in Mapfumo 2002, Novoplansky and Goldberg 2001). Plant growth and metabolism decelerate when soil water becomes less available (Horn et al. 2002). When drought continues, plants may enter into dormancy. This results in a reduction of the total amount of above- and below-ground plant biomass that is produced in a given growing season (Horn et al. 2002). During drought, plants use carbohydrates previously produced and stored in the roots or shoots. Oosthuizen and Snyman (2001) showed that the C4 grass *Themeda triandra* in South Africa increases the total non-structural carbo-hydrates under water stress, mainly in the shoots. Non-structural carbohydrates are used for a regrowth when the water stress ends. But though plants are dormant during drought, they continue to respire and to use energy. Brown (1965) in

Horn et al. (2002) suggests that this increased use of reserved carbohydrates can result in the loss of root vigour and mass may as well reduce the number of basal buds that are developed for the potential growth in the following year. Such empirical findings underline that memory effects within perennial grasses seem to exist. Thus, moisture stress could cause not only a reduction in forage production in the year of the drought, but also in subsequent years. Novoplansky and Goldberg (2001) found linear effects of water both on shoot and root biomass. Pavón and Briones (2000) found a high correlation between rainfall and fine root biomass production. Fuhlendorf et al. (2001) found a high correlation between precipitation and the basal cover of perennial grasses within a semi-arid savannah. Bertiller et al. (1996) show that water stress has negative effects on root growth of *F. pallescens* seedlings. Though information about the effect of water stress on adult *F. pallescens* tussocks does not exist, we can expect, that dry years will have a negative effect on vigour or vitality respectively – as I will call plant vigour in this work – of an individual tussock.

I assume that the vitality of an individual tussock can be affected both by a reduced ability to intercept photosynthetic active radiation (PAR) and by a restricted capacity of water extraction out of the soil due to the reduction of fine root biomass. Though the exact mechanisms of these complex processes are yet not completely understood, it is biologically plausible and reasonable to include such an effect as a simple biological rule into our simulation model.

Grazing induced vitality change. — The consequences of grazing become most evident by regarding its effect on the cover of a specific species. Bertiller (1996) demonstrates clearly the strong effect of grazing on the cover of *F. pallescens* in grazed uplands after at least 25 years of grazing. An exclosure, lasting for 10 years, had a *Festuca* cover of approximately 60%, whereas the corresponding grazed reference site showed a *Festuca* cover of only 20%. How this population level effect emerges out of the grazing effect on individual tussocks is poorly understood and has been investigated only theoretically up to date. One obvious process is defoliation itself; but it is unclear, if grazing affects the mortality of a tussock or if grazing affects vigour or vitality of a tussock. The model will include both options. In grazed areas fully grown tussocks (16.0 ± 1.8 cm diameter in upland areas) are smaller than in ungrazed areas where a diameter of 30 cm is characteristic (M. Bertiller pers. comm.). This is taken as a argument that grazing affects vitality negatively as it reduces the potential productivity of a tussock. Mapfumo et al. (2002) found that grazing has negative effects on root biomass of two perennial grasses of the genus *Bromus*, though their findings were not unidirectional. Briske (1991) states that one can expect that root biomass is negatively affected by grazing. Oosthuizen and Snyman (2003) found, that grazing removed important fractions of non-structural carbo-hydrates, which are gathered within the shoots in *Themeda triandra*, an important forage grass in South Africa. Thus, it is reasonable to include a non-mortal negative effect effect of grazing on the the vitality of a tussock, which will be mediated by a defoliation threshold and a transition probability.

Plant Production. – Data on *Festuca* productivity are scarce, which is due to the lack of a long-term monitoring. But at least I have estimations showing the order of magnitude in which productivity for *F. pallescens* ranges. Defossé and Bertiller (1991) report the following numbers from the Media Luna Ranch, where they measured annual net primary production (*ANPP*) in newly erected exclosures: for 300 days in 1981/82 *ANPP* was ca. 100 g/m²; during the following year it was 150 g/m² in 369 days. At a *Festuca* site near to Media Luna Ranch (45°58' S, 71°43' W) with a 372 mm long-term mean annual rainfall *ANPP* is ca. 120 – 150 g/m² (J. M. Paruelo pers. comm.). Primary productivity in clipped plots lagged 30-60 days behind controls during the vegetative period and showed compensation under grazing. In contrast, during the reproductive period primary productivity showed undercompensation under grazing (Bertiller and Defossé 1990a). How can we translate productivity on the individual tussock level and how do we consider precipitation and grazing effects? As has been shown for many grasslands and shrubland areas of the world (Milchunas and Lauenroth

1993), *ANPP* increases approximately linearly with the mean annual precipitation (Paruelo et al. 2000, Wiegand et al. 2004c). So it is assumed that precipitation has direct effects on productivity on the tussock level, too. The grazing effect will be indirectly included due to its modification of vitality as precipitation will act additionally indirectly due to its effect on vitality.

Defoliation. — As mentioned above, grazing has a general negative effect on *Festuca* cover. In Media Luna Ranch exclosures, the grass cover reached 55-58% with a low CV of 15% Defossé et al. (1990). In order to understand the grazing process on the individual tussock level I use the simulation model to test the hypothesis that during continuous grazing within large paddocks, sheep forage strong selectively on individual tussocks and select them after their compositional state. I assume that an increasing amount of aboveground dead biomass leads to a lower defoliation probability, a tussock and vice versa if the relative amount of dead biomass (*dfrac*) is low. This hypothesis will be contrasted with non-selective scenarios and it will be tested, if selective grazing leads to a higher vulnerability of the system than other grazing scenarios. Field data will be collected to test the selective grazing hypothesis and some assumptions of this hypothesis will be tested in the following Chapter 3.

Colonization. — Bertiller (1992) concludes that since grazing may reduce the cover, several consecutive years of high grazing disturbance may severely affect the seed production and can lead to the disappearance of *Festuca* from the seed bank.

The recruitment of new *F. pallescens* individuals is a rare event (Defossé et al. 1995). The causes precluding *F. pallescens* seedlings from natural regeneration are not yet totally clear and were investigated with priority. *Festuca pallescens* reproduces strictly from seeds (Soriano 1960 in Soriano 1983, Bertiller 1992). The soil seed bank for *F. pallescens* is replenished after the seed dispersal during fall. After the seed dispersal has taken place, the seed bank diminishes steadily during the growing season to a minimum at the end of summer (Bertiller and Coronato 1994). *Festuca pallescens* has a transient seed bank constituted by seeds that germinate in greater numbers immediately after the dispersal, which is due to the lack of a dormancy mechanism Bertiller and Aloia (1997). The persistence of the seed bank of *F. pallescens* is very low, particularly at canopy gaps (Bertiller and Coronato 1994). This short persistence might be a primary control of the regeneration of this species in Patagonia. The majority of seeds germinate in autumn and only a small fraction remains in the seed bank (Bertiller 1992). The second peak of emergence is in early to mid spring (Defossé et al. 1997a). Interspecific competition of adult *F. pallescens* tussocks affects the *Festuca* seedlings negatively (Defossé et al. 1997b). In the stage of 5 leaves up to 1 tiller, the seedling density in bare soil patches is higher than next to tussocks (Defossé et al. 1997b). Root competition of adult Festuca tussocks against *Festuca* seedlings did affect the density of seedlings in the 5-leaves-to-1-tiller stage: its density was significantly higher when there was no competition by neighbouring adult tussocks (Defossé et al. 1997b). It seems therefore probable that seedling survival is higher within the bare patches between adult *Festuca* tussocks, where the competition is reduced. But Bertiller and Coronato (1994) found that these 'interspaces' have no germinable seed bank before the next replenishment starts in summer. The causes for seed loss are not clear (Bertiller 1996). Bertiller and Aloia (1997) conclude that the establishment of plants seems to be dependent on the annual replenishment of the seed bank and the coupled occurrence of favourable water conditions, a dependence which explains the limited re-establishment potential under grazing disturbance.

Soil water effect on seeds. — Seedling emergence is significantly correlated with soil moisture content in 0 to 5 cm soil depth (Defossé et al. 1997a). During summer, when the soil water content reaches a minimum, the seedling emergence reduces to nearly zero and the mortality rates for seedlings up to four leaves (approximately 4 months old) increases (Defossé et al. 1997a). Experiments in the laboratory showed that 60 % of the seed germinated at a soil water content of 8%.

Such higher soil water contents and thus germination usually occurs in fall. A water content of 4% inhibits germination almost completely (Defossé et al. 1995). Such low soil water contents normally occur in summer. Seedlings that germinate in fall already show comparatively deep roots at the beginning of the following summer, so that they survive with higher probability than seeds germinated in spring (Defossé et al. 1997a). The seedling survival depends on locally available soil water (Bertiller et al. 1996, Defossé et al. 1997a, Defossé et al. 1997b). Water availability is likely to restrict the establishment of seeds (Bertiller et al. 1996); therefore, favourable years with above average rainfall may promote seed establishment.

Grazing effect on seeds. — In clipped plots reproductive structures occurred only to a limited extent (Bertiller 1996, Defossé et al. 1997a). During three seasons, grazing had significant negative effects on two- and four-months-old seedlings. The effect on 6-month-old seedlings was negative, but not significant in one year (Defossé et al. 1997a). Defossé et al. (1997a) discuss, that large bare patches, a result of long-term grazing, are detrimental to the survival of *Festuca* seedlings. Seed production is proportional to grass cover (Bertiller 1992). In summer, after the seed rain, seed distribution is spatially homogeneous in patches of bare soil (Bertiller 1992) if the grass cover remains above a minimum threshold of 40 % (M. Bertiller pers. comm.). The total germinable seed bank density of perennial grasses after seed rain in late summer is positively correlated with the total vegetation cover (Bertiller 1996, see also seed production Bertiller 1992). Bertiller (1996) showed that over a range of total plant cover from 30 to 75%, the total germinable seed bank density increases ca. from 180 to 480 seeds / m². Seedling density increases linearly with the cover, in the case of *F. pallescens* from 0 to 30% cover (Bertiller et al. 1996). Defossé et al. (1997a) state that seedling survival is lower under grazing, on slopes, and on windward sides of adult plants. Defossé et al. (1997b) conclude concerning the effect of grazing in the Patagonian *Festuca* grassland, that grazing seems to be detrimental to seedling establishment.

Concluding the empirical evidence about the seedling dynamics, it is obvious that seedling dynamics is a highly complex process. Thus, modelling seedling dynamics in an adequate way has to consider as minimum the following processes and factors: precipitation, vegetation cover, grazing, competition of adult *Festuca* tussocks against its own seedlings and saplings, seed loss in bare patches or 'interspaces' respectively. Important gaps in the knowledge are – apart from the uncertainty of the details of the processes and possible parameter values – mainly the uncertainty about seed loss in bare patches and the fate of one and more-year-old seedlings. It is highly probable that after the first growing season a surviving *F. pallescens* seedling consists only of one tiller (Defossé et al. 1997a). A one year old seedling therefore by no means can be considered as an adult tussock having at least 15 cm diameter. I do not know how long a recently recruited seedling needs to reach a fully reproductive and structural state, corresponding to a fully-grown tussock. We will include a delay of two years until a seedling reaches the adult state for the following reason: at the beginning of the second year the fate of an approximately one-tiller-individual will be highly susceptible to the amount and timing of the first precipitations after the first summer drought. We assume that the growth from a one-tiller-state to a tussock with a diameter of ca. 10-15 cm will take at least two years. These assumptions are in accordance with qualitative observations of different empirical ecologists (M.B. Bertiller, L. Ghermandi, J.M. Paruelo, pers. comm.). During the sapling stages and the first year of the adult tussock stage, one may assume that the accumulation of dead material is not yet relevant, due to the low biomass production until this stage. Thus, it is reasonable to assume, that if grazing is selective in relation to the relative amount of dead material, grazing might have a stronger impact on a two year old recruit than on an adult tussock. Intraspecific competition and seed loss in bare patches will be considered indirectly by the spatial redistribution of plant available soil water. The negative effect of a reduced vegetation cover will be applied linearly to the survival of the first seedling state.

13

Senescence and littering. — Information about senescence and littering rates is very scarce. Bertiller and Defossé (1990a) mention that senescence rates are 'very low' during 'early and mid-spring' and that they are 'very high' during 'mid-summer'. As I will use a one-year time step in the simulation model, the senescence rate will describe the transition from the green biomass of the actual year to the dead biomass of the following year. The senescent biomass which goes senescent during the actual year will not be modelled explicitly and thus stays available for forage in the actual year. The seasonal effect of senescence on forage selection will be considered implicitly at the seasonal grazing scenarios. About littering rates I actually do not have quantitative information. If the dead biomass accumulates over years when grazing is excluded, the littering rate of *F. pallescens* might be lower than the senescence rate.

Mortality. — Until December 2004 I have not found published data on tussock mortality of *F. pallescens*. Into the simulation model we will include rules, considering both precipitation by soil water status and grazing as possible causes for the individual tussock mortality. The mortality caused by grazing will only occur at the lowest vitality state and with a low probability.

Summary. — As I have demonstrated above, detailed information about several biological processes in the *Festuca* steppe exists. Thus, more than 15 years of investigation have gathered enough information for a fully individual based simulation model to be developed. The model is individual based and introduces the specific impact of precipitation and grazing on specific biological processes e. g. the seedling dynamics, the tussock vitality and the mortality. However, there are some information gaps to be filled for the construction of a complete model that describes the vegetation dynamics of *F. pallescens*. Further, when presenting the essential concept of the simulation model, it will become obvious that I have to include a number of parameters with unknown ranges to fill the data gaps. Similarly I do not know a priori if all hypothesized processes are relevant. Consequently, I have to investigate, which of the included detailed biological processes is relevant to the behaviour of the system and I have to estimate reasonable parameter ranges for the different parameters, processes and sub-processes. This will be done by using inverse pattern-oriented modelling techniques (see Chapter 4). However, in this Chapter and in Chapter 3 I will study the dynamics of the model under an expert parameterisation and test the ability of the model to reproduce several observed population level patterns not used for model construction.

2.3 MODEL DESCRIPTION

2.3.1 Essential concept of the *F. pallescens* simulation model

I built an individual-based, spatially explicit model to simulate the dynamics of a homogeneous stand of a typical grass steppe of *F. pallescens* of the Subandean district in Northwest Patagonia. The model simulates the behaviour of the system during the early stages of the degradation process. My focus was on individual tussocks of *F. pallescens*, the dominant species of the system. Therefore, I did not include invasive shrubs (*Mulinum spinosum* or *Acaena splendens*) into the model which play in important role during later stages of degradation. I considered, but did not simulate explicitly the dynamics of preferred but scarce species of forbs and small mesophytic grasses.

Temporal and spatial grain. — The model simulates the dynamics of individual *F. pallescens* tussocks within a homogeneous patch of the *Festuca* steppe. The simulation of individuals is essential, because I assume that the grazing decision of the herbivore depends on the actual compositional state of each encountered tussock. Consequently the simulation model has to be spatially explicit and is implemented on a grid of 128 x 128 rectangular cells. Each cell represents an area of 30 x 30 cm, the typical size of a fully grown tussock of *F. pallescens*. The simulated patch size is hence approx.

1.500 m² (i.e. 1475 m²) in size. This patch is homogeneous with respect to soil, topographic characteristics and the precipitation regime.

The model has an annual time step and the influence of different seasonal grazing regimes was simulated by modifying the forage selectivity of herbivores. The model description is provided at different levels of detail: in the rest of this section I describe the essence of the model, mostly related to the impact of precipitation and grazing on vegetation. A conceptual description of the implemented biological processes is given in the following section 2.3.2. The detailed description of the rule set follows is given in APPENDIX I.

Cell states, essential properties and variables. — Each grid cell can take several discrete states, e.g. bare soil or empty, live tussock and dead tussock (see Fig 2.1, Tab. 2.2 for variable definitions). Seedlings S_i – with the index i representing the age of each seedling – occur in empty cells only, and a new tussock recruits only, if seedling survive during three time steps. Qualitative field observations suggest that one-year old seedlings grow vegetatively for at least an additional two years, before they fructificate and can be considered as a fully grown tussock (Bertiller, M., Paruelo, J.M., and Ghermandi, L., pers. comm., see section 2.2.2). Seedlings S_i are implemented as a transient state within an empty cell (Fig. 2.1 and Tab.2.2).

The different cell states are related to each other by different ecological and biological processes (see Fig. 2.1-2.3), such as homogeneous precipitation (Global water input), small-scale neighbourhood water redistribution (Water redistribution), growth (Plant production, Vitality change), grazing (Defoliation), colonization, senescence (includes littering) and tussock mortality. A cell representing a live tussock is characterized by following state variables: green biomass (gb_i), dead biomass (db), the dead biomass fraction ($dfrac_i$) and the tussock vitality (vit, see Fig. 2.1 and Tab. 2.2). The compositional state of a tussock consists of the dead fraction of biomass ($dfrac_i$) and the tussock vitality (vit). $Dfrac_i$ is calculated as the relative proportion of dead biomass over total tussock biomass ($gb_i + db$). Both fractions appear interspersed in the tussock. I assume that herbivores select tussocks strongly for tussock characterized by low $dfrac_i$ (O´Connor 1992). Dead biomass may last in the tussock for several years (Soriano et al. 1976 in Soriano 1983, Jobbagy and Sala 2000).

Vitality. — The second characteristic, tussock vitality (vit) is an aggregated variable, which describes the capacity of the tussock to intercept photosynthetic active radiation and thus its potential primary production. The aboveground component of 'vitality' (vit) is basically determined by the density of tillers and the amount of standing dead material. However, vitality can also be interpreted as an aggregated description of the compositional state of the root biomass. Hence the tussock vitality is a property which stores the history of the tussock. It is assumed that the state of the root system is affected both by precipitation and grazing (see section 2.2.2). The concept of vitality (or vigor) is used in rangeland ecology (Kirkman 1995, Peddie et al. 1995, Kirkman and Moore 1995), despite its definition may differ. Kirkman 1995 defines vigor as the plant potential to regrowth during a season after grazing occurred. The vitality concept used in this model uses Kirkman's definition, as it reflects both the impact of the previous seasons on each tussock, and the effect of the actual time step.

The concept of vitality has been successfully introduced into simulation modelling of vegetation dynamics (Jeltsch et al. 1995, Jeltsch et al. 1996, Stephan et al. 1996, Stephan et al. 1998).

Philosophy of the simulation model. — The general idea of this model is to simulate the effect of the most important drivers – precipitation and grazing – at a scale, where both drivers act on the dominant species of an ecosystem. This scale is the small-scale of an individual grass tussock. So the approach is a cross scale-approach (Rietkerk et al. 2002), because it translates the effect of a large scale driver (precipitation) and a patch and landscape driver (herbivore grazing) onto the fine grain of individual plants. As I consider sub lethal effects of both drivers, it is necessary to include the impact of each driver into the ecological and biological processes (see Tab. 2.1). Tab. 2.1 shows the number

of parameters, which are included into each process of the simulation model, and how much of them are related to one of both drivers. Nearly all processes considered in the simulation model are affected by precipitation or by grazing or both, at least indirectly. Only senescence and littering are assumed to be just biological processes which are not affected directly neither by precipitation nor by grazing. Fig. 2.2 gives an overview over the implemented processes in order of implementation and indicates the included rules, which are given in Appendix I.

Tab. 2.1.: Overview of how the drivers precipitation and grazing affect the ecological and biological processes.

(i) means indirect effect of the driver on the process, e.g. water redistribution is influenced by tussock density, which is affected by grazing (see detailed Rule-Set). Processes are summarised compared to Fig. 2.2-2-3.

Number of parameters of a driver with causal effect on process	Number of parameters Driver		
Process	**Total**	**Precipitation**	**Grazing**
Global water input	1	1	0
Local Water redistribution	2	2	(i)
Plant growth	3	1	(i)
Grazing	4	(i)	2
Colonization	6	4	2
Vitality dynamics	6	4	2
Senescence and Littering	2	(i)	(i)
Mortality	6	4	2
Sum of parameters	30	16	8

2.3.2 Short description of the included biological processes

This section gives a short overview over the included processes and how the model works in principle (compare Fig. 2.1-2.3). An overview of model variables is given in Tab. 2.2, while an overview of model parameters is given in Tab. 2.3.

Initialisation. — The model is initialised with a tussock distribution of an assumed natural steppe with high *Festuca* cover of ~58%, oriented at observations of the oldest exclosure at the Media Luna Ranch. Hence the model is always initiated in an assumed optimal state.

Biomass carry over. — The procedure Biomass Carry over calculates all the remaining living (green) biomass from the last simulated time step, which will be available as forage during the actual time step.

Global Water input. — The procedure Global Water input simulates annual precipitation and calculates plant available soil water w, which initially is spatially homogeneous, as it is precipitation for the whole simulated area of 38.4 x 38.4 m ~ 1.500 m². Precipitation data are derived from a modelled precipitation time series derived from meteorological data out of the region (see section 2.2.2). One parameter is introduced, which gives the fraction of total plant available soil water w which will be available for plant growth. This parameter (WI.1/PUE, Tab. 2.3) is equivalent to precipitation use efficiency per tussock of 0.09 m² area and is estimated from Paruelo et al (2000). Total annual water loss (1-WI.1*annual rainfall) is not further specified and may be caused by superficial water run off, deep percolation or evaporation.

Water redistribution. — After precipitation two processes of small scale soil water redistribution are considered (Fig. 2.3 and Appendix I). The first process is water gain of living tussock due to lateral water uptake by roots from neighbouring empty or dead tussock cells, and vice versa water loss of empty or dead cells. The second process simulates higher soil water loss due to higher evaporation or run off at 'larger bare patches' with size of 3 x 4 cells or larger. This process is

Fig. 2.1: *Festuca pallescens* **simulation model: grid cell states and transitions-scheme.**
Shaded boxes show possible cell states. Biological processes (thin framed boxes) mediate between the cell states. Dotted arrows indicate the influences of the external driver grazing on processes and variables, whereas complete arrows show the influences of precipitation on cell states and processes. Dashed lines indicate biological relationships within a live tussock.
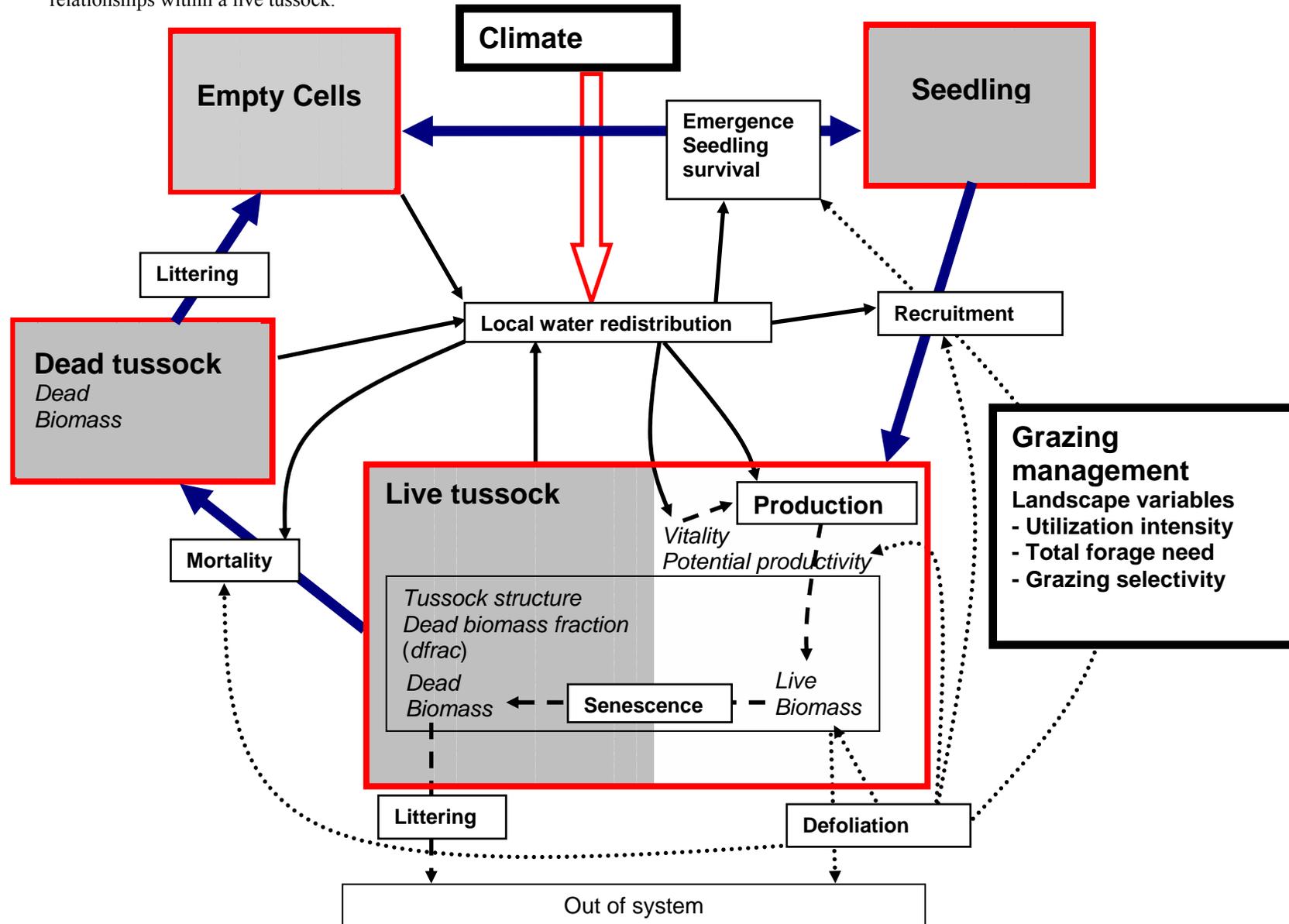
included as a hypothesis to explain the difficulties to observe surviving seedlings of *F. pallescens* in the field. The local water redistribution is an essential process, because neighbourhood effects are modelled exclusively due to the indirect redistribution of plant available soil water. Adult tussocks behave neutral to each other, no water gain or loss is assumed between neighbouring living tussocks cells. Asymmetric competition (Weiner 1990) of adult tussocks against neighbouring seedlings is mediated by local water redistribution. After local water redistribution plant available soil water shows heterogeneous distribution on a small scale with dry, average or humid patches. The heterogeneous soil water distribution modifies the whole behaviour of the *F. pallescens* dynamics of the actual time step.

Water induced vitality change. – After water redistribution tussock vitality changes according to its actual plant available soil water status (Fig. 2.3). Four parameters are included which change tussock vitality according to soil water thresholds, two may increase and two may decrease tussock vitality. Vitality is assumed to be deterministic, if there is a humid year all tussocks will profit, and not only a certain fraction. Water induced vitality change occurs before plant growth, because I assume that the soil water status of the actual time step has a strong effect on plant growth. Root growth starts in early spring at *F. pallescens* (Ares et al. 1990), so for humid years it is reasonable to assume that a tussock can profit from that to some extent. Increase of vitality is limited to one vitality class per time step. So it is assumed that a weak tuft (vitality = 1) can not grow to a strong tuft of vitality = 3 within one time step.

Plant production. — Plant growth is simulated as a function of plant available soil water and vitality of a tussock. I used a Michaelis-Menten function to simulate plant growth. I assume that plant growth at low precipitations shows no delay, because *F. pallescens* steppe is a cold temperate semi-arid steppe, so one can expect that in early spring there will always be a good soil water status at least for the upper soil layers due to snowfall in winter. Plant growth includes three parameters: one indicating the plant available soil water w at which a tussock produces 50% of its annual production, one parameter which estimates maximum tussock productivity (per m²) for a tussock at the lowest vitality class 1, and finally the parameter which estimates the increase in productivity for a tussock with a higher vitality. The differences in productivity are similar between two neighbouring vitality classes and the differences in productivity between minimum and maximum rainfall.

Defoliation. — I distinguish two spatial scales for the grazing process: the local or tussock level, and the patch or landscape unit level scale. The latter scale 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) results from a fixed forage need per capita (i.e. 1 kg sheep^{-1} day^{-1}) and a fixed stocking rate (e.g. 1 sheep / ha). The total amount of available forage *TF* (kg / ha) 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*). I 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 (values for the standard parameterisation P_S). To calculate the forage consumed from *F. pallescens, PF* is discounted from total forage need *FN*, so I get forage needed from *F. pallescens*. Landscape level mean utilization intensity *M* for *F. pallescens* then is given as

$$M = (FN\text{-}PF) \, / \, AF \qquad\qquad\qquad\qquad\qquad \text{(eqn. 2.1)}$$

Defoliation: Grazing process. — The grazing process is considered as 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 $dfrac_i$), 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 a probability that depends on the structure of the tussock ($dfrac_i$) and the mean utilization intensity.

Under very low utilization intensity (M close to 0), grazing probability shows a close to linear decrease with increasing fraction of standing dead. With 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 ($dfrac_i$) and it is calculated only once, prior to the grazing routine. That is, $dsmax$ is not altered during the grazing process.

A tussock that has been accepted for grazing is defoliated with local defoliation intensity (lc_i). 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 ($dfrac_i$) as well as on the overall utilization intensity (M). With increasing utilization intensity, the grazing probability of a tussock with a given structure ($dfrac_i$) increases. In addition maximum defoliation intensity of a grazing event is determined by tussock structure.

Defoliation: Grazing regimes. — To simulate different grazing regimes in a more realistic way, I introduced different grazing regimes according to the seasonality of the defoliation: continuous year round grazing or all forage needed is consumed in spring, summer-fall, or winter. Because the time step of the model is one year, grazing seasonality was simulated trough its influence on $dfrac_i$ 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. Further details are given in Appendix I.

Colonization. — Seedlings are not modelled explicitly, so they carry no biomass and only general survival of seedlings per cell are modelled without density dependent mortality. There are one seedling stage and two sapling stages, each lasting one year, according to field observations (see section 2.2.2). Seedling and sapling survival are triggered by plant available soil water (three parameters), combined with a certain probability of survival (one parameter for seedlings, one for saplings). Seedling survival additionally depends on adult *F. pallescens* tussock cover as was observed in the field. This aggregated parameter thus includes additionally the history of the paddock, and thus considers both the grazing and the climatic history which may have influence on recruitment. Sapling survival may also be directly affected by grazing, mediated by the relative grazing intensity M. So here it is not necessary to introduce an additional parameter.

Grazing induced vitality change. — After defoliation the vitality of each individual tussock might change, depending on its vitality and the individually suffered relative defoliation intensity. The higher the tussocks vitality, the higher is the tolerated grazing intensity. Two parameters are introduced, one threshold for the tolerated defoliation intensity at the lowest vitality of a tussock and one parameter for the probability of occurrence.

Senescence and littering. — Senescence and littering are modelled at the end of the time step and it is the only process which is not influenced by climate or grazing. Two parameters determine a fixed rate of senescence and littering of the living and the dead biomass. As the *Festuca* steppe

accumulates dead biomass above ground I assume a higher senescence than littering rate for the standard model parameterisation P_S. As I strongly simplify the process of senescence by using an annual time step, I assume that dry biomass, which went senescent at the actual time step may be consumed at the actual time step. Dry biomass is not modelled explicitly. Biomass which goes senescent is transferred to dead standing above ground dead biomass in the following year. Hence the senescence parameter is an aggregated parameter for the transition between green biomass at the actual time step and standing dead biomass at the next biomass. Green biomass thus also includes dry biomass of the actual time step, which will be consumed by livestock if no alternatives exist, as e.g. in late summer or during winter.

Mortality. — Mortality occurs only for tussocks in the lowest vitality class. The probability of dying depends on thresholds related to soil water availability and defoliation severity.

Conclusion. — As the sub lethal effects of grazing and precipitation are included, the medium complex model includes approx. 30 parameters. This complexity is necessary to investigate the combined effect of precipitation and grazing, as the basic grazing decisions take place at the plant individual scale (Parsons and Dumont 2003), if an individual plant is accepted for grazing, Simulating a coarser grain might miss the essence of the grazing process and so it would not be possible to simulate different forage selection scenarios or other characteristics of the grazing process in a biologically plausible way. Understanding how the effect of individual processes at lower levels determines the behaviour of an ecosystem is a major challenge in ecology (Levin 1992) and that will be tackled here.
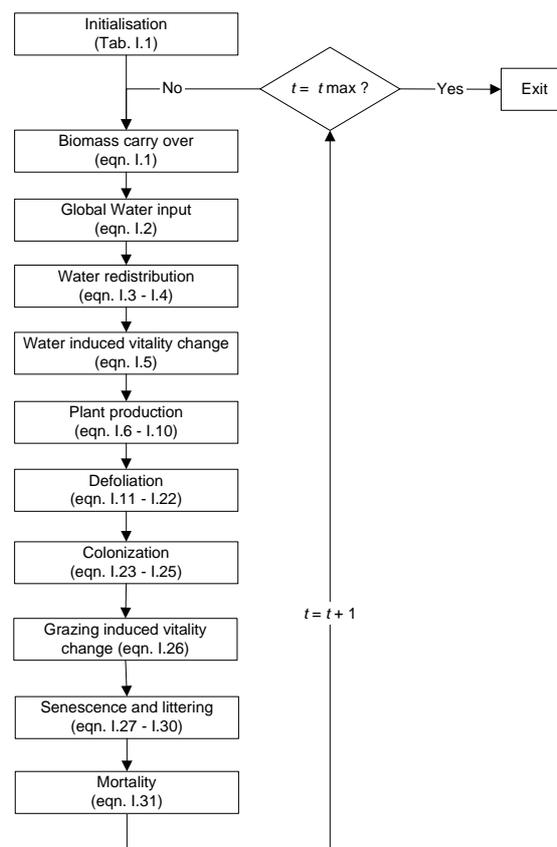
Fig. 2.2: Process flow-chart for the *F. pallescens* steppe simulation model.
All biological processes are listed, which have effect on the behaviour of the system in the order of implementation. Within the boxes, which include the process-names, equation numbers are provided, which correspond to the included rules (see Appendix I).

Tab. 2.2: State variables of the *Festuca pallescens* simulation model at the tussock, population and patch/landscape level.

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. Variables only used in the Rule-Set see Tab. I.2.

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.	$cs = \{0, 1, 2\}$
db, $db(cs)$	Dead *F. pallescens* tussock biomass	dead biomass / cell area · year (g DM / 0.09 m² 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 i-th tussock; defines tussock structure	
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	
$dsmax$	Maximum defoliation severity	-	Maximum relative defoliation severity depends from $dfrac$, calculated once before grazing routine	
gb_i	Green *F. pallescens* tussock biomass	live biomass / cell area · year (g DM / 0.09 m² 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.	
$gprob$, $gprob_{GR.5}$	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 m² y)	Minimum residual biomass after grazing is calculated before grazing and depends on $dfrac$ and gb	
lc_i	Local defoliation severity	gb_{prod} / cell area · year (g DM / 0.09 m² y)	Local consumption: total removed green biomass per tussock and time step during i defoliation events	
$prod$	*ANPP* per tussock	gb / cell area · year (g DM / 0.09 m² y)	Annual plant production is modelled as a function of vit and w with Michaelis-Menten kinetics	
S_i	Seedling of state i	-	Seedling of state i; i = 0: emerged from empty cell ($cs = 0$); 1: One year old seedling; 2: two year old seedling; survival of S_2 leads to a fully grown tussock and to transition from $cs = 0 \rightarrow cs = 2$.	$i = \{0, 1, 2\}$
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.	$vit = \{0, 1, 2, 3, 4\}$

Tab. 2.2 continued: Population level

w	Plant available soil water	H_2O / area (mm / cm²)	Local plant available soil water after local water redistribution
$dfrac$	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
$Min\ dfrac$	Minimum $dfrac$ per simulation	-	-
$dfrac_{CV}$	-	-	Spatial variability of $dfrac$ per time step and grid
fT_{dfraci}	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
$Mean\ vit_{dfraci}$	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%] $dfrac$)

Patch / Landscape level

-	Seedling survival Si	%	Seedling survival Si is expressed in % per grid with i = 0 (germinated seedlings), 1 (sapling 1st year), 2 (saplings, 2nd year)
Recruitment	Tussock recruitment	%	Tussockrecruitment is expressed in % per grid area and time step t
Mortality	Tussock mortality	%	Tussock mortality is expressed in % per grid area and time step t
Td_S	Tussock density	Tussocks / area (n / m²)	The simulated tussock density (Td_S) is calculated directly as ratio of all live tussocks / total grid size (~1500 m²). Due to the resolution of the grid (1 tussock = 0.09m²) 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.
$Min\ cov_i$	Min cover$_i$		Minimum cover (cov_i) of cell state i per simulation
Mean prod	Mean *ANPP* per tussock	gb / cell area · year (g DM / 0.09 m² y)	Mean *ANPP* per tussock and 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
Mean ANPP	-	Mean *ANPP* / grid area · year (kg DM / ha t)	Mean *ANPP* per simulation
Min ANPP	Minimum *ANPP*	Min *ANPP* / grid area · year (kg DM / ha t)	Minimum *ANPP* per simulation

Tab. 2.2 continued: Patch / Landscape level

Max ANPP	-	Max *ANPP* / grid area · year (kg DM / ha *t*)	Maximum *ANPP* per simulation
Mean gb$_i$	Mean green biomass per tussock i	*gb*$_i$ / cell area · year (g DM / 0.09 m² 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.
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).
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*$_S$.
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
Max Mreal	Maximum realised defoliation severity *M*	-	Maximum realised *Mreal* per simulation
Min Mreal	Minimum realised defoliation severity *M*	-	Minimum realised *Mreal* per simulation
C	Consumed forage	*gb*$_P$ / area (g DM / 1500 m² *t*)	Landscape / patch level consumed forage per time step: sum of *lc*$_i$ for all live tussocks of the whole grid
Min C	Minimum consumed forage	Min *gb*$_P$ / area (kg DM / ha)	Minimum consumed forage *C* per simulation during time steps where grazing occurs
Mean C	Mean consumed forage	*gb*$_P$ / area (kg DM / ha)	Mean consumed forage *C* per simulation during time steps where grazing occurs
*f*T$_G$	Fraction of grazed tussocks	-	Relative proportion of grazed live tussocks
Mean PUE	Mean precipitation use efficiency, whole grid	-	Landscape/patch level average precipitation use efficiency, ratio *w* (all live tussocks) / *w*G (all cells), i.e. the sum of all plant available soil water for live tussocks / total precipitation input for all cells per time step.
-	*Festuca state*	-	Classification of *F. pallescens* into degradation states, for more details see Tab. II.1

Tab. 2.3: List of the parameters of the *Festuca pallescens* steppe simulation model.
Parameters are grouped according to the processes they influence directly. The 'Typical value' column values correspond to the most reasonable values derived from the literature and from expert opinion (Standard parameterisation P_S). The last two columns correspond to the estimated upper and lower boundary for each parameter. These values were used in the sensitivity analysis (Chapter 4). For Calibration and sensitivity analysis in Chapter 4 all parameters were varied independently (calibration scenarios NG_i, G_i) and in groups to **driver-related processes**, calibration scenarios NG_g and G_g). The parameters were grouped according the column 'Parameter group for sensitivity analysis'. Legend: Column 1: Parameter abbreviation (Abb.) used in Chapters (C.) 2, C. 3, and C. 5; Column 2: Abbreviations used in C. 4.

Para-meter abb. C. 2, 3, 5	Para-meter abb. C. 4	Units	Processes (bold) and explanation of parameters	Typical value (P_S)	Parameter group for sensitivity analysis	Lower level	Upper level
			Water Inputs (WI)				
WI.1	PUE	-	Fraction of annual global rainfall which represents an input to plant available soil water w	0.57	1. WI	0.40	0.74
			Water Redistribution (WR)				
WR.1	WredT	water (mm / cm²)	Fixed amount of lateral soil water loss of a empty cell or a dead tussock due to water uptake from a neighbouring live tussock cell	5	2. WR L	1	20
WR.2	WredO	water (mm / cm²)	For empty cells in "large bare patches" only; fixed amount of soil water loss, for each empty neighbouring cell unaffected by lateral roots	20	3. WR O	10	30
			Plant growth (PG)				
PG.1	ProdV1	gb / cell area ·year (g DM / 0.09 m² y)	Annual net primary production (dry matter, DM) of a live tussock with vitality =1 ($vit = 1$) and year	150	4. PG V	105	195
PG.2	ProdincV 2-4	idem	Annual production increment of gb per unit increment of vitality > 1 and time step t	50	4. PG V	35	65
PG.3	MMconst	water (mm / cm²)	Constant of Michaelis-Menten equation for plant production: Indicates soil water status which enables half of maximum plant production (equation 1)	55	5. PG W	38	72
PG.4	SEN	%	Fixed % annual rate of senescence of green biomass left over after grazing	60	6. SEN	40	80
PG.5	LIT	%	Fixed % annual rate of littering of dead biomass both from live and dead tussocks	40	7. LIT	20	60
			Grazing (GR)				
GR.1	Stock	Sheep / area (n / ha)	Stocking density: number of sheep (n) per hectare; experimental parameter	0.5	Fix (varied in G_i, G_g)	0.0	2.0
GR.2	FNd	green biomass / day (g DM / d)	Daily (d) forage need in green biomass (DM) per head	1000	fix	fix	fix
GR.3	G_{Rej}	-	Fraction of $dfrac$, at which tussock is completely rejected from livestock. The parameter is related to the calculation of maximum defoliation severity ($dsmax$) as a function of a tussocks relative amount of dead biomass ($dfrac$).	0.95	fix	0.95	0.99
GR.4	Gshape	-	Shape parameter of equation (19): Determines shape of defoliation severity ds as a function of $dfrac$; Defines impact of increasing $dfrac$ on ds	0.5	8. GR T	0.3	0.7

Tab. 2.3 continued:

GR.5$_i$	G$_S$	-	Seasonal shift of the effect of tussock structure *dfrac* on grazing acceptance probability *gprob;* Alters the probability of a tussock to be accepted for grazing, which is a function of *dfrac* and grazing season (eqn. 22); *GR.5* = 1.0 for continuous grazing (a); 1.5 for spring grazing (b); 0.6 for summer and autumn grazing (c); 0.3 for winter grazing (d).	GR.5$_a$=1.0 GR.5$_b$=1.5 GR.5$_c$=0.6 GR.5$_d$=0.3	fix	fix	fix
			Colonization (CO)				
CO.1	ColWS0	water (mm / cm²)	Minimum soil water for emergence	200	9. CO W	140	260
CO.2	ColS0p	-	Probability (prob.) of emergence at cover > 40 % if soil water *w* > CO.1	0.3	9. CO W	0.1	0.5
CO.3	ColWS1	water (mm / cm²)	Soil water for survival of first year seedlings	170	9. CO W	119	221
CO.4	ColWS2	water (mm / cm²)	Soil water for survival of second year seedlings	140	9. CO W	98	182
CO.5	ColS0Cov	%	Minimum *F. pallescens* cover for maximum emergence and survival probabilities.	40	10. CO D	20	60
CO.6	ColS12p	-	Survival prob. for seedling 1st and 2nd year if soil water *w* > CO.3 and *w* > CO.4 respectively	0.9	10. CO D	0.7	0.99
			Vitality dynamics (VD)				
			Water thresholds				
VD.1	VincW1	water (mm / cm²)	*w* threshold for transition of *vit* = 1 → *vit* = 2	200	11. VD W	140	260
VD.2	VincW2	water (mm / cm²)	*w* threshold for transition of *vit* = 2 → *vit* = 3 or *vit* 3 → *vit* = 4	250	11. VD W	175	325
VD.3	VdecW1	water (mm / cm²)	*w* threshold for transition of *vit* = 4 → *vit* = 3	260	11. VD W	182	338
VD.4	VdecW2	water (mm / cm²)	*w* threshold for transition of *vit* = 3 → *vit* = 2 or *vit* = 2 → *vit* = 1	200	11. VD W	140	260
			Defoliation severity threshold				
VD.5	VdecG	-	Minimum relative defoliation severity threshold for tussock transition *vit* n → *vit* n-1	0.5	12. VD D	0.3	0.7
VD.6	VdecGp	-	Prob. of grazing induced vitality transition	0.8	12. VD D	0.6	0.99
			Mortality (MO)				
MO.1	MortW1	water (mm / cm²)	Water threshold 1: combined with *MO.3*	180	13. MO W	126	234
MO.2	MortW2	water (mm / cm²)	Water threshold 2: combined with *MO.4*	200	13. MO W	140	260
MO.3	MortWp1	-	Prob. of mortality if *w* < *MO.1*	0.2	13. MO W	0.05	0.4
MO.4	MortWp2	-	Prob. of mortality if *MO.1* <= *w* < *MO.2*	0.1	13. MO W	0.01	0.2
MO.5	MortG	-	Relative defoliation severity (*ds*) threshold for grazing induced mortality (only for *vit* = 1): combined with *MO.6*	0.6	14. MO D	0.4	0.99
MO.6	MortGp	-	Prob. of mortality if defoliation severity > *MO.5*	0.05	14. MO D	0.01	0.1
			Primary forage (PF)				
PF.1	PFmax	%	Minimum relative amount forage provided by other items	5	15. PF	0	5
PF.2	PFinc	%	Increment in per cent for *PF.1* per % *cov* increment of *F. pallescens*	0.83	15. PF	0	0.83
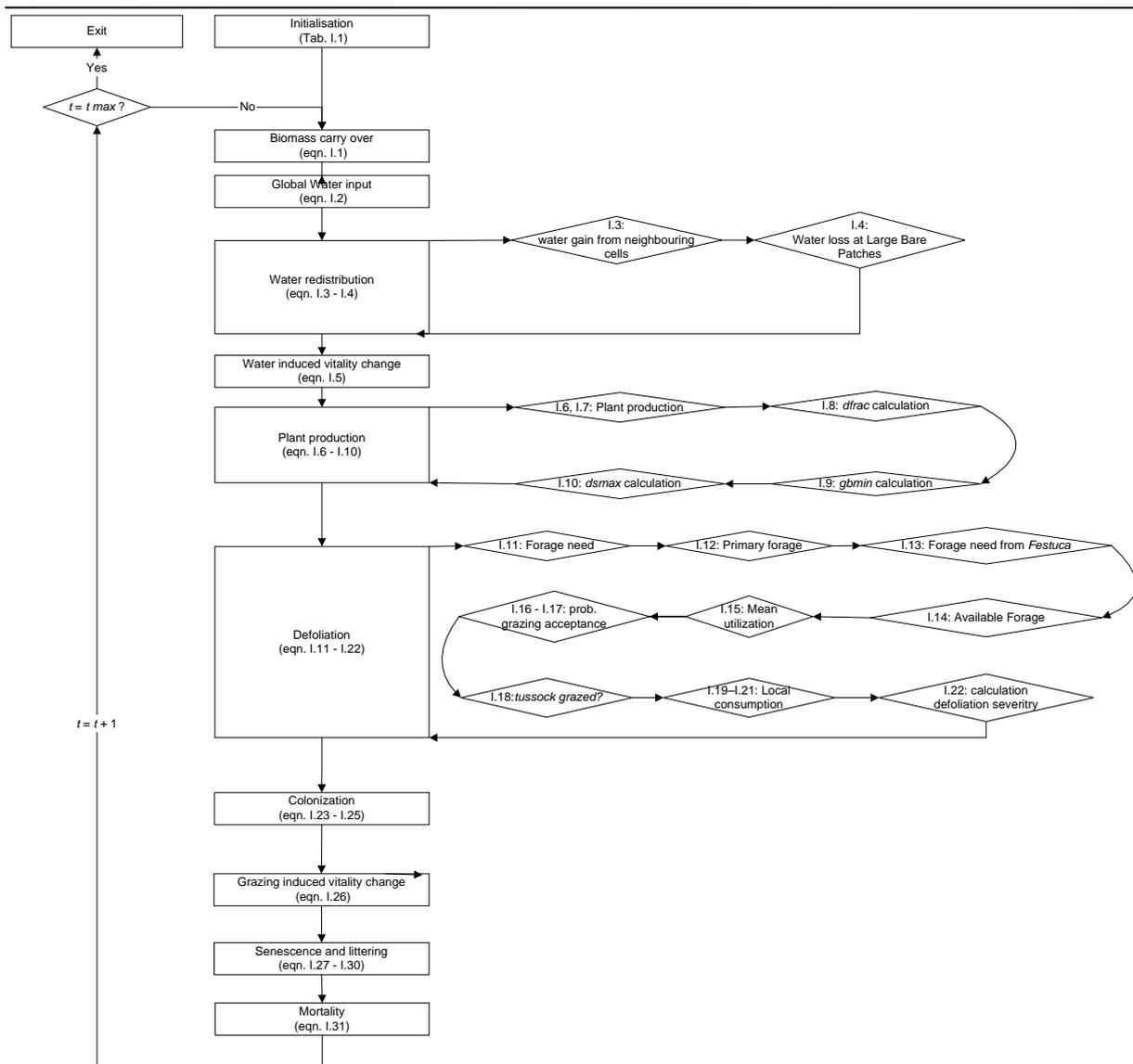
Fig. 2.3: Detailed process and equation flow-chart for the *F. pallescens* steppe simulation model.
All biological processes and routines are listed, which have effect on the behaviour of the system in the order of implementation. Equation numbers are also provided, which correspond to the following rule (for the detailed Rule-Set see Appendix I). For the most complex processes the sub-processes are provided in order of implementation including equation numbers.

2.3.4 Performed simulations and analysis

Model behaviour – To obtain a first understanding of how the simulation model behaves I compared individual simulation runs which are all based on the same specific climate data set but different grazing levels (no grazing vs. highly selective continuous grazing).

The first question I addressed was if the simulation model shows equilibrium or non-equilibrium behaviour. To answer this question I analysed the response variables tussock density (Td_S) and the demographic behaviour, i.e. tussock recruitment and tussock mortality. If recruitment and mortality are highly episodic then non-equilibrium behaviour of the system is highly probable. I compared demographic behaviour for different grazing levels ('No grazing', 'Light grazing' (stocking rate = 0.5 sheep / ha), 'Moderate grazing' (stocking rate = 1.0 sheep / ha) and 'Heavy grazing' (stocking rate = 1.5 sheep / ha). I put these qualifications in quotation-marks, because it was not yet known, which stocking rate can be qualified as light or moderate grazing. The selected grazing levels

were chosen in accordance with expert estimations of normally performed average stocking rates for the *F. pallescens* steppe (see Chapter 3). The comparison of demographic events including grazing should answer the question, if grazing alters the type of dynamics found for the assumed 'natural dynamics' without grazing.

The reference model parameterisation used for this analysis was the model parameterisation estimated by the field experts (standard parameterisation P_S). This parameterisation produced good accordance between the simulated and the observed patterns. These observations were made during preliminary simulations. Chapter 3 will demonstrate in detail that the reference model parameterisation leads to reasonable results by comparing the model output with field data.

The simulations for investigating the demographic behaviour are based on one repetition per grazing level and the standard precipitation time series and were run for 100 time steps. To investigate to which extend demography was triggered by the precipitation events I calculated the Spearman rank correlation coefficient between demographic variables and actual precipitation. Hence, each calculation included 100 data points.

To investigate the basic model behaviour I run two simulation experiments: the first experiment included a grazing gradient of stocking rates ranging from 0.0 to 2.0, with intervals of Stock = 0.1 and compared the trajectories for different stocking rates. The second simulation experiment investigates the time scales of natural recovery if livestock was removed after a grazing period of specific duration.

Each simulation of the first simulation experiment was run for 150 time steps, using the same precipitation time series as above but I adding 50 randomly chosen data points. The first 50 time steps were run without grazing to equilibrate the model from initial conditions. Thus, each simulation included 100 time steps with grazing. These simulations were used to demonstrate the basic model behaviour and to investigate qualitatively if regeneration or grazing threshold were evident. The second simulation experiment repeated the first one, but including grazing duration as a parameter. I varied duration of grazing for each grazing level between 30 and 120 time steps. After the grazing period, I simulated 200 to 290 time steps without grazing to let the system recover from grazing. Thus, each simulation was undertaken for 370 time steps (50 time steps to equilibrate + 30-120 time steps of grazing + 200-290 recover time steps). Time to recovery was defined as the number of time steps the grazed scenario took to reduce the difference in tussock density Td_S compared to the No grazing control to a difference $Td_{S=0}$ - $Td_{Sgrazed} \leq 3\%$.

The effect of stochastic rainfall on the demographic processes, the compositional state of *F. pallescens*, and landscape level *ANPP*, and how they are modified by grazing, was investigated as follows: 100 repetitions of the standard parameterisation with different stochastic climates were performed for 100 time steps and the four grazing levels described above. For each grazing level, for all 100 climate repetitions and for all time steps I calculated the frequency distribution of the different demographic events. For the compositional state of *F. pallescens* (i.e. the tussock density Td_S) I calculated the frequency distributions for the discrete time steps $t = 10, 20, 50$ and 100 years. This enabled me to take into account the environmental noise (or climatic uncertainty) to study the basic behaviour of the simulation model. Additionally the Spearman rank correlations between the demographic behaviour and several variables describing precipitation history were investigated for this simulated data. The precipitation history parameters were: precipitation at the actual time step t and at previous time steps t_{-i}; i = {1,2,3,4,5}, and the running means including the actual precipitation plus the precipitations up to 5 years before actual precipitation.

27

2.4 RESULTS

2.4.1 Model behaviour and equilibrium dynamics of the *Festuca* steppe

At the beginning I describe some general features of the model behaviour (see Fig. 2.4). Fig. 2.4 A shows the event-driven behaviour of the system without grazing, the assumed natural dynamics of *F. pallescens*. Tussock recruitment and mortality occur sporadically. In this example (i.e. the standard parameterisation P_S estimated by the field experts, and the specific precipitation time series), tussock recruitment occurs approximately once every four years, and tussock mortality occurs nearly every second year. However, one third of the mortality events is below 1.5% of the whole area and are thus
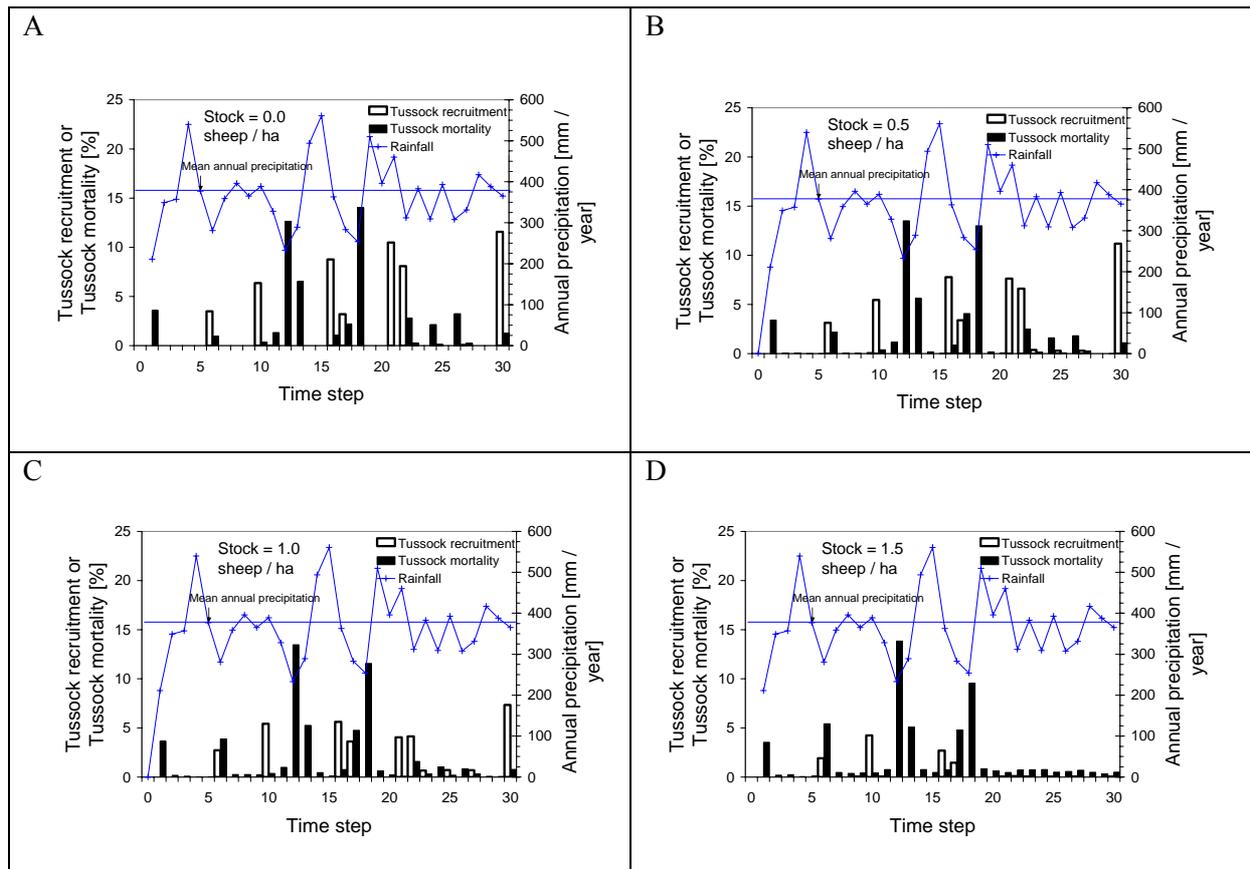
Fig. 2.4: Demographic Behaviour of the *Festuca* steppe simulation model.
Shown are the first 30 time steps of one specific time series with stochastic precipitation, and the demographic behaviour of Festuca pallescens, i.e. tussock recruitment and tussock mortality [%]. The model parameterisation used was estimated by the field experts (standard parameterisation, P_S). A) tussock recruitment and mortality without grazing; B) Grazing = 0.5 sheep / ha; C) Grazing = 1.0 sheep / ha; D) grazing = 1.5 sheep / ha. The event-driven behaviour of the model for recruitment and mortality is evident. Grazing decreases consecutive tussock recruitment to an equilibrium, which is characterized by low constant tussock mortality rates and a complete lack of tussock recruitment (D, after time step 18).
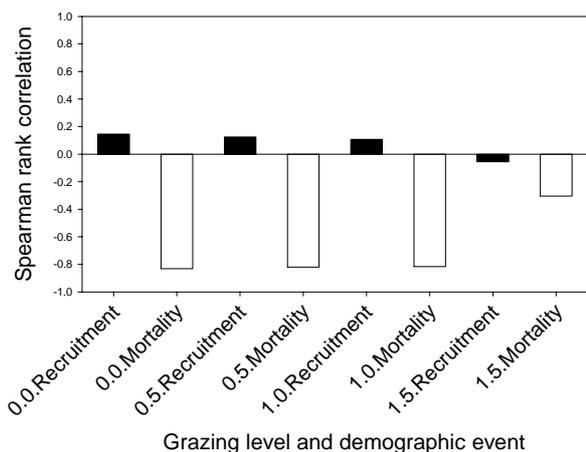
Fig. 2.5: Correlation of demographic behaviour with precipitation.
Shown are the Spearman rank correlations for the four grazing levels with the actual precipitation for each one run and 100 time steps. Recruitment is weakly correlated for all grazing levels to precipitation, indicating a complex behaviour. Mortality is highly correlated to precipitation for the three lowest grazing levels. Correlation between mortality and precipitation is reduced for the highest grazing level.
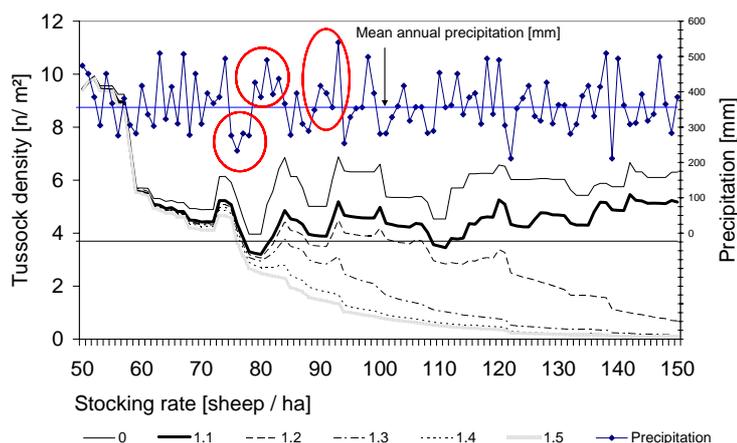
Fig. 2.6: Model Behaviour of the *Festuca* steppe simulation model.
Shown is a time series (150 time steps) of one precipitation time series and the change of tussock density with different grazing levels. The first 50 time steps were run without grazing and are not shown. The model parameterisation used was estimated by the field experts (standard parameterisation, P_S) for the high impact of precipitation on tussock density is evident (grazing pressure = 0.0 sheep / ha), as it is for heavy grazing (e.g. 1.5 sheep /ha).

less important. As precipitation is the only factor varied during this scenario, it is evident that tussock mortality occurs nearly every second year, but one third of mortality events are below 1.5% and variability in precipitation is responsible for the discrete recruitment and the mortality events. Fig. 2.5 shows the Spearman correlation coefficients between actual precipitation and the demographic behaviour for the four grazing levels. Recruitment is weakly correlated to actual precipitation for all grazing levels which indicates that recruitment is a complex behaviour. Thus it occurs not only sporadically, but the events cannot be explained directly with actual precipitation. However, mortality is strongly correlated to actual precipitation for the three lowest grazing levels. The highest grazing level leads to a weaker correlation to actual precipitation.

Temporal variability and grazing. — Fig. 2.6 shows the temporal variability of tussock density, fluctuating with annual precipitation and under the complete grazing range from

0.0 sheep / ha to 2.0 sheep / ha. This time series provides several interesting qualitative insights. Without grazing the tussock density fluctuates strongly, between tussock densities ranging from approx. 4 – approx. 8 tussocks / m². Thus, the variation of extreme values of tussock density is similar to the variation of extremes for annual precipitation (range differs ca. 40% from mean). On the other hand, the time series demonstrates that tussock density shows a more 'stable' behaviour than precipitation. Tussock density may remain relatively unchanged, or is consistently increasing or consistently decreasing for several consecutive years. For example, for the No grazing scenario precipitation alternates between the time steps 60-70 on a yearly time step between 'good years' (above MAP) and 'bad years' (rain below MAP), but tussock density changes very little. During a series of either 'bad' years with precipitation below average or a series of 'average' and 'good' years, tussock density changes consecutively. For example a series of four bad years (time step approx. 75-80) leads to a strong decrease in tussock density. Increases in tussock density become evident if combinations of good and mean precipitation years occur, e.g. time step 72-75 or 80-84.

The next interesting result is related to the grazing effect on tussock density. I observe three groups of stocking rates: the first one (Stock 0.1- ca. 1.1) decreases tussock density moderately and the temporal variation follows the no-grazing temporal variation of tussock density. This group of stocking rates leads to long-term stable vegetation, without a stable or exact equilibrium, but a dynamic or 'pseudo-equilibrium'. This 'stability' may be related to the fact that herbivore saturation is not reached, i.e. the consumed forage is always considerably lower than the total standing consumable biomass.

The second group (Stock ca. 1.4 - 2.0) shows a trend to strong degradation (tussock density < 1.0 after 50 years of grazing at time step 100). A strong decline in tussock density was induced by four dry years (time steps approx. 75-80). A strong reduction in tussock density occurred for all grazing scenarios during these time steps. But under these high stocking rates tussock density is already after 25-30 years in such a reduced state, that it cannot respond positively to favourable climatic conditions following the four year drought. A **regeneration threshold** is evident at a tussock density of approx. $Td_S = 2.5$. Below this threshold, tussock density is unable to recover.

Finally a third group of stocking rates (parameter Stock, GR.1) is evident, namely Stock = 1.2 – 1.3. With these stocking rates, tussock density tends to decrease in the long-term below the recover threshold, but considerably slower than at higher stocking rates. This regeneration threshold holds only for constant grazing.

The qualitative different behaviour of the system under these three groups of stocking rates indicate that a second threshold, a **grazing threshold,** exists for the tussock density as a response to the increasing stocking rate. The first group lies below the threshold, so tussock density fluctuates similarly to its response to climate when no grazing occurs. The intermediate group seems to lie over the threshold, within the range of the decreasing slope. So it is an interesting question if a threshold can be detected with a quantitative analysis and if it has similar values for different rainfall scenarios or model parameterisations.

Regeneration without grazing. — For Stocking rates Stock < 1.1 sheep / h the vegetation was able to recover within shorter time frames (Fig. 2.7). For this range of stocking rates recovery time did not depend much on the number of years grazed and was basically linearly related to stocking rate. However, for Stock > 1.1 sheep / h the relation between recovery time and stocking rate becomes non-linear and recovery time exploded if the steppe was grazed longer than 30 years. An interesting question is if this threshold has similar values for different rainfall scenarios or model parameterisations.
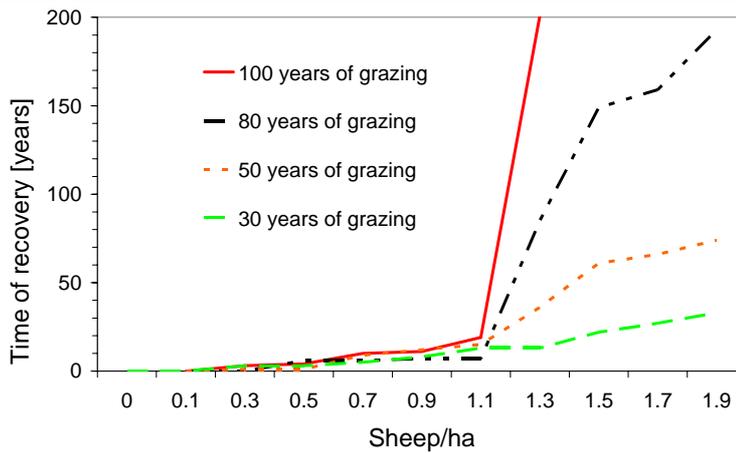
Fig. 2.7: Natural Recover of the model *Festuca* steppe under a grazing and a grazing duration gradient.
Time of recovery was defined as the number of time steps the vegetation needed to reach a tussock density equal to tussock density for No grazing $\leq$ -3%. A regeneration threshold is evident at Stock = 1.1 sheep/ha when grazing took longer than 30 years. Recover times increases exponentially above both thresholds. Simulations were run with the standard parameterisation P_S; each simulation was run for 370 time steps, over a gradient of 30 to 120 time steps of grazing and a stocking rate from 0.0 to 2.0 sheep/ha. Each scenario was repeated once and each simulation was first run 50 years without grazing for equilibrating from initial distribution.

2.4.2 How does grazing modify the demographic processes of *Festuca pallescens*

Fig. 2.4 shows how grazing modifies the demographic processes of *Festuca pallescens* for one exemplary precipitation time series. Tussock recruitment is not reduced substantially at 'low' grazing of 0.5 sheep / ha. At 'moderate' grazing of 1.0 sheep / ha tussock recruitment is already reduced to approximately half the rates observed with *No grazing* (compare Fig. 2.4 A with C). Finally, under Heavy grazing (Fig. 2.4 D), no recruitment occurs at all after some 20 time steps, indicating that Heavy grazing is detrimental for tussock recruitment. Thus the behaviour of tussock recruitment, which was event-driven and showed non-equilibrium behaviour for Moderate grazing and less grazing intensity, changes qualitatively to a new 'equilibrium' behaviour which consists out of no-recruitment-events.

Tussock mortality shows a different pattern of change, which seems to be dynamic. During the first 15 time steps, grazing increases mortality events moderately (e.g. time step 5, mortality during one dry year, Fig. 2.4 A-D). High mortality events, which occur during a series of dry years and during such a series mostly at the second year, are not influenced substantially by grazing. But Heavy grazing leads to another change of the event driven and non-equilibrium dynamics of the tussocks: it leads to a constant low mortality rate for Heavy grazing. Interesting is also the finding that under Heavy grazing mortality rates decline after a certain time (e.g. time step 18) in comparison with lower or *No grazing*. The reason for this is that the already strongly reduced tussock density of *F. pallescens*, cannot be further reduced to such a high extend. These results show that grazing has a strong impact on the type of dynamics shown by *Festuca pallescens,* and produces a negative effect on recruitment. The high mortality rates may explain the decrease of *F. pallescens* due to grazing.

2.4.3 How does stochastic rainfall affect the demographic processes of *Festuca pallescens*?

After the presentation of the model behaviour for specific simulations and time series I investigate if the observed event-driven behaviour can be generalised for different rainfall time series. Fig. 2.8 shows the frequency distributions for the demographic behaviour which was generated by repeating

100 time steps simulation with 100 different stochastic climates for the four grazing scenarios. The event-driven behaviour under stochastic rainfall with a variability of CV = 20% can be considered as a general model behaviour (Fig. 2.8).

Recruitment. — Under the no-grazing scenario more than 60% of the time steps have no recruitment at all, 15 to 20% of the time steps show recruitment below 2%, while the remaining time steps show recruitment above 2%. Grazing with 0.5 sheep / ha modifies this result only slightly. But Heavy grazing with 1.5 sheep / ha changes the recruitment pattern strongly: under this scenario 76% of the years show no recruitment, just 15% of the time steps show very low recruitment $\leq 2\%$, and just around 9% of the time steps show medium or larger recruitment events. With respect to large recruitment events (i.e., larger than 8%) dramatic effects of grazing become evident (Fig. 2.8 A-C). Without grazing 7.2% of all time steps show large recruitment events, Light grazing modifies this result slightly to 5.6%, and Heavy grazing does not allow large recruitment events at all. Whereas the increase of no-recruitment events under low and Moderate grazing is gradually, Heavy grazing extinguishes large recruitment events. Only low (<2%) and medium sized recruitment events (>2>x<8%) were observed. Thus, grazing does not modify the event-driven behaviour of the model system with respect to recruitment, but Heavy grazing significantly modifies the frequency of recruitment events, and the frequency of larger recruitment events above 6%.
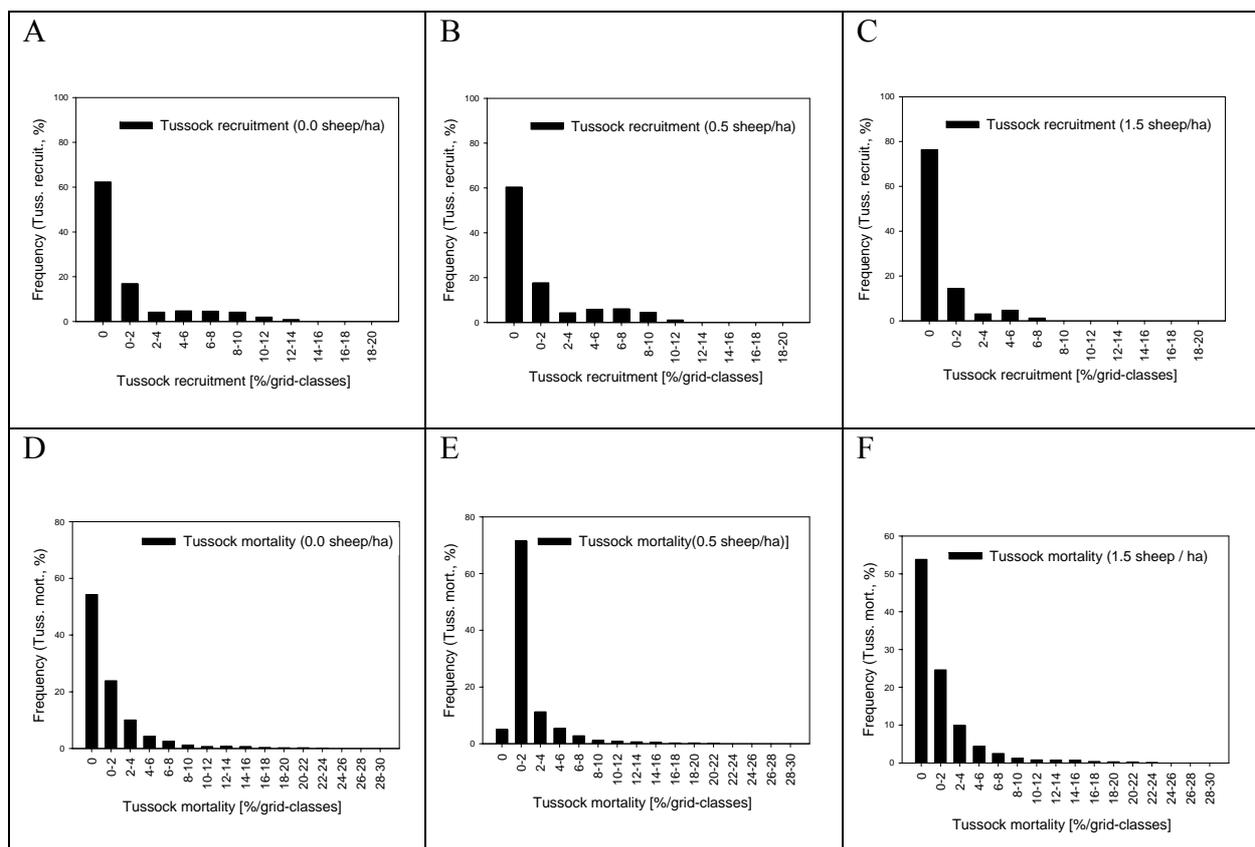
Fig. 2.8: Demographic behaviour of *F. pallescens* under 100 stochastic climates and different grazing levels.
A)-C) Tussock recruitment; A) No grazing; B) Light grazing: 0.5 sheep / ha; C) Heavy grazing: 1.5 sheep / ha; D-F) Tussock mortality: D) No grazing; E) Light grazing: 0.5 sheep / ha; F) Heavy grazing: 1.5 sheep / ha; shown are frequency distributions for demographic events; all simulations were run with the standard parameterisation (P_S, estimated by the empirical ecologists), including 100 repetitions with different stochastic climate rainfall time series and containing the annual data for each 10.000 time steps.
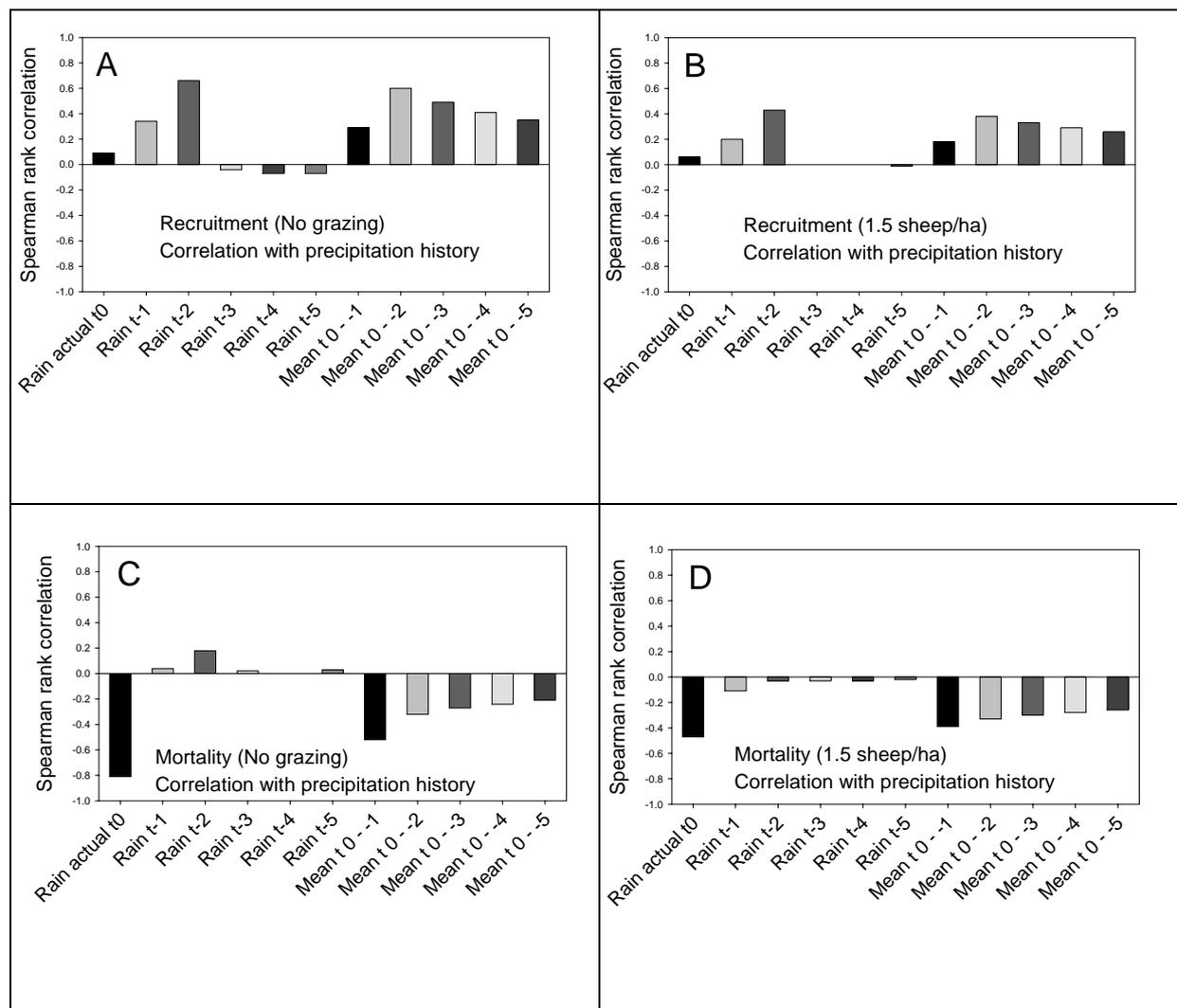
Fig. 2.9: Correlation between precipitation history and demographic events.
A), B) recruitment; C), D) mortality; A), C) No grazing; B), D) Heavy Grazing; Shown are the Spearman rank correlation between 9.500 data points for each demographic event with one of the given precipitation history parameters: Rainfall for specific years ($t=t$ to $t=-5$ and running mean of $t=t$ to $t=i$, $i=-1, -2,-3,-4,-5$).

Tussock mortality. – Tussock mortality under grazing behaves somewhat different from tussock recruitment. Under *No grazing* the results are similar: approx. 60% of time steps show no mortality events, while approx. 20% show below 2% mortality. But already under low grazing of 0.5 sheep / ha the mortality pattern is modified. Under this scenario at least some mortality occurs in 95% of the simulated time steps, though in most time steps mortality is low (in 71% of the cases it is below 2%). Time steps without mortality occurred only in 5% of the simulated time steps (Fig. 2.8 E). The frequency of larger mortality events (>2%) is not much modified compared to No grazing (Fig. 2.8 D-E). The shift in mortality which occurs already in 95% of the cases under Light grazing is a consequence of the rule that mortality may occur if a certain defoliation severity level is executed. This shift of the event-driven behaviour of the model system was unexpected.

Under Heavy grazing an unexpected shift in system behaviour is observed (Fig. 2.8 F): now a similar pattern as for No grazing can be observed since during most time steps no mortality occurs. The explanation for this finding is different from that for the No grazing scenario. For the No grazing scenario tussock mortality occurs only under unfavourable environmental conditions, e.g. dry years.

During most time steps no mortality occurs. At Heavy grazing mortality occur rarely because no tussocks are left (they died early during the simulation) and no recruitment occurred. This indicates that overgrazing occurred. Constant low mortality rates were observed for intermediate stocking rates as 0.5 or 1.0 sheep / ha respectively. Thus the question arises, if the systematic shift from event-driven mortality to constant mortality or the subtle shifts in tussock recruitment would be responsible for changes in *F. pallescens* dynamics – if they occur – due to grazing.

Correlation with precipitation history: recruitment. — Fig. 2.9 A and Fig. 2.9 B show the correlations between recruitment and current and past precipitation events for No grazing and Heavy grazing, respectively. Both show similar patterns: Recruitment is weakly correlated with actual precipitation. The correlation increases subsequently until reaching the highest value at a time lag of $t = -2$. For longer time lags the correlation drops near to zero. The correlation with the running means of precipitation show a similar pattern. The mean between actual precipitation and that of the year before shows a similar correlation as that for t = -1; the highest correlation is reached for the running mean of the actual rainfall plus that of the two anterior years. The correlations drop consecutively for running means including earlier rainfalls. The correlations for Heavy grazing are in general lower than for No grazing. Light and Moderate grazing show similar behaviour as No grazing (data not shown).

Correlation with precipitation history: mortality. — Fig. 2.9 C-D give the analogue correlations for mortality. For mortality the correlation picture changes completely: for both grazing scenarios, mortality is highest correlated with actual precipitation. The correlation to precipitation of the previous year drops already to approx. -0.1. The correlations of the running means with mortality are strongly dominated by the correlation with the actual time step. All correlations of running means have lower correlation value than that for the current time step t and drop consecutively for each added former rainfall. As shown for recruitment, correlations for Heavy grazing are lower with actual precipitation than for No grazing. Light and Moderate grazing show similar behaviour as No grazing (data not shown).

2.4.4 How does stochastic rainfall affect the compositional state of *F. pallescens* and how is the compositional state modified by grazing?

How is tussock density affected under the more general view including 100 different stochastic climates? After 10 years of grazing the simulations result show no differences between No grazing and Light grazing (Fig. 2.10 A). The peak density perceivable after 10 time steps is caused by the initial distribution (Fig. 2.10 A). 'Moderate' and Heavy grazing show already a slight change within the peak of the distribution, but it changes not qualitatively (Fig. 2.10 B). After 20 time steps the peak at Td_S =7.8 disappears for the No grazing scenario (Fig. 2.10 C), and Light grazing shows no significant differences to No grazing. Moderate and Heavy grazing does not lead to significantly different tussock density distribution (Td_S), but a few occurrences of *F. pallescens* cover below 20% ($Td_S \leq 2.2$) are evident, under Heavy grazing this fraction amounts more than 10% of all occurrences (Fig. 2.10 D), whereas at No grazing Td_S does not fall below $Td_S \leq 2.2$.

After 50 time steps of continuous high selective grazing strong qualitative differences are obvious (compare Fig. 2.10 E with F). Approximately 65% of the samples show a $Td_S \leq 2.2$ or cover $\leq 20\%$ respectively and a strong negative effect of grazing on *F. pallescens* structure. 'Moderate' grazing leads to 15% of the samples with Td_S below 2.2. Such a pronounced change means that negative structural changes have a high probability of approx. 65% to occur after 50 years, but under specific rainfall time series remains a probability of approx. 35% that they will not occur and thus the negative changes would be masked by climatic stochasticity. After 100 time steps the trend found after 50 time
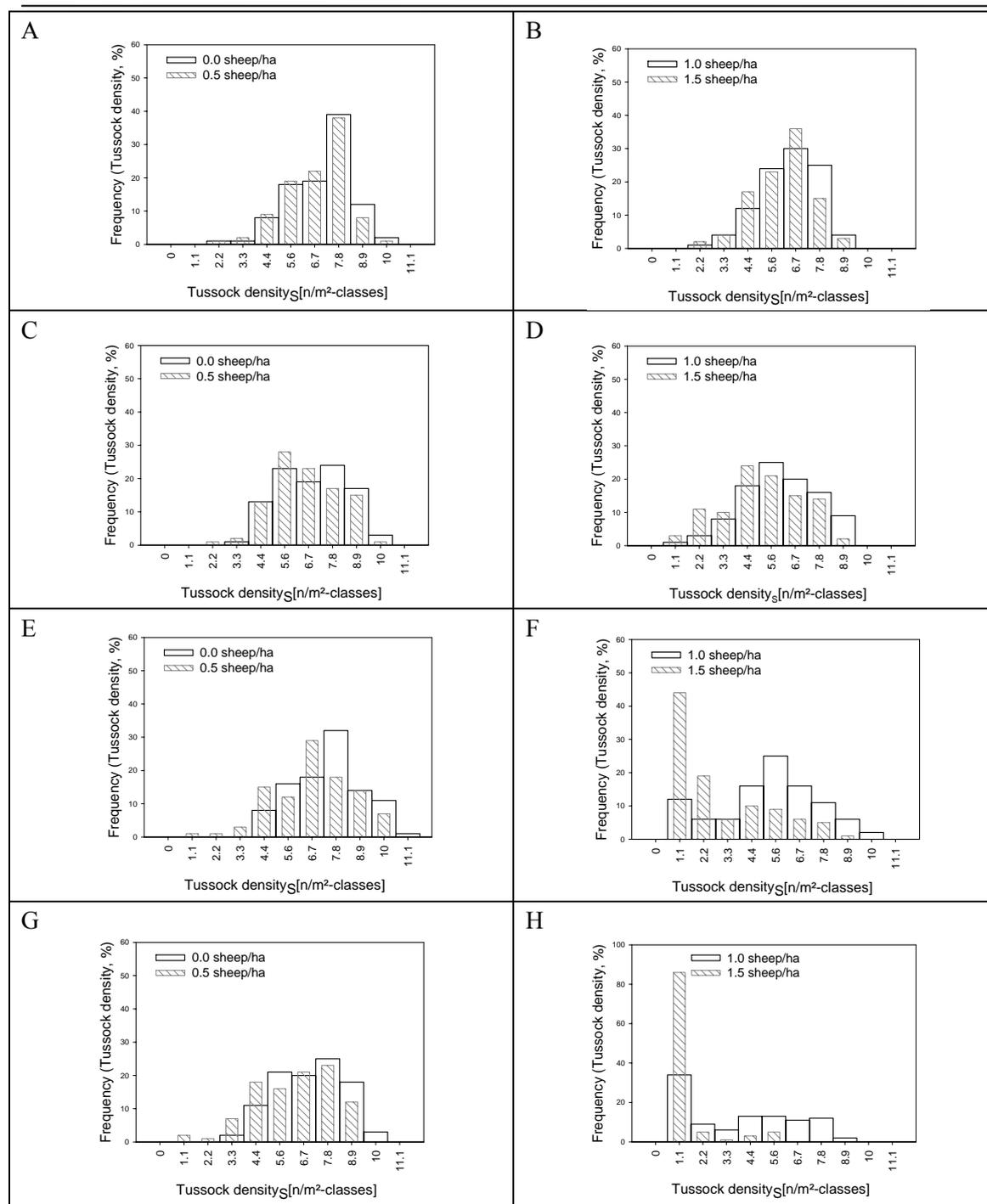
Fig. 2.10: Frequency distribution for tussock density at different time steps after 100 stochastic climate repetitions.

Shown are the frequency distributions of tussock density for 100 data points, consisting of 1 discrete time step repeated 100 simulations, each simulation run with a different stochastic climate (mean annual precipitation for the 10.000 data points MAP = 375 mm, CV = 20%, min. = 211 mm, max. = 561 mm). Tussock density classes á Td_S =]1.1] equal cover of 10%. A)-B): Td_S after 10 years of grazing for stocking rates A) 0.0 and 0.5 sheep / ha respectively; B) 1.0 and 1.5 sheep / ha respectively. C)-D): Td_S after 20 years of grazing for stocking rates C) 0.0 and 0.5 sheep / ha respectively.; D) 1.0 and 1.5 sheep / ha respectively. E)-F): Td_S after 50 years of grazing for stocking rates E) 0.0 and 0.5 sheep / ha respectively.; F) 1.0 and 1.5 sheep / ha respectively. G)-H): Td_S after 50 years of grazing for stocking rates G) 0.0 and 0.5 sheep / ha respectively.; H) 1.0 and 1.5 sheep / ha respectively.

Tab. 2.4: Mean and standard deviation for tussock density and *ANPP* distributions for discrete time steps.
Given are means and standard deviations (SD) for the tussock density distributions shown in Fig. 2.10 and *ANPP* frequency distribution (Fig. 2.11).

	Tussock density variability of frequency distribution											
	Stocking rate [sheep/ha]											
	0.0			**0.5**			**1**			**1.5**		
Time step	Mean	SD	CV%	Mean	SD	CV%	Mean	SD	CV%	Mean	SD	CV%
10	6.5	1.4	22	6.2	1.4	22	5.8	1.4	23	5.5	1.4	25
20	6.3	1.6	25	5.9	1.6	27	5.3	1.7	32	4.5	1.8	41
50	6.8	1.6	24	6.2	1.8	29	4.7	2.3	50	2.4	0.6	25
100	6.3	1.6	25	5.7	1.8	33	3.3	2.7	82	2.2	1.3	58
	ANPP variability of frequency distribution											
	Stocking rate [sheep/ha]											
	0.0			**0.5**			**1**			**1.5**		
Time step	Mean	SD	CV%	Mean	SD	CV%	Mean	SD	CV%	Mean	SD	CV%
10	1053	295	28	1004	285	28	941	275	29	870	268	31
20	1030	325	32	963	320	33	862	323	37	721	329	46
50	1135	372	33	1031	384	37	769	431	56	382	364	95
100	1010	330	33	898	346	39	523	457	87	100	216	216

steps of grazing is reinforced (Fig. 2.10 G-H): 'Light grazing' leads only to subtle changes of the *F. pallescens* structure, which might be difficult to detect in the field system. 'Moderate' grazing leads in more than 50% of the applied climatic sequences to a reduction of *F. pallescens* to a cover below 20%, the Td_S-class ≤ 1.1 is the most frequent one, and the other Td_S-classes up to $Td_S \leq 7.8$ are approx. equally distributed. Thus, the typical frequency distribution of Td_S shown for the no or low grazing scenario is changed significantly. The Heavy grazing scenario leads to a nearly complete decline of *F. pallescens*, in more than 80% of the cases only a *Festuca* cover of 10% or less is remaining.

After 20 years of grazing no negative impact of Heavy grazing can be detected because of the stochasticity of the rainfall. After 50 years of Heavy grazing however, negative impacts are clearly evident, but not for 'moderate' grazing, whereas 100 years of grazing show, that 'moderate' grazing would eventually lead to a strong reduction in *F. pallescens* cover and thus would not be sustainable on the longer term. A comparison with the single run (Fig. 2.6) shows clearly, that a long term sustainable stocking rate has to lie considerably lower than the first estimation of the stocking rate 1.1 sheep / ha, which was 'sustainable' for the single run with a specific precipitation series. For the standard model parameterisation P_S a sustainable stocking rate has to lie clearly below 1.0 sheep / ha. The shown tussock density distributions show that the model system has no stable equilibrium point, but would provide a stable probability distribution, which changes not over time. I expect that a higher number than 100 repetitions per time step would provide a normal distribution of tussock densities (compare Tab. 2.4).

2.4.5 How does grazing affect the annual productivity of *F. pallescens*, considering the stochasticity of rainfall?

How does the simulation model behave in relation to landscape level annual net primary production (*ANPP*), one of the key variables expressing the functioning of the ecosystem and a key variable also for key management? Fig. 2.11 shows the frequency distribution of *ANPP* for 100 simulations with different stochastic climates averaged for 100 repetitions for the specific time steps t = 10, 20, 50, and 100 respectively and the four grazing levels. The picture is in general similar to the analogue frequency distributions of tussock density (compare with Fig. 2.10). The distribution for the No grazing scenario seems to be normally distributed, with a more shallow/flat distribution than for tussock density, indicating higher variability than tussock density. Similar to tussock density, pronounced changes due to grazing are perceivable after 50 years of grazing, to some extent for
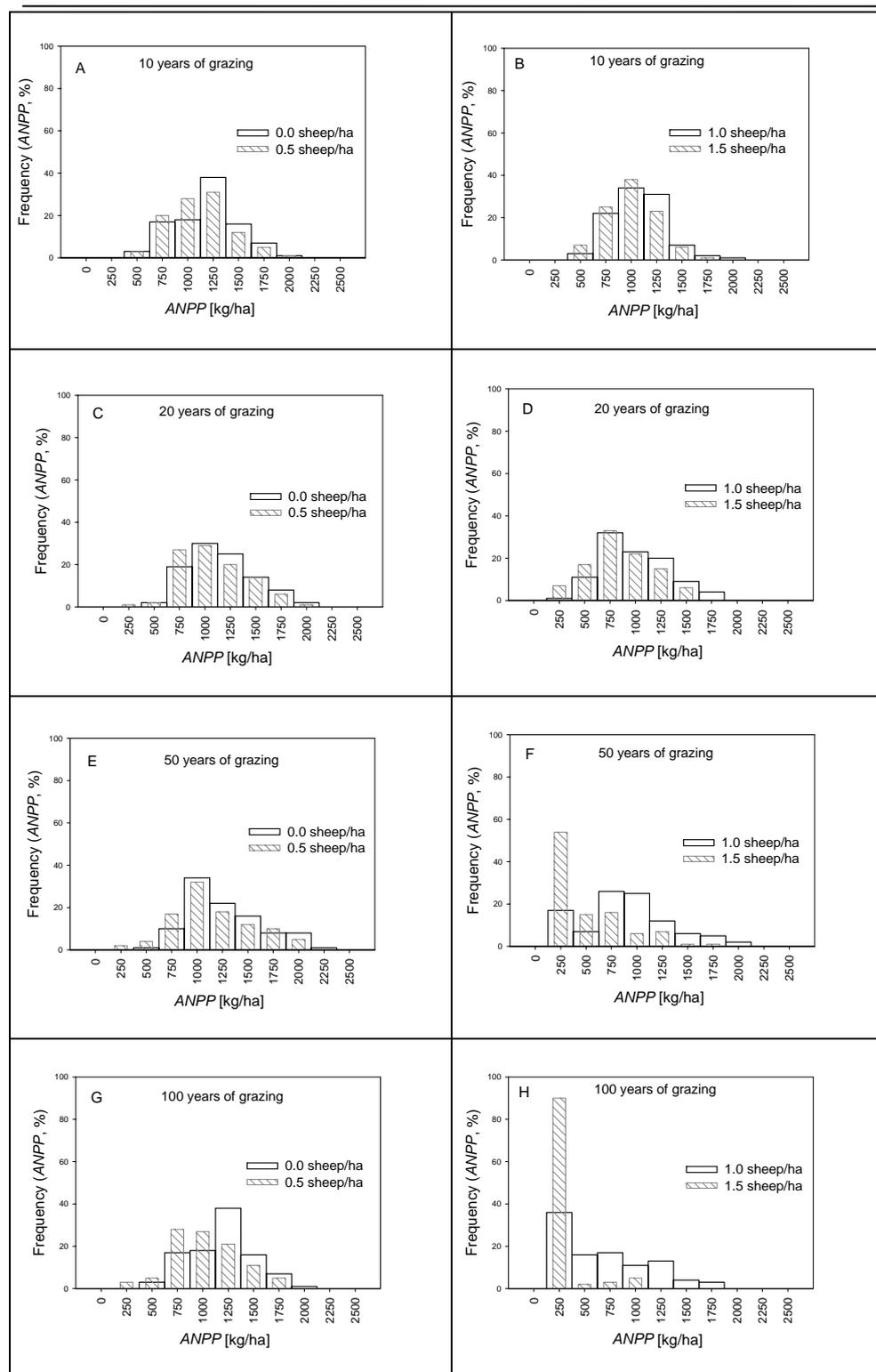
Fig. 2.11: Frequency distribution for annual productivity *ANPP* at four time steps including 100 stochastic climate repetitions.

Shown are the frequency distributions of landscape level annual net primary production (*ANPP*) for *F. pallescens* for 100 data points per specific time step A, B: 10; C, D: 20; E, F: 50; G, H: 100 years of simulation. The four grazing levels are plotted. Each distribution consists out of 100 simulations, each run with a different stochastic climate Annual net primary productivity-classes á *ANPP* =]0-250] kg / ha.

moderate and clearly for Heavy grazing. The most interesting case here is 'Moderate grazing': after 20 years 11% of the cases show $ANPP \leq 500$ kg / ha, after 50 years this value increases to 24%, and after 100 years to approx. 50%. $ANPP \leq 500$ kg / ha is the assumed lower limit for No grazing. For No grazing $ANPP$ felt below this value at maximum in 3% of the cases (see Fig. 2.11). Thus, after 50 years, a decline in productivity will be masked by stochasticity of the precipitation time series with high probability, and after 100 time steps a significant decrease would be detected only with 50% probability. Tab. 2.4 shows the variabilities for the $ANPP$ frequency distributions, which are in general higher than those for the tussock density frequency distributions.

2.5 DISCUSSION

During this Chapter 2 I presented in detail a simulation model which investigates the grazing effect on a dominant grass species of a semi-arid steppe. As the variability of rainfall varies strongly between years, the biological effects of highly variable soil water on individual plants has to be considered for investigating the combined effect of grazing and the highly variable rainfall on the dynamics of a dominant tussock grass. Additionally I investigated basic properties of the model dynamics responding to the following questions:

i)   What type of vegetation dynamics shows the *Festuca* steppe in terms of equilibrium vs. non-equilibrium dynamics?

ii)   Does grazing alter substantially the type of dynamics found for the assumed 'natural dynamics' without grazing?

iii)   What is the effect of stochastic rainfall on the demographic processes and the compositional state of *F. pallescens*, and how are they modified by grazing?

An analysis of the results for specific rainfall sequences reveals clear non-equilibrium behaviour of the model system (Fig. 2.4, 2.8). In approx. 60% of the simulated time steps, no tussock recruitment or no tussock mortality occurred in the scenario without grazing. Additionally most of the recruitment of mortality events had no strong effect on the change of tussock density. Thus, relevant changes occur only in one over 4 or 5 years **(i)**.

Grazing changes the dynamics of the assumed natural ungrazed system in two aspects: tussock recruitment changes gradually, so that the 'no events' increase slightly with 'Light' and 'Moderate grazing', but strongly with 'Heavy grazing', and the large recruitment events disappear, whereas the low and medium recruitment events occur more seldom (Fig. 2.8). Tussock mortality changes to a constant low rate of mortality, so that the term 'event-driven' may be applied only in parts. Larger mortality events (> 2%) might be event-driven by precipitation, but Heavy grazing adds a constant rate to the event-driven aspect **(ii)**.

Stochastic rainfall without grazing leads to sporadic recruitment and mortality events. (iii) The stochasticity of rainfall leads to an unpredictability of demographic behaviour (Fig. 2.8), and response variables such as tussock density (Fig. 2.10) and annual net primary production (Fig. 2.11). The frequencies of recruitment and mortality events are similar to distributions of exponential decay, whereas tussock density and simulated $ANPP$ resemble more a normal distribution. A higher sample size than 100 repetitions or pooling the 100 repetitions x 100 time steps for both variables would provide a clearer picture.

Grazing under the influence of 100 different stochastic climates leads to moderate to strong shifts within the distributions, which are perceivable only after 50 times steps, but for 'Moderate grazing' only after 100 time steps (Fig. 2.10, Fig. 2.11) **(iii)**.

2.5.1 Individual based modelling of stochastic climate and grazing

The presented simulation model integrates stochastic rainfall and a biologically based grazing model on the individual plant level. Even though a number of simulation models exist, which deal with stochastic rainfall, plant growth and grazing (compare Introduction, section 2.1), no study exist to date which combines a biologically based grazing model with the individual level of plant representation. This approach allows integrating the interaction between precipitation and grazing and their effects on biological processes such as seedling survival, tussock mortality and others. The results presented here highlight that the approach can provide valuable insights into the process of interaction between stochastic climate and grazing and how natural and anthropogenic drivers lead to observations we are facing and want to explain.

The presented model is a rule-based approach where several biological processes are formulated in an aggregated and phenomenological way, e.g. plant growth as an annual integrated response of individual plants to plant available soil water. Despite the rule is based on a physiological approach, many processes are explicitly formulated as aggregated rules because the detailed biological process is not yet known. An alternative approach might be to formulate such a model consequently as a process based model. A series of simulation models exists, which follow more the process based approach, emphasizing the physical details of different processes related to water dynamics, plant production or grazing (Riedo et al. 2000, Laio et al. 2001a, Laio et al. 2001b, Mitchell and Csillag 2001, Parsons et al. 2001, Pierson et al. 2001, Porporato et al. 2001, Schulte 2003, Schulte et al. 2003, Janssen et al. 2004, compare section 2.1). But each of these models represents only parts of the complex interacting processes between plant available soil water, individual plants, individual grazing events which further interact with highly variable rainfall. A complete physically based formulation of the problem of my thesis would require such a high number of parameters that even a first parameter estimate might become extremely difficult as it would be the case for model calibration and validation.

2.5.2 Investigation of the demographic behaviour

Demography: Colonisation/Recruitment. – The finding that the simulation model for the *F. pallescens* dynamics shows non-equilibrium behaviour can explain the difficulties to observe natural regeneration of *Festuca pallescens* in the field (Bertiller 1996, Defossé et al. 1997a, 1997b). Non-equilibrium behaviour means that tussock recruitment and mortality occur sporadically. The chance to observe newly observed tussocks under natural conditions would be only 2/5, if one assumes that the expert parameter estimation is realistic. From these recruitment events, one third is nearly negligible, because recruitment events are of 0.5% or lower, which is equivalent to recruitments of maximum 6 tussocks / 100 m² (data not shown in that detail, compare Fig. 2.8). Additionally it is very probable that the whole area of the *Festuca* steppe is grazed at least with 'moderate' stocking rates (1.0 sheep / ha) or higher. Hence, recruitment would be additionally reduced due to grazing.

Role of saplings for recruitment. — Further it is highly probable that an additional state during life-history of *F. pallescens* was identified, which has not yet been in the focus of empirical studies: the sapling state between seedling survival (1st year after germination), and the date a tussock can be considered as a fully grown tussock. There remains uncertainty regarding the age at which a recruited seedling reaches a size, vitality and a root system which is comparable to a fully grown tussock. However, it is estimated that reproduction might be reached after 2-4 years (M. Bertiller, L. Ghermandi, J. M. Paruelo, pers. comm.). Thus, my implemented rule for tussock recruitment after the third time step is a simplification, but in principle biologically realistic. The correlations between precipitation history and recruitment showed however that they are highest for the rainfall two years earlier, than the three years earlier one, as one could expect (Fig. 2.9 A-B). This result suggests that either the seedling survival or the survival of the one-year-old saplings are the most important for

tussock recruitment. But as I record the simulation results at the end of each time step, the survival of the germinated seedlings two years earlier may show the highest correlation with actual recruitment. However, it is not known, if recently recruited tussocks after 2 to 3 years reach vitality comparable to a tussock in the lowest vitality class and may also resist to grazing and dry years with the same strength. Therefore the model rules are optimistic within the time scale of 3 years until recruitment and recruitment might even be lower in reality. Additionally it is unknown, how sensitive saplings are to grazing and dry years, before they maturate.

Mortality. — Mortality shows also an event driven behaviour (Fig. 2.4, 2.8). This was expected, as plant soil water related mortality threshold were implemented into the model. Surprising was the high negative correlation of mortality to actual rainfall (Fig. 2.9). Despite a similar result was expected, I expected additionally relatively high correlations to rainfall one year earlier, due to high mortalities which may occur after two or more years of consecutive drought.

2.5.3 The type of vegetation dynamics the *Festuca* model shows

The analysis of the demographic behaviour and the results with a specific rainfall series (Fig. 2.6) revealed an event-driven behaviour of the model system, but also that tussock density reacts with some delay to climatic variability which indicates that a certain memory lies within the system (Wiegand et al. 2004c). Two hypotheses may explain this finding: firstly, not only survival of seedlings is relevant, but also that from saplings and newly recruited tussocks, which have considerably higher survival probabilities than seedlings, but considerably lower ones than vital adult tussocks with vitality > 1 (compare section before). Second, precipitation and grazing have sub lethal effects on tussock vitality. So a change in tussock density might occur in an unexpected time step, because during the years before, tussocks were weakened step by step due to grazing and/or dry years, and thus mortality events occur also with temporal delay. These aspects of population dynamics and episodic events are worth to be investigated empirically and with simulations more in detail and are treated in Chapter 5. Despite the found memory effects within the model, the event-driven and thus non-equilibrium character of the model is evident through the demographic behaviour.

Non-equilibrum dynamics. — The concept of non-equilibrium dynamics was introduced by DeAngelis and Waterhouse (1987). Wiegand et al. (1995) showed with a simulation model for the shrub steppe in the South African Karoo the non-equilibrium dynamics of a shrub ecosystem. They simulated the population dynamics for five shrub species, which responded differently to precipitation. They included some parameters and processes which can be found also within the *F. pallescens* simulation model: 'Age of establishment', which is an analogy to the three seedling/sapling stages of *F. pallescens*, 'Minimum size of safe sites', which has an analogy with *F. pallescens* recruitment dynamics, which is less probable both close to live tussocks and within 'large bare patches', and 'Rain thresholds for germination and seedling survival' which exist in the *F. pallescens* model, too. Other parameters of the Wiegand et al. (1995) model concern mostly seed production, which was not modelled explicitly in the *F. pallescens* model, and life-span, which is difficult to define for tussock grasses (M. Bertiller, pers. comm.). Two main causes Wiegand et al. (1995) discuss which are responsible for event driven behaviour of the model: at first, it is the effect of highly variable rainfall on survival of seedlings, and additionally a relevant high number of available safe sites for colonisation, which have to be available during one year of favourable abiotic conditions. The coincidence of both independent events leads to the event-driven behaviour.

Comparison of Karoo and Festuca steppe. — In principle one can expect that similar mechanism may work at the *Festuca* steppe. In difference to the model of Wiegand et al. (1995) is that *F. pallescens* have no defined maximum age. This is due to the impossibility to define one grass tussock as exact one individual (Soriano and Sala 1986). Thus, in analogy to the Karoo model,

recruitment events need favourable abiotic conditions to generate large recruitment events, but they need safe sites too. In difference to the Karoo model, *F. pallescens* mortality is not endogenous, but also triggered by precipitation (Fig. 2.4-2.6, 2.8-2.9). If a similar mechanism would underlie the dynamics of the Karoo and the *Festuca* steppe, than for natural dynamics of the *Festuca* steppe drought would provide the natural mortality of tussocks which would be necessary to create a sufficient high number of available safe sites for natural large recruitment events. That hypothesis would be interesting for further investigations. It would offer one explanation, why natural recruitment was not yet observed in the field (Bertiller 1992, Bertiller and Coronato 1994, Defossé et al. 1995, Bertiller 1996, Bertiller and Aloia 1997).

Further Wiegand et al. (1995) proposed two concepts to distinguish 'state' and 'transitions' for event-driven systems: the 'integral' events, as e.g. tussock recruitment and tussock mortality are. They occur sporadically and in consequence community structure changes discontinuously, but these changes are essentially to the population dynamics in this semi-arid system with highly variable rainfall. The second concept is that of the 'transition triggers' which are events which are able to change the dynamics of the system essentially and thus lead to a different state. I identified grazing as an event which changes basically tussock mortality from a sporadic event to a constant event at low rates.

Could this qualitative change be valued as a 'transition trigger' which leads to another state of the *Festuca* steppe? The low constant tussock mortality alone does not explain a transition between states, because the constant mortalities occur already at 'Light grazing' (0.5 sheep / ha), but the structure of *F. pallescens* does not change after 100 years of grazing (Fig. 2.10). I argue that the highest contribution to the transition from a dynamic equilibrium of sustainable *Festuca* cover to strong reduction in cover is mediated by the lack of recruitment due to Heavy grazing (1.5 sheep / ha, Fig. 2.4). This transition of the sporadic-event of recruitment to non-event occurs after some decades of heavy grazing. Thus an abrupt but non predictable lack of recruitment under heavy grazing may occur. Such non-event may be an irresolvable task for a range manager.

The explanation for this finding may be sapling survival: the biological rule says, if the relative grazing intensity *M* is near to 1, sapling survival tends to zero. So, first there might be lower seedling survival, due to a reduced *Festuca* cover after a series of dry years. During the following years sapling survival is restricted by grazing, when the available biomass does not exceed the needed forage any more by a relevant factor. The biological assumptions about seedling mortality due to grazing and also that of reduced seedling survival at reduced *Festuca* cover should be investigated more in detail, as tussock recruitment seems to be one of the essential processes to understand *Festuca* dynamics. Wiegand et al. (1995) identified recruitment as the key process for the dynamics in the Karoo shrub steppe in South Africa, too. 'Moderate grazing' (1.0 sheep / ha) reduces tussock recruitment gradually. But on the long term it has the potential to change the structure of *Festuca* cover (Fig. 2.10). It would be interesting to investigate, if the change in recruitment occurs completely gradually or if it includes thresholds, and under which conditions thresholds might occur.

2.5.4 The effect of stochastic rainfall on demography

In general the effect of stochasticity on model behaviour is as could be expected from theoretical models (Wissel 1989). Including environmental noise leads not to a stable equilibrium, but to a long-term stable probability distribution. Such behaviour was shown for tussock density and *ANPP* (Fig. 2.10-2.11). Instead the frequency distributions for recruitment (No grazing) showed exponential decay. This result is explained by the inclusion of thresholds of plant available soil water for colonisation and mortality.

Recruitment. — The event-driven behaviour of recruitment is not only explained by stochastic rainfall. The effect of stochastic rainfall is reinforced due to the interaction with the biology of *F. pallescens*: I explain the sporadic occurrence of tussock recruitment events with the necessity of a series of at least three average or humid years, which allow a age-cohort of seedlings not only to survive the year of germination, but also the following sapling years. As the probability of dry years in this region is roughly 12 up to 20%, the probability is high that one age cohort does not survive until maturation.

Mortality. — Stochastic rainfall influences tussock mortality in a similar way as recruitment: the inclusion of thresholds favour the event driven behaviour. One dry year may lead to mortality of recently recruited tussock, and additionally of other weak tussocks, which accidentally were within the lowest vitality class. A series of drier years, however, may weaken a high proportion of tussocks and lead to high mortality during the second dry year or even later. On the other hand, no mortality may occur during several years, if average, humid or years slightly below-average years occur.

2.5.5 Grazing effects on *Festuca* dynamics

Grazing leads to strong structural and functional changes, depending on the grazing scenario. 'Light grazing' showed only small changes in comparison to No grazing (Fig. 2.8, 2.10, 2.11). 'Moderate grazing' showed weak to moderate effects after 20 and 50 time steps, but strong effects both on structure and function after 100 time steps. 'Moderate grazing shows one fundamental problem in semi-arid systems: the long time scales of change which may surpass human horizons (Wiegand et al. 1995, Wiegand and Milton 1996, Jeltsch et al. 1997, Weber et al. 1998, Weber et al. 2000). 'Heavy grazing' shows extreme negative effects both on tussock density and productivity and should be qualified as heavy overgrazing.

Grazing under stochastic rainfall leads for the standard parameterisation to threshold behaviour in two aspects: a **grazing threshold** appears to exist (Fig. 2.6), below which grazing might be sustainable on the long-term. Below this threshold a dynamic 'pseudo-equilibrium' is evident around which tussock density fluctuates driven by the stochastic rainfall sequence. The grazing threshold will be further investigated in Chapter 5.

Regeneration threshold under constant grazing. — Additionally a **regeneration threshold** exists at approx. $Td_S = 2.5$ (Fig. 2.6). If tussock density falls below this value, recovery of *F. pallescens* is not possible anymore. This regeneration threshold holds only for the case of constant grazing. I propose this threshold as a first degradation threshold for constant grazing, and I will use this threshold during this thesis.

Time to recover, when grazing is stopped. — If grazing is stopped after a certain number of time steps, the regeneration threshold changes (Fig. 2.7). No tussock density value could be found, despite extinction of all tussocks, which impedes *F. pallescens* from recovering when grazing is stopped. But a relative regeneration threshold can be found (Fig. 2.7). This relative regeneration threshold can be expressed as the ratio between time of recovery needed to reach again a tussock density as the ungrazed control and the total grazing time. If this threshold lies below 1, recovery is shorter than the grazing time, recovery time increases linearly and is not prolonged significantly. If the ratio 'time to recover / grazing duration' changes to values > 1, this indicates that recovery time increases non-linearly in relation to the grazing time and the relative regeneration threshold was surpassed (Fig. 2.7).

This ratio could be used as a measure for degradation in the model. If time to recover of the *F. pallescens* steppe for a specific stocking rate takes longer than grazing lasted before, the steppe shows severe degradation. Walker et al. (2002) proposed a time frame of up to a maximum of 200 years as basis for an assessment if a system is degraded or not. Underlying this proposal, Fig. 2.7 tells

us, that for the *F. pallescens* steppe 80 years of grazing would lead to recovery times of 200 years. However, this time frame is unrealistic since already a recovery time of ~ 20 years would force a farmer to give up. Thus, an optimal minimum requirement would be not to surpass the 'time of recover' for the grazing intensity x grazing duration threshold, which lies at approx. 20 to 25 years at stocking rate = 1.1 and 30 years of grazing. For grazing management also such a value seems not to be realistic, and a farmer would only accept at maximum, if ever, recovery times, which naturally might occur after a heavy drought has reduced tussock density strongly. Such natural recovering time frames would be a next step to investigate.

2.5.6 Equilibrium vs. non-equilibrium dynamic paradigm

For nearly two decades ecologists have controversially discussed if and how resource (vegetation) and consumer (herbivores) are coupled and how this coupling affects dynamics of grazed semi-arid systems and its management (see Ellis and Swift 1988, Ellis 1994, Illius and O'Connor 1999, Illius and O'Connor 2000, Fuhlendorf et al. 2001, Briske et al. 2003, Archer 2004). The main disagreement is about the question if grazing exerts a long-term effect on vegetation or not. If resource and consumer are uncoupled, the consumers are expected to have no effect on the resource, but otherwise this would be the case (Illius and O'Connor 1999). Ellis and Swift (1988) postulated that high variability in precipitation may lead to uncoupled herbivore-resource dynamics and to non-equilibrium dynamics (Ellis and Swift 1988). As my investigations of correlations between demographic events and precipitation history show, this may be true for the *F. pallescens* only in parts (Fig. 2.9). As at least recruitment is correlated highest with the precipitation history two years earlier, vegetation dynamics may remain stronger coupled than expected, if such interactions between the biology of a perennial species with climate occur over several years.

Caughley et al. (1987) in Ellis (1994) postulated that in a semi-arid system where the precipitation exceeds a CV of 30% will show non-equilibrium dynamics. However, if herbivores and vegetation are coupled the system will show equilibrium behaviour, where grazing should lead to a negative linear effect on vegetation. The latter position is maintained mainly by Illius and O'Connor (1999). The equilibrium behaviour of a coupled system is explained by the deterministic behaviour of the system if herbivore saturation is reached. That means, if herbivore consumption exceeds plant standing crop, the system will go to extinction deterministically, otherwise the system will reach onee equilibrium point (van de Koppel et al. 1997). This simple theoretical models assumes no interaction between resource and herbivores i.e. the both interacting components have o negative on each other. Coupled resource-consumer models like that of Lotka (1925) and Volterra (1926), where both species have negative effect on each other, lead to a stable equilibrium point with damped oscillations under a certain threshold for the reproductive success of the resource (Wissel 1989). Above a certain threshold for reproduction of the resource the system becomes instable and the consumer goes extinct.

I contribute the following results to this debate: the *Festuca* steppe simulation model shows non-equilibrium dynamics caused by episodic recruitment and mortality (Fig. 2.4 A), although precipitation varies only with a CV of 20%. I argue that the effect of herbivores on vegetation will depend on its relation to a threshold in stocking rate above which coupling of vegetation and herbivores occurs (see Fig. 2.6). Stocking rates below the threshold cause only a moderate reduction in tussock density (Fig. 2.6), and no strong effect is exerted on vegetation. I determined the threshold qualitatively for the *Festuca* steppe.

However, if stocking rate exceeds the threshold, tussock density declines strongly at time scales, which are shorter if stocking rate increases (Fig. 2.6). The interpretation of this result is that herbivore and vegetation are coupled near herbivore saturation (van de Koppel and Rietkerk 2000). Herbivore saturation means that the forage consumed by livestock reaches the actual grazeable forage,

so that the realized relative grazing intensity (*Mreal*) ~ 1. At this grazing intensity the negative biological impact of grazing will surpass any potential recovery of *F. pallescens*. As a consequence tussock density will decline below the regeneration threshold if stocking rate is above the grazing threshold. The regeneration threshold ranges for the used parameterisation at tussock density Td_S of approx. 2.5 (Fig. 2.6). Clearly this deterministic degradation due to a tight coupling between herbivores and vegetation occurs only because I assume that grazing has negative effects on vegetation such as higher tussock mortality, reduced vitality, and reduced regeneration (see further discussion below).

If stocking rate is far higher than the grazing threshold, herbivore saturation is already reached after 20 years, and the system degrades towards a stable state of nearly complete loss of vegetation cover. However, such extreme degradation is outside the range of application of the model since in this case shrub encroachment mostly by *Mulinum spinosum* was observed (J. Paruelo, pers. comm., and own observation). We constructed our model only for at maximum moderate degradation.

The interesting point here is that a stocking rate coinciding with threshold stocking rate at approx. 1.1 sheep / ha yields for the specific time series analysed only to moderately reduced tussock density. The difference to tussock density under No grazing would probably not be statistically significant. However a slight increase in stocking rate leads to degradation on the long term (Fig. 2.6).

Fig. 2.6 shows that degradation occurs after a specific series of a combination of unfavourable rainfall events. This result was observed for constant stocking rates. I did not investigate natural herbivore dynamics. Therefore I can not decide if the variability of precipitation is sufficient to decouple vegetation and herbivores, but I expect that the coupling will be weaker than under a constant stocking rate (van de Koppel and Rietkerk 2000).

My results clearly indicate that variability of precipitation has a negative effect on vegetation. However I would partially contradict the hypothesis of Illius and O'Connor (1999) that the grazing effect is especially severe during drought. My results indicate that reduced tussock recruitment after drought and under heavy grazing seems to be a more important factor. During drought grazing increases mortality only moderately, but in the following years recruitment fails under grazing (Fig. 2.4). These results are obviously related to the biological constraints included in the simulation model, mainly the reduced seedling survival at reduced tussock density. In humid years reduced sapling survival is obviously under grazing. Under heavy grazing recently recruited tussocks might be especially vulnerable, because they are preferred by sheep due to the low proportion of dead biomass. Without negative effect of drought or grazing regeneration of vegetation should be possible. Clearly, in some cases my study can be too optimistic because soil erosion is included only implicitly. With higher evaporation in larger bare soil patches, an explicit inclusion of irreversible soil erosion would possibly increase the negative effects, if high rainfall would follow a series of dry years. But soil erosion will only be important for heavy degradation which is outside of the scope of this study

I argue that a model investigating the interaction of grazing with stochastic rainfall aimed to contribute to the debate about the equilibrium dynamics of semi-arid rangelands needs to include at least three essential characteristics: the most important factor of environmental variability (here: precipitation), an explicit representation of the small scale spatial processes and the biological effects of grazing on the resource. Neglecting one of these features, a study will fail to improve the understanding of or to make useful predictions on the interaction of drought and grazing.

The modelling approach. — I included grazing as an explicit spatial process at a small scale. My model assumes that space is limited, i.e. herbivores are fenced in large paddocks, so tussocks have a certain probability of being re-grazed during one time-step. The biological constraints and the role of space are partly neglected in the debate concerning equilibrium dynamics in semi-arid grazing systems (compare Briske et al. 2003). The *Festuca* steppe in general is completely fenced and grazed all year

round. Thus, there is no buffering space available, which makes it a more vulnerable system. The theory of non-equilibrium dynamics developed by Ellis and Swift (1988) is based on additional available space to buffer lack of forage during drought. Illius and O'Connor (2000) included space in a simulation study. They investigated the effect of increasing resource variability in areas, which are accessible only during the dry season on the supported animal numbers in the presence of different large buffering areas, which are accessible during the wet season. They found that additional accessible space during the wet season increases the mean number of supported animals, but they neglect a possible negative biological effect of grazing on the key resource. Briske et al. (2003) conclude, that the question, which model applies best - the equilibrium or the non-equilibrium model – might be resolved only with the development of a model that accommodates both the equilibrium and non-equilibrium paradigm.

The simulation model for the *Festuca* steppe is able to show both, equilibrium and non-equilibrium dynamics and applies a biologically realistic grazing model. The conceptual framework of the model could also be applied to other semi-arid systems. I argue that existing simple theoretical models are not sufficient to investigate the grazing effect under highly variable rainfall. Although theoretical approaches may predict the stable states for simple grazing models (van de Koppel and Rietkerk 2000), they must fail if we want to investigate specific systems and grazing effects at concrete time scales.

The consideration of the biological constraints, i.e. to estimate if grazing affects recruitment, mortality or other vegetation processes, is also essential and is often neglected during the equilibrium-non-equilibrium debate. Ellis and Swift (1988) postulate, that vegetation and thus productivity is not negatively affected by grazing, but they give only a qualitative evaluation without evidence. Illius and O'Connor (2000) assume in their simulation model, that grazing has no negative effect on plant production. Briske et al. (2003) report, that empirical evidence is very scarce about how vegetation is affected by grazing in highly variable environments. In O'Connor (1994) I find the only empirical study which investigates the effect of grazing on distinct population processes of vegetation, but the time scale was too short to separate the effect of rainfall and grazing completely.

2.6 SUMMARY

During this Chapter 2 I presented in detail a simulation model which investigates the grazing effect on a dominant species of a semi-arid steppe. It integrates a biological plausible grazing model at the level of biological processes occurring at the individual plant level and the effect of plant available soil water at the same level as grazing. Thus, the model has the potential to separate anthropogenic effects (i.e. grazing) from natural effects (e.g. highly variable rainfall) from each other. I show that tussock recruitment and tussock mortality show event-driven behaviour which is induced and maintained by the highly variable rainfall. The investigations of the correlations between demographic behaviour and precipitation history parameters revealed that tussock recruitment is mainly related to precipitation two years before the actual time step, but mortality is mostly correlated with actual rainfall.

Then I show that 'moderate' and 'heavy' grazing change the demographic behaviour in a complex manner, so that finally heavy grazing is hypothesized to be responsible for the observed strong reduction in *Festuca* cover. Heavy grazing leads to a lack of recruitment after a certain time lag of some 20 years, probably due to the reduced survival of seedlings and/or saplings under heavy grazing. I developed the hypothesis that at such point herbivore saturation is reached, were available and needed forage equal. In this case a deterministic tight coupling of resource and consumer occurs

and leads to a negative feedback response due to the possible tussock mortality due to grazing. The *Festuca* cover will decline deterministically near to extinction below the regeneration threshold.

Thus, the results of Chapter 2 lead to a hypothesis explaining the reduction of *Festuca* cover under grazing including, which explains the causality between grazing, demographic behaviour of *F. pallescens* and the reduction in tussock density of *F. pallescens*.

Conclusion. — I presented a model, which may show both equilibrium and non-equilibrium dynamics, depending on the biological and environmental constraints. Thus, it presents one further step in the understanding of long-term quantitative dynamics of the interaction between stochastic environment and grazing.

2.7 VIEW

In Chapter 2 I presented a simulation model, which simulates the interaction between grazing and stochastic precipitation on the biological relevant spatial scale – the individual level – and includes a biologic realistic grazing model. An analysis of the model behaviour using an expert parameterisation revealed event-driven behaviour of the model system, and how heavy overgrazing modifies the assumed natural model behaviour.

The following Chapter 3 will explore the model behaviour under the expert estimation in more detail. It will present a first sensitivity analysis of the model, a qualitative comparison of field data with model predictions, three tests of essential model assumptions, and an analysis of annual net primary production (*ANPP*) and precipitation use efficiency under different grazing regimes.

Chapter 3 represents to certain extend model development done previous to my thesis. However, this chapter does not portray the model as it was when I took over the project. I revised the model rules substantially and all analyses were based on the current model rules. Chapter 3 was submitted to 'Ecological Applications'. For that reason I include the manuscript completely into my thesis. Only the formatting was adjusted to the format of the thesis. Some shorter repetitions of material of previous chapter occur, for example in the study site description (3.3.1) and the model description (3.3.2), Tab. 3.1 and Fig. 3.3. These sections are recommended to be read very roughly. The first author of Chapter 3 is Jose M. Paruelo and I am the second author. My contributions to this chapter, beside model development, are: Co-author of sections 3.1, 3.2, 3.3.2, 3.3.6, 3.4.2, the figures 3.3, 3.6, 3.8 were produced with equal contributions by both main authors; and Tab. 3.1 was mainly my contribution. I estimate my contribution to the manuscript of Chapter 3 as high as approx. 25%.

3 ASSESSING THE LONG-TERM DYNAMICS OF A SEMIARID GRASS STEPPE UNDER STOCHASTIC CLIMATE AND DIFFERENT GRAZING REGIMES[1]

3.1 ABSTRACT

To investigate the impact of *small* scale grazing events on vegetation dynamics at the patch scale, we built a grid-based spatial explicit stochastic simulation model to upscale vegetation dynamics to the landscape. The model simulates grazing events and basic processes like seedling establishment, growth or mortality of the dominant species. Field data, generate at the same scale than the output variables of the model, were used to evaluate the model at the level of the predictions and to test some of its basic assumptions. Simulation experiments analyzed the interaction of precipitation and grazing regimes.

Simulated tussock density and green biomass lies within the range defined by the extreme values observed in the field. Except for the heavily grazed paddock, simulated and observed values of the proportion of standing dead biomass per tussock were similar, ranging between 0.30 and 0.60. As we observed in the field, grazing increased the relative abundance of tussock with a low proportion of standing dead biomass.

Grazing generated a reduction in tussock density which results in a decline in Aboveground Net Primary Production (*ANPP*). Both variables presented a non-linear behaviour including high temporal variability and delay effects, which may prolong for decades. Changes in *ANPP* were minimum for winter grazing and maximum for continuous grazing and they become evident only at high stocking densities. Under high stock density conditions precipitation use efficiency (PUE) was 82% lower than the values for non-grazed runs. Grazing reduced also the sensitivity of *ANPP* to interannual changes in precipitation. The variability and autocorrelation of the precipitation data had a significant effect on tussock density, and hence on *ANPP*. The interannual variability of precipitation was more important than the grazing regime in explaining differences in tussock density. Tussock density was higher and less sensitive to the grazing regime under a low-variability scenario.

The results of the simulation model highlight some 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.

3.2 INTRODUCTION

Desertification has been identified as one of the major environmental problems that arid and semiarid systems face at the beginning of the century (Dregne, 2002). The concept of desertification is used in a wide range of situations and contexts. Probably due to the widespread use of the term its definition has been controversial and vague (Reynolds and Stafford-Smith 2002). The meaning of the term desertification becomes highly dependent on which specific aspect of the socio-economic, political, cultural or ecological system the analysis is focusing. In an ecological context one of the most useful ways to characterize these phenomena has been coined by Le Houreou (1984), who stated

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that desertification is the reduction of the precipitation use efficiency (PUE, the ratio of net primary production to mean annual precipitation) of an ecosystem. Such reduction in PUE involves profound structural and functional changes both in the biota and the soil. Although climatic and geologic forces may be behind the desertification process (Oba et al. 2001, Harthey and Chong, 2002, Hillel and Rosenzweig 2002), at ecological time frames, grazing by domestic herbivores has been identified as the one of the major agents (Soriano and Movia 1986, Manzano et al. 2000, Paruelo and Aguiar 2003, Ares et al. 2003). Grazing promotes changes at different levels and on different components of the system. 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 playing a key role in changing the structure of the plant community. 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), species composition (León and Aguiar, 1985; Altesor et al. 1998) or nutrient balance (McNaughton 1990). 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 2003). Each of these actions will impact differentially on individual plant, population and community processes.

Since its introduction by European settlers at the beginning of the XIXth century sheep stocks start to rise in Patagonia, an extensive arid and semiarid area in the southern tip of South America (Soriano and Paruelo 1990). Livestock numbers peaked in the '60s and decreased since then (Golluscio et al. 1998). Ecologists started to recognize signs of degradation in the steppes in the '50s (Soriano 1956b, Boelcke 1957). The grass steppes dominated by a tussock grass, *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 the cover of *Festuca pallescens* and, in the latest states of degradation, to shrub encroachment (León and Aguiar 1985, Bertiller et al. 1995). In grazed communities of *F. pallescens*, decreased senescence in grazed tussocks starts a positive feedback between successive grazing events. Due to the extremely selective defoliation regime, grazing pressure is not homogeneously distributed over the tussock population in a grazed area. Livestock persists on only a fraction of the total grassland 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. Therefore, predictions of livestock impacts based on landscape level mean utilization intensity given by consumed over produced biomass are inappropriate, since such point model approaches ignore the high grazing impact on the preferred sites. Based on the particular traits of the *F. pallescens* grazing system, we hypothesize that livestock impacts on landscape level vegetation dynamics depend on the small-scale tussock level pattern of the grazing regime.

Understanding how the effect of individual processes at lower levels determines the behavior of the systems at higher levels is a major challenge in ecology (Levin 1992) and it is critical to device management schemes capable to operate at the ecosystem level. The nature and the scale of the processes involved make the analysis of the degradation extremely difficult from a pure experimental approach. Difficulties arise from many unanswered methodological questions: In how many years can we detect the impact of a management strategy on the vegetation? Which are the variables that allow one for an early detection of the degradation processes? Given the spatial variability of the vegetation variables, how many samples need to be taken to detect grazing-induced changes? The answer to these questions is essential to device monitoring programs and to design management plans. 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. Additionally, semiarid rangeland dynamics are 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. Because of the mismatch between time scales for observation and vegetation change (Wiegand et al. 1995; Wiegand and Milton 1996) and its inherently complex dynamics, little is known about the long-term dynamics of semiarid plant communities.

With the development of powerful computers a new approach to the modelling of natural systems, especially for applied questions, has being adopted (e.g., Coffin and Lauenroth, 1990; Wiegand et al. 1995; Jeltsch et al. 1996; Wiegand and Milton 1996; Wiegand et al. 2003; Grimm and Railsback *in press*). These new models describe directly the dynamics of biological processes by simulating the fate of individuals or assemblages of individuals including the essential biological information in the form of rules rather than mathematical equations. Even with the most complex problems these models allow for the direct inclusion of expert knowledge (i.e. they are not necessarily restricted to hard data) and they do not rely on equilibrium concepts. Although there is little (long-term) field data available on the full dynamics of arid plant communities, attributes of individual plant behavior are relatively easy to observe. The basic idea is therefore to incorporate the short-term knowledge in form of simple rules 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. *Festuca* steppes are an ideal system to device such model 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.

Our goal in this article was to provide a quantitative understanding of the impact of grazing and different scenarios of precipitation on vegetation dynamics at the scale of a *Festuca pallescens* steppe patch (10-100 hectares). The temporal scale of the analysis spans over decades and has a temporal resolution of one year. Our approach is based on a simulation model. Based on the available knowledge on the spatially small-scale processes at the tussock level and on the controls of the defoliation regime, we built a grid-based spatially explicit stochastic simulation model to upscale vegetation dynamics to the landscape. Our model built on several studies on the effect of grazing on semiarid ecosystems that use rule based simulation models including stochastic rainfall (Jeltsch et al. 1996, Wiegand and Milton, 1996, Jeltsch et al. 1997, Stephan et al. 1998, Weber et al. 1998, Weber et al. 2000, Weber and Jeltsch 2000, Beukes et al. 2002). We studied the long-term effects of livestock grazing with respect to two groups of factors: factors open to direct management (utilization intensity, timing of defoliation), and non-manageable factors (climatic conditions). Our study included also field measurements aimed to generate data at the same hierarchical level that the output variables of the model. Such data were used to evaluate the model at the level of the predictions and to test some of its basic assumptions. We analyzed the patterns generated by the model in the context of desertification processes. The evaluation of the model included a test of some of the assumptions of the model using field data, a sensitivity analysis, and the comparison of model outputs against field data. Finally, we performed simulation experiments to evaluate the response of the grass steppes to different climate and grazing scenarios.

3.3 METHODS

3.3.1 Description of the study area

Our analyses focused on the grass steppes of *Festuca pallescens* ("coirón blanco") that characterize the Sub Andean district of the Patagonian Phytogeographic Province (Soriano 1956a, Paruelo et al. 1991, León et al. 1998, Paruelo et al. 2004) (Figure 3.1). They occur where mean annual precipitation is higher than 300 mm. As in most of Patagonia, precipitation is concentrated in winter (Paruelo et al. 1998). Mean temperatures are lower than 5 °C, with mean monthly maximum of 10.5 °C (January) and mean monthly minimum of –2.2 °C in July. Winter temperatures and the distribution of precipitation determine an asynchrony between the wet and the growing seasons (Paruelo and Sala, 1995, Paruelo et al. 2000).

The Subandean district limits to the east with the shrub steppes of the Occidental district, and toward the west with the subantartic forests. Both the west and east boundaries correspond to a wide ecotone where the physiognomy of the vegetation change gradually (León and Facelli 1981, Bertiller et al. 1995, Jobbágy et al. 1996). *Festuca* grasslands are concentrated in a narrow North-south strip between 71° W and 71 ° 30' W that is continuous only between 43 ° 30' S and 46 ° S (León et al. 1998, Paruelo et al. 2004) (Figure 3.1). Towards the north, grass steppes occurred in an intricate mosaic due to the complexity of the landscape (Jobbagy et al. 1996, Paruelo et al. 2004). The grass steppes have been defined phytosociologically as the "community of *Festuca 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 *Festuca* 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*) (León and Aguiar 1985, Bertiller et al. 1995). Such structural modifications were associated to changes in water dynamics, net primary production and herbivore biomass (Aguiar et al. 1996, Golluscio et al. 1998). A number of field studies analyzed the impact of grazing on single processes at the population or ecosystem level (Bertiller 1992, 1996, Bertiller and Coronato 1994, Defossé et al. 1990, 1997a, b, Paruelo et al. 2000).

In *Festuca* grasslands, standing dead biomass is not consumed by sheep, and may last in the tussock for several years (Soriano et al. 1976, Jobbágy and Sala 2000). As a consequence, green biomass located in tussocks with high fractions of standing dead biomass is protected from defoliation, due to the spine-like character of standing dead material. Hence, the selection of a grazing site at the spatial scale of a single-tussock is affected by tussock composition. Stock densities vary over the region according to the productivity and vegetation physiognomy of the paddocks (Golluscio et al. 1998a). The stock density on the *Festuca* grass steppes ranges from 0.4 to 1.6 sheep.ha^{-1}.
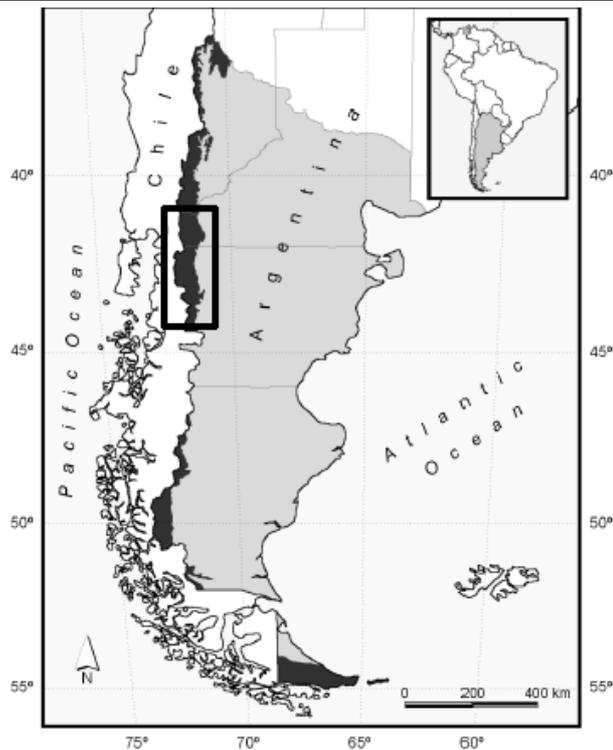
Fig. 3.1: Map of the study region.
   The black areas corresponded to the *Festuca pallescens* grass steppes (Subandean district). Redrawn from León et al. 1998.

Fig. 3.2: General view of the grass steppes of the Subandean district.
   Below: a detail with a Festuca pallescens tussock. (Photo JMP).

3.3.2 The model

We built an individual-based, spatially-explicit model (COIRON) to simulate the dynamics of a homogeneous stand of a typical grass steppe of *F. pallescens* of the Subandean district in north western Patagonia (Figure 3.2). The model simulates the behavior of the systems during the early stages of the degradation processes. 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 (*Mulinum spinosum* or *Acaena splendens*). We considered, but did not simulate explicitly the dynamics of preferred but scarce species of forbs and small mesophytic grasses.

Temporal and spatial grain.—The model simulates the dynamics of a homogeneous stand of a typical grass steppe of the Subandean district (Figure 3.2). The spatial resolution (cell-size) of the model is equivalent to a fully-grown individual tussock (30 x 30 cm). This is the spatial scale at which most of the plant processes and livestock forage decisions take place. The model has an annual time step but we simulated the influence of different seasonal grazing regimes by modifying the selectivity of herbivores. Model description is provided at three levels of detail: in the rest of this section we describe the conceptual model, the equations and rules are presented in Appendix I and, finally, the code is available on request (paruelo@ifeva.edu.ar or sandro.puetz@ufz.de).

51
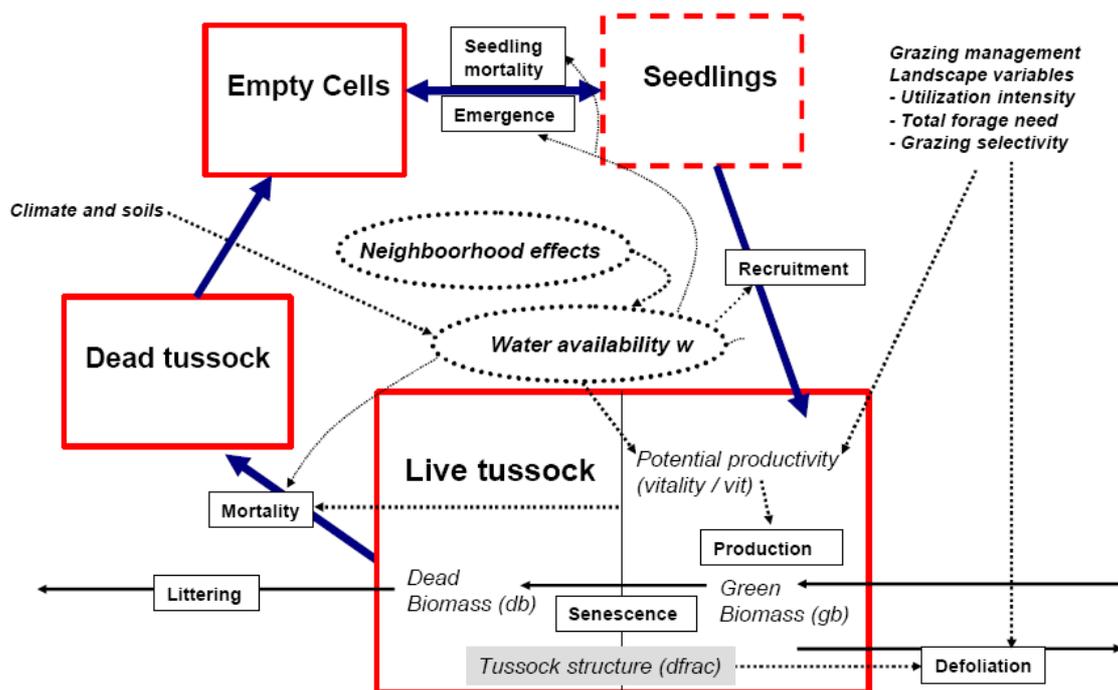
Fig. 3.3: Diagram of the COIRON model.
State variables are presented in shadowed boxes (seedlings are not explicitly modeled). Non-shadowed boxes correspond to the different processes associated to the dynamics of the systems. Internal and external driving factors are represented in italics.

Basic variables and states.— There are three possible states for a cell (Figure 3.3). 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*) (Figure 3.3). Both fractions appear interspersed in the tussock. Tussock composition or structure (*dfrac)* denotes the fraction of standing dead *db* over total standing biomass *db + gb*. A tussock is characterized by a discrete level of "vitality" (*vit*), a property accounting for tussock's memory of its history, which is basically determined by 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. The dynamics of the state variable is basically controlled by plant available soil water (*w*) throughout its influence on the input and transference fluxes of matter (production, senescence). Dead biomass may last in the tussock for several years (Soriano et al. 1976, Jobbagy and Sala 2000). 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. For production response to soil water – the only resource considered – we assumed Michaelis-Menten kinetics. Potential production (*vitality*) determines the maximum production of the tussock.

Water dynamics. — Annual rainfall is assumed to be spatially homogenous. A fixed fraction of annual rainfall is transformed into an annual amount of plant available soil water *w*. Such fraction is based on observed and simulated values of the ratio between transpiration and precipitation for the grass steppe (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). 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 tussock sites due to lateral influx (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*.

Mortality. — Mortality occurs only for tussocks in the lowest vitality class. The probability of dying depends on thresholds related to soil water availability and defoliation severity. Grasses reproduce exclusively from seeds, and seed distribution is considered to be spatially homogeneous (Bertiller 1992); seed production and distribution are not modeled explicitly. Seedling emergence occurs only in empty cells . Seedling mortality, emergence and recruitment probabilities depend on locally available soil water, and grazing.

Grazing pressure. — We distinguish two spatial scales for the grazing process: the local or tussock level, and the patch or landscape unit level scales. The last scale 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. To calculate the forage consumed from *F. pallescens, PF* is discounted from total Forage need *FN*, so we get forage needed from *F. pallescens*. Landscape level mean utilization intensity *M* for *F. pallescens* then is given as

$$M = (FN\text{-}PF) \, / \, AF \tag{3.1}$$

Grazing process. —The grazing process is considered as a sequence of local grazing events that continue until the total forage need has been met, available forage reach 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 increasing fraction of standing dead. With 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, *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.

Grazing regimes. —To simulate different grazing regimes in a more realistic way, we

introduced different grazing regimes according to the seasonality of the defoliation: continuous year round grazing (a) or all forage needed is consumed in spring (b), summer-fall (c), or winter (d). Because the time step of the model is one year, grazing seasonality was simulated trough 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.

Table 1 summarizes the parameters of the model and the values used in the simulations. Further details on the parameters and the specific rules and equations of the model are provided in Appendix I. Parameter values were derived or estimated from the literature, unpublished data and the opinion of experienced local ecologists and range scientists. This version of the model, then, has been parameterized without indirect calibration using the field patterns of the output variables. 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 sensitivity analysis varying the level of 14 groups of parameters, and we compared model outputs against field data.

3.3.3 Field studies

We conducted field studies a) to compare field data with model outputs, and b) to test some model assumptions. We selected 16 grazed paddocks in 5 private ranches and 3 exclosures distributed across the Subandean district. We had, then, estimates of 6 sites, one ungrazed with 3 replicates (exclosures) and 5 grazed with a variable number of replicates (1 to 5 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 paddock were excluded from the analysis because *F. pallescens* is not longer the dominant species (León and Aguiar 1985). Reliable estimates of long-term stock densities are very difficult to derive 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 three meters, 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 Colman, 1982):

Density (tussock.m^{-2}) = (distance (m) . 2)^2)$^{-1}$ (3.2)

- On each of the target 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; and 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. From the original data, we calculated the *diameter* (cm) and the *total volume of the tussock (= π . (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 to April).

On a subset of the sites, we estimated the fraction of the photosynthetically active radiation intercepted (fPAR) by the tussock. It was assessed using the Normalized Difference Vegetation Index, 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). Monteith (1981) showed that the product of fPAR and PAR, the intercepted PAR (IPAR) is the main determinant of productivity. Based on this rationale, we used the NDVI as a linear estimator of the potential productivity of the tussock and hence as an alternative way to estimate the vitality of the tussock. We measured the reflectance of two or three portions of aprox. 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).

3.3.4 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 c.a. 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 to 10. Simulations were performed for three of stocking density 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 field plot.

3.3.5 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. 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. To test the last assumption, we generated (for the average precipitation conditions of the sampled *Festuca* steppes), values of biomass production per tussock using the equation included in the model (see Appendix I). 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).

3.3.6 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 (table 1) 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 (Table 1). 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).

3.3.7 Modeling experiments

To understand the dynamics of the grass steppe we designed modeling experiments based on 5 climatic scenarios and 32 management scenarios. The 5 climatic scenarios were built on a series of mean annual precipitation (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 re-arranged in order to generate two periodic scenarios, one having a period of 10 years (C10) and the other of 20 years (C20),with a higher autocorrelation than the original data. 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 8%. Every scenario had the same MAP (375 mm). The management scenarios derived from combining stocking 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 ha and 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 4 stocking density scenarios, from 0 up to 1.5 sheep.ha^{-1}. According to the information available for the area on grazing management (Golluscio et al. 1998), we defined 4 scenarios of seasonality: continuous, winter, spring and summer/fall grazing.

3.4 RESULTS

3.4.1 Testing model assumptions

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,) (Figure 3.4, inset).

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 (Figure 3.4). 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) (Figure 3.5). The consumption level and the frequency of defoliated tussock decreased as the proportion of standing dead material (*dfrac*) increased. 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 2) (Figure 3.6a). At low grazing pressures (low mean degree of consumption) highly defoliated tussocks coexist with no-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 increases, reducing the variance among tussocks. The model (using the standard parameterization Table 1) was able to simulate the same exponential decline in variability as the proportion of the biomass consumed augmented (Figure 3.6b). 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) (Figure 3.7). NDVI, an independent estimate of light interception and hence carbon gains showed also a positive relationship with tussock vitality (Figure 3.7).
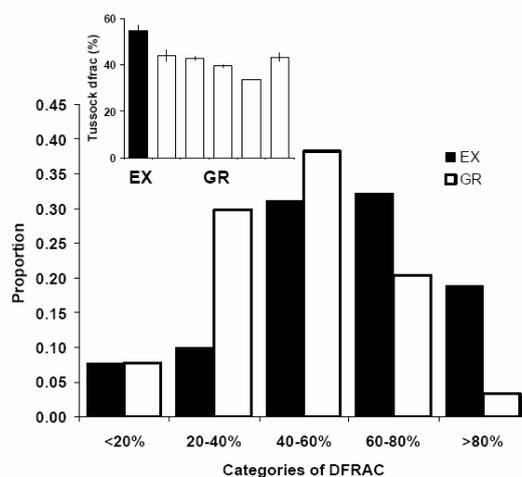
Fig. 3.4: Relative frequency of *F. pallescens* tussocks corresponding to different structural classes
Shown are the tussock distributions (proportions) over dfrac (proportion of dead biomass over total biomass) for grazed (GR, n=90) and ungrazed (exclosures, EX, n=480) areas. The inset graph showed the average dfrac (as %) for ungrazed (exclosures, EX) and 5 different grazed paddocks (GR). The lines on top of the bars correspond to the standard errors.
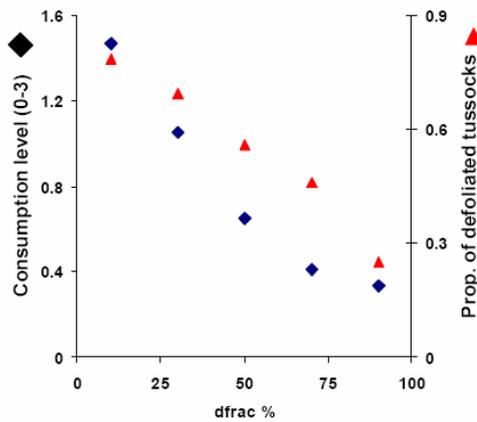
Fig. 3.5: Average consumption level and proportion of tussocks defoliated.
Consumption level: (0= ungrazed, 3 = all the tillers defoliated) for different classes of percentage of dead biomass per tussock (*dfrac*).
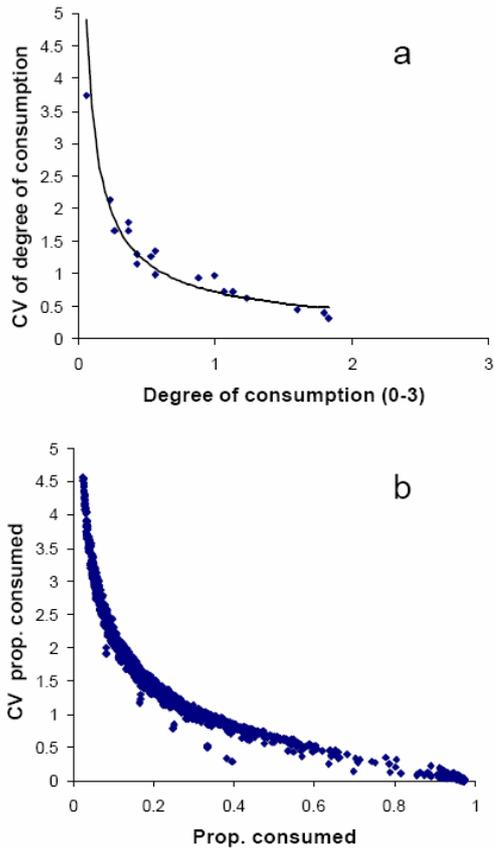
Fig. 3.6: Relationship between the degree of consumption per paddock and the coefficient of variation of the degree of consumption among tussocks
CV: (STD/mean) ; (a). field measurements, (b) model runs for stocking densities ranging from 0.3 to 1.5 sheep/ha.
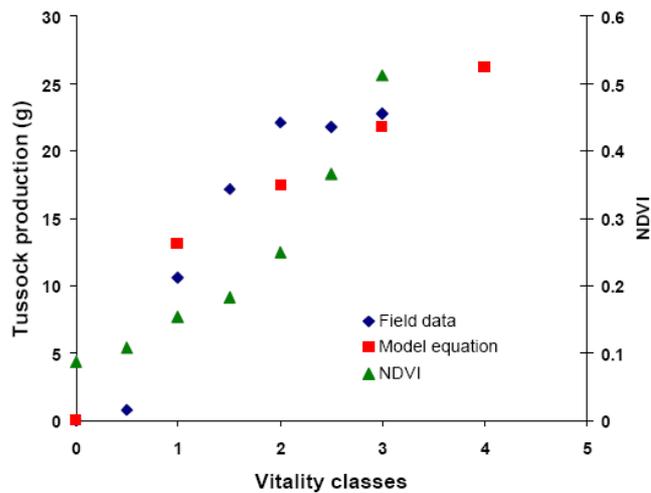
Fig. 3.7: Average tussock production per vitality class.
Average tussock production per vitality class was derived from model equation (squares) and field data (peak biomass, diamonds) (n = 570). Triangles represent the NDVI recorded on 216 tussocks. Vitality was assessed visually.

3.4.2 Sensitivity analysis

Only six of the 14 groups of parameters have a relative mean effect on the output variables higher than 10%. The model was particularly sensitive to those parameters related to water inputs (Figure 3.8). The relative mean effect (RME) of the fraction of the precipitation available for plants (WI.1) on tussock density was 0.38. The rain factor parameter WI.1 (parameter group 1) represents the proportion of the incoming water transpired by the vegetation. Our estimates (0.57, Table 1) 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. There is no data available to support directly the values used, but data on root lateral spread of Patagonian 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 of *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* ($\left|\text{RME}\right| > 0.23$) and a lower but strong impact ($\left|\text{RME}\right| = 0.10$) 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 (Figure 3.8).

59
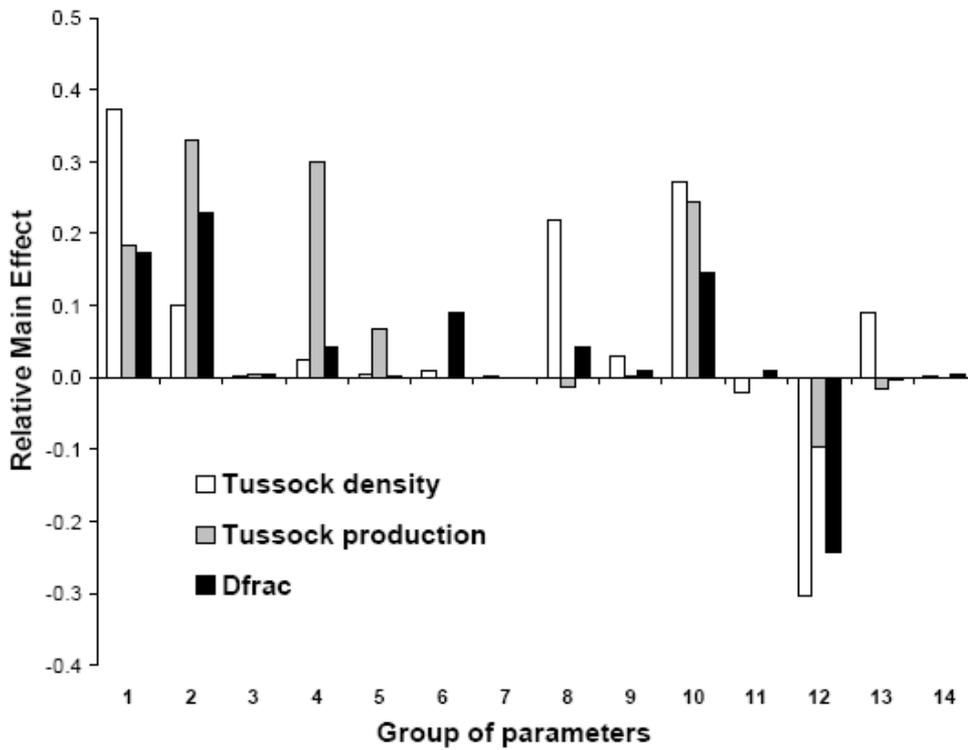
Fig. 3.8: Relative main effect of 14 groups of parameters on three output variables of the model.
Tussock density, tussock production and the fraction of dead biomass per tussock (*dfrac*).
Parameter groups are defined in Tab. 3.1.

Tab. 3.1: List of the parameters of the *COIRON* model.

Parameters are grouped according to the processes they influence directly. The column value corresponds to the most reasonable values derived from the literature and from expert opinion. The last two columns correspond to the estimated upper and lower boundary for each parameter. These values were used in the sensitivity analysis.

Parameters,	Units	Processes (bold) and explanation of parameters	Typical value	Parameter group for sensitivity analysis	Lower level	Upper level
		Water Inputs (WI)				
WI.1	-	Fraction of annual global rainfall which represents an input to plant available soil water w	0.57	1. W Inputs	0.40	0.74
		Water Redistribution (WR)				
WR.1	water (mm / cm²)	Fixed amount of lateral soil water loss of a empty cell or a dead tussock due to water uptake from a neighbouring live tussock cell	5	2. W Dis1	1	20
WR.2	water (mm / cm²)	For empty cells in "large bare patches" only; fixed amount of soil water loss, for each empty neighbouring cell unaffected by lateral roots	20	3. W Dis2	10	30
		Plant growth (PG)				
PG.1	green biomass / cell area · year (g DM / 0.09 m² y)	Annual net primary production (dry matter, DM) of a live tussock with vitality =1 ($vit = 1$) and year	150	4. Prod 1	105	195
PG.2	green biomass / cell area · year (g DM / 0.09 m² y)	Annual production increment of gb per unit increment of vitality > 1 and time step t	50	4. Prod 1	35	65
PG.3	water (mm / cm²)	Constant of Michaelis-Menten equation for plant production: Indicates soil water status which enables half of maximum plant production (equation 1)	55	5. Prod 2	38	72
PG.4	%	Fixed % annual rate of senescence of green biomass left over after grazing	60	6. Sen	40	80
PG.5	%	Fixed % annual rate of littering of dead biomass both from live and dead tussocks	40	6. Sen	20	60
		Grazing (GR)				
GR.1	Sheep / area (n / ha)	Stocking density: number of sheep (n) per hectare; experimental parameter	0.5	Experiment	0.0	2.0
GR.2	green biomass / day (g DM / d)	Daily (d) forage need in green biomass (DM) per head	1000	Fixed	fix	fix
GR.3	-	Fraction of $dfrac$, at which tussock is completely rejected from livestock. The parameter is related to the calculation of maximum defoliation severity ($dsmax$) as a function of a tussocks relative amount of dead biomass ($dfrac$).	0.95	7. Def max	0.95	0.99
GR.4	-	Shape parameter of equation (19): Determines shape of defoliation severity ds as a function of $dfrac$; Defines impact of increasing $dfrac$ on ds	0.5	7. Def max	0.3	0.7
GR.5$_i$	-	Seasonal shift of the effect of tussock structure $dfrac$ on grazing acceptance	GR.5$_a$ = 1.0	Fixed	fix	fix

		probability *gprob;* Alters the probability of a tussock to be accepted for grazing, which is a function of *dfrac* and grazing season (eqn. 22); *GR.5* = 1.0 for continuous grazing (a); 1.5 for spring grazing (b); 0.6 for summer and autumn grazing (c); 0.3 for winter grazing (d).	$GR.5_b = 1.5$ $GR.5_c = 0.6$ $GR.5_d = 0.3$			

Colonization (CO)

CO.1	water (mm / cm²)	Minimum soil water for emergence	200	8. Col W	140	260
CO.2	-	Probability (prob.) of emergence at cover > 40 % if soil water w > CO.1	0.3	8. Col W	0.1	0.5
CO.3	water (mm / cm²)	Soil water for survival of first year seedlings	170	8. Col W	119	221
CO.4	water (mm / cm²)	Soil water for survival of second year seedlings	140	8. Col W	98	182
CO.5	%	Minimum *F. pallescens* cover for maximum emergence and survival probabilities.	40	9. Col D	20	60
CO.6	-	Survival prob. for seedling 1st and 2nd year if soil water w > CO.3 and w > CO.4 respectively	0.9	9. Col D	0.7	0.99

Vitality dynamics (VD)

Water thresholds

VD.1	water (mm / cm²)	w threshold for transition of $vit = 1 \rightarrow vit = 2$	200	10. Vit Wat	140	260
VD.2	water (mm / cm²)	w threshold for transition of $vit = 2 \rightarrow vit = 3$ or $vit\ 3 \rightarrow vit = 4$	250	10. Vit Wat	175	325
VD.3	water (mm / cm²)	w threshold for transition of $vit = 4 \rightarrow vit = 3$	260	10. Vit Wat	182	338
VD.4	water (mm / cm²)	w threshold for transition of $vit = 3 \rightarrow vit = 2$ or $vit = 2 \rightarrow vit = 1$	200	10. Vit Wat	140	260

Defoliation severity threshold

VD.5	-	Minimum relative defoliation severity threshold for tussock transition vit n $\rightarrow$ vit n-1	0.5	11. Vit Def	0.3	0.7
VD.6	-	Prob. of grazing induced vitality transition	0.8	11. Vit Def	0.6	0.99

Mortality (MO)

MO.1	water (mm / cm²)	water threshold 1: combined with *MO.3*	180	12. Mort wat	126	234
MO.2	water (mm / cm²)	water threshold 2: combined with *MO.4*	200	12. Mort wat	140	260
MO.3	-	prob. of mortality if w < *MO.1*	0.2	12. Mort wat	0.05	0.4
MO.4	-	prob. of mortality if *MO.1* <= w < *MO.2*	0.1	12. Mort wat	0.01	0.2
MO.5	-	Relative defoliation severity (*ds*) threshold for grazing induced mortality (only for $vit = 1$): combined with *MO.6*	0.6	13. Mort def	0.4	0.99
MO.6	-	prob. of mortality if defoliation severity > *MO.5*	0.05	13. Mort def	0.01	0.1

Primary forage (PF)

PF.1	%	Minimum relative amount forage provided by other items	5	14. Prim.for	0	5
PF.2	%	Increment in per cent for *PF.1* per % *cov* increment of *F. pallescens*	0.83	14. Prim.for	0	0.83

3.4.3 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}) (Figure 3.9a). Tussock green biomass simulated by the model laid within the range of observed average values per ranch (Figure 3.9b). The simulated green biomass was slightly lower than the values measured in the field data. Simulated plots were much less variable than the sites surveyed. Observed biomass per tussock was more variable among plots than the simulated values. The indirect approach used to generate field estimates may be responsible of their high spatial variability. Except for the heavily grazed paddock, simulated and observed values of *dfrac* (the proportion of standing dead biomass per tussock) were similar, ranging between 0.30 and 0.60 (Figure 3.9c). As we observed in the field, grazing increased the relative abundance of tussock with low *dfrac*.
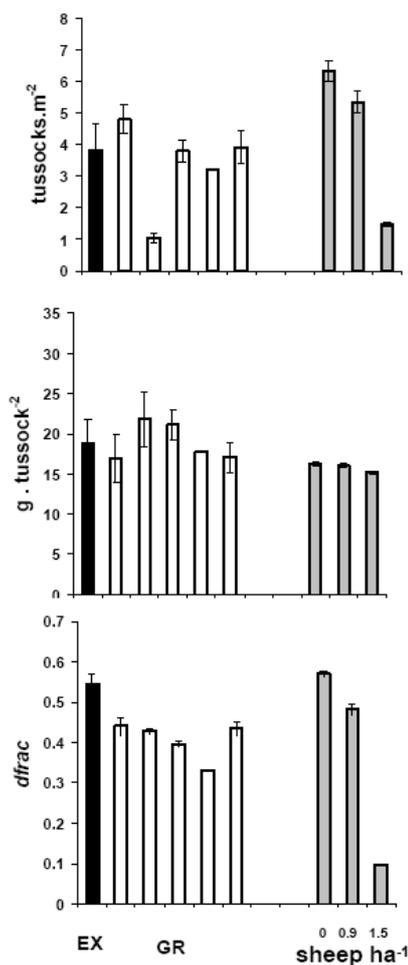
Fig. 3.9: Field and simulated data for Tussock density, tussock green biomass and the fraction of dead biomass per tussock.

Field data in 6 sites corresponded 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 3 stocking densities (0, 0.9 and 1.5 sheep.ha^{-1}).The lines on top of the bars correspond to the standard error.

3.4.4 Simulation experiments

Long term simulation of the dynamics of the *Festuca pallescens* steppe showed that the structural and functional attributes simulated are highly variable in time regardless of the grazing management or the stock density (Figure 3.10). Grazing generate a reduction in tussock density (Figure 3.10a). Under non-grazing conditions the 10-year mean tussock density varied between 4 and 9 tussocks m^{-2} (Figure 3.10a). There was a clear delayed effect of grazing on tussock density (Figure 3.10a). After 10 years of grazing, even under the high selectivity regime (continuous grazing), the differences among stock density scenarios were small.). The proportion of grazed tussocks varied through time for a particular grazing scenario.The magnitude of the differences differed through time and can become minimum after a sequence of good years (decades 6 and 7, Figure 3.10a, b). For moderate stocking densities, it ranged between 22 and 44%. As grazing 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 (Figure 3.10b). Grazing modified the structure of the steppe by reducing the amount of dead material per tussock (*dfrac*) and the spatial variability of this attribute.
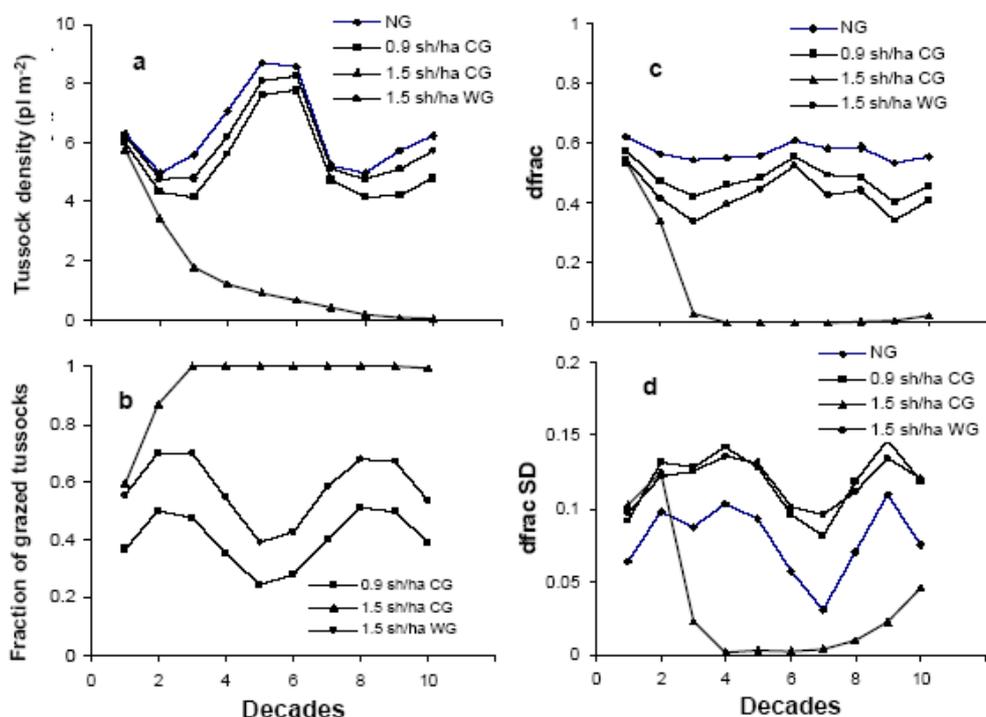
Fig. 3.10: Ten-year average values of simulated tussock density.
(a), fraction of grazed tussock per grid (b), proportion of dead biomass per tussock (*dfrac*)(c) and standard deviation of *dfrac* (d). Simulations were performed for the ungrazed (NG) and continuous grazing (CG) conditions, at 3 different stock densities, 0, 0.9 and 1.5 sheep.ha^{-1} and for winter grazing (WG) at 1.5 sheep.ha^{-1}. The climate scenario was the control.
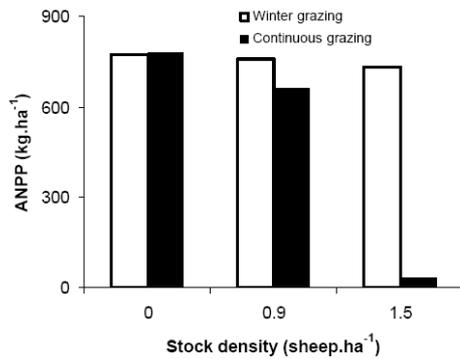
Fig. 3.11: Average Aboveground Net Primary Production for different stocking densities and grazing systems.
ANPP is shown for the last decade of the simulation for the grazing scenarios continuos vs. winter grazing. The climate scenario was the control.
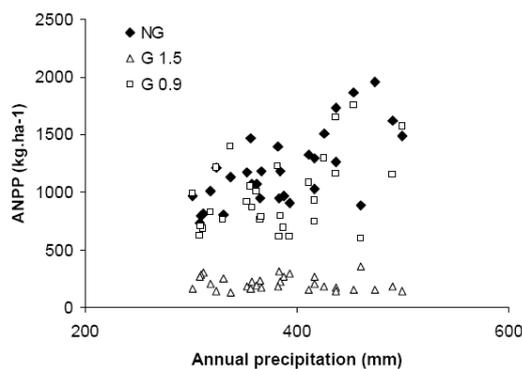
Fig. 3.12: Simulated Aboveground Net Primary Production as a function of current year precipitation.
ANPP is shown for different stocking densities (NG: ungrazed, 0.9 and 1.5 sheep.ha$^{-1)}$.

The proportion of dead biomass per tussock (*dfrac*) was less variable among years than tussock density, ranging from 0.53 and 0.62 (Figure 3.10c). The spatial variability of *dfrac* (standard deviation) varied between 0.03 and 0.11 (Figure 3.10d). The temporal CV of the average potential productivity (vitality) of the tussocks was 11% (data not shown

The reduction in tussock density by grazing (Figure 3.10a) resulted in a decline in *ANPP* (Figure 11). Tussock density explained 82% of the inter-annual variability in aboveground net primary production (*ANPP*). *ANPP* showed a temporal coefficient of variation of 23% (data not shown) with extremes values of 1561 and 456 kg.ha^{-1}. Under non-grazing conditions the precipitation use efficiency (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 precipitation use efficiency (PUE) was 82% lower than the values for non-grazed runs (0.055 g.m^{-2}.mm^{-1}). Grazing reduced also the

65
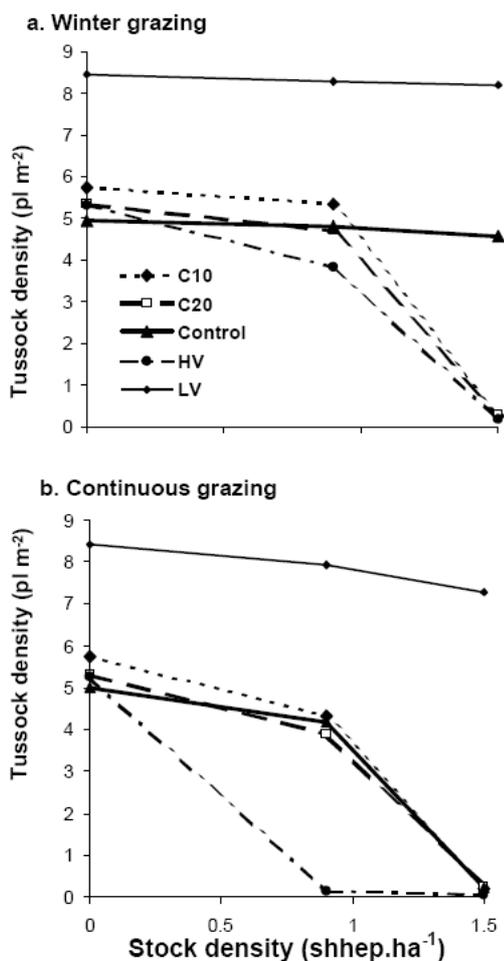
Fig. 3.13: Simulated tussock density as a function of the stocking density.
Shown are two grazing systems: (a) winter grazing, and (b) continuous grazing for five climate scenarios: control, 10 year period cycle (C10), 20 year period cycle (C20), low interannual variability (LV) and high interannual variability (HV).

sensitivity of *ANPP* to inter-annual changes in precipitation (Figure 3.12). The slope of the relationship between simulated *ANPP* and 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 current year precipitation under non-grazing conditions (Figure 3.12). The precipitation from the two previous years accounted for a substantial portion of the unexplained variance (an additional 19%). For high grazing pressures (1.5 sheep.ha^{-1}) the system became insensitive to changes in annual precipitation (Figure 3.12). The variability and autocorrelation of the precipitation data had a significant 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 (Figure 3.13). Tussock density was higher and less sensitive to the grazing regime under a low-variability scenario (Figure 3.13 a,b). The autocorrelation of the precipitation data increased the sensitivity of the system to high stock densities under winter grazing (Figure 3.13b).

3.5 DISCUSSION

Long-term dynamic of semiarid plant communities are often inherently complex because they may exhibit non-equilibrium dynamics where nonlinear processes (Westoby et al. 1989) and stochastic event-driven behavior (Walker 1993; Wiegand et al. 1995; Jeltsch et al. 1999) are involved. Our model results confirmed these findings. Moreover, we found that the structure of the *Festuca* steppe may be highly variable in time. This characteristic of the system makes difficult the evaluation of model performance using observed 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. An additional difficulty arises because temporal and spatial scales in semiarid plant communities 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. Similarly, driving events such as large recruitment events may change the structure and composition of the plant community rapidly but once large cohorts of non-palatable plants are established they may persist for decades (Wiegand and Milton 1996).

3.5.1 Our modelling approach

Models with applied orientation aimed to assess the long-term dynamics of semiarid plant communities and the impact of grazing need to include a considerable degree of detail to be meaningful. Although spatially explicit and individual-based simulation models are ideally suited to include the level of detail necessary to respond to these questions, they have been heavily criticized (DeAngelis and Mooij 2003; Wiegand et al. 2003). The main reasons are an inherent lack and uncertainty of data, the complexity of realistic simulation models which hinders a thorough model understanding and analysis, problems of error propagation, and the problem that it is because it is often not clear a priori which mechanistic details are relevant and which details can be safely abstracted. Appropriate methods to overcome these difficulties have only been recently developed (e.g., Wiegand et al. 2003, 2004a). In model construction and analysis we followed such a method, termed pattern-oriented modelling (Grimm et al. 1996; Wiegand et al. 2003, 2004a), which enabled us to handle and analyse our relatively complex simulation model, and to include many kinds of information.

The first essentially ingredient of our approach was that we constructed our model on a spatial scale (i.e., the scale of individual tufts) which facilitated direct and easy comparison with field observations. This had two advantages: first, because the unit of the model was also the unit of observation we could transform our knowledge directly as rules into the model, and second, we could basically measure the same variable we measured in the field. The second essentially ingredient of our approach was that we compared the model against multiple field data. This is especially important to assure that the model performance is reasonable. While it might be relatively simple to reproduce one feature of a system (e.g., tussock density) with a number of substantially different models versions, the simultaneous agreement with multiple data each describing a different key-features of the system is by far non-trivial (e.g., Kendall et al. 1999; Railsback and Harvey 2002; Wiegand et al. 2003, 2004 a). Because the initial conditions and the variability of the driving forces of the *Festuca* system (stock density, grazing seasonality, etc.) are difficult to access and because the simulated structure of the *Festuca* 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 (Figure 3.9) 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 (Figure 3.6). The changes in tussock density and primary production associated with grazing matched the trends reported in the literature (León and Aguiar, 1985, Aguiar et al. 1996). The third essential element of our approach was performance of a sensitivity analysis to find critical model processes and parameters which deserve 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 relative main effect) to changes in the parameter values within a plausible range (Figure 3.8). 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 Yadhjian and Sala 2002) We found that the behaviour of our model was surprisingly stable and even the initial parameter estimates yielded reasonable model behaviour. This shows that our model indeed captures "the essence" of the dynamics of the *Festuca* steppe in a robust way. Once gained confidence in the model, we performed simulation experiments to address our specific questions. The approach taken in this study can be widely applied for investigating long-term rangeland dynamics and for assessing implications of different management regimes under unpredictable rainfall.

Despite its ability to reproduce observed field patterns, the model has some shortcomings. One of them is that it does not consider the dynamics of shrub encroachment described for the area (León and Aguiar 1985, Bertiller et al. 1995). The model only simulates the early states of degradation by grazing, which can be observed in the field. An additional shortcoming is the absence of explicit simulation of erosion processes. Erosion alters water redistribution and dynamcis, and it also constrains recruitment processes (Defossé et al. 1997a,b). To investigating 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.

3.5.2 The long-term dynamics of the *Festuca* steppe

The long-term simulations of the dynamics of the *Festuca* grass steppe highlighted some interesting characteristics of the systems that are not 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 (Figure 3.10). The temporal variability would be associated with an important autocorrelation of the output variables. This autocorrelation generates a memory in the system that may last many years. Different variables showed different memories: tussock density > *dfrac* > *fraction of tussock grazed*. Such differences among ecosystem attributes are critical in evaluating the response of the system to management practices. Assessing the status of a plot based on the density or cover of *Festuca* would be, then, extremely difficult. The inter-annual variability of tussock density was higher than the variability among some of the grazing management and stock densities analyzed (Figure 3.10). 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. (2000) 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 (Figure 3.12). This is because the memory of the system determines an important effect of the distribution of "good" and "bad" years on tussock density dynamics and hence on *ANPP* interannual changes (Figure 3.13). 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 mean annual precipitation. Interestingly, the response of the system to the inter-annual pattern of precipitation variability changes under different management scenarios.

A highly degraded system can not respond to inter-annual changes in precipitation (Figure 3.12). In such conditions, most of the incoming water is lost as deep percolation or runoff. An increase in runoff may generate serious erosion problem 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 Houreou 1984, Prince et al.1998) a degradation of the system lead to an important reduction of precipitation use efficiency (PUE). O´Connor et al. (2001) observed a reduction in PUE in experimental plots as degradation increases in Southafrican grasslands. Such reduction 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 become unresponsive to annual changes in precipitation. The slope of the *ANPP*-PPT relationship has been proposed as a descriptor of PUE and hence of desertification (Veron et al. submitted, Paruelo et al. in press). Our simulation results showed that long term grazing reduced significantly the sensitivity of *ANPP* to inter-annual changes in PPT (Figure 3.12).

Stock density was the most important factor to account for differences in tussock density, *ANPP* and the fraction of standing dead material of a tussock among simulations (Figure 3.9). The total amount of biomass removed decreased the productivity of the steppe because its impact on tussock potential production ("vitality"). The magnitude of this change varied for different grazing management layout. Those that increase the selectivity of grazers generated more differences in tussock density and *ANPP* between non-grazed and grazed treatments (Figure 3.11). The response of tussock density and *ANPP* to stock density and grazing seasonality was non-linear. Such kind of response, added to the lag in the response of the system to management practices and to the interactions with climate, turn highly risky the definition of optimum stock densities and grazing systems on the base of "trial and error" approaches.

3.5.3 Implications for management

The model developed provide an important tool to explore the long term behaviour 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 landuse 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.).

3.6 LITERATURE CHAPTER 3

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CHAPTER 4: BIOLOGICAL PROCESSES AFFECTING THE SIMULATION RESULTS: CALIBRATION AND SENSITIVITY ANALYSIS

4.1 INTRODUCTION

The model presented in Chapters 2 and 3 includes a high number of independent parameters (30). Most of them cannot be parameterised directly, due to the lack of field data. Additionally, the empirical estimation of parameters proves to be very difficult because they depend on a detailed way of unknown history of grazing and climate. Direct field estimates would require intense long-term field studies. It was evident from the beginning of the project, that the model cannot be parameterised directly from field estimates. Therefore I used and further developed an approach of model calibration and validation, which does not require direct empirical estimates of model parameters, but uses field data at higher aggregated population levels as they are usually provided by empirical studies, for indirect parameter estimation.

This method can be called 'indirect pattern oriented modelling', because it indirectly derives parameter estimates for processes operating at smaller scales from comparison with patterns observed at larger scales. The method is a further development of the 'pattern oriented modelling approach' developed by Grimm (1994), Grimm et al. (1996), Grimm (1999), Grimm (2002), Wiegand et al. (2003), Wiegand et al. (2004b), and Grimm and Railsback (2005) and was applied e.g., by Jeltsch et al. (1996); Wiegand et al. (1998), Jeltsch et al. (1999), and Wiegand et al. (2004a).

Uncertain or unknown parameters at the individual level are estimated indirectly by using observed patterns on a higher aggregated level (e.g. the vegetation cover or the observed dead biomass fraction). The basic idea of this approach is to select a high number of model parameterisations (several thousands) which are well dispersed in the entire plausible parameter space and to apply the model for all of these parameterisations. The calibration procedure basically consists in comparing several model outputs (= patterns) with field data. Some statistical criteria are necessary to prove that the simulated pattern and the observed pattern agree. All parameterisations which do not produce agreement between observed and simulated patterns are rejected. Parameterisations which produce agreement between all observed and simulated patterns are accepted because they generated model dynamics which are in agreement with the data about the system. The variation within the accepted model parameterisations reflects the remaining uncertainty about the system.

Additionally to model parameterisation my basic interest is (1) to investigate in more detail the contribution of precipitation and grazing to different biological processes (e.g. colonisation, growth or mortality), and (2) how important these processes are in determining the resulting observable empirical data at the higher aggregated population dynamics or community levels. If I understand the relationship between these different levels, I may gradually advance the understanding about the combined effect of anthropogenic and highly variable natural factors such as precipitation in semi-arid regions.

Detailed data about a certain ecosystem is often limited and in most cases very scarce. This is one reason to use simulation models when facing long-term questions. One major challenge in ecological modelling is to bridge the gap between theoretical ecology and empirical ecology (Bolker et al. 2003). Many ecological models make useful theoretical considerations, but they are weakly related to 'real' systems (Wiegand et al. 2003). Top down approaches, which do not use real systems as starting points, use often abstract variables or operate at scales which cannot be directly compared with field observations. The main challenge I am going to face in this chapter is the parameterisation and analysis of a medium complex simulation model with 30 free parameters, which are based only on a small empirical data set.

The main aims of this chapter are:

i) to calibrate and validate the simulation model presented in Chapter 2 and Chapter 3 by means of a multi-criterial, hierarchical indirect pattern oriented approach based on limited empirical data (calibration and validation).

ii) to analyse the relative importance of the independent parameters and processes with respect to the key variables of the *Festuca* steppe (sensitivity analysis).

iii) to discuss the biological and ecological implications for the *Festuca* steppe and the general implications which result out of the sensitivity analysis.

The presented calibration and validation protocol is based on the methods of the multi-criterial pattern oriented model calibration presented by Wiegand et al. (2003), and Wiegand et al. (2004b) and is further developed in this Chapter 4. Due to the complexity of the actual model with 30 independent parameters, the scarcity of available field data, and the strong stochastic behaviour of the model induced by the stochastic precipitation, I improved the indirect pattern oriented calibration by using a stepwise approach, which includes four steps of calibration and is combined with one step of validation. This stepwise approach was necessary to account for the stochastic behaviour of the model due to the stochastic precipitation. After the first calibration step I introduce an additional validation with field data that were not used before for calibration. The entire calibration procedure yields a set of model parameterisations which produced agreement between observed and simulated patterns. The set of accepted parameterisations (= calibrated simulation model) can be used for systematic experiments e.g. of varying grazing effects, different climates etc. The methods used during model calibration and sensitivity analysis are similar to those proposed by Saltelli et al. (2000).

4.2 MATERIAL AND METHODS

4.2.1 General strategy: Parameter estimation and uncertainty reduction

The methodological section contains the following parts: first, it provides a short summary of the approach's overall philosophy and a general description how model calibration is performed. Second, I will provide an overview about the detailed procedure of model calibration. The detailed explanation contains the following parts: (i) it explains how the available field data are used for calibration, and (ii) it describes how field data are processed to be used for calibration. Third, the steps of model calibration and validation are explained as well as the methods used for sensitivity analysis and the evaluation of the relative importance of one parameter for the outcome of the simulation model.

General strategy. — I face the following challenge: **a complex simulation model has to be parameterised with a high number of uncertain parameters, for which field estimations do not exist**. I use a multi-criterial analysis of empirical data at the higher aggregated population dynamics level to derive indirect estimations of those parameters driving the biological processes which finally generate the observed outcome on the population and community level. The empirical data are a snap shot of reality (Jeltsch et al. 1999), since long-term monitoring is still lacking. A sophisticated and complex procedure is necessary because most of the biological processes are influenced by the two drivers of the system we are interested in: stochastic precipitation and grazing (see Chapter 2).

The fact that precipitation, which is a driver on the largest spatial scale, also acts on the individual level of each tussock plant, makes it necessary to build a model on the individual tuft level. An approach like this is called a cross-scaling approach (Rietkerk et al. 2002).

Pattern-oriented modelling approach. — The approach used for model calibration, validation, and sensitivity analysis, follows in general the concept of the 'Pattern oriented modelling' (Grimm

1994, Grimm et al. 1996). For the purpose of model calibration this approach actually passes a significant further development (Wiegand et al. 2003, Wiegand et al. 2004b). This further development of the pattern oriented modelling with the purpose of model calibration can be called **'inverse/indirect pattern oriented model calibration'**. The main aim is to gain confidence into the biological plausibility of the simulation model and to reduce the parameter uncertainty substantially (Clark 2003, Higgins et al. 2003, Wiegand et al. 2004b) by a calibration of all parameters during one multi-criterial calibration step.

A multi-criterial calibration means that different types of field data with varying quality are used together to exclude biologically unrealistic model parameterisations. It allows combining data from different hierarchical scales (e.g., community, population level and individual level if available) in a simulation model. Data from higher hierarchical levels are used to understand which processes or factors on a lower hierarchical level determine the aggregated results we observe at the higher level, e.g. the overall cover at the community level. It is a powerful instrument to reduce parameter uncertainty for simulation models.

Another subsequent question to this model is, if the inverse pattern oriented method mediates between a medium complex simulation model with approx. 30 independent parameters and a scarce amount of available field data. A special feature of this approach in this respect is that it can also use data of weaker quality (i.e., data with larger uncertainties). Such data are used to exclude extreme improbable model behaviour since they indicate at least coarsely the order of magnitude where the model output should range. While one or two of such 'weak patterns' may not transport much information, several weak patterns together can reduce the uncertainty considerably because each of the weak patterns eliminates parameterisations which produce extremely wrong model behaviour.

The main aspect of this approach is the transformation of different variables being sampled in the field into **observed patterns** (as general abbreviation: **Pi**, **Pj**, **Pk**, e.g. **Pi** = **P1** (*tussock density* of *F. pallescens*), **Pj** = **P2** (*mean tussock biomass*), that provide the criteria for the selection of model parameterisations using the simulation results. If several variables are available, several patterns can be derived from the variables. In this case I combine them to a **pattern filter combination (Pj + Pk + Pl**, e.g. **P1** (*tussock density*) + **P2** (*mean tussock biomass*) + **P3** (*mean tussock annual productivity*: **P1 P2 P3**). I use these filter combinations (general syntax: **Pi Pj Pk**) to judge the similarity of the output of the simulation model with the field data. Combining different patterns to calibrate a model is a type of multi-criterial assessment (Reynolds and Ford 1999). The systematic and hierarchical comparison of the pattern with the model output, allows me to reject those parameterisations that lead to unrealistic results. Thus, I am able to reduce the parameter uncertainty in a substantial way.

Hierarchical comparison of the pattern means, that first, one certain pattern which is assumed to be most essential, e. g. tussock density of *F. pallescens* (**P1**), has to be fulfilled by the output of the actually compared model parameterisation. During the following steps of comparison additional patterns (**P2** and so on) are applied systematically to find those model parameterisations which fulfil the imposed filter combination. Each simulated pattern is compared with the observed pattern using a specific test statistic, which decides if both pattern are significantly different or not, which in general has to be developed newly for each step of comparison.

This approach also requires testing the different confidence intervals of the observed patterns which are used for model calibration during the development of specific test statistics. This involves especially the question how much uncertainty can I tolerate in particular field data to still achieve realistic results. Additionally I test which filter combination is necessary and sufficient to obtain a satisfying model calibration. This includes the question, how much data (or pattern) are needed to calibrate the model sufficiently. After this analysis, I select the appropriate filter combination which provides the model parameterisations for further sensitivity analysis and simulation experiments.

The 'indirect/inverse pattern oriented model calibration' requires the following steps:

- The characterisation of the available field data and evaluation of their uncertainty
- The transformation of field data into 'patterns' for the comparison with field data
- The definition of a test statistic and investigating the effect of its tolerance limits for the multi-criterial pattern fulfilment
- The definition of the range within uncertain simulation model parameters are varied and the generation of the tested model parameterisations
- The Calibration: multi-criterial comparison of the observed patterns with simulated patterns.
- Sensitivity analysis of the calibrated model: exploration of the parameter space remaining after the Calibration.
- Additional validation of the calibrated model parameterisations with independent data is performed (Rykiel 1996, Higgins et al. 2001, Gardner and Urban 2003), if independent data are available.

This seven steps were performed for four different calibration scenarios of model parameterisations in different levels of detail. The different investigated scenarios were necessary to in- or exclude grazing as a parameter into the calibration (scenarios **NG** (No grazing included) or **G** (Grazing included, see Tab. 4.3)), and additionally to vary the parameters independently (index i, e.g. G_i) or in groups, to so called driver-related processes (see Tab. 2.3). Each driver-related process combines all parameters, which refer to a specific biological process (e.g. Colonization) and to one driver (precipitation or grazing). The grouped calibration scenarios were analysed up to the step of sensitivity analysis. Both independent calibration scenarios (NG_i, G_i) were analysed and calibrated until the remaining parameterisations were considered as useful for simulation experiments.

This general calibration scheme was later modified, which will be described in detail during the following sections. Additional calibration steps were necessary due to the inclusion of the stochastic driver precipitation. During the first calibration step (see below) only one climate was run for each parameterisation. For the calibrated parameterisations after the first step 100 repetitions with different climate scenarios were run to test the remaining parameterisations in detail.

4.2.2 Detailed Approach: Indirect pattern oriented process analysis

The detailed stepwise calibration approach is illustrated in Fig. 4.1. I modify the general strategy for the 'indirect pattern oriented model calibration' described in Chapter 4.2.1, due to the fact, that the *Festuca* steppe model has 30 free parameters, which is more than e.g., in Wiegand et al. (2003) and Wiegand et al. (2004b). On the other hand, I dispose over data for more qualitatively different response variables (pattern). This enables me to use some field data for calibration and others for validation. Thus, I can use additional options to control the model against independent response variables that were not 'trained' before the calibration (Gardner and Urban 2003). I use calibration in the sense of testing one parameterisation against several patterns with specific confidences intervals (tolerance limits) which were calculated from empirical data. If the output of the model using a given parameterisation produces results lying simultaneously within the ranges given by the confidence intervals of all patterns, the parameterisation is accepted and I assume that it has the potential to mimic the observed system dynamics.

Detailed reasoning for the several calibration steps. — The calibration and the sensitivity analysis were performed in several steps (see list below). **A first step** (Step 4 of the list below) **of model calibration** sorted out all those model parameterisations showing system dynamics, which

were highly improbable to be biologically realistic, e.g. grasses died out in unrealistic short time horizons or grasses colonised the grid completely. Next, additional response variables for which field estimates were available were included (Step 6). This was a second selective criterion. These additionally variables were used during the 2nd calibration step both first for validation of the calibrated parameterisation out of the 1st calibration step, and then used for the 2nd calibration step. Only if an accepted parameterisation passed first this validation after comparison against the new included independent response variables, it was considered for further calibration steps. During the first two steps of calibration I performed only one repetition with one stochastic climate time series per parameterisation. I assumed that a parameterisation, which produced extremely improbable model behaviour for one stochastic climate will do so also for the most of the other stochastic climates. Additionally, the selection criteria during the first steps of calibration were weaker than during the following steps. This procedure was necessary due to the high number of free parameters. **The third and fourth steps of Calibration** (Step 7 and 8) provided the 'fine-tuning' of Calibration and considered repetitions of different stochastic rainfall time series. Thus, with the parameterisations validated during step 1 and 2 of calibration I performed 100 repetitions with different stochastic climates but no grazing and contrasted the results with a set of response variables.

Evaluation of 3rd calibration step simulations. — For the evaluation of model parameterisations during the 2nd step of calibration I used an aggregated criterion for the selection of the parameterisation. It counted how many pattern were fulfilled at least in 80 out of 100 repetitions with different precipitation scenarios. The output of each simulation was compared to a set of patterns. For these patterns, stricter confidence intervals than during the first calibration step were used to fulfil the both. Additionally, the simulation results were evaluated against all patterns at different time steps (see Tab. 4.4), and I counted the number of repetitions (climate scenarios) leading to pattern fulfilment for each model parameterisation. So as a response I received a percentage of positive fulfilment for each pattern per model parameterisation, e.g. 17% from for the pattern tussock density, plus 23 % for the pattern annual net primary production etc. I demanded a threshold of 80% for the fulfilment of each pattern to accept the model parameterisation, and a threshold of 90% of positive fulfilment for all evaluated patterns.

Fourth step of calibration. — Only if the evaluated results for the 100 repetitions of one model parameterisation exceeded the threshold so that they fulfil 90% of the pattern/time step evaluation at 80% or higher each, they passed over to the next step. The 4th step of Calibration included 100 climate repetitions per parameterisation and it included the whole range of stocking rates. I defined a criterion which sorted out model parameterisations leading to unrealistic stable results under heavy grazing. If this criterion was passed, the remaining parameterisations were accepted as fully accepted and were used for the subsequent simulation experiments. This method cannot exclude the possibility of false negative evaluations completely during the calibration step. But this is not problematic because I can assume that the false negative evaluations will occur at random and I assure systematic sampling of the parameter space.

Calibration scenarios. — As mentioned in chapter 4.2.1, I chose four groups of calibration scenarios. One group consisted of a calibration with grazing (**G**) and one without grazing (**NG**). This approach was not only necessary, because grazing parameters could only be calibrated varying those parameters, but it was also necessary to calibrate the model without grazing, because a feedback between grazing and non-grazing parameters could not be excluded a priori.

The second division I performed was the comparison of the calibrations of independent and grouped parameters (e.g. **NG$_i$** and **NG$_g$**). The idea of this approach is the following: independent calibration of each parameter is the most accurate approach, because one can test the sensitivity for each parameter individually. The disadvantage of this approach was that I had to test a large amount of

parameterisations due to the high degree of freedom and the high probability was high to test biological unrealistic parameter combinations. Therefore I grouped different parameters to parameter groups (driver-related processes, Tab. 2.3), which represent sub-processes mostly driven by one of the two exogenous drivers. Consequently, I grouped mortality parameters that are related to the soil water status and those parameters related to the grazing impact. The justification for this calibration procedure was, that it was biologically plausible to assume, that if one parameter of this group changed in one direction, it is probable that the other parameters also would change into this direction For example, if the water threshold for the first year seedlings increased, the water threshold for the second year seedling increased, too. It would be biologically implausible to generate parameterisations, where young seedlings survived better in drier conditions than the older saplings. The advantage of the approach is a considerable reduction of the dimensions of the parameter space, which reduced the simulation effort. The disadvantages are the additional assumptions on parameter grouping. One aim of this chapter was to compare both types of calibration to find the systematic effects concerning their results and to find out if different interpretations result out of these different approaches.

The comparison of the simulation model with field data consisted of following steps:

1. The characterisation of the available field data, the evaluation of uncertainty.
2. The transformation of field data into 'patterns' for the comparison with field data, and the definition of test statistics and of statistical confidence intervals for the multi-criterial pattern fulfilment.
3. The definition of the range within which uncertain simulation model parameters were varied and generation of model parameterisations.
4. The Calibration, 1st step: multi-criterial comparison of the observed patterns with the simulated patterns, and the exclusion of highly unrealistic model parameterisations.
5. Sensitivity analysis of the calibrated model: exploration of the parameter space remaining after Calibration.
6. The Calibration, 2nd step: validation and calibration of the remaining parameterisations against the newly included pattern *ANPP* and green biomass.
7. Calibration, 3rd step: Calibration including 100 different climates against a series of predictions (primary and secondary).
8. Calibration, 4th step: compared the accepted parameterisations of the 3rd calibration step with tussock density over variable stocking rates.

4.2.3 The characterisation of the available field data, evaluation of uncertainty

The empirical data were collected for two purposes: The first purpose was to test directly three basic hypotheses made about the model: the vitality increment with increasing potential productivity, the distribution of the dead fraction of biomass at grazed sites compared to exclosures, and the relation between the mean grazing intensity and variability of the grazing intensity distribution at the individual tussocks (compare Chapter 3). The second purpose of the field data collection was the indirect parameterisation of the simulation model. Since the model was developed at the level of individual tussocks, most of the empirically measured variables corresponded directly to variables in the simulation model. Thus, the high degree of structural realism in the simulation model allows a one to one comparison between model and reality.

The field data were sampled between 2000 and 2003 at four sites (ranches) and 20 paddocks. Six of them were paddocks excluded from grazing (exclosures), whereas 14 were grazed paddocks. The duration of time a paddock was excluded from grazing varied between 10 and 17 years. A detailed grazing history including data on the mean grazing intensity was in general not available. The detailed

Tab. 4.1: The sample size of field data for model calibration.

Per site, 30 tussocks were measured. Dead tussocks were not included into the database. One paddock of the grazed paddocks included only 20 tussocks, and two samples for vitality. These data were used to estimate confidence intervals by bootstrapping used for model calibration.

Pattern	Observed pattern/response variable	Abb.	Exclosure		Grazed	
			n paddocks	n tussocks	n paddocks	n tussocks
P 1	*Tusssock density*	*Td*	6	178	14	409
P 2	Green biomass (density estimated)	gb_{dens}	6	178	14	409
P 3	Green biomass (diameter estimated)	gb_{diam}	6	178	14	409
P 4	Mean dead biomass fraction	*dfrac*	6	178	14	409
P 5	Tussock distribution over *dfrac*	fT_{dfrac}	6	178	14	409
P 6	*Mean vitality*	*mean vit*	3	88	10	279

description of the data sampling of the empirical variables was given in Chapter 3. Additionally to the data used in Chapter 3 we collected data from another 7 paddocks at two sites in 2002 and 2003, of which 3 were exclosures and 4 grazed paddocks. Precipitation data for the years after 1998 are not available. So the empirical data have to be regarded as 'random samples' within the possible range of values, assumed to depend largely on precipitation. For the calibration of the simulation model, I will choose the widest possible confidence intervals for model calibration to avoid strong assumptions about real values for the used variables, i.e. excluding only highly improbable model behaviour. I can do this because one advantage of this method is that excluding model dynamics which deviate strongly from observed several weak patterns will constrain the model dynamics considerably. This issue is discussed in detail in Wiegand et al (2004b).

Field data. — Tab. 4.1 shows the sample size for grazed paddocks and exclosures. For each paddock the mean value was calculated, and median and range-of-paddock means are used to compare grazed paddocks with exclosures (Fig. 4.2). Possibly due to the different age of the exclosures and the presumably wide range of unknown stocking rates applied to grazed paddocks, significant differences cannot be detected for tussock density (*Td*, **P1**).

Also for the biomass estimations, gb_{dens}(**P2**) and gb_{diam}(**P3**), an expected significant decrease for grazed paddocks is not evident. Nevertheless, some important variables show significant differences between grazed and ungrazed paddocks: as expected, the mean *dfrac* per paddock (**P4**, p = 0.017, U-test) is lower than in grazed paddocks. As expected, too, for two out of five *dfrac*-classes the tussock distributions over dead biomass fraction $fT_{dfrac1-5}$ differ significantly: as expected; tussock distribution over *dfrac*-class 2 (20 - 40% relative amount of dead biomass, fT_{dfrac2}, **P52**, p = 0.0282) is lower for exclosures. Analogically, exclosures have a larger amount of tussocks with a higher fraction of dead biomass (60 - 80%, fT_{dfrac4}, **P54**, p = 0.0293) than grazed paddocks. Finally *mean vitality* (*mean vit*) differs significantly in grazed paddocks and exclosures (**P6**, p = 0.026, U-test).

Concluding the description of field data, it is obvious that some patterns will have a weak potential in discriminating between grazed paddocks and exclosures. Nevertheless, some important variables that help to discriminate between both factors will in conjunction show a significant behaviour. For the essential task, the overall calibration of the model regardless of grazing, it is essential to have a rough estimate of the possible range of the variables. The assumption is that several patterns, which are weak when used alone, will become strong patterns, when they are combined (Wiegand et al 2004b).

Fig. 4.1: Scheme of model calibration and sensitivity analysis
Explanation see sections 4.2.1-4.2.2. The calibration scheme guides through whole Chapter 4 and shows to which step of the procedure each Table and Figure refer to.
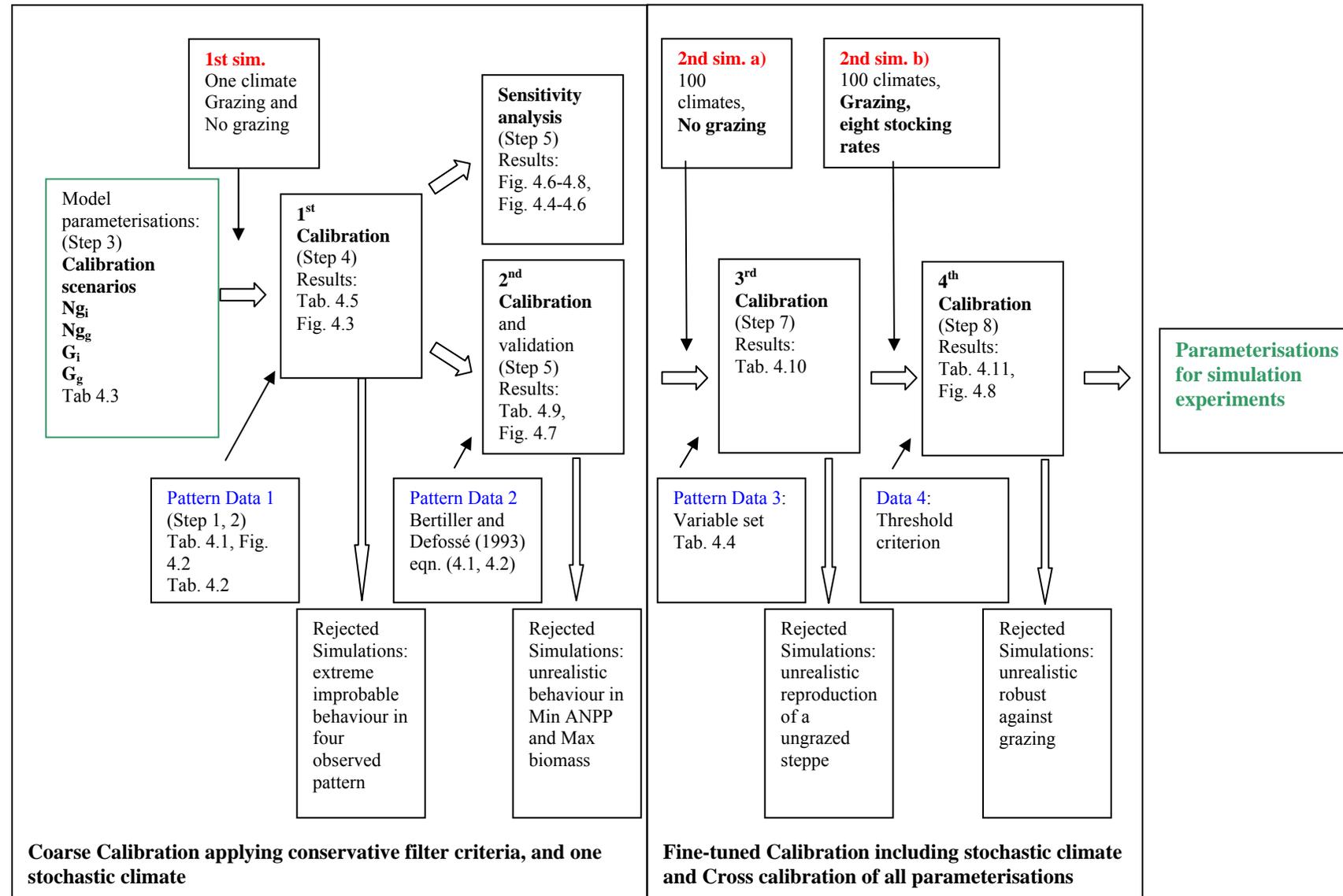
4.2.4 The transformation of field data into 'pattern' for the comparison with field data

In this section I define the criteria for pattern fulfilment. The general philosophy of the approach for this calibration step was given in section 4.2.1. It consisted of a comparison of observed patterns with simulated patterns. During this comparison a yes/no decision was applied for the simulated data, depending weather or not they reproduced the observed pattern. This required defining a statistical criterion, which decides if a significant difference between the simulated and the observed pattern exists. This approach takes two types of uncertainty into account: the uncertainty due to scarce data, and the pattern data uncertainty of both simulated and observed patterns. Here, I summarize the performed steps. As field data, especially from exclosures, are scarce, and detailed knowledge about the distributions of the data is limited, I decided to perform a bootstrap approach (Manly 1996).

Sub-pattern. — Additionally to the standard approach, where one observed pattern is compared with a simulated pattern, a more sophisticated approach was necessary for pattern **P5,** the frequency distribution over *dfrac*-classes. The field data provided an estimate of the relative amount of the dead biomass fraction. As it was hypothesized, that exclosures and grazed paddocks differed in the distribution of tussocks over *dfrac*-classes, the classified frequency distribution had to be compared. Thus, the pattern was divided into five sub-patterns, which at first were compared individually with the simulated data (i.e., sub-patterns); secondly it was assessed if the simulated tussock distribution fulfilled all five sub-patterns of the observed patterns or less. Finally I generated a complex, sensitive and strict pattern for comparing simulated with observed pattern.

Pattern filter definition by bootstrapping. — Bootstrapping was used to estimate upper and lower confidence intervals for each pattern used for model calibration. Bootstrapping is an advantageous approach, as only a small sample size was available, but for each empirical field variable $88 - 409$ data points exist (see Table. 4.1, n of individual measured tussocks). Each of the 10.000 bootstrapping data samples performed for each variable mimicked the available field samples. For exclosures, 6 samples of 30 tussocks were sampled with replacement out of the exclosure tussocks data set, analogically 14 samples for the bootstrapping out of the 'grazed' data set (for *mean vitality*, **P 6**, 3 or 10 samples respectively). In the following, for each sample the mean, the minimum and the maximum was calculated. I used the range of minimum and maximum values out of the bootstrapping procedure for those observed patterns, were the uncertainty about their range was highest (see Tab. 4.2); for the other observed patterns, I used the mean values out of each bootstrap sample to generate the frequency distribution, which was the basis to define the confidence intervals. Further, for the most observed patterns, for one 'mimicked field sample' of 6 exclosures or 14 grazed paddocks respectively the maximum mean and the minimum mean was recorded. For pattern including higher uncertainty the maxima and minima out of minima and maxima were recorded. Consequently, 10.000 ranges of mimicked field samples were taken. Finally, I calculated the frequency distribution for both the maximum range and the minimum range test statistic based on the 10.000 bootstrapped data sets. Next, I tested the different confidence intervals which could be derived from these distributions. Finally, I chose a two-tailed 99.8% confidence interval for the acceptance of the simulation output, which is equivalent to a lower confidence interval of 0.1% and a upper confidence interval of 99.9%. This means that the simulated values that would lie below the 0.1% or above the 99.9% limit were rejected. Thus, nearly the whole range of the pattern generated by the bootstrapping procedure was accepted as a valid simulation result. The cut of 0.1% at both ends was used to exclude zero values out of the tussock distribution over *dfrac*-classes 2-4 (**P52-P54**, for exclosures), which are assumed to be unrealistic and returned biased calibration results in preliminary studies. Thus, I used a criterion for pattern fulfilment, which rejected parameterisations which would produce unrealistic behaviour, i.e. produced at least one pattern which was outside the observed field range. Considering the
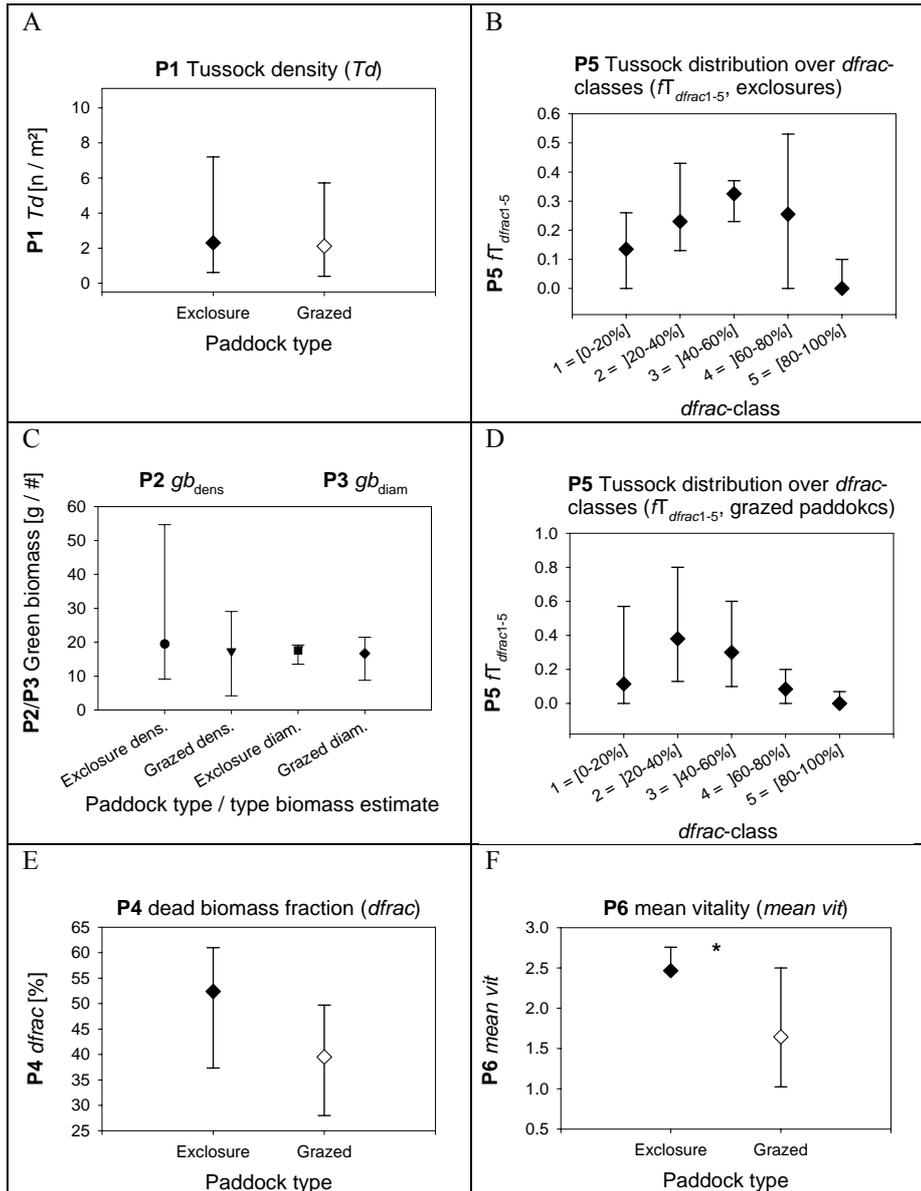
Fig. 4.2: Field data used for multi-criterial model calibration.
Median and range of data are shown for Exclosures (n = 6), and Grazed paddocks (n = 14). **P1 - P6**: Abbreviations of observed patterns used for indirect model calibration. *: Medians between grazed and exclosure significant different with $p < 0.05$ (U-test, Mann-Whitney). **A**): **P1**: tussock density Td; **B**): **P2**: green biomass gb_{dens}, estimated via biomass density (mg green biomass / cm³) with relationship: green biomass = 70.727 * tussock diameter $^{-0.4803}$ ($R^2 = 0.31$, n = 35, compare Chapter 3); **P3:** green biomass gb_{diam} estimated linearly as a function of tussock diameter: green biomass = 0.928 * tussock diameter ($R^2 = 0.611$, n = 62); **C**): **P4**: mean dead biomass fraction (*dfrac*) per paddock/sample, p = 0.016763 ; **D**): **P5** (for exclosures): tussock distribution over *dfrac*-classes, divided into 5 sub-patterns **P51-P55** for each *dfrac*-class: **P51**: frequency of tussocks with *dfrac* [0-20%], **P52**: frequency of tussocks with *dfrac*]20-40%] and so on; **E) P5** (grazed paddocks); **P52** and **P42** differ significantly between exclosures and grazed: **P52** (fT_{dfrac2}): p = 0.023, and **P54** (fT_{dfrac4}): p = 0.028840; **F**): **P6**: *mean vitality* (*mean vit*), p = 0.027993 (n = 13).

83

Tab. 4.2: Definition of pattern fulfilment.
Listed are the upper and lower values for the selected 99.8% confidence interval values derived from bootstrapped field data. Column 1 indicates the used observed pattern (compare Tab. 4.1, Fig. 4.2). Column 2 gives the pattern identifier; column 3 and 4 list the correspondent simulated variables, which were used for calibration. **Subpattern**: A sub-filter was necessary if i) more than one simulated variable was compared with one pattern (e. g. **P2**, **P3**, **P4**); or ii) if one pattern consists out of different classes (**P5**). **Range of means**: min. and max. of means of each bootstrap sample was used for calculation of the frequency distribution, which was used for determination of the confidence interval. **Range of Min/Max**: Min. and Max of each bootstrap was used for confidence interval determination. Range of Min/Max was used for biomass data of exclosures to include fewer assumptions about the exclosure biomass data.

Observed Pattern		compared with simulated			Used upper/lower confidence interval	**No grazing** Range of means	**Grazing** Range of means
					data base for bootstrapping	n = 178	n = 409
					n paddocks	6	14
		Pattern	or sub-pattern	Explanation		**Type of confidence interval calculation**	
Td	**P1**	$Td_S(t = 100)$	-		0.01%	0.70	0.43
					99.9%	5.17	4.59
						Range of Min/Max	Range of means
gb_{dens}	**P2**	*Mean prod*	**P21**	Biomass estimation from biomass density	0.01%	1.1	7.2
		Mean gb$_S$	**P22**		99.9%	61.2	27.1
gb_{diam}	**P3**	*Mean prod*	**P31**	Biomass estimation linear to tussock diameter	0.01%	4.1	10.8
		Mean gb$_S$	**P32**		99.9%	42	22.7
						Range of means	Range of means
dfrac	**P4**	*Mean dfrac*	**P41**		0.01%	36.5	26.1
		Min dfrac	**P43**		99.9%	62.7	51.4
fT_{dfrac}	**P5**	fT_{dfrac}	**P5**	Tussock distribution over *dfrac*-class			
$fT_{dfrac\,1}$	**P51**	$fT_{dfrac\,1}$	**P51**	[0%-<=20%]	0.01%	0.00	0.03
					99.9%	0.37	0.57
$fT_{dfrac\,2}$	**P52**	$fT_{dfrac\,2}$	**P52**	]20%-<=40%]	0.01%	0.03	0.07
					99.9%	0.57	0.74
$fT_{dfrac\,3}$	**P53**	$fT_{dfrac\,3}$	**P53**	]40%-<=60%]	0.01%	0.03	0.00
					99.9%	0.63	0.60
$fT_{dfrac\,4}$	**P54**	$fT_{dfrac\,4}$	**P54**	]60%-<=80%]	0.01%	0.03	0.00
					99.9%	0.60	0.30
$fT_{dfrac\,5}$	**P55**	$fT_{dfrac\,5}$	**P55**	]80%-<=100%]	0.01%	0.00	0.00
					99.9%	0.10	0.14
Mean vit	**P6**	*Mean vit*	**Step 2**		0.01%	2.07	1.40
					99.9%	3.07	2.40

whole range of the field data is a weak criterion. However, because I demanded fulfilment of several patterns (i.e. the model should produce simulated patterns which lie all simultaneously within the observed ranges) my filter algorithm as a whole was very strict (see Wiegand et al. 2004b).

Detailed description of field data. — Two alternative tussock biomass/annual net primary productivity pattern filter criteria were generated, because of high uncertainty about the biomass estimations. To estimate the observed **pattern 2** (used for comparisons with *mean prod* (**P21**) and mean gb_S **P22**), which estimates tussock biomass referring to biomass density, the method applied in Chapter 3 was used. Here, we fitted using an estimate of biomass density gb_{dens} [mg green biomass / cm³], to a data set comprising 35 oven-dried tussocks. Then the tussocks were measured from the Media Luna Ranch: the pattern **P2** green biomass (biomass density, tussock diameter) is estimated as $gb_{dens} = 70.727 *$ tussock diameter $^{-0.4803}$ (R² = 0.31, n = 35). As the diameter was known from perimeter measurements, the volume of each tussock was calculated and the biomass density was estimated as a function of tussock diameter. The alternative biomass estimate for each tussock employed to calculate the observed **pattern 3** (**P32 and P32**) additionally 27 tussocks measured at two other sites, and estimates green biomass as a function of tussock diameter assuming a direct linear relationship: the pattern **P3** green biomass (tussock diameter) $gb_{diam} = 0.928 *$ tussock diameter (R² = 0.61, n = 62). As biomass can be carried over from the year before, we could not totally separate actual biomass data from the annual production. Additionally, as field data for the paddocks provide indirect estimates based on regressions, derived from a small tussock sample size, it is reasonable to test different alternative patterns for annual production and biomass. The two patterns for biomass/annual net primary productivity (**P2**, **P3**) tested both for mean tussock biomass after senescence at the end of each time step (*mean gb_S*) and the mean annual net primary production per tussock (*mean prod*). This was because the available data could be split clearly into both components. However, both variables are important and had to be tested. I therefore used a similar pattern filter for both variables. Since senescence occurs mainly during fructification (Bertiller and Defossé 1990a, and 1990b, see Chapter 2). It is improbable that the tussock's annual production is substantially higher than the standing green biomass including dry biomass which becomes senescent during the actual year /time step.

4.2.5 Range of varied parameters and generation model parameterisations

For calibration and sensitivity analysis four calibration scenarios were investigated: at first, grazing (**G**) and no grazing (**NG**) scenarios were calibrated separately, and secondly, parameters were calibrated independently (index i) or in groups (g) of 15 (for scenario **NG$_g$**) or in groups of 16 (for scenario **G$_g$**) driver related-processes respectively (Table 4.3). The definition of parameter groups is given in Chapter 2, Table 2.3.

I tested as much different parameterisations as necessary to obtain a sufficient number of accepted parameterisations. Experience tells that about 0.1% of all parameterisations would be positive evaluated (T. Wiegand, pers. comm.). Of most parameters the range was not known. Therefore, the parameter range investigated was in general wide: I selected the estimation of the field experts' ± 30%. For some parameters however, the whole possible parameter range was estimated (e.g. senescence SEN and littering LIT). The selection of a conservative wide range is necessary because the biological uncertainty is high. The defined pattern will filter out all those model parameterisations, which produce highly improbable behaviour, which does not agree with the field observations.

The values of 29 or 30 model parameters respectively remained unknown or uncertain (see Table 4.3 and Table 2.3, Chapter 2). To sample this parameter space systematically, I used a Latin hypercube design (Stein 1987, McKay et al. 2000, Saltelli et al. 2000), a stratified sampling method

Tab. 4.3: Number of parameterisations used for calibration and sensitivity analysis.
Abbreviations: calibration scenarios: **NG**: No grazing included; **G**: Grazing included; indices: ₍ᵢ₎: parameter independently estimated; ₍g₎: parameter estimation in groups of sub-processes. Groups are defined in Tab. 2.3.

Scenario x parameter block	NG_i	G_i	NG_g	G_g
N parameterisations	196301	195428	161999	196347
N independent parameters or sub-processes	29	30	15	16
N intervals/subcubes the parameter space is divided	11	11	21	21

without replacement. For each parameter, I selected an interval within which the parameter was varied (lower and upper limits given in Table 2.3, Chapter 2). Then, I divided each interval into 21 or 11 equidistant subintervals respectively (Table 4.3). I used 21 subintervals to obtain almost continuous relationships between model parameters and model predictions. For the scenarios (NG_i and G_i) with 29 or 30 parameters respectively I used 11 subintervals, ensuring that searching through the resulting high-dimensional parameter space was still practically possible. Thus, my 15-30 dimensional parameter space was subdivided into 11^{29}, 11^{30}, 21^{15} or 21^{16} sub-cubes respectively defining a hypercube. This hypercube was used in the following way to select parameter combinations for which simulations were run. At first, a sub-cube was randomly chosen. Then, all sub-cubes that coincided with the chosen sub-cube in at least one parameter subinterval were deleted from the hypercube and another sub-cube was randomly chosen from the reduced hypercube. This was repeated as long as possible, resulting in 11 or 21 selected sub-cubes defining 11 or 21 model parameterisations respectively. I repeated the above procedure until obtaining the number of parameterisations given in Table 4.3.

Because the sampling points in the Latin Hypercube sensitivity analyses were well distributed within the parameter space, relatively few simulations are necessary to achieve significant results compared to a random or a full grid parameter selection (Stein 1987; Helton 1993). The simulations were all run with one identical stochastic climate for 100 time steps. The initial condition reflected a potential natural state of the *Festuca* steppe with a high cover of approx. 60% (see Appendix I).

4.2.6 Calibration, 1ˢᵗ step: multi-criterial comparison of observed patterns with simulated patterns

During this step, different methods to calculate the confidence interval, different confidence intervals, and different pattern filter combinations were explored. Finally the most appropriate pattern filter combination (**P1 P2 P4 P5** for calibration scenarios **NG** and **P1 P3 P4 P5** for calibration scenarios **G** respectively) was selected and used to filter all generated model parameterisations for a given calibration scenario. In the first calibration step I used conservative filter criteria to remove only parameterisations which produce highly improbable model behaviour in the five basic properties tussock density (equivalent to cover), tussock biomass and tussock annual productivity, mean *dfrac*, and tussock distribution over *dfrac*-classes. This 'prefiltering' was necessary because more detailed filters (i.e. in steps 3-4) required simulations with different climatic scenarios (i.e. including environmental stochasticity) and the computational effort would be too large. Therefore I filtered in this step only using conservative wide confidence intervals and with only one precipitation series assuming that a parameterisation which e.g. went extinct without grazing will do so for almost all precipitation series.

The results of this 1ˢᵗ step of Calibration were model parameterisations which reproduced the different patterns simultaneously and were called accepted parameterisations. The most restrictive pattern during this procedure was the pattern tussock distribution over *dfrac*-classes (**P5**, $f T_{dfrac1-5}$).

This pattern is a complex pattern and was the 'eye of the needle'. The accepted parameterisations were used for the sensitivity analysis. Frequency distributions of the calibrated parameters over the whole investigated range (Tab. 2.3) are plotted. Frequency distributions of the calibrated parameters show, if the process related to the parameter is necessary, if parameter values unequal to zero are included and the value zero was included into the range. Further, one can test, if the valid parameter range was limited during calibration, and if the distribution differs significantly from an even distribution. Finally, one can try to estimate an optimal value, if the frequency distribution shows a clear maximum. I assume that approximately 100 accepted parameterisations are necessary to analyse the calibrated parameterisations and to obtain insight into the distribution of the parameters over their range.

4.2.7 Sensitivity analysis of the calibrated model

The sensitivity analysis was mainly performed with Spearman's rank correlation. This is one possible method to relate the model input (parameterisations) and the model output (primary and secondary predictions) to each other (Saltelli et al. 2000). I chose Spearman's rank correlation because it makes no assumptions about the relationship between the tested parameter and the response variable. For sensitivity analysis I use only those model parameterisations which fulfilled the conservative 1st Calibration step filter combination (**P1 P2 P4 P5**, for no grazing calibration scenarios **NG**, and **P1 P3 P4 P5** for the grazing calibration scenarios **G**). Hence, the sensitivity analysis investigated the remaining parameter uncertainty after the first step of calibration. The reasoning for this approach was that I assume that only those parameterisations, which fulfil the requested pattern combinations are potentially biologically appropriate. The sensitivity of the response variables within the remaining parameter range is of special biological interest.

24 response variables were tested which describe different characteristics of population dynamics such as tussock density, live biomass, annual production, and vitality distribution. Nine of the variables included into the sensitivity analysis were primary predictions, and 15 were secondary predictions. The primary predictions are those used as patterns for the first step of calibration (Tab. 4.2). Secondary predictions are response variables which may be used for further model validation or model analysis, but which were not used as pattern for calibration. Additionally, a semi-quantitative index was calculated to compare the relative importance of the parameters on all investigated variables. This *relative correlation strength* (*rcs*) is calculated from the sum of the absolute values of all significant correlations between the response variable and one parameter. For each scenario *rcs* is normalized by dividing all *rcs* for each parameter through the highest value. As each parameter is part of a sub-process and a process (see Chapter 2, Table 2.3), a qualitative comparison between the grouped and the independent scenarios for calibration is possible.

4.2.8 Model validation: comparison of the 1st step calibrated model with secondary predictions

Additional empirically observed or estimated variables were available (i.e. secondary predictions), which allowed validating the parameterisations accepted during the 1st calibration step. I use validation in the term of Rykiel (1996), Higgins et al. (2001), and Gardner and Urban (2003), which means that independent empirical data that were not necessary for calibration, are used. The result of the validation was that model parameterisations having produced model predictions lying outside the range of the variables used for validation, were also rejected like those during first calibration step. This filtering is equivalent to the 2nd calibration step. Thus, I used this step in two ways: as validation and as an additional calibration which rejects some parameterisations accepted during the 1st step of Calibration.

The data base for validation was formed by the accepted parameterisations from the 1st calibration step. As example I show results from those calibration scenarios where parameters were

run independently, both the in- and excluding grazing calibration scenarios (G_i and NG_i). As the number of calibrated parameterisations was high for G_i, I made a selection of exemplar parameterisations of the calibration for G_i. For the three most influencing parameters Stock, SEN, and LIT two parameterisations were included out of each positively calibrated interval. They were chosen randomly out of the pool of the calibrated parameterisations.

The following variables were selected for the validation: the mean simulated vitality (*mean vit*), the minimum of mean annual productivity per hectare (*min ANPP*), and the maximum standing biomass (*max B*). *Mean vit* was chosen, because this variable is difficult to estimate in the field and the field data for vitality were not yet tested for plausibility (see Chapter 3). As only little was known about *mean vit*, I applied a less restrictive criterion, *mean vit* > 1. Only parameterisations showing a uniform tussock distribution at the lowest vitality level are discarded. Biomass and productivity were chosen, because they are essential variables for a simulation of grazing and thus I aim to avoid strong over- and underestimation of productivity and biomass estimations. For these variables only weak estimates were available. For the variable minimum of annual net primary production (*min mean prod*) a very rough estimate was available: min mean prod > *750* kg / ha (Bertiller and Defossé 1993, for a *Festuca* steppe in very good state). For maximum standing phytomass (*max B*) no estimation was available. So I derived a theoretical quantitative estimate for both biomass variables using the bootstrapped range values for tussock density *Td* (**P1**, Table 4.2) and the green biomass per tussock estimated by biomass density gb_{dens}, **P 21**, see Table 4.2) as a basis for a theoretical estimation of a possible range for both variables. The data for exclosures were used as follows:

min ANPP $\qquad = ((\textit{max } Td_E \text{ [n/m}^2] * \textit{max } gb_{densE}\text{[g/n]} - \textit{min } Td_E\text{[n/m}^2] * \textit{min } gb_{densE}\text{[g/n]}) / 2) * 0.4 * 10$ (4.1)

max B $\qquad = ((\textit{max } Td_E \text{ [n/m}^2] * \textit{max } gb_{densE}\text{[g/n]} - \textit{min } Td_E\text{[n/m}^2] * \textit{min } gb_{densE}\text{[g/n]}) / 2) * 1.5 * 10$ (4.2)

min ANPP	Minimum ANPP for a *Festuca* steppe in an assumed natural state [kg/ha];
max/min Td	Maximum/minimum *tussock density* for the bootstrapped exclosure field data (compare Fig. 4.2 A), Tab. 4.2. pattern **P1**);
max/min gb_{dens}	Maximum/minimum bootstrapped biomass per tussock data, estimated from biomass density estimation for exclosure paddocks (compare Fig. 4.2 B), pattern **P21**, Tab. 4.2);
max B	Theoretical derived maximum standing green phytomass [kg/ha]

The idea of this estimation is the following: the first term estimates a theoretical mean biomass per m², using the extreme values for tussock density (range of means) and tussock biomass (range of min./max.) and adding an estimated confidence interval to it (0.4 for *min ANPP*, 1.5 for *max B*). The last factor (10) scales the unit to [kg/ha]. The estimated value for the minimum annual net primary production *min ANPP* = 630 kg / ha lies 10% below that given by Bertiller and Defossé (1993) and the estimated value for *max B* ~ 2.365 kg / ha is about 20% higher than the estimated maximum possible *ANPP* in the field (2.000 kg / ha, Bertiller and Defossé 1993). Thus, I assume that the maximum biomass carry over from a year preceding a year of maximum annual productivity will not exceed 25% of the maximum *ANPP*.

2^(nd) step of Calibration. — The validation of the results of the first step of calibration showed partly biologically implausible results (see 4.3.3). Thus I used the results of the validation for the 2^(nd) calibration step for both calibration scenarios (NG_i and G_i), using the variables derived above; for the Grazing calibration scenario (G_i) I used stricter mean vitality values ($1.4 \leq \textit{mean vit}_S \leq 2.4$, Tab. 4.2) than for the No grazing calibration scenario (NG_i), due to the larger amount of accepted parameterisations.

Variability of accepted parameterisations. — The parameters of the remaining parameterisations after the 2nd step of calibration are ranked by their relative correlation strength (*rcs*) calculated after the 1st calibration step and characterised by i) their median values, ii) the % deviation of the standard parameterisation P_S from the median, iii) the average deviation (%) of the accepted parameterisations from the median, iv) the in mean standard deviation (%) and v) the mean coefficient of variation (CV) of the average deviation of one parameterisation from the median. At this step all parameterisations from the scenarios **NG$_i$**, **G$_i$** and the standard parameterisation P_S are analysed together. The relative correlation strength (*rcs*) was then calculated newly as the median of both specific *rcs* - values for the scenarios **NG$_i$** and **G$_i$**.

4.2.9 Third step of Calibration, including repetitions of stochastic climate, No grazing

Overview. — After the validation and the 2nd step of calibration, two further calibration steps were performed. This approach was due to the high stochasticity of precipitation acting upon the model. The remaining parameterisations after validation were run with 100 repetitions over 100 different stochastic climates and over the whole range of stocking rates. The output of these simulations — first of all the output without grazing — was calibrated against a series of further patterns, and I calculated an aggregated index indicating how much patterns fulfilled the 100 repetitions of one model parameterisation with a frequency of 80% (details see below). The approach of repeating 100 times each parameterisation was chosen to avoid false positive calibration due to the use of only one random precipitation regime. However, this more sophisticated and computationally intensive calibration makes only sense for biologically reasonable parameterisations. Therefore I use only the parameterisations accepted after the 2nd calibration step. The following final 4th calibration step investigated the resulting parameterisations with regard to their behaviour of tussock density at the whole stocking rate range. A criterion was established to reject all unrealistic stable parameterisations (details see next section).

3rd step of calibration: *Concept of Cross calibration.* — As mentioned above, I used the remaining parameterisations from the previous calibration step and applied them with 100 climatic repetitions over the whole range of stocking rates. So the parameterisations selected from the no grazing calibration scenario (**NG$_i$**) were tested for how they behaved under grazing and vice versa (**Cross calibration (Cc)**). Cross calibration means that parameterisations, which were calibrated under the non-grazed pattern filter combination were now tested additionally against the grazed conditions and vice versa. This approach ensures that all parameterisations, weather they were calibrated during the first both calibration steps, were both tested under both conditions and are accepted only, if they showed reasonable behaviour under both conditions. The 3rd calibration step test all parameterisations against no-grazing conditions, the 4th calibration step tests the same parameterisations under grazing conditions.

Details of 3rd calibration step. — The simulations were run 150 time steps, where the first 50 time steps were performed without grazing to allow the system to equilibrate from the initial conditions. From these simulations, the runs without grazing were separated and calibrated against a series of primary and secondary predictions (see Table 4.4). For each pattern a threshold was defined to select parameterisations showing a biologically reasonable behaviour under natural conditions (without grazing) and under most of the stochastic climates applied. The selected thresholds are more restrictive than the confidence intervals used in the 1st calibration step (see Table 4.4). The calibration of most variables occurred at two time steps ($t = 50$ and $t = 150$). Therefore, a stability criterion could be included into the calibration. Additionally, some patterns ask for a minimum or maximum value throughout the whole run, and thus, the pattern selects parameterisations showing certain system stability.

Tab. 4.4: Third step of Calibration: used variables for calibration of No grazing simulations repeated with 100 stochastic climate repetitions.

41 exemplar parameterisations, selected from the calibration scenarios G_i and NG_i, calibrated during the 1st and 2nd step of calibration, were run 150 time steps with 100 different stochastic climates. The results of these runs without grazing were calibrated against the listed variables. Each parameterisation had to fulfil the given threshold at least 80 times out of 100 repetitions. A parameterisation was accepted, if the **Cross calibration** index (**Cc**) counted 9 out of 11 (~ 80%) fulfilled patterns (column 1, 2) and thus the evaluation was positive.

3rd step of calibration: Cross calibration (Cc) 1st step						
Nr. Cc - evaluation	Variable	Abb.	Explanation	Criterion / threshold	Confidence intervals tested	Evaluated at time step t
1	Tussock density	Td_S	-	> 3.3 / m²		50
2	Tussock density	Td_S	-	> 3.3 / m²		150
3	$Min\ cover_F$	$Min\ cov_F$	-	> 23%		1-50
4	$Min\ cover_F$	$Min\ cov_F$	-	> 23%		1-150
5	$ANPP$	-	-	> 750 kg/ha	80% / 90% / 95% fulfilment out from 100 simulated stochastic climates	50
6	$ANPP$	-	-	> 750 kg/ha		150
7	$Festuca\ state$ [1]	Cov_F*ANPP	cover: 30-90% ANPP 750-2000 kg/ha	States: 7-9, 13-15		50
8	$Festuca\ state$ [1]	Cov_F*ANPP	idem	idem		150
9	$Min.\ ANPP$	$Min\ prod$	-	>350 kg/ha		1-150
10	$Mean\ ANPP$	-	-	600-2200 kg/ha		1-150
11	$Max\ green\ biomass$	$Max\ B$	-	1500-2500		1-150

Further, an integrating index **Cc** (**C**ross **c**alibration) including an aggregated threshold was defined, which summarizes the results of the calibration for each parameterisation. The variable thresholds select a reasonable, good compositional state under natural conditions after a long-term run of 150 time steps (compare with Bertiller and Defossé 1993). Three one-sided confidence intervals were tested (80%, 90% and 95%), which set the limit how many repetitions out of the 100 performed stochastic climate repetitions should lead to results lying within the variable thresholds. Finally, the confidence interval 80% was used. The integrating index **Cc** counts the number of fulfilled patterns per parameterisation under the given variable thresholds and confidence intervals (Table 4.4). A parameterisation was accepted during this step if the index **Cc** reached or surpassed the aggregated threshold 9 accepted patterns from the 11 possible ones, i.e. one parameterisation fulfilled at least 80% out of all patterns tested at the different time steps within at least 80 repetitions out of 100 different stochastic climates.

During the 4th calibration step, the accepted parameterisations out of this 3rd calibration step were checked over the whole range of stocking rates.

4.2.10 Fourth Calibration step

Finally, the remaining parameterisations were checked against the whole range of stocking rates. I simulated the first 50 years without grazing to allow the system to equilibrate from the initial conditions, and applied different stocking rates for time steps 51-150. The median out of 100 stochastic climate repetitions was calculated for time step 50 (not grazed) and for time step 150 (whole stocking rate range). This calibration step is a control of the performed calibration steps before. The reason for this is that some of the accepted parameterisations under no-grazing conditions might show an unrealistic stability against grazing, i.e. heavy grazing might not lead to the observed reduction in

tussock density (Bertiller 1996). Thus, a selection criterion sorting out such biologically unrealistic stable parameterisations was introduced. As biologically unrealistic I define a model parameterisation that does not lead to a reduction in tussock density after 100 years of heavy grazing. Such a model parameterisation may occur, due to conservatively criterion for pattern fulfilment to accept a simulation result as valid. The stability criterion was defined as follows: if the median of tussock density at stocking rates of 1.5 sheep / ha or higher was higher than 3.3 (i.e. 30% cover) at time step 150 (after 100 time steps of grazing), the parameterisation was rejected as unrealistically stable. The guideline for the threshold for discarding biologically unrealistic parameterisations is a statement from Bertiller (1996): She found that at least 25 years of grazing with stocking rates of 1.5 sheep / ha between May and December (approximately 1.0 sheep / ha for continuous grazing) reduced *Festuca* cover in uplands to approx. 30%. A criterion for biologically unrealistic unstable parameterisations is very difficult to develop, because there is a high danger of generating overly optimistic estimations for sustainable stocking rates. Thus, such a criterion was not yet tested.

4.3 RESULTS OF PARAMETER ESTIMATION

4.3.1 First step of Calibration

Table 4.5 gives an overview over the results of the first step of calibration. Different filter combinations, confidence intervals and calculations of tolerance limits were tested. After testing several pattern filter combinations (Tab. 4.5), I decided to use the pattern filter combination **P1 P2 P4 P5** for the no grazing calibration scenarios **NG$_i$** and **NG$_g$** and the pattern filter combination **P1 P3 P4 P5** for the grazing scenarios **G$_i$** and **G$_g$**. These filter combinations include the patterns tussock density (**P1**), mean annual net primary production per tussock (**P21** for No grazing /**P31** for Grazing), mean total live biomass after senescence (**P22** for **NG** / **P32** for **G**), mean dead biomass fraction per grid (**P4**, includes both *dfrac* (**P41**), and *min dfrac* (**P43**)), and finally tussock distribution over *dfrac-*classes (**P5**, divided in five sub-patterns, see Tab. 4.2). The final confidence interval I use is two-sided accepting all values, which lie within the 99.8% range of the by bootstrapping generated frequency distributions.

For the no grazing scenario (**NG**) the more conservative biomass filter (**P2**) was applied where frequency distributions were calculated using the minima and maxima of each bootstrap sample instead of the mean values, as for other confidence intervals. The reason was the lack of knowledge about biomass for ungrazed situations, thus, it is appropriate to filter with fewer assumptions. Additionally, it was more difficult to find accepted parameterisations out of the No grazing calibration scenario (see below). Thus, I widened the confidence interval to obtain more accepted parameterisations.

Two main results arise from the calibration. First, the numbers of accepted parameterisations are at least one dimension higher for the scenarios including grazing in comparison with those without grazing (Tab. 4.5, see the bold and shadowed marked results within the row No grazing). This result was unexpected. My null hypothesis about the system was that the No grazing situation was the most probable to reflect the natural situation.

The number of calibrated parameterisations without grazing was relatively low. The second result is that the number of positive calibrations within the scenarios that grouped the parameters was higher than the scenarios run with independent parameters. This result was expected due to the reduced degree of freedom of the parameter space. There are at two possible explanations for the finding that I could accept only a low number parameterisations for the scenario **NG$_i$** without grazing. First, it is possible, that one or more filters were set too strictly. **Pattern 5**, the frequency distribution over *dfrac-*classes is extremely selective, especially on the No Grazing scenario (see Table 4.5), i.e. only few

Tab. 4.5: Overview over the results of the 1st calibration step.
Shown are the percentages of parameterisations fulfilling a certain pattern filter combination (left column). All four possible calibration scenarios including Grazing and No grazing run each with independent parameters or grouped parameters runs are listed (NG_i, NG_g, G_i, G_g). Pattern filter combinations further used for the following 2nd step of calibration are bold marked and grey shadowed. **P1 P2 P5 P6>1**: pattern filter combinations used for calibration step 2: **P6>1**: parameterisations were accepted, if mean vitality was > 1.0. Pattern and confidence interval definition: see Tab. 4.2. Definition of calibration scenarios see Tab. 4.3. Definition of parameters and parameter groups (NG_g, G_g) see Tab. 2.3.

Results 1st step of Calibration				
% Fulfilllment of total parameterisations				
Data base and calibration scenarios	**No grazing (NG)**		**Grazing (G)**	
	Calibration scenarios			
	NG_i: 29 free p.	NG_g:14 groups of p.	G_g: 30 free p.	G_g: 15 groups of p.
Range of confidence interval	99.8%	99.8%	99.8%	99.8%
Type of confidence interval calculation for bootstrapped biomass data	Range of Min/Max	Range of Min/Max	Range of means	Range of means
Filter combination \ Nr. of parameterisations	196347	161999	196347	196347
% Parameterisations fulfilling pattern filter combination				
P1	25.79	22.96	19.01	15.66
P1 P21	25.79	22.96	18.90	15.66
P1 P22	16.98	15.65	5.15	14.93
P1 P31	25.79	22.96	16.47	12.85
P1 P32	11.91	11.05	2.80	4.38
P1 P41	9.25	8.63	4.69	5.62
P1 P43	9.86	9.20	4.77	7.85
P1 P5	0.11	0.24	1.92	2.21
Multiple criteria analysis with different biomass estimators				
Biomass confidence intervals calculated by biomass density				
P1 P2	16.98	15.65	5.12	14.93
P1 P2 P4	5.51	4.76	1.56	4.65
P1 P2 P4 P5	**0.05**	**0.08**	0.33	1.06
P1 P2 P5 P6>1	0.04	0.05	0.33	0.98
P1 P2 P5 P6	0.01	0.01	0.06	0.23
Biomass confidence intervals calculated by linear biomass estimation				
P1 P3	11.91	11.05	2.50	3.92
P1 P3 P4	3.91	3.49	0.76	1.79
P1 P3 P4 P5	0.04	0.06	**0.13**	**0.27**
P1 P3 P5 P6>1	0.03	0.04	0.13	0.26
P1 P3 P5 P6	0.01	0.00	0.03	0.05

parameterisations pass this filter. The demand to fulfil all five sub-patterns of pattern 5 (**P51**-**P55**) was possibly a too strong assumption. Second, it is possible that the whole system evolved under grazing and thus better calibration is generally achieved if light grazing is included. I assume both points are relevant, but I did not test a more tolerant **pattern 5**, because the 1st calibration step provided enough parameterisations for further work. Thus, the 1st calibration step has fulfilled his aims: to generate new hypothesis to understand better the *Festuca* steppe dynamics: i) one might test if relaxed assumptions about the tussock distribution over *dfrac*-classes (e.g. generating a sub-pattern consisting only out of 2

Frequency distribution of accepted parameters (1st Calibration:
Calibration scenarios (parameters independent):
No Grazing (**NG$_i$**)   Grazing (**G$_i$**)
P1 P2 P4 P5 (N= 105)   **P1 P3 P4 P5** (N = 250)
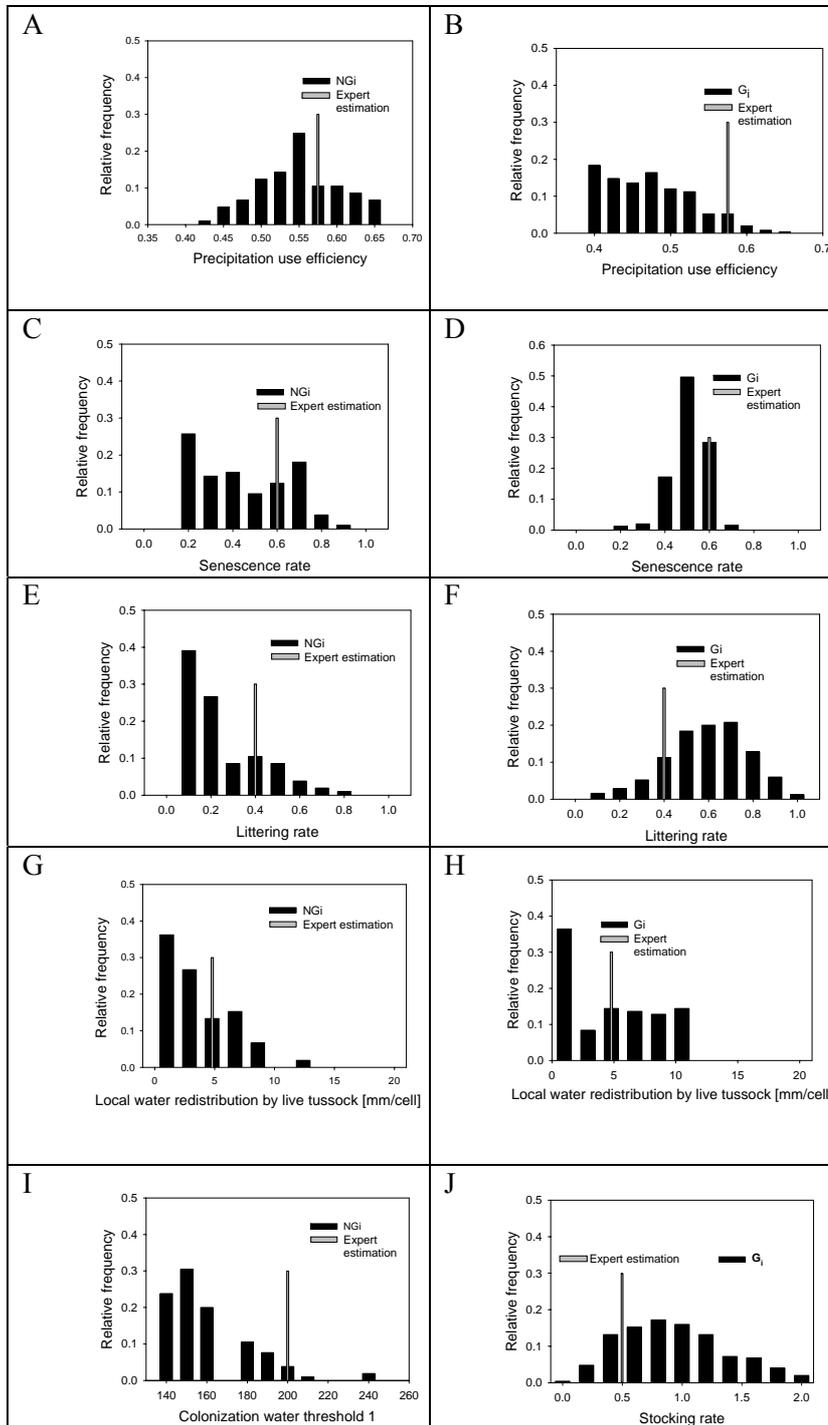
Fig. 4.3: Frequency distributions for exemplar parameters after the 1st step of calibration.
Shown are the frequency distributions of the accepted parameters over the whole investigated range. Exemplar parameters are shown where the parameter range could be limited during the 1st calibration step. Left column shows the calibration scenario No grazing, each parameter independent (**NG$_i$**, calibrated with filter combination **P1 P2 P4 P5**, N = 105); right column shows the calibration scenario Grazing, each parameter independent (**G$_i$**, calibrated with filter combination **P1 P3 P4 P5**, N = 250). Each parameter space was divided equally into 11 intervals. Parameters are defined in Tab. 2.3. Expert estimation: the thin bar indicates the expert estimation (see Tab. 2.3).

or 3 sub-pattern) lead to a wider acceptance of parameterisations and ii) the *Festuca* steppe evolved under light grazing.

Frequency distributions. — Fig. 4.3 shows the frequency distributions of the accepted parameterisations for most parameters for which the parameter space was restricted through the 1st step of Calibration (calibration scenarios **NG$_i$**, left column, **G$_i$** right column). Restrictions of parameter space for both calibration scenarios was possible for precipitation use efficiency (PUE), senescence rate (SEN), littering rate (LIT), and local water redistribution by live tussocks (WredT). For the calibration scenario No grazing (**NG$_i$**) additionally the soil water induced mortality threshold 1 and 2 (MortW1, MortW2) and one vitality change parameter, the soil water induced vitality decrease 1 (VdecW1, data not shown) can be limited within the investigated range. For the parameters stocking rate (Stock) and the grazing shape parameter (Gshape, eqn. I.10, Appendix I, data not shown), which are part of the Grazing (**G$_i$**) calibration scenario, the parameter space could be restricted. For the parameters senescence and littering I investigated the whole parameter range. As expected, exclusion of one of both processes (i.e. SEN = 0 or LIT = 0) is not possible, there are on accepted parameterisations without these processes. Other parameters might show a specific maximum within their distribution, but cannot be restricted within their range. A restriction of the parameter space for all parameters was not possible because i) the applied pattern filter combination is still too tolerant to restrict more parameters, or ii) the parameters range is already reasonably well estimated. A further more detailed analysis would be interesting to resolve the question if further parameters could be restricted within their range under the condition of a better estimation of some assumed basic parameters (e.g. senescence rate SEN or littering rate LIT).

4.3.2 Sensitivity analysis

For sensitivity analysis I use the model parameterisations which were accepted at the 1st Calibration step. I show and discuss in detail the results for the most important parameters out of the calibration scenarios, were parameters were run independently. The results for the grouped calibration scenarios are given in Appendix II. For the calibration scenario No grazing (**NG$_i$**) I used 105 accepted parameterisations, **NG$_i$** = 122, Tab. 4.5), and for the Grazing calibration scenario **G$_i$** I used = 250 parameterisations. First I discuss the ranking of parameters after their relative correlation strength (*rcs*) for each calibration scenario (Fig. 4.4). Secondly I discuss some results for important response variables in detail.

Parameter ranking after relative correlation strength (rcs): Calibration scenario No grazing. — The most important parameters for the calibration scenario No grazing (**NG$_i$**, Tab. 4.6 and Fig. 4.4 A, and **NG$_g$**, Fig. 4.4 B and Tab. II.3, Appendix II) are the senescence rate (SEN) and the littering rate (LIT); thus these processes have the highest overall mean correlation with the investigated response variables. At the first glance this is a surprising result but it becomes understandable when we consider that senescence has a high influence on the biomass variables, from which 5 are included into this analysis. But senescence and littering show also significant correlations with classes 2 and 3 of the tussock distribution over the dead biomass fraction (*f*T$_{Sdfrac2-3}$, Tab. 4.6), i.e. tussocks with a dead biomass fraction of 20-40% and 40-60% are significant correlated with the senescence rate. The next important parameters at the calibration scenario **Ng$_i$** with high mean relative correlation strength values (*rcs*) are vitality increase by water 2 (VincW2), basic plant productivity (ProdV1), vitality decrease by water 2, colonization 1st year water threshold (see Fig. 4.4 A, Tab. 4.6) and one water threshold for mortality. The most important parameter for tussock productivity estimates the maximum potential productivity for a tussock with lowest vitality (ProdV1 at vit = 1). This result is an expected one, because this parameter estimates the largest fraction of the tussocks' maximum potential productivity.

Tab. 4.6: Spearman rank correlation for calibration scenario No grazing, parameters independent (NG$_i$).
Shown are the descriptive statistics and significant correlations of important response variables against the 12 parameters with the highest rank correlation strength (*rcs*). Variables are defined in Tab. 2.2, parameters in Tab. 2.3.

Calibration scenario No Grazing, parameters independent (Ng$_i$), N = 105, Filter: P1 P2 P4 P5	Ranking after rcs →								1	2	3	4	5	6	7	8	9	10	11	12
Process									SEN/LIT	SEN/LIT	VD	WR	VD	PG	VD	CO	MO	CO	PF	PG
Sub-process									SEN	LIT	VD W	WR L	VD W	PG V	VD W	CO W	MO W	CO W	-	PG V
Parameters									SEN	LIT	VincW1	WredT	VincW2	ProdV1	VdecW2	ColWS0	MortW1	ColS0p	PFinc	ProdincV2-4
Variables	Min	lower confidence	Median	upper confidence	Max	Mean	Sd	Cv	PG.4	PG.5	VD.1	WR.1	VD.2	PG.1	VD.4	CO.1	MO.1	CO.2	PF.2	PG.2
Td_S	0.7	1.6	3.1	4.7	5.1	3.1	1.2	39			-0.25	0.22								
$Min\ cov_F$	0.3	0.6	1.5	3.7	3.7	1.7	0.8	47	0.24		0.24	0.20				0.22	0.24	0.26		
$Mean\ prod$	6.9	8.7	11.7	4.7	19.6	12.0	3.0	25					0.33	-0.37	**0.72**				0.31	0.22
$Mean\ gb_S$	1.2	15.1	14.8	45.1	57.6	20.7	16.0	77	**-0.95**	**-0.78**						0.21				
$Mean\ gb_P$	11	11	27	70	70	33	17	51	**-0.88**	**-0.69**					0.20	0.25				
$dfrac$	0.4	0.4	0.5	0.5	0.6	0.5	0.0	10	0.33						0.21					
fT_{dfrac1}	0.0	0.1	0.1	0.3	0.4	0.1	0.1	56	-0.43	-0.46					-0.27			0.21		
fT_{dfrac2}	0.0	0.1	0.1	0.2	0.3	0.1	0.1	42	0.24									0.24		
fT_{dfrac3}	0.1	0.2	0.3	0.4	0.6	0.3	0.1	46		0.21	-0.30							-0.35		
fT_{dfrac4}	0.1	0.3	0.5	0.6	0.6	0.4	0.1	24			0.20									
fT_{dfrac5}	0.0	0.0	0.0	0.0	0.1	0.0	0.0	427		-0.20					-0.26			0.25		
$mean\ vit$	1.0	1.0	1.6	2.2	3.2	1.6	0.5	34			-0.23	0.39	**-0.47**		-0.34		**0.42**		0.27	
$mean\ vit_{dfrac1}$	0.0	1.0	1.0	1.2	1.7	1.0	0.2	18	-0.33	-0.29	**-0.45**			-0.19	-0.36					
$mean\ vit_{dfrac2}$	1.0	1.0	1.0	2.0	3.0	1.3	0.5	35			**-0.49**	0.36					0.20			
$mean\ vit_{dfrac3}$	1.0	1.0	1.6	2.1	4.0	1.6	0.7	42			-0.30	0.34	**-0.41**		-0.26		0.34		0.19	
$mean\ vit_{dfrac4}$	1.0	1.0	1.8	2.7	3.8	1.7	0.7	41				0.35	**-0.53**		-0.36		0.40		0.30	
$mean\ vit_{dfrac5}$	0.0	0.0	0.0	0.0	3.0	0.1	0.5	383		-0.23					-0.30			0.30		
$mean\ ANPP$	215	383	530	857	1323	587	225	38		0.23				-0.37	**0.45**		0.27		0.21	0.31
$min\ ANPP$	37	111	189	340	585	215	108	51				-0.21	0.29			0.33	0.24			
$max\ ANPP$	662	714	1147	2426	2754	1251	410	33		0.25				-0.40	**0.44**					0.38
$ANPP$	92	113	380	907	966	411	201	49		0.23		-0.20	0.34	-0.24	0.37					
B_S	26	40	416	2403	2425	643	583	91	**-0.84**	**-0.69**						0.26				
$max\ B$	125	516	1420	3394	4896	1763	1239	70	**-0.90**	**-0.73**						0.24				
relative correlation strength (*rcs*)									0.21	0.21	0.12	0.12	0.12	0.11	0.11	0.07	0.07	0.06	0.05	0.05

Tab. 4.7: Spearman rank correlation for calibration scenario Grazing, parameters independent (G$_i$).
Shown are the descriptive statistics and the significant correlations of important response variables against the 9 parameters with the highest rank correlation strength (*rcs*). Variables are defined in Tab. 2.2, parameters in Tab. 2.3.

Calibration scenaro Grazing, parameters independent (G$_i$):N = 254, Filter: P1 P3 P4 P5	Ranking after rcs →								1	2	3	4	5	6	7	8	9
Process									SEN/LIT	GR	WR	SEN/LIT	PG	WI	VD	PG	VD
Sub-process									SEN	GR M	WR L	LIT	PG V	-	VD W	PG V	VD W
Parameters (1st row: names of Chapter 4, 2nd row: as in other chapters)									SEN	Stock	WredT	LIT	ProdV1	PUE	VincW2	ProdincV2-4	VdecW2
Variables	Min	lower confidence	Median	upper confidence	Max	Mean	Sd	Cv	PG.4	GR.1	WR.1	PG.5	PG.1	WI.1	VD.2	PG.2	VD.4
Td_S	0.96	2.23	3.80	4.47	4.59	3.60	0.83	23		**0.41**	0.33	0.15					
$Min\ cov_F$	1.0	2.1	3.7	4.5	4.6	3.5	0.9	24	0.17	**0.44**	**0.42**	0.18				-0.13	
$Mean\ prod$	11.19	13.56	18.77	21.70	22.58	18.12	2.82	16	**0.45**	0.36	0.37	0.15		-0.19		0.18	-0.20
$Mean\ gb_S$	10.82	11.11	13.55	18.09	22.67	14.05	2.53	18	**-0.48**					0.15	-0.14		
$Mean\ gb_P$	23.41	27.36	33.22	38.24	45.14	33.18	4.02	12		0.21	0.18		**0.43**	-0.18	-0.20	0.14	-0.12
$dfrac$	0.26	0.31	0.35	0.39	0.51	0.35	0.03	8	0.19							0.16	
fT_{dfrac1}	0.03	0.04	0.08	0.18	0.52	0.09	0.07	67	0.16				0.13	0.12			
fT_{dfrac2}	0.09	0.36	0.53	0.69	0.74	0.52	0.13	25	**-0.45**	0.24		-0.19				-0.16	
fT_{dfrac3}	0.08	0.19	0.39	0.56	0.60	0.38	0.13	34	0.37	-0.27		0.15				0.14	
fT_{dfrac4}	0.00	0.00	0.00	0.00	0.27	0.00	0.03	782	-0.22		-0.13	-0.34			0.13		
fT_{dfrac5}	0.00	0.00	0.00	0.00	0.10	0.00	0.01	1581									
$mean\ vit$	1.01	1.77	2.87	3.72	4.00	2.80	0.64	23	0.34	0.18	0.34	0.23	-0.17	-0.29	-0.32	-0.14	-0.33
$mean\ vit_{dfrac1}$	1.00	1.19	2.62	3.42	4.00	2.49	0.78	31	0.29	0.13	0.35	0.26		-0.39	**-0.44**	-0.20	-0.21
$mean\ vit_{dfrac2}$	1.00	1.73	2.86	3.73	4.00	2.81	0.66	24	0.33	0.15	0.31	0.26	-0.15	-0.29	-0.32	-0.13	-0.33
$mean\ vit_{dfrac3}$	1.01	1.75	2.93	3.83	4.00	2.87	0.66	23	0.33	0.23	0.30	0.14	-0.17	-0.16	-0.22		-0.34
$mean\ vit_{dfrac4}$	0.00	0.00	0.00	0.00	3.50	0.12	0.53	425	-0.17	0.15	-0.13	-0.37			0.17	0.14	
$mean\ vit_{dfrac5}$	0.00	0.00	0.00	0.00	1.00	0.00	0.06	1581									
$mean\ ANPP$	369	572	829	1049	1237	822	177	21	0.28	**0.56**	0.23		0.35	0.13	-0.15		
$min\ ANPP$	133	309	625	805	932	586	177	30	0.31	**0.57**	**0.50**	0.13	0.31				
$max\ ANPP$	663	940	1194	1449	2447	1200	186	15	0.15	0.38			**0.55**	0.30		0.26	
$ANPP$	133	367	694	894	983	659	187	28	0.33	**0.54**	**0.44**	0.17	0.23				
B_S	119	305	496	728	892	506	152	30	-0.19	0.31	0.25						
$max\ B$	412	638	861	1295	2330	931	282	30	**-0.78**	0.17	**-0.43**	**-0.50**	0.21	0.34			
Relative correlation strength (*rcs*, out of 24 variables):									0.25	0.22	0.20	0.15	0.14	0.11	0.07	0.07	0.06
fT_G	0.00	0.29	0.54	0.22	1.00	0.55	0.21	0.38		**0.63**		-0.66		0.16			
cov_{EL}	0.00	0.11	0.00	0.12	0.38	0.02	0.05	3.03	-0.21	**-0.43**	**-0.54**						
cov_{ES}	0.00	0.01	0.00	0.00	0.01	0.00	0.00	1.29	-0.21	-0.40	**-0.49**	-0.16					
$mean\ PUE$	0.06	0.11	0.27	0.19	0.41	0.25	0.07	0.27	0.18	**0.47**	**0.68**		-0.12	0.15	0.26		
C	0	72	281	63	649	295	136	0.46		**0.96**	0.30	**-0.55**	0.14				
$Mean\ C$	0	71	278	64	629	291	135	0.46	-0.13	**0.96**	0.29	**-0.56**	0.15	0.13			
$Mreal$	0.00	0.12	0.24	0.09	0.55	0.25	0.10	0.41	-0.20	**0.75**		**-0.74**		0.15			

The ranking of parameters indicates that each biological process (colonization, mortality, and vitality dynamics) has at least one parameter with relatively high correlations with the response variables and thus can be interpreted as important process for vegetation dynamics. Although this finding was intuitively expected, it was not clear if a rigorous analysis would confirm this expectation. This was because I have no data about the relative ranking of soil water related processes and I tried to include only important processes. An interesting finding is that the water threshold parameters show a stronger *rcs* than the correspondent survival probability parameter, e.g parameters ColWS0 vs. ColS0p, survival probability for seedlings (Fig. 4.4 A). Another interesting finding is that if I compare parameters from scenario **NG$_i$** which were later grouped within the grouped scenario **NG$_g$** (Tab. 2.3) is that in most cases one or two parameters of a given sub-process (e.g. MortW1 from the parameter group water induced mortality MO W, Tab. 2.3) are strongly correlated, while the other parameters of the given sub-process show only weak correlations (see Tab. 4.6, and Tab. II.2 for **NG$_i$**). This indicates that a sub-process is driven by one or two parameters only and that it may thus be possible to abstract some parameters and thus reduce the model's complexity without loosing much of information. This is an one important step towards an up-scaling of this model to the next larger spatial scale. A priori it was not clear which parameters of a sub-process would be the most important ones, because it was unknown how the model would behave.

Comparing both No grazing calibration scenarios. — Comparing the grouped and the independent parameter run for the No grazing scenario (Fig. 4.4 A and Fig. 4.4 B), I find that the most relevant parameters (senescence and littering) are the same. Modifications of the ranking can be observed in parameter groups with lower *rcs*. The parameter group water induced mortality (MO W, Fig. 4.4 B, for parameter group definition see Tab. 2.3) shows higher correlations than the parameter-group water induced vitality change (VD W). Parameters of the Colonization group (CO G), which comprises the parameter for seedling emergence colonization cover threshold (ColS0Cov) and colonization probability in the 1st – year (ColS0p), show higher average correlations than the soil water threshold related parameter group (CO W, Tab. II.3). Thus, grouping of parameters may lead to shifts in the relative ranking of sub-processes within one process (e.g. Colonization). An explanation for this is that a sub-process is more reduced in relative correlation strength the more parameters it includes which show no significant correlations to the investigated response variables. This finding shows that it is not straight forward to find the most important sub-process for reduction in model complexity. Thus, at this point it becomes evident that up-scaling of a bottom up simulation model is by far a non-trivial challenge.

Parameter ranking for calibration scenarios Grazing. — The calibration scenarios including grazing (**G$_i$**, Tab. 4.7, Fig. 4.4 C, Tab. II.4, and **G$_g$**, Fig. 4.4 D and Tab. II.5 (Appendix II) show important similarities with the no grazing scenarios: the senescence rate is the most important, the littering rate is nearly as important as senescence (at 4th position), then the basic plant productivity (ProdV1), water induced vitality increase 2 (VincW2) and the water induced vitality decrease 2 (VdecW2) follow. However, there are also important differences between grazed and ungrazed calibration scenarios: Colonization and mortality related parameters show reduced relative correlation strengths for the grazed scenarios and are reduced within the ranking. The most important new parameter is the stocking rate, which is absent for the No grazing calibration scenarios and is nearly as important as senescence, and shows the highest correlations for the grouped scenario (Fig. 4.4 D). This finding was expected, because stocking rate affects several processes. The biological interpretation of the finding that both senescence and stocking rate show the highest correlations is that both processes (grazing and senescence/littering) compete for the available living biomass. This interpretation emphasizes the importance of adequate estimations of senescence and littering rates.

Small scale water redistribution by live tussocks. — The second new parameter with high
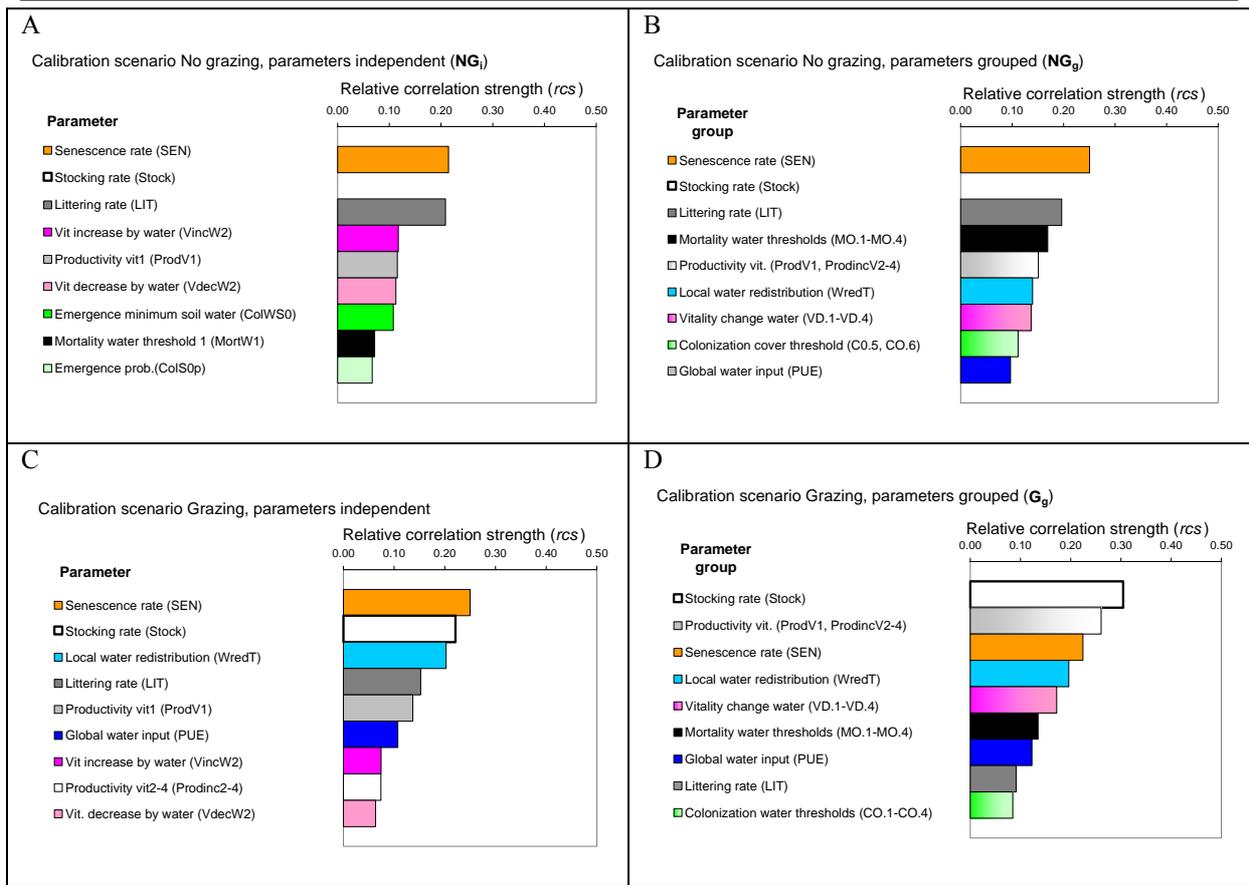
Fig. 4.4: Sensitivity analysis: Relative importance of parameters for the calibration scenarios after calibration.

Shown are the aggregated results of the sensitivity analysis performed after the 1st Calibration step for the four calibration scenarios defined in Tab. 4.3 and Tab. 2.3. Parameters are ranked using the mean relative correlation strength (*rcs*) of one parameter/sub-process with 24 variables. The mean relative correlation strength is the mean out of the absolute values of all significant correlations between the regarded response variables and one parameter/sub-process (detailed results see Tables 4.6, 4.7, II.2-5, Appendix II). calibration scenarios: **A)** No grazing, all 29 parameters run independently (**NG$_i$**); the parameter Stocking rate (Stock) is included for illustrative purposes at the rank it contains for scenario **G$_i$**; **B)** No grazing, parameter grouped (**NG$_g$**, 15 parameter groups); **C)** Grazing, all parameters run independently, (**G$_i$**, 30 parameters); **D)** Grazing, parameter grouped (**G$_g$**, 16 parameters). Same colours refer to the same sub-process (e.g. black = soil water induced mortality). In brackets the included parameters are listed. If one colour passes over to white more than one parameter is included into this sub-process.

ranking is the local water redistribution by tussocks (WredT, see Fig. 4.4 C-D). This result indicates that small-scale processes like water gain by live tussocks from the neighbourhood may play an important role for the vegetation dynamics in a grazed system. This finding was not expected, because the maximum value I chose for this parameter during parameter variation (20 mm, see Tab. 2.3) was low relative to the mean annual precipitation (MAP = 375 mm). A biological interpretation is that vegetation dynamics under grazing becomes more stable, if the tussocks are able to provide themselves with resources from the neighbourhood. This improves both tussock vitality and plant productivity, and reduces the overall relative grazing pressure. This also may reduce the decrease of the tussock vitality if a tussock is grazed. But there is also a trade-off included within this dynamics, so the interpretation is not straight forward. A tussock which improves productivity gaining water from its neighbourhood increases its probability of being accepted for grazing and exerts higher competition against neighbouring emerged seedlings. Nevertheless, this finding is a highly interesting

non-trivial result of the spatial component of this simulation model. The next important parameters within the ranking of scenario G_i are Global water input (PUE) and Productivity increment by vitality 2-4 (ProdInc2-4) reflecting that parameters contributing to plant productivity become more important, i.e. the functional component of the vegetation dynamics increases in importance relative to structural components.

Comparing both grazing calibration scenarios. — The grazing scenario with grouped parameters (G_g) shows similar results as G_i, which parameters were run independently (compare Fig. 4.4 C and 4.4 D). Differences are, that stocking rate and the parameter group plant productivity by vitality (PG V) rank higher than senescence rate (SEN), the parameter groups vitality change by water (VD W), mortality by water (MO W) and colonization water thresholds (CO W) increase in ranking, whereas littering rate (LIT) decreases in rank. These differences suggest that within the grazing scenarios the grouping of parameters leads to stronger changes in ranking than within the calibration scenarios without grazing. The strong decrease in relative correlation strength of the littering rate might reflect therefore that under grazing less biomass is available for littering due to the removal of biomass by grazing.

Conclusion of the aggregated sensitivity analysis. — Concluding this overview over the sensitivity analysis, which investigated the relative importance of the parameters, I state that the parameters (for independent parameter runs) or sub-processes (for grouped parameters calibration scenarios) senescence and littering rate, the stocking rate, the local water redistribution by live tussocks and tussock vitality change by water, are those parameters/sub-processes which show the highest correlations with the investigated response variables and thus are evaluated as the most important parameters or sub-processes. Grazing and senescence are the parameters with the highest importance because they compete against each other for the available plant biomass. Water redistribution on the small scale (WredT) is an important parameter contributing to vegetation dynamics of the grazed scenario. There are normally one or at most two parameters per sub-process, which show strong correlations to model predictions. This is an important finding which indicates that model complexity can be reduced by removing parameters of a sub-process.

I assume that a parameter is important if it shows high ranking. This is only true, however, if an important parameter could not be restricted considerably in range by calibration. In this case it would show a low ranking. As most parameters retained a wide initial range, low correlations can be correctly interpreted as low effect on the response variables.

Detailed analysis of specific response variables and specific parameters. — Now I analyse if there are strong correlations between specific response variables and specific parameters, parameter groups or other response variables. Such an analysis should indicate whether response variables exist which are highly correlated to a small number of parameters or variables. If this is the case for a variable it might be easily predicted by a small number of parameters or with a relative simple linear model. I consider the key variables tussock density (Td_S), ANPP per tussock (gb_P), simulated mean vitality per grid (*vit mean*), the mean dead biomass fraction per grid (*dfrac*), and additionally for the Grazing calibration scenarios the available forage per tussock (*TB*), mean consumed forage (*Mean C*), and mean precipitation use efficiency (*mean* PUE). All significant rank correlation coefficients for the variables Td_S, gb_P, *vit mean*, and *dfrac* with specific parameters are given for the calibration scenario NG_i at Fig. 4.5 A (for the six most relevant parameters), Tab. 4.6 and Tab. II.2 (Appendix II); for scenario G_i at Fig. 4.5 B (for the six most relevant parameters), Tab. 4.7 and Tab. II.4 (Appendix II; for NG_g and G_g at Tab. II.3 and Tab. II.5 (Appendix II) respectively.

Selected correlations of response variables are given in Tab. 4.8 for the independent calibration scenarios NG_i and G_i. Correlations for grazing related response variables are given in Tab. 4.7 below and at Fig. 4.5 C.

Tussock density. — *Tussock density* shows the highest correlation with stocking rate (scenario $\mathbf{G_i}$, $cor._{Stock} = 0.41$ (Fig. 4.5 B). This result is not intuitive because one would expect a negative correlation between Td_S and Stocking rate, i.e. tussock density should decline with increasing stocking rate. For a specific model parameterisation this hypothesis is true (see following sections), if only stocking rate is varied. But during the calibration scenario Grazing, independently run parameters $\mathbf{G_i}$ each model parameterisation was run only with one stocking rate out of the whole range. Thus, a model parameterisation including a high stocking rate (e.g. Stock = 2.0 sheep / ha) may fulfil the applied pattern filter combination only, if other parameters are combined with that stocking rate in such a way that the specific filter combination is still fulfilled. E.g. the parameterisations might be selected with the highest productivity parameter values, low senescence and littering rates, low mortality thresholds etc. If such parameterisations are biologically plausible, should be tested in a following step.

Tussock density, further correlations. – The second significant correlation is that to local water redistribution ($\mathbf{G_i}$, $cor._{WredT} = 0.33$, Fig. 4.5 B). This correlation is biologically meaningful; it means that the more water tussocks may extract from the neighbourhood, the higher the probability is to remain at higher tussock density. The third significant correlation is a negative one to Vitality increase by water 1 (VincW1, $cor_{VincW1} = -0.25$, $\mathbf{NG_i}$, see Tab.II.2, Appendix II)) and finally to Global water input (PUE, $cor._{WUE} = 0.19$ ($\mathbf{NG_g}$, Tab.II.3, Appendix II). The negative correlation between Td_S and VincW1 shows how the water threshold for vitality changes affects tussock density, e.g. if vitality increases already at relatively low soil water status levels, we would observe higher densities than otherwise. The empirical knowledge about sub-lethal effects of soil water on plant vigour is scarce and was not yet investigated at the *Festuca* steppe.

The analysis for tussock density shows that no strong correlations (i.e. cor. $> \pm 0.70$) exist, which would allow to predict tussock density with a relative simple linear model and a few independent parameters. Most correlations between the investigated response variables and model parameters show values below cor. $< \pm 0.70$. This reflects the complex interplay of different processes which finally lead to the value at the higher level variable, as e.g. tussock density.

Mean vitality. — The next very important variable is *mean vitality* of tussocks, because it co-determines strongly (together with precipitation) annual production of a tussock (*prod*) and thus is highly correlated, as expected, with the mean annual production per tussock (*mean prod*), with values $cor._{gbP} = 0.63$ and 0.55 ($\mathbf{NG_i}$ and $\mathbf{G_i}$, respectively, Tab. 4.8)). For the scenario No grazing with independent parameters ($\mathbf{NG_i}$) mean vitality shows a complex picture of medium strong correlations with the following parameters (Stocking rate (Fig. 4.5 B), VincW2 (Fig. 4.5 A), MortW1 (Tab. II.5, scenario $\mathbf{G_g}$, WredT (Fig. 4.5 A), VdecW2, PFinc, ColWS2 and others, see Tab. II.2 and Tab. II.3). Thus, nearly all biological processes contribute significantly to mean vitality: vitality dynamics by water, mortality by water, Colonization, and local water redistribution.

Mean annual net primary production per tussock. — Mean annual net primary production per tussock (*mean prod*) shows two strong correlations with response variables: one with *mean vit* ($cor._{mean\ vit} = 0.63$, Tab. 4.8, see above), and with basic plant productivity (ProdV1, $cor._{ProdV1} = 0.72$, $\mathbf{NG_i}$, Fig. 4.5 A). These correlations are expected, because they reflect the plant productivity equation (see Appendix I, eqn. I.6). Correlations between *mean prod* and ProdV1 are weaker for grazed scenarios ($cor._{ProdV1} \sim 0.45$, Fig. 4.5 B).
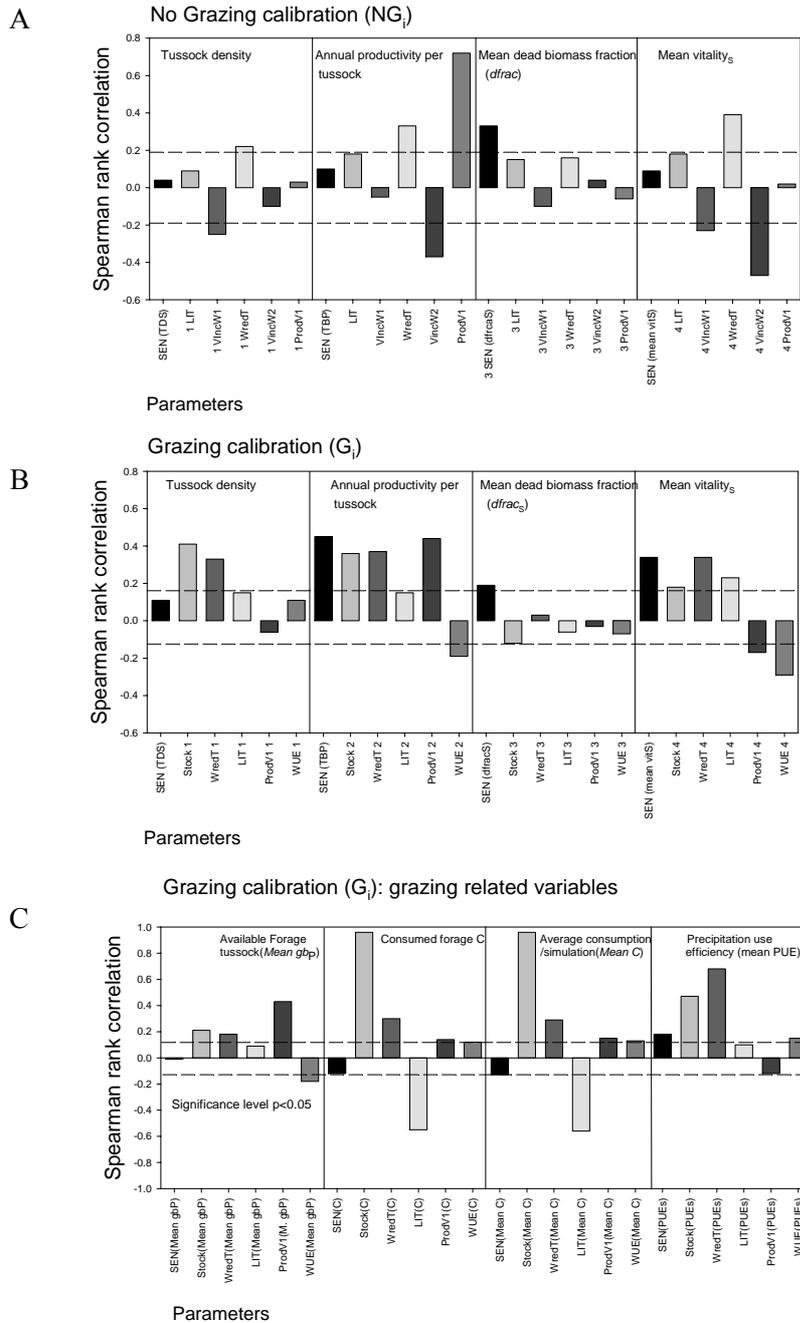
Fig. 4.5: Sensitivity analysis: Correlations between exemplar response variables and parameters.
Shown are the Spearman rank correlations for the calibration scenarios No grazing and Grazing, run with independent parameters. **A)** Calibration scenario No grazing, independent parameters (**NG$_i$**), significance level: $p = 0.05$ (for cor. $\geq \pm 0.19$, $N = 105$); correlations of the variables tussock density, Annual net primary production per tussock, mean dead biomass fraction and mean vitality with: SEN: senescence rate; LIT: littering rate; VincW1: vitality increase due to soil water status 1; WredT: local water redistribution by tussocks; VincW2: vitality increase by soil water status 2; ProdV1: basic plant productivity at vitality = 1; **B)** Calibrations scenario Grazing, parameter independent (**G$_i$**); significance level: $p = 0.05$ (for cor. $\geq \pm 0.12$, $N = 250$); correlations of the variables as in A) with the parameters: SEN, Stock: stocking rate; WredT; Lit; ProdV1; PUE: precipitation use efficiency per tussock. **C)** Calibrations scenario Grazing, parameter independent (**G$_i$**), correlations with grazing related response variables: available forage per tussock (*mean g$_P$*); Consumed forage (*C*) at time step (*t*); mean consumed forage per simulation (*mean C*).

100

Tab. 4.8: Correlations between response variables for the calibration scenarios NG_i and G_i.
    A): Calibration scenario No grazing, parameters independent (NG_i, N = 105); significance level: $p < 0.05$; **B)** Calibration scenario Grazing, parameters independent (G_i, N = 250); significance level: $p < 0.05$; Variables are explained in detail in Tab. 2.2. Bold: Correlations (cor.) $\geq \pm\,0.4$

A

NG_i	Td_S	Mean prod	Mean gb_S	dfrac	mean gb_P	fT_{dfrac1}	fT_{dfrac2}	fT_{dfrac3}	fT_{dfrac4}	fT_{dfrac5}	Mean vit	mean vit_{dfrac1}	mean vit_{dfrac2}	mean vit_{dfrac3}	mean vit_{dfrac4}	mean vit_{dfrac5}
Td_S	■					-0.15		0.18			0.15		0.21	0.13	0.13	
Mean prod		■	0.17		0.34			0.25	-0.21		**0.63**		0.24	**0.54**	**0.59**	
Mean gb_S	0.17		■	-0.25	**0.97**	0.35	-0.31	0.17	-0.19	-0.14	0.13	0.33		0.20	0.19	-0.13
dfrac			-0.25	■	-0.20	**-0.74**			**0.50**	0.19		-0.23				0.15
mean gb_P		0.34	**0.97**	-0.20	■	0.27	-0.33	0.27	-0.25	-0.17	0.24	0.31	0.16	0.29	0.28	-0.17
fT_{dfrac1}	-0.15		0.35	-0.74	0.27	■	-0.14	-0.30	-0.18			0.31	-0.16			
fT_{dfrac2}			-0.31		-0.33	-0.14	■	**-0.46**		0.24	-0.28	-0.13	-0.39	**-0.40**	-0.13	0.26
fT_{dfrac3}	0.18	0.25	0.17		0.27	-0.30	-0.46	■	**-0.69**	-0.34	0.21		**0.41**	0.36		-0.37
fT_{dfrac4}		-0.21	-0.19	**0.50**	-0.25	-0.18		-0.69	■		-0.14	-0.12	-0.23	-0.24		
fT_{dfrac5}		-0.14	0.19		-0.17		0.24	-0.34		■					0.13	**0.93**
Mean vit	0.15	**0.63**	0.13		0.24		-0.28	0.21	-0.14		■	0.25	**0.44**	**0.86**	**0.94**	
mean vit_{dfrac1}			-0.23		0.31	0.31	-0.13		-0.12		0.25	■		0.30	0.24	
mean vit_{dfrac2}	0.21	0.24			0.16	-0.16	-0.39	**0.41**	-0.23		**0.44**		■	**0.46**	0.27	-0.13
mean vit_{dfrac3}	0.13	**0.54**	0.20		0.29		-0.40	0.36	-0.24		**0.86**	0.30	**0.46**	■	**0.74**	
mean vit_{dfrac4}	0.13	**0.59**	0.19		0.28		-0.13			0.13	**0.94**	0.24	0.27	**0.74**	■	0.15
mean vit_{dfrac5}			-0.13	0.15	-0.17		0.26	-0.37		**0.93**			-0.13		0.15	■

B

G_i	Td_S	Mean prod	Mean gb_S	dfrac	Mean vit	mean vit_{dfrac1}	mean vit_{dfrac2}	mean vit_{dfrac3}	mean vit_{dfrac4}	Mean gb_P	mean ANPP	B_S	max B	Mean PUE	C	Mean C	Mreal
Td_S	■				0.23	0.20	0.22	0.20		**0.66**		**0.77**		**0.84**	**0.41**	**0.41**	
Mean prod		■	0.13		**0.55**	**0.46**	**0.55**	**0.53**		**0.73**	**0.64**	0.20	-0.18	0.21	**0.40**	0.39	0.15
Mean gb_S	0.13		■						-0.13	**0.72**		**0.58**	**0.60**				-0.35
dfrac		0.55		■					0.14				-0.17				-0.14
Mean vit	0.23	**0.55**			■	**0.86**	**0.97**	**0.91**	-0.17	0.34	0.31	0.20	**-0.42**	0.25	0.20	0.19	
mean vit_{dfrac1}	0.20	**0.46**			**0.86**	■	**0.86**	**0.68**	-0.17	0.31	0.27	0.19	-0.40	0.21	0.17	0.16	
mean vit_{dfrac2}	0.22	**0.55**			**0.97**	**0.86**	■	**0.82**	-0.17	0.36	0.31	0.22	-0.38	0.23	0.17	0.16	
mean vit_{dfrac3}	0.20	**0.53**			**0.91**	**0.68**	**0.82**	■	-0.16	0.28	0.29	0.13	-0.40	0.25	0.26	0.25	
mean vit_{dfrac4}			-0.13	0.14	-0.17	-0.17	-0.17	-0.16	■	-0.12		-0.16	0.20		0.15	0.15	0.28
Mean gb_P		**0.73**	**0.72**		0.34	0.31	0.36	0.28	-0.12	■	**0.54**	**0.52**	0.29		0.23	0.23	
mean ANPP	**0.66**	**0.64**			0.31	0.27	0.31	0.29		**0.54**	■	**0.63**		**0.58**	**0.58**	**0.58**	0.13
ANPP	**0.78**	**0.65**			**0.46**	0.39	**0.46**	**0.43**		**0.50**	**0.91**	**0.69**		**0.74**	**0.56**	**0.56**	
B_S	**0.77**	0.20	**0.58**		0.20	0.19	0.22	0.13	-0.16	**0.52**	**0.63**	■	0.32	**0.62**	0.31	0.30	-0.24
max B		-0.18	**0.60**	-0.17	**-0.42**	-0.40	-0.38	-0.40	0.20	0.29		0.32	■	-0.18	0.15	0.15	0.14
mean PUE	**0.84**	0.21			0.25	0.21	0.23	0.25		**0.58**		**0.62**	-0.18	■	**0.48**	**0.47**	
C	**0.50**	**0.41**	0.32		0.17	0.15	0.19		-0.26	**0.49**	**0.56**	**0.64**		**0.46**	■	-	**0.93**
Mean C	0.17											0.18		0.16	-	■	**0.93**
Mreal	**0.40**	0.34	-0.26		0.31	0.28	0.27	0.36		**0.45**		0.19	-0.13	**0.52**	**0.93**	**0.93**	■

A — Parameter: Local water redistribution (calibration scenario Gi)

Variables	-1.00 … -0.60 … -0.20 … 0.00 … 0.20 … 0.60 … 1.00
Tussock density	(positive)
Mean vitality	(positive)
Mininum ANPP	(positive)
Cover large bare patches	(negative)
Precipitation use efficiency	(positive)
Min. forage consumed	(positive)
Min. Mreal	(positive)

Significant rank correlation (Spearman)

B — Parameter: Gshape (calibration scenario Gi)

Variables	-1.0 … -0.6 … -0.2 … 0.0 … 0.2 … 0.6 … 1.0
Fraction of grazed tussocks	(positive)
Mean Forage consumed (mean C)	(negative)
Minimum Forage consumed	(negative)
M Real	
Minimum M real	(negative)
Maximum M real	(negative)

Significant rank correlation (Spearman)

Fig. 4.6: Correlations of local water distribution and grazing shape with exemplar response variables.
    Shown are data from the Calibration scenario Grazing, parameters independent (G_i). **A)** Parameter local water redistribution by tussocks (WredT). **B)** Parameter Gshape, which triggers forage selectivity of herbivores in dependence of *dfrac*.

Dead biomass fraction. — Dead biomass fraction (*dfrac*) shows a complex behaviour due to relatively weak correlations with several parameters: the highest one which was expected is that with senescence rate (SEN, $cor._{SEN} = 0.33$, **NG$_i$**, Fig. 4.5 B). Other significant correlations exist to one vitality decrease parameter (VdecW2, **NG$_i$**, Tab. II.2), to local water redistribution WredT (**NG$_g$**, Fig. 4.5 B) and to plant productivity parameters.

Mean available forage per tussock. — Mean available forage per tussock (*mean gb$_P$*) is a key variable which indicates the potentially available biomass for livestock. *Mean gb$_P$* shows strong negative correlations both to senescence ($cor._{SEN} = -0.89$, **NG$_i$**) and littering ($cor._{LIT} = -0.69$, **NG$_i$**, both see Tab. 4.6) These correlations emphasize the importance of both parameters as 'competitors' to stocking rate as a biomass consumer. Weak positive correlations were found with plant productivity ProdV1 and to the water threshold parameter for seedlings (ColWS0, both **NG$_i$**, see Tab. 4.6). The correlations of *mean gb$_P$* with *mean vitality* are weak for the two calibration scenarios, with independent parameters: at the No grazing scenario correlation is $cor._{mean\ vit} = 0.24$, (**NG$_i$**, Tab. 4.8), and at the Grazing scenario $cor._{mean\ vit} = 0.34$, (**G$_i$** Tab. 4.8). The weak correlation for both scenarios is unexpected. This finding might reflect the effect of the wide range of both parameters SEN and LIT into sensitivity analysis. Hence available forage may include a highly variable fraction of biomass carry over remaining from several years before, which dies at highly different rates and thus reduces correlation between mean vitality of tussocks and available forage.

Mean consumed forage per simulation. — Mean forage consumed per simulation and year (*Mean C*) has got a strong correlation with grazing ($cor._{Stock} = 0.96$, **G$_i$**, Fig. 4.5 C, Tab. 4.7), a intermediate correlation with littering ($cor._{LIT} = -0.56$, **G$_i$**, Fig. 4.5 C, Tab. 4.7), but only a weak correlation with senescence ($cor._{SEN} = -0.13$, **G$_i$**, Fig. 4.5 C, Tab. 4.7). This result reflects the finding, that littering rate is a stronger antagonist to stocking rate than senescence rate under grazing. But it is not an intuitive result. One might expect that senescence should be more important, because it directly reduces the available green biomass which is available for consumption. But grazing reduces green biomass and with it the absolute amounts of biomass available for senescence. Thus the relative importance of senescence rate decreases. Now littering rate takes over the importance, because lower littering rates lead to higher and longer lasting fractions of dead biomass, which increase forage selectivity and thus reduce the relative amount of green biomass which is consumed. This explanation emphasizes the importance of our initial hypothesis that forage selectivity is increased by above ground standing dead material.

Defoliation shape. — A very interesting result is that the minimum of consumed forage (*min C*) is strongly correlated to the defoliation shape parameter ($cor._{Gshape} = -0.83$, G$_i$, Fig. 4.6 B). Also the realized minimum relative grazing intensity (*min Mreal*) is strongly correlated to the defoliation shape parameter ($cor._{Gshape} = -0.63$, **G$_i$**, Fig. 4.6 B). Both correlations show that if forage selectivity increases with increasing values of the parameter Gshape, the minimum consumed forage is reduced, which might be relevant during drier years. Finally, precipitation use efficiency is strongly correlated with local water redistribution WredT ($cor._{WredT} = 0.68$, **G$_i$**), and with stocking rate ($cor._{Stock} = 0.47$, **G$_i$**, see Fig. 4.6).

Conclusion. — I conclude this section emphasizing that due to the complexity of the interacting processes some central variables might not be easily predicted with simple linear models, as e.g. tussock density and mean vitality. In contrast annual productivity (*mean prod*) shows two high correlations. Thus, this essential variable seems to be more accessible to prediction. However, one of the highly correlated variables is mean vitality; thus, *mean prod* is not easy to predict. These findings justify the use of a complex simulation model for understanding the complex processes governing the impact of grazing and precipitation on the biological processes of the *Festuca* steppe. Interesting results are the high correlations of local water redistribution with precipitation use efficiency and the

correlation of the grazing shape parameter with minimum consumed forage.

4.3.3 Validation of 1st step calibrated parameterisations

After the first step of calibration I performed a validation, since additional estimates are available for several secondary predictions, which were not used during the 1st step of calibration. Fig. 4.7 exemplifies two important secondary predictions: the *min ANPP* per patch and the maximum green and dry standing biomass (*max B*). Only rough expert estimates are available for both variables (Compare section 4.2.8). Fig. 4.7 shows that the accepted parameterisations are likely to underestimate the *min ANPP* in most cases, if I assume a potentially natural *Festuca* steppe. The underestimation of *ANPP* could be a consequence of the confidence interval for tussock density in the No grazing scenario (**NG**). Some of the exclosures were only established recently and grazing was only excluded for few years. Thus, these data might reflect the grazing history rather than the natural state without grazing.

The validation of maximum biomass (*max B*) shows a contrary result (Fig. 4.7 B). An important fraction of the accepted parameterisations overestimates the theoretical estimation the maximum biomass (*Max B* ~ 2.400 kg / ha). The intuitive explanation for this overestimation is that too low senescence and littering rates lead to a long-term accumulation of biomass, which is biologically unrealistic. Alternatively, the overestimation could also be a consequence of a too tolerant biomass pattern filter **P21** (Tab. 4.2).

Conclusion of validation. — As a consequence of these validation results, a further model calibration was essentially necessary at this point.
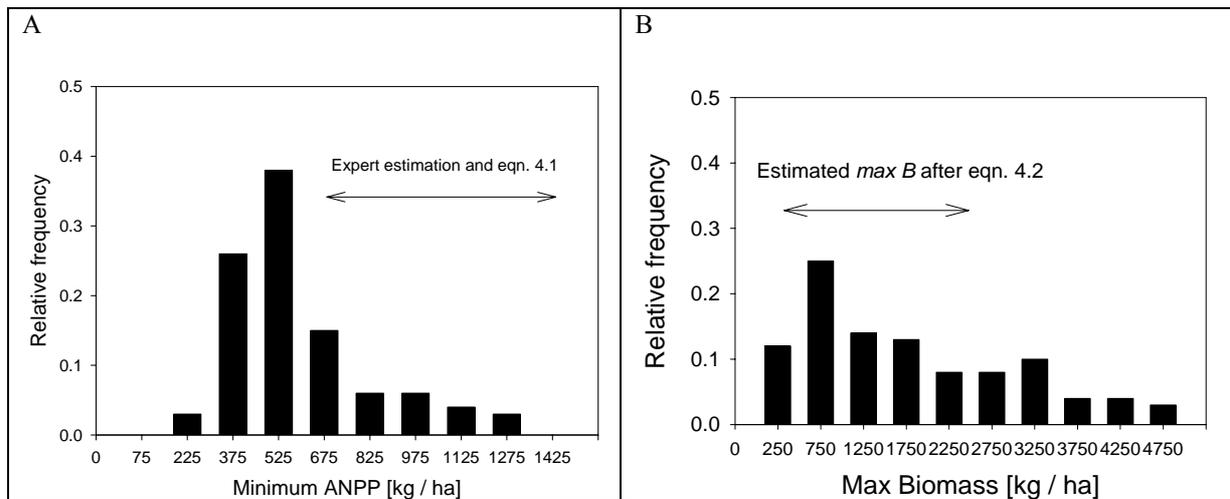
Fig. 4.7: Validation of accepted parameterisations after 1st step of Calibration
Shown are the frequency distributions of all accepted parameterisations from Calibration 1st step over the secondary predictions **A)** Minimum annual net primary production *ANPP* and B) maximum live biomass (*max B*) for validation against the range estimated in section 4.2.8. Used was the Calibration scenario No grazing, independent parameters (**Ng$_i$**, N = 105). In many cases *ANPP* and *max B* are under- or overestimated: values for *ANPP* < 631 kg / ha, and values for *max B* above approx. 350 kg / ha < *max B* < 2365 kg / ha are biologically unrealistic. These findings require additional calibration of the accepted parameterisations out of the 1st step of Calibration. A minimum *max B* could not be determined; a determination of a maximum for *ANPP* was not necessary because maximum values lie within the expert estimation.

Tab. 4.9: Variability of parameters accepted after the 2nd Calibration step.

Shown are: (row 3) the median for each parameter taken from the 41 accepted parameters after the 2nd step of calibration. The median is regarded as a 'best fit'. Row 4 shows the parameter values from the expert estimation. Mean deviations from the best fit are shown for the expert parameter estimation (row 5) and for the mean out of the 41 accepted parameterisations (row 6). Row 7 and 8 indicate the standard deviation and the coefficient of variation (CV) of the 41 deviations from the median ('best fit'). Row 9 gives the mean rcs calculated out of the scenarios NG_i and G_i. **Legend**: NG_i: calibration scenario No grazing, independent parameters; G_i: Grazing, parameter independent; Row 5 and 6: white with bold margins: Parameter deviation $\leq 15\%$ from median; **grey shadowed**: deviation $15\% \leq p \leq 30\%$; **grey shadowed and bold**: deviation $p > 30\%$.

Rank mean correlation strength (*rcs*, mean of **G**i + **NG**i calibration)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Parameter	SEN	Stock	LIT	WredT	ProdV1	VincW2	VdecW2	VIncW1	WUE	ProdncV2-	MortW1	ColWS0	MortWp1	ColS0p	PFinc
Median out of 41 parameterisations	0.5	0.4	0.4	9	160	250	270	200	0.53	51.5	195	180	0.26	0.28	0.5
Expert estimation	0.6	0.5	0.4	5	150	250	260	200	0.57	50	180	200	0.2	0.3	0.83
Expert estimation: % deviation from median	20	25	0	44	6	0	4	0	9	3	8	11	23	7	66
Parameter mean deviation from median out of 41 valid parameterisations	24	142	40	50	17	15	15	14	12	16	14	14	37	42	53
Standard deviaton of mean deviation from median	18	117	34	38	10	11	7	11	8	11	9	11	25	22	32
CV of mean deviation from median	0.75	0.82	0.86	0.76	0.59	0.75	0.46	0.76	0.67	0.67	0.67	0.77	0.67	0.52	0.60
Mean relative rank correlation strength (**G**i + **NG**i calibration)	1.00	0.89	0.79	0.68	0.54	0.42	0.38	0.28	0.26	0.26	0.24	0.23	0.16	0.16	0.15
Rank mean correlation strength (*rcs*, mean of **G**i + **NG**i calibration)	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Parameter	VdecG	VdecW1	ColWS2	VdecGp	PFmax	ColWS1	ColS0Cov	Gshape	MMconst	WredO	MortGp	ColS12p	MortW2	MortWp2	MortG
Median out of 41 parameterisations	0.5	210	135	0.8	22	170	40	0.79	52	24	0.06	0.84	205	0.12	0.67
Expert estimation	0.5	200	140	0.8	30	170	40	0.50	55	20	0.05	0.9	200	0.1	0.60
Expert estimation: % deviation from median	0	5	4	0	#	0	0	36	6	17	17	7	2	17	10
Parameter mean deviation from median out of 41 valid parameterisations	31	13	17	12	48	19	24	66	18	19	28	9	16	46	23
Standard deviaton of mean deviation from median	18	9	10	9	30	11	15	48	11	17	25	5	10	26	14
CV of mean deviation from median	0.58	0.70	0.59	0.78	0.62	0.59	0.64	0.74	0.63	0.88	0.91	0.57	0.65	0.55	0.60
Mean relative rank correlation strength (**G**i + **NG**i calibration)	0.13	0.11	0.09	0.08	0.07	0.07	0.06	0.06	0.05	0.03	0.02	0.00	0.00	0.00	0.00

Calibration against validation variables: 2nd Calibration step. — As a consequence of the result of validation I filtered the accepted parameterisations (1st calibration step) with the variables *mean vit*, *min mean prod*, and *max B*, using the values described in Chapter 4.2.8. More restrictive confidence intervals were applied for the calibration scenario Grazing (G_i, e.g. $1.4 \leq$ *mean vit* ≤ 2.4, Table 4.2), whereas *mean vit* > 1 for No grazing (NG_i) was left more tolerant. The stricter use for scenario G_i was possible due to the high number of accepted parameterisations. A lower limit for *min mean prod* could not be defined and *max B* was validated positively for all parameterisations after validation against *mean vit*. The result of 2nd step of Calibration were 40 accepted parameterisations for the scenarios NG_i and G_i plus the standard parameterisation P_S which were used for the following two steps of calibrations which included the stochasticity of precipitation sequences.

Variability of validated parameters. — Table 4.9 shows the median for each parameter out of the 41 accepted parameterizations (Tab. 4.9, 2nd and 3rd row). The parameter ranking corresponds to the *mean relative correlation strength* (*rcs*), calculated out of the *rcs* from calibration scenarios G_i and NG_i (first row, Tab. 4.9, values for *rcs* are normalized between 0 and 1). The five parameters with the highest correlation strength show mostly high variability $> 30\%$ (Tab. 4.9, 5th row 'Parameter mean deviation from median'), only the parameters senescence rate SEN and 'basic productivity' (ProdV1) show a moderate one ($15\% \leq x \leq 30\%$). The next seven ranked parameters mostly show low mean variability ($\leq 15\%$) around the median.

Comparing the best fit estimates with expert estimation. — I calculated the median values for all parameters out of the accepted parameterisations after the 2nd calibration step. Assuming independence between parameters, this median could represent a first rough estimate of a 'best fit-parameterisation'. The correlations between parameters are in general weak (see Tab. II.6, Appendix II). A very strong positive correlation between LIT and SEN (littering and senescence) exists, as expected. A weak significant negative (cor. ~ -0.3 between precipitation use efficiency PUE and water distribution by tussocks (WredT) exists, which might indicate a weak compensatory effect between both parameters. Nevertheless, this correlation is that weak that for a first rough analysis, it is justified to regard them as independent.

The standard parameterisation estimated by the field ecologists (P_S) deviates slightly from the calculated median which represents my first 'best fit'. The field experts estimation (P_S, Tab. 4.9, 4th row 'Expert estimation: % deviation from median') shows in general lower deviation from the 'best fit' estimates than the mean variability of the 41 parameterisations (Tab. 4.9, compare 4th and 5th row). From the 10 parameters with the highest relative correlation strength (*rcs*) only local water redistribution (WredT) shows a high deviation from the best fit. Senescence (SEN) and stocking rate (Stock) deviate moderately, the other parameters deviate only slightly.

High variability of stocking rate. — The high variability of the parameter stocking rate (Stock, Tab. 4.9, 5th row) after the 2nd step of calibration was expected, because I did not yet include a pattern which controls the effect of grazing. However, in the next two steps all accepted parameterisations will be run over the whole stocking rate range and calibrated as run for No grazing and for Grazing (**Cross calibration**).

The variability of the other 4 highly ranked parameters to reflect the remaining uncertainty within these parameters. The low variability of the following seven parameters (VincW2 to ColWS0, 5th row) can be attributed to a good estimate of these parameters or to the limited degree of freedom which is left for a stable system.

Conclusion. — I conclude that the independent parameter estimation from the field experts provided values which lie very close to the 'best fit' estimate of the model parameters. The five parameters with the highest ranking show moderate variability. This variability may be attributed to a lacking of cross calibration or it reflects the remaining uncertainty about these parameters, assuming their biologically plausibility.

4.3.4 Calibration 3rd step

Now I present the results of the cross calibration including stochastic climate repetitions (Step 7 of the protocol, section 4.2.2). This calibration step takes the stochastic variability of precipitation into account. This is important, because precipitation has a strong effect on some model variables. Additionally, parameterisations, which were calibrated under grazing conditions, are now calibrated under No grazing conditions and vice versa (Cross calibration). The 3rd calibration step calibrates the results of the accepted 41 model parameterisations only against a restrictive set of variables which represents a *Festuca* steppe in good compositional state (compare Tab. 4.4).

Main result. – Only 15 of the 41 parameterisations were accepted and are selected for the next calibration step (Tab. 4.10, first row, framed parameterisations). Most of the accepted parameterisations (12) came from the Grazing calibration scenario, only 2 from the No grazing scenario. The expert estimation was also accepted. Thus the Grazing parameterisations provide more stable results, when averaged over 100 climates than the No grazing parameterisations. The reason why the No grazing parameterisations perform weaker is not clear. They reproduce in most cases *mean ANPP* well, but fail in *Min ANPP*. The threshold for *Min ANPP* may still be too restrictive, despite that it was chosen below the 50%-value of the minimum estimate for annual productivity for a

Tab. 4.10: Results of 3rd Calibration step: Cross calibration against no grazing conditions.

Shown is the ranking of how well the 41 calibrated model parameterisations fulfil the criteria for 11 primary and secondary predictions (patterns) after 100 repetitions with different stochastic climates (compare Tab. 4.4). All runs exclude grazing. Selected parameterisations for the final calibration step are framed and marked in bold (first row). The applied aggregated Cc-index threshold was: 9 out of 11 patterns (approx. 80%) had to fulfil the given variable thresholds and ranges during at least 80 out of the 100 simulations with different stochastic precipitation sequences (the applied confidence interval). Two groups of model parameterisations can be described after this calibration step. The selected group fulfils 90% of the given criteria, whereas the rejected group fulfils only less than 50% of the given criteria. This threshold behaviour is mainly correlated with two variables: $ANPP(t)$ and the aggregated variable *Festuca state*, which is a classification of the degradation state as a combination of tussock cover and $ANPP(t)$ (compare Tab. II.1). $ANPP(t)$ and *Festuca state* seem to be highly correlated, so a mismatch of one threshold normally leads to a mismatch in both pattern. The most sensitive variable is *max B* (last row). The selection threshold for *Max B* was probably too strict. The next sensitive variables are *Min ANPP* and *Min Td*$_S$.

Model parameterisation			5	6	24	26	28	1	2	3	4	7	8	23	41	9	25	15	16	20	22	29	11	18	21
			Cc index: N fulfilled patterns for all variables for the given confidence interval																						
Applied confidence interval (% fulfillment out of 100 repetition)		80%	11	11	11	11	11	10	10	10	10	10	10	10	10	9	9	5	5	5	5	5	4	4	4
		90%	11	11	11	11	11	10	10	7	10	10	10	10	9	9	9	3	2	4	4	2	0	2	1
		95%	10	11	11	11	10	10	10	7	10	10	10	10	9	9	9	1	2	4	0	0	0	2	1
Variable	**Threshold criterion**	**time step**	N fulfilled threshold criteria for one variable and 100 repetitions with stochastic precipitation																						
Tussock density $Td_S(t)$	>3.3	50	100	100	100	100	100	100	100	97	100	100	99	100	100	99	100	93	97	98	95	86	83	93	84
Tussock density $Td_S(t)$	>3.3	150	100	100	100	100	100	100	100	97	100	100	97	100	100	100	100	67	90	97	94	87	84	37	40
Min. Tussock density $Td_S(t)$	>2.1	1-50	100	100	100	100	100	100	100	100	100	100	98	100	100	100	100	99	96	96	95	94	85	100	100
Min. Tussock density $Td_S(t)$	>2.1	1-150	100	100	100	100	100	100	99	100	100	97	100	100	100	100	100	80	89	88	87	78	60	99	80
$ANPP_S(t)$	>750 Kg/ha	50	95	100	97	100	100	100	100	82	100	100	100	100	96	99	100	47	25	43	33	30	31	14	25
$ANPP_S(t)$	>750 Kg/ha	150	94	100	97	99	100	100	100	81	100	100	96	100	98	97	100	17	17	50	30	31	33	2	3
Festuca state	7-9/13-15	50	95	100	97	100	100	100	100	82	100	100	98	100	83	99	100	47	25	43	33	30	31	14	25
Festuca state	7-9/13-15	150	94	100	97	99	100	100	100	81	100	100	95	100	95	97	100	17	17	50	30	31	33	1	3
Min ANPP $_S$	>350kg/ha	1-150	98	100	100	100	100	100	100	100	100	100	100	100	100	100	100	87	45	56	36	26	10	90	60
Mean ANPP $_S$	600-2200 kg/ha	1-150	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	93	85	98	95	93	86	72	82
Max B	1500-2500 kg/ha	1-150	100	100	98	100	91	0	0	23	64	75	100	0	16	0	53	78	0	32	56	86	0	0	1

Tab. 4.10 (continued).

Model parameterisation			27	38	32	35	30	31	34	36	10	12	13	14	17	19	33	37	39	40
			Cc index: N fulfilled patterns for all variables for the given confidence interval																	
Applied confidence interval (% fulfillment out of 100 repetition)		80%	4	4	3	2	1	1	1	1	0	0	0	0	0	0	0	0	0	0
		90%	2	2	1	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0
		95%	2	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Variable	**Threshold criterion**	**time step**	N fulfilled threshold criteria for one variable and 100 repetitions with stochastic precipitation																	
Tussock density Td_S	>3.3	50	72	94	77	81	64	70	43	71	24	17	4	62	0	74	55	53	36	44
Tussock density Td_S	>3.3	150	29	86	82	61	67	76	37	77	5	0	0	52	0	65	55	46	9	31
Min. Tussock density Td_S	>2.1	1-50	98	85	82	53	40	35	53	51	15	79	37	60	3	68	12	35	35	34
Min. Tussock density Td_S	>2.1	1-150	86	54	37	12	6	3	16	9	0	17	0	18	0	23	0	6	2	2
ANPP	>750 kg/ha	50	24	51	64	76	51	52	33	60	6	2	2	13	0	40	22	38	27	13
ANPP	>750 kg/ha	150	1	51	62	57	55	53	27	62	0	0	0	4	0	35	22	37	6	6
Festuca state	7-9/13-15	50	24	51	64	70	51	52	32	59	6	2	2	13	0	40	22	38	27	13
Festuca state	7-9/13-15	150	1	51	60	56	55	53	25	62	0	0	0	4	0	35	22	37	6	6
Min ANPP	>350 kg/ha	1-150	100	57	79	17	10	5	53	18	0	1	0	5	0	10	0	7	1	12
Mean ANPP	600-2200 kg/ha	1-150	84	100	99	91	95	95	81	93	0	5	0	12	0	77	48	69	30	34
Max Biomass	1500-2500 kg/ha	1-150	33	0	0	0	52	8	0	0	12	0	0	14	0	24	0	0	0	0

F. pallescens steppe in a good compositional state. I assume that it should have taken into account climatic variability in a sufficient way. The selection criteria for model calibration were probably too wide, so that also less stable parameterisations were accepted. Additionally No grazing parameterisations were not selected for productivity, whereas the Grazing calibration scenarios where

indirectly selected for productivity. A further reason might be a too favourable precipitation scenario obtained by chance, which leads to erroneous positive calibrations.

Conclusion. — Fifteen parameterisations were accepted during the 3rd calibration step, of these 12 come from the Grazing calibration scenario with independent parameters (G_i), 2 from the ungrazed scenario with independent parameters (NG_i), and the expert estimation P_S was also accepted. These parameterisations reproduce consistently an assumed natural *Festuca* steppe under no grazing conditions. The most critical response variables are *Min ANPP* and *max B*. It is difficult to find reasonably good estimates for both variables. Both variables were already identified as very sensitive during validation.

4.3.5 Calibration 4th step

The fourth step of Calibration and the second of **Cross calibration** (**Cc**) filtered the 15 selected parameterisations against the median of pattern **P1**, tussock density Td_S, but over the entire range of stocking rates. This procedure is necessary to avoid too optimistic estimations of the

Tab. 4.11: Results of the 4th calibration step.
Parameterisations are filtered by using the median of tussock density out of 100 stochastic climate repetitions separately for each stocking rate. Shown are those parameterisations, which were accepted during the 3rd step of calibration (Tab. 4.10). The acceptance criterion was: tussock density < 3.3 at stocking rate 1.5 or higher. Accepted parameterisations are framed (1-8, 41).

Results 4th Calibration step	Stocking rate [n / ha]								
	0.0	0.0	0.3	0.6	0.9	1.2	1.5	1.8	2.1
Time step \ Parameterisation	50	150	150	150	150	150	150	150	150
1	5.1	4.6	4.4	4.0	3.1	0.1	0.0	0.0	0.0
2	4.9	4.4	2.6	0.2	0.0	0.0	0.0	0.0	0.0
3	5.3	5.1	5.0	4.8	4.5	4.1	3.2	1.4	1.1
4	6.2	6.0	5.6	5.2	3.6	0.0	0.0	0.0	0.0
5	6.2	6.1	5.9	5.6	5.3	4.8	1.7	0.5	0.3
6	6.3	6.4	5.8	5.2	4.7	4.0	1.6	1.2	1.1
7	6.0	5.9	5.4	5.0	4.7	4.3	3.0	1.2	0.8
8	6.3	6.0	5.7	5.4	5.1	4.4	3.1	1.1	0.7
9	6.7	6.6	6.5	6.4	6.0	5.5	4.7	2.6	0.5
23	7.0	7.4	7.4	7.2	6.9	6.2	4.4	0.5	0.3
24	5.3	4.9	4.7	4.5	4.4	4.2	3.9	3.5	2.6
25	6.2	6.2	6.0	5.7	5.4	5.1	4.7	4.1	2.0
26	6.4	6.3	6.3	6.2	6.2	6.1	5.7	5.0	3.9
28	5.1	4.8	4.8	4.7	4.6	4.4	4.0	3.4	2.3
41	8.0	8.1	7.7	7.4	6.9	6.0	1.1	0.1	0.0
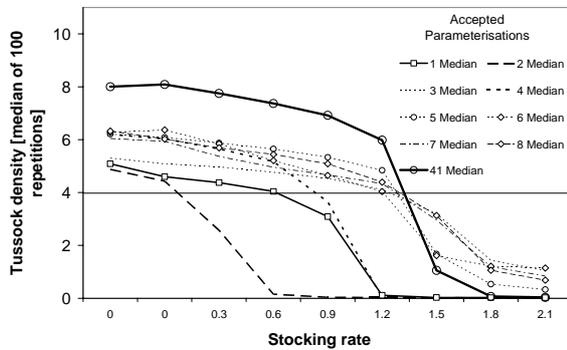
Fig. 4.8: Finally accepted parameterisations.
Shown are the median of tussock density over the whole range of stocking rates for 100 repetitions of stochastic climates.

sustainable stocking rate. Such parameterisations may lead to extreme stable dynamics of *F pallescens* (i.e. no reduction of *Festuca* cover) under unrealistically high stocking rates. To avoid this I defined the threshold criterion that tussock density should decrease below $Td_S < 3.3$ after 100 time steps of grazing at a stocking rate of 1.5 sheep / ha or higher. Nine out of 15 parameterisations fulfilled this condition (Tab. 4.11, and Fig. 4.8). These 9 parameterisations are finally used for further model simulation experiments. Only one of these parameterisations results from the No grazing scenario with independent parameter run (**NG$_i$**), one is the field expert estimation, and finally 7 parameterisations come from independent parameter run including Grazing (**G$_i$**).

As I calibrated only the calibration scenarios run with independent parameters (**NG$_i$** and **G$_i$**) completely, but not the grouped parameters, more parameterisations will be accepted if the grouped calibration scenarios will be calibrated analogically. But I expect, that for the grouped calibration scenarios, too, the No grazing scenario will provide less accepted parameterisations than the Grazing scenario.

4.4 DISCUSSION

The chapter had the following aims:

- to investigate if calibration and partially validation of the simulation model presented in Chapter 2 and Chapter 3 was possible despite limited empirical data. and a new calibration
- to analyse the relative importance of the independent parameters and processes with respect to the key variables of the *Festuca* steppe in a sensitivity analysis using the remaining parameterisations after the first step of calibration.

The main results from model calibration were:

First, it was possible to calibrate the presented simulation model of the *F. pallescens* steppe, despite limited data of 14 samples á 30 tussocks for grazed paddocks, and 6 samples á 30 tussocks for non grazed exclosures. Thus, the inverse pattern oriented approach is a powerful tool to parameterise medium complex simulation models with some 30 unknown parameters.

Second, calibration using grouped parameters lead to a higher number of accepted parameterisations than calibration with independent parameters. The calibration of the No grazing, parameter independent calibration scenario yielded only few accepted parameterisations. This was due to the extreme selectivity of pattern **P5** which describes the tussock distribution over *dfrac*-classes.

Third, a stepwise approach of calibration was developed which was necessary because of the stochasticity of precipitation. In a first step I excluded parameterisations which produced highly improbable simulation results compared with the observed pattern. For this coarse assessment I used only one stochastic climate series. In a second step I used the reduced set accepted parameterisations for fine-calibration considering the full range of stochastic climates (i.e., 100 stochastic series).

Fourth, validation of parameterisations accepted in the 1st calibration step with independent data (not used during this calibration step) was possible and necessary and improved the calibration considerably.

Fifth, I defined an aggregated criterion for model calibration which allowed excluding unrealistic parameterisations in a more objective manner, because 100 stochastic rainfalls were considered and the strong impact of one stochastic rainfall was eliminated.

Sixth, I defined for sensitivity analysis a multi-criteria index (relative correlation strength, *rcs*), which summarizes the significant correlations between an independent parameter and important response variables. This enabled me to assess the relative importance of one parameter (or process) for the whole model. For the calibration scenario No grazing, the most influencing parameters were

senescence rate and littering rate, for the Grazing scenarios they were senescence rate, stocking rate, littering rate, basic tussock productivity, and local water redistribution by tussocks. The weighted correlation strength for both grazing and no grazing lead to following ranking in importance for following parameters and processes: senescence rate, stocking rate, littering rate, local water redistribution and basic plant productivity.

4.4.1 Discussion of the Calibration method

First calibration step. — Model calibration was possible despite the limited data due to the multi-criterial pattern oriented approach of filtering the simulation results. This approach combines several weak patterns which would have, taken in isolation, a high uncertainty. However, several weak patterns together constrained the model dynamics successfully because each pattern removes parameterisations which produce highly improbable behaviour in one pattern. An important tool enabling such a calibration was the bootstrapping of the field data for the definition of confidence intervals (compare Tab. 4.2). The bootstrapping allows considering the uncertainty inherent to the field data. The selectivity of the filtering approach was highly improved by the generation of hierarchical filters (**P5**, tussock distribution over *dfrac*-classes1-5, $fT_{dfrac1-5}$), which consisted out of five sub-patterns (**P51-P55**) and thus generated a strong selecting pattern.

Calibration yielded a reasonable amount of accepted model parameterisations for all calibration scenarios (No grazing and Grazing, parameters independent, **NG$_i$** and **G$_i$** respectively, and for the grouped scenarios, Grazing or No grazing (**G$_g$** and **NG$_g$**, respectively).

However, one scenario showed a limited amount of accepted parameterisations: the calibration scenario No grazing, independent parameters (**NG$_i$**). Several reasons may explain this finding. First, the complex pattern **P5**, tussock distribution over *dfrac*-classes 1-5 filtered too strict. This occurred probably due to a high inverse correlation of *dfrac*-class3 and *dfrac*-class 4 to precipitation: *dfrac*-class 3 is positively correlated with rainfall while *dfrac*-class 4 is negatively correlated. Thus, during a good year, *ANPP* is high and *dfrac* will be reduced and vice versa, consequently, tussocks change between both *dfrac*-classes depending on the rainfall (see Chapter 5). I discovered this effect too late to repeat the subsequent calibration steps.

A biological explanation is that 'no grazing' is not a natural state of the *Festuca* steppe, because it is assumed that the steppe evolved under light grazing (Lauenroth 1998, Baldi et al. 2001, M. Bertiller, pers. comm.). Therefore, under no grazing, the dead biomass fraction would become larger than field values for no grazing exclosures. One can assume that the exclosure excluded only grazing by large herbivores such as sheep or guanacos, but not rodents, hares and others.

Finally, it is possible, that a biological process is lacking, at least for the no grazing scenario: a density dependent reduction of biomass production by tussock with high dead biomass fraction. A high dead biomass fraction may shade the remaining living tillers and lead to reduced productivity. This effect may reduce *dfrac* and later cause a recovery in productivity. This hypothesis could be tested in the field. However, this process may not influence the quality of the calibration. Our biomass growth rule includes already a general assumption of growth saturation, which may be induced by shading or saturated response at high soil water levels. Such biomass production rules are applied for individual plants (Passioura 1982, Richter 1985, Richter and Söndgerath 1990).

Multi-criterial comparison in Sensitivity Analysis. — The most important result of the sensitivity analysis consists in a quantitative evaluation of the relative sensitivity of different parameters for a large number of response variables. This was done using the mean absolute significant values of the Spearman rank correlation of one parameter with all compared response variables. Multi-criteria model evaluation is a complex, non-trivial task (Reynolds and Ford 1999), so an intuitive interpretable and easy calculable approach to compare the influence of a large number of

parameters on a large number of response variables may help generating a fast and comprehensive understanding of a complex system.

A limitation of this approach is that the selection of response variables will have an important impact on the ranking. To obtain comparable results, I included for each analysis the same set of variables. For the analysis of the Grazing calibration scenarios (G_i, G_g), it would be useful to analyse additional variables, not giving response within the No grazing scenarios, e.g. mean consumed forage (*mean C*). Including such grazing related variables will lead to a relatively stronger importance of the stocking (Stock) and littering rate (LIT) than senescence (SEN, data not shown). Another point of consideration is that I did not normalize the comparison to the number of analysed parameterisations. If one uses very low numbers of parameterisations for sensitivity analysis, results may be biased due to relatively stronger effect of stochasticity, because of the reduced sampling of the parameter space. Thus, I avoided sensitivity analysis with less than 100 parameterisations. A lower limit of a reasonable number of good estimates of sensitivity has yet to be determined.

Regarding this approach it is important to have in mind that the relative importance of one parameter or process does not decide about the quality of the parameters' estimation. Parameters, which show low correlations with most variables and are ranked low may be estimated very good, so that they do not have further impact on the response variable within the remaining parameter space. Such an evaluation has to take into account the variability of the remaining parameters (compare Tab. 4.9).

Validation. — An in-between validation of the accepted parameterisations was possible and necessary after the first step of calibration. As aggregated data for large scale *ANPP* or standing green phytomass were not available, theoretical, from literature derived values (Bertiller and Defossé 1993) were used for validation. For the remaining parameterisations I calculated after this validation the variability of the parameters, and a weighted relative correlation strength (*rcs*), that integrates the results for the grazing and no grazing scenarios. Tab. 4.9 shows that the four parameters with the highest influence on the response variables showed high variability, whereas the following eight medium sensitive parameters show low variability. So the last group might be estimated appropriately with remaining but reduced sensitivity, whereas the first group should be specified more in detail for specific situations or scenarios.

4.4.2 Biological interpretation of the results of the Sensitivity analysis

The most important parameters found during parameter estimation and sensitivity analysis were: Grazing or stocking rate respectively, senescence and littering, local water redistribution, and finally basic plant productivity at the lowest vitality level. The second most important group is lead by three parameters of water induced vitality change, and then water use efficiency and finally one parameter group of soil water induced mortality and seedling survival in the first year. Thus, within the 15 most important parameters all processes of the model are found to have some relevance for the model results.

The importance of stocking rate is intuitive, as it modifies a series of processes. The importance of senescence and littering is also intuitive, because they are competitors of herbivores in consuming the green biomass. But the high correlation with the investigated variables as e.g. with tussock biomass after senescence (B_S), tussock distribution at dfrac-class1 (0-20% dead material, $fT_{Sdfrac1}$), mean tussock biomass before senescence (*Mean gb_P*), and maximum biomass (*max B*) – all examples for calibration scenario **NG_i** (No grazing, parameters independent) was somehow surprising. The importance of both processes emphasizes the importance of an adequate estimate of these parameters, which is especially difficult in perennial species with evergreen leaves.

The importance of the basic plant productivity parameter (ProdV1) is also clear. Nevertheless

our knowledge about the link between structure and function on a small scale individual level is scarce. However, for an adequate description of the productivity dynamics of perennial plants one need to understand better how the compositional state of a perennial plant is related to its history, because this may decide about its productivity for the future. This analysis proved that a good estimate of the potential productivity of a 'standard tussock' is essential for estimating productivity and in consequence the grazing impact on a specific system.

The high correlation of local water redistribution at live tussocks (WredT) with the investigated variable was unexpected. Though being theoretically easy to postulate and intuitively relevant, the role of spatial local water redistribution was neglected to date. Tongway et al. (2001), Sparrow et al. (2003) and Maestre et al. (2002) discuss the importance of small-scale water redistribution for the pattern formation in semi-arid regions.

Local water redistribution has both a stabilizing and inhibiting effect on the system. It stabilizes the adult tussocks, because they benefit from resources in the neighbourhood, and survive better during drier years. On the other hand, resource competition reduces the survival probability of neighbouring conspecific seedlings and thus limits recruitment. If local water redistribution is working within this system, the best site for *Festuca* seedling to recruit should be theoretically a larger distance away from all *Festuca* adults. This would be a larger bare soil or matrix patch. But these bare soil interspaces often loose their seed bank very fast (see Chapter 2, discussion of empirical evidence). Seed bank loss in interspaces is probably due to second phase dispersal. However, the indirect consideration of a reduced recruitment within 'large bare patches' was not an important factor during sensitivity analysis (WredO, see Table II.2-5, Appendix II). However, seed bank loss may also take place in interspaces smaller than the size of the defined large bare patches. The model shows theoretically optimal recruitment if one seedling has in each direction two cells distance (approx. 60 cm) to an adult tussock. Thus optimal recruitment results within an interspace of 90×90 cm. If the interspace is smaller, competition with adult tussocks occurs. The larger an interspace the higher the probability of seed bank loss due to wind. How interspace area and seed bank loss by wind are correlated, was yet investigated. I assume that 90 cm $\times$ 90 cm interspaces are sufficiently large to be subject to larger seed loss due to wind.

I postulate a trade-off between asymmetric competition of adults against juveniles (Weiner 1990) and the size of interspaces, which increases the probability of seed loss due to second phase dispersal. That would be the **competition-second phase dispersal trade-off**. The larger the distance of a seed to its mother plant, the higher the survival probability. However seed bank loss due to wind dispersion increases with interspace size. Possibly, additional factors exists which could modify or determine the fate of a seedling. At first, the adult tussock density around an interspace may play a role. A high density around a medium sized interspace could protect the seeds better from wind dispersion. Lower wind dispersion enhances the probability of seedling germination in an interspace and thus seedling survival. Secondly, a process which leads to buried seeds could enhance recruitment in interspaces. This finding was highlighted by Rotundo and Aguiar (2004). Accordingly, it would be interesting, which processes could contribute to the burying of *Festuca* seeds in interspaces. Trampling by herbivores, burying by dispersion of litter, potentially the role of insects, or rodents should be considered. Despite the fact that a systematic investigation with the simulation model lacks to date, some features can be highlighted which are important for recruitment.

Some interesting findings from the analysis concern parameters which seem to have low impact on model output. E. g. seedling survival in the second and third year had low correlations with the investigated variables. Nearly all grazing related parameters, besides stocking rate itself, had low correlations. The parameter with the highest correlation was vitality decrease by grazing (VdecG, 12th highest correlation, (**G$_i$**) see Table II.4, Appendix II). This can be interpreted in two directions: first, it

is mainly the stocking rate itself that has an impact on the vegetation dynamics, because relative grazing intensity has effect on several processes directly. Secondly, each process is affected by grazing in a subtle way and the overall negative long-term effect is an additive effect of a large number of small negative effects, which for itself are difficult to detect.

Senescence and littering. – The sensitivity analysis highlighted the importance of both littering and senescence for the grazing system. It is intuitive that these processes are important, because these are the biological 'consumers' of living biomass, hence reducing the forage amount and quality for herbivores. Despite the importance of these processes, it is very difficult to find parameter estimates for both processes. Coupland (1973) in Coupland (1992) [163] estimated mass fluxes in Canada. Bertiller and Defossé (1990b) calculated relative senescence on a daily basis for the *Festuca* steppe. These estimates could not be translated to a yearly time step, because daily biomass estimates were not known. But otherwise, senescence is mostly neglected both in empirical and in modelling studies. Crawley (1997) named senescence one of the myths of botany, probably from an evolutionary point of view, because its biological 'meaning' seems not to be intuitive nor evident, but this statement underlines how few this phenomenon has been investigated to date.

4.5 CONCLUSION

I presented a sophisticated and new method for calibration of complex simulation models which can be applied when scarce empirical data are available. It can be named as inverse or indirect pattern oriented calibration and is a further development of Wiegand et al. (2003, and 2004b). Despite calibration of simulation models to field data is often neglected in ecology, a series of examples for calibrated or validated models in ecology do exist: Dieckkrüger et al. (1995), Higgins et al. (2001), Nathan et al. (2001), Clark et al. (2003), Gordon et al. (2004), Wiegand et al. (2003), Wiegand et al. (2004a/b), Risch et al. (2005), and Schurr et al. (2005). To date I could not find any example in Ecological Modelling, where 30 uncertain model parameters were calibrated in one step, as I presented within this chapter. The strength of model calibration is that it increases the confidence in the simulation model and that it ensures that model simulations produce an outcome which is within the biologically plausible range, given that the implemented biological rules are reasonable. Based on an extensive documentation of the biological knowledge about *F. pallescens* and its implementation as rules into the model, combined with the calibration, I showed that the model is biologically reasonable. Consequently, it was possible to estimate nearly 30 parameters at one step. Obviously, it would be desirable that some of the most relevant parameters would be further estimated empirically or by experiments.

4.6 VIEW

This chapter provided a novel approach for a step wise pattern oriented calibration and indirect parameter determination for a medium complex simulation model with 30 parameters, which could not be estimated in the field. The method developed by Wiegand et al. (2003, and 2004b) was further developed and applied successfully on a situation with strongly limited field data for model calibration and highly stochastic model behaviour due to the occurrence of stochastic precipitation sequences. Additionally the sensitivity analysis of the calibrated model parameterisations gave interesting new insights into biological mechanism of a semi-arid grazing system. The accepted model parameterisations, which represent the range of remaining biological uncertainty, are used in the following Chapter for simulation experiments. This will additionally show how the remaining biologically uncertainty will affect the simulation results.

5 INTERACTING BIOLOGIC AND ABIOTIC MECHANISMS EXPLAINING STRUCTURAL CHANGE OF A SEMI-ARID STEPPE

5.1 INTRODUCTION

Degradation of drylands occurs on a global scale, with an estimated minimum of 70% of the area affected in Africa, Asia and the Americas and more than 50% in Australia (Cardy 1994). However, the true extent of the problem is difficult to quantify (Pickup et al. 1998) due to the non-equilibrium behaviour of the ecosystems (DeAngelis and Waterhouse 1987, Westoby et al. 1989, Walker 1993) caused by rainfall variability, which imposes dramatic changes in vegetation within short-terms. This causes a masking of the negative trends in vegetation condition except in the most extreme cases (e.g. Foran et al.1986). A controversy about the status and trend of rangelands exists, particularly in the African Sahel. The debate continues on whether the environmental changes labelled as `desertification´ represent massive land degradation or a misinterpretation of climatic variability (see Pickup et al. 1998, Fuhlendorf et al. 2001, Archer 2004). Non-equilibrium behaviour also makes it difficult to determine if land continues to degrade, remains in a stable condition, or improves, even when remote sensing data is indicating a change over time (Pickup et al. 1998). The presented work aims to investigate the interplay between short-term stochastic precipitation and grazing and how this interplay affects degradation of vegetation on the long term.

Degradation refers to different characteristics of an ecosystem: to soils, vegetation (Rubio and Bochet 1998), and animal productivity (Illius and O'Connor 2000). Degradation of vegetation cover can be defined by structural destruction or removal of the vegetation cover (Rubio and Bochet 1998) and, as a consequence, a functional degradation of productivity of plant species important for foraging in rangelands (Milchunas and Lauenroth 1993, Oesterheld et al. 1999). For a more detailed discussion of the effect of grazing on plant productivity see Chapter 3.

The semi-arid areas of Patagonia in Argentine are one of the large areas menaced by degradation (Del Valle et al. 1998). Increasing desertification in Patagonia is the main socioecological problem of the region (Soriano and Movia 1986). Del Valle et al. (1998) classified the desertification of arid Argentine Patagonia with satellite data for the whole region (approx. 780.000 km²). They found that more than 60% of the area was in the category of moderate to severe desertification or even in a stronger desertified state. However, they focussed strongly on soil characteristics and neglected to some extent the role of vegetation. Additionally, they could not separate the effects of natural and anthropogenic impacts on desertification. The separation of both effects in a stochastically fluctuating environment is one of the keys to understanding grazing impact on vegetation in an unpredictable environment (Fuhlendorf and Briske 2001, Archer 2004).

The aim of this chapter is to gain an understanding of how grazing affects vegetation under highly variable, unpredictable precipitation. I use a simulation model, which includes the effects of grazing and precipitation on the essential biological processes of the dominant species of the *Festuca* steppe, *Festuca pallescens* (see Chapter 2 and 3). This approach allows for separating the effects of grazing and climate on different hierarchical levels, both on a higher one (e.g. vegetation or population dynamics), and a more detailed one (e.g. specific biological processes such as establishment or mortality). Additionally, the simulation approach allows evaluating sustainable management strategies, under climatic uncertainties and uncertainty regarding the knowledge about the biological dynamics. Remaining biological uncertainty is mostly expressed as remaining parameter uncertainty (Clark 2003, Clark et al. 2003, Higgins et al. 2003, Wiegand et al. 2004a/b, see Chapter 4). The determination of a sustainable grazing regime aims to avoid a decline of the key variable, tussock density below threshold values, from which regeneration of *F. pallescens* will be difficult.

Consequently this chapter is focussed mainly on the changes of tussock density under grazing and stochastic climate. Tussock density is a key structural component of vegetation dynamics (Briske et al. 2003). Additionally I assess the long-term effects on consumable biomass exerted by livestock under different grazing regimes and stochastic climate. This perspective provides the link to animal productivity which has been investigated thoroughly during the last years (Fynn and O'Connor 2000, Illius and O'Connor 2000). However the impact of grazing on vegetation under stochastic climate is poorly understood (Fuhlendorf et al. 2001, Archer 2004). I will use the simulation model presented in Chapter 2 and Chapter 3 and the accepted parameterisations gained in Chapter 4 to address the following topics:

1a) I analyse the impact of grazing on tussock density under stochastic climate and the remaining parameter uncertainty.

1b) I analyse the grazing impact on tussock density for different time scales, different types of forage selection and different grazing regimes.

2) I derive a criterion for long-term sustainable grazing management under stochastic climate conditions which considers the remaining parameter uncertainty.

3) I analyse the temporal autocorrelation between the precipitation time series and the former state of the vegetation on key variables of the *Festuca pallescens* dynamics.

4) I analyse how grazing and the stochastic climate interact and how this interplay affects the dynamics of *F. pallescens*.

Both the combined consideration of environmental and parameter uncertainty into the analysis of grazing effects on vegetation, and the separation of the natural and the anthropogenic components of the interaction between stochastic climate and grazing, are of general interest and might provide an additional step in advancing our understanding of the complex dynamics of grazing systems.

5.2 MATERIAL AND METHODS

5.2.1 Conduction of experiments

General approach. — The aim of this chapter is to separate the effects of natural exogenous variability, represented here by annual stochastic precipitation, and the anthropogenic effect, represented by grazing, on the dynamics of *Festuca pallescens*. The general assumption is that the high variability in precipitation affects almost all essential biological processes such as establishment, mortality, and the important response variables of *F. pallescens* as e.g. annual productivity, standing green biomass, tussock density and (mean) tussock vitality. Therefore the negative effects of grazing are difficult to detect. The range of precipitation in sites of the *Festuca pallescens* steppe (e.g. Media Luna Ranch) differs up to 40% in both directions from the mean annual precipitation (MAP = 375 mm / year). Thus, a strong impact of precipitation on the dynamics of *F. pallescens* can be expected.

The key questions are: can the effect of grazing be disentangled from the high variability introduced by precipitation? And furthermore, under which conditions does grazing have a negative effect on the primary response variables, simulated tussock density (Td_s) and mean consumed forage (*mean C*)? The contributions of different uncertainties (Clark et al. 2003, Higgins et al. 2003, Wiegand et al. 2004a/b) influencing the variation in the results, have to be separated. I separate three components of uncertainty i) the inherent stochasticity included into the model, ii) the environmental uncertainty represented by precipitation and iii) the remaining parameter and process uncertainty representing mainly the uncertainty of biological processes.

Investigation of the three components of uncertainty. — At first, the inherent stochasticity implemented into the model had to be considered. The inherent stochasticity is given by several processes of the model which include stochastic components, e.g. random selection of tussocks for grazing and other processes (compare model description Chapter 2, Appendix I). I tested the inherent uncertainty by repeating one parameterisation and one climate several times. In this case parameter uncertainty and environmental noise were excluded, because both parameters and the climatic sequence were constants. Then I calculated the coefficient of variation (CV) for important variables and derived their maximum for a certain number of repetitions.

Second, the effect of the environmental noise or climatic uncertainty had to be estimated. I did this by repeating only one parameterisation with 100 different stochastic climates. So the resulting variability of the results is due to both the climatic and the inherent model uncertainty. When the inherent uncertainty was known (see step before), the contribution of climatic uncertainty to total uncertainty could be estimated.

Third, the effect of parameter uncertainty on the behaviour of the response variables was estimated by using simulation results including one repetition of all accepted model parameterisations (see Chapter 4, 4th Calibration step). All these parameterisations produced dynamics in accordance with our data on the *Festuca* steppe. I performed simulations and repeated them with a single climate sequence, so the results reflected the effect of the parameter variation and thus the parameter uncertainty.

Finally, a combination of environmental uncertainty and parameter uncertainty provided a complete picture. In this analysis the simulations described in Chapter 4 (2nd and 3rd calibration step) were used. In total 41 model parameterisations were repeated with 100 stochastic climates for 150 time steps. Only parameterisations were used which passed the calibration process. These were 9 model parameterisations. The first 50 time steps were run without grazing, so that the model reached its equilibrium which is independent from initial conditions. Initial conditions were chosen representing an assumed natural *F. pallescens* steppe with a high cover of around 55-60% (see Chapter 2). Grazing was represented by 8 stocking rate levels between 0 and 2.1 sheep / ha or between 0 and 210 sheep / km². 21 grazing levels between the same ranges were used for the standard model parameterisation (P_S), which was estimated from the empirical field ecologists (see Chapters 2-4). These grazing levels covered and even surpassed the whole theoretically possible range of mean grazing intensities. To my knowledge, stocking rates higher than approx. 1.6 sheep / ha were not observed to date (Bertiller 1996, Chapter 3). The response variables were registered at time steps 50, 75, 100, 125 and 150, from which the first 50 years were discounted. Hence grazing occurred for time steps 51 - 150 or 100 years. Three simulations were run for each investigated scenario (see below). Each scenario consists of 8 grazing levels x 9 parameterisations x 100 climates = 7.200 simulations.

Quantitative estimation of a grazing threshold. — After estimating the impact of different uncertainties I asked if the grazing impact on vegetation showed threshold behaviour. A quantitative analysis to estimate a threshold for the effect of grazing on tussock density was investigated with a standard logistic curve with four parameters (see Fig. 5.1 and eqn. 5.1). I performed simulations for 150 time steps, the 100 last included grazing, with different parameterisations and different numbers of stochastic climatic sequences: with

A)   the standard parameterisation (P_S) and one stochastic climate (21 grazing levels between 0 – 2.0 sheep / ha;

B) P_S and 100 stochastic climate sequences (21 levels of grazing);

C)   9 accepted parameterisations (includes P_S, see Chapter 4) and one stochastic climatic sequences (8 grazing levels, see above); and finally

D)   the same parameterisations as in C) but repeating them with 100 stochastic climates (and the same 8 grazing levels).

These simulations represent a gradient of increasing grazing pressure under constant conditions. I fitted tussock density to a standard logistic curve (eqn. 5.1) which describes threshold behaviour. The threshold behaviour of grazing on tussock density was observed in preliminary simulations and was a general characteristic of the remaining accepted parameterisations (see Fig. 4.8 and Tab. 4.11 Chapter 4).

The threshold parameter *EC50* (eqn. 5.1, Fig. 5.1) estimates the stocking rate at which the fitted tussock density (*max*), which is reached without grazing, is reduced by 50%. The *slope* indicates how strongly tussock density decreases with increasing stocking rate and determines together with the threshold, the stocking rate at which tussock density begins to decrease. The analysis was performed with SigmaPlot (2001).
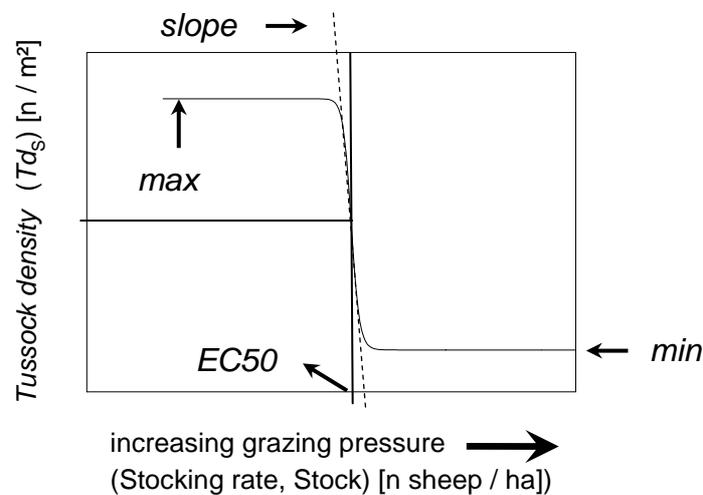
Fig. 5.1: Graphical scheme for estimating the grazing threshold parameter.
The grazing threshold (EC50) denotes that stocking rate, which leads to a decrease of tussock density by 50%. The slope indicates the strength of the decline and that stocking rate at which the initial tussock density begins to decline. Further explanations see text and equation 5.1.

Estimation of the grazing threshold:

$$Td_{S\ fitted} = min + \frac{max - min}{1 + 10^{(\log(EC50 - Stock)) \cdot slope}}$$

eqn (5.1)

$Td_{S\ fitted}$	tussock density fitted by the equation
Td_S	simulated tussock density after 100 time steps of grazing (data used for the fit)
Stock	Applied stocking rate per simulation

Fitted parameters by nonlinear regression (Standard four parameter logistic curve):

min	minimum tussock density estimated for maximum stocking rate
max	maximum tussock density estimated for no grazing
EC50	parameter estimating the threshold stocking rate, at which tussock density declines to 50%
slope	parameter estimating the slope of decrease of tussock density

Forage selection. — After the threshold analysis the effect of different grazing scenarios, including uncertainty, was simulated. These scenarios analyzed the type of forage selection and the seasonality of the grazing regime. A non-selective and a highly selective forage strategy was tested (see Fig. 5.2, eqn. 5.2): the non-selective scenario leads to tussock defoliation as a function of mean grazing pressure, independently of tussock state or its structure, e.g. the dead biomass fraction (*dfrac*).

On the other hand, the highly selective forage model leads to forage selection as a function of the dead biomass fraction (*dfrac*) for each tussock. I assumed that the highly selective foraging model is the more realistic one for situations were sheep are kept in large paddocks with thousands of hectares (compare Chapter 2 and 3).
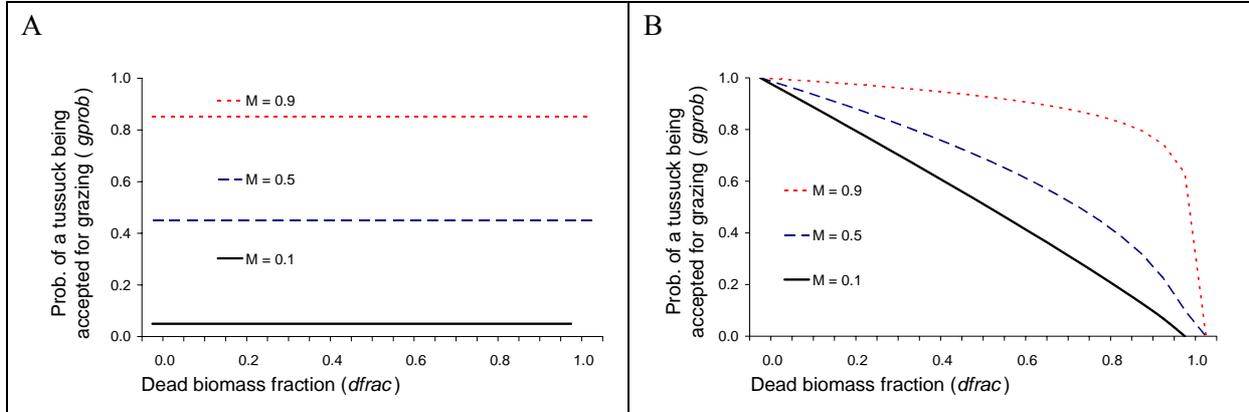
Fig. 5.2: Applied models of forage selection by sheep at the tussock level.
A) Non-selective model: probability of a tussock being accepted for grazing (*gprob*) depends only on relative mean grazing intensity (*M*); **B)** Highly selective forage model: the probability of a tussock being accepted for grazing depends strongly on the tussock structure and hence the dead biomass fraction (*dfrac*).

Probability of a tussock being accepted for grazing, depending on foraging scenario:
Highly selective forage selection (HS), continuous grazing:

$$gprob_{HS}(dfrac, M) = \begin{cases} (1 - dfrac)^{1-M} & , \text{if} \quad 0 < M \le 1 \\ \\ 0 & , \text{else} \end{cases} \quad (5.2a)$$

Non-selective forage selection (NS):

$$gprob_{NS} = M \qquad , \text{for} \quad 0 < M \le 1 \qquad (5.2b)$$

$gprob_{HS/NS}$ Probability of a tussock being accepted for grazing within the High selective forage scenario (HS) or the Non-selective forage scenario (NS)

dfrac   Dead fraction of tussock biomass (tussock structure)

M   Relative grazing intensity

Note that for each tussock a minimum residual biomass (*gbmin*) remains which cannot be grazed. For scenario HS (high forage selectivity) *gbmin* is calculated individually for each grazing event (see eqn. I.9 Appendix I), whereas for the non-selective scenario it is a fixed amount of biomass.

    Seasonal grazing. — Four scenarios of seasonal grazing were analyzed. They included:
i)   continuous grazing all the year round, and seasonal grazing which is represented by grazing during
ii)   only spring grazing,
iii)   grazing during summer and autumn, and finally
iv)   grazing only during winter.

    Since the simulation model acts on a yearly time step, modelling of seasonal grazing is implicit (eqn. I.17, see Appendix I): I assumed that forage selection on tussock structure changed with

season. In relation to continuous grazing, tussock selectivity is assumed to be higher in spring, i.e. the effect of tussock structure is relatively higher compared to the assumed all year mean, which is due to the high supply of fresh green biomass (see eqn 5.2 and, eqn. I.24 and eqn. I.32, Appendix I). On the other hand I assume that forage selection will be reduced in summer, autumn and mainly in winter, when senescence mostly has taken place and a low proportion of green biomass is available.

Seasonal grazing with seasonal altered *dfrac* (only for High selective grazing, HS):

$$
dfrac_S \; = \;
\begin{cases}
dfrac_i \cdot GR.5 & \text{, if } dfrac_i \cdot GR.5 \leq 1, \text{ for } GR.5 \in \left[1.0, 1.5, 0.6, 0.3\right] \\
1 & \text{, if } dfrac_i \cdot GR.5 > 1
\end{cases}
\tag{5.3}
$$

$dfrac_S$ seasonal altered dead fraction of live tussock biomass *dfrac* by weighted herbivore selectivity, only at high selective grazing (HS)

$dfrac_i$ Original dead biomass fraction of live tussock i

$GR.5$ seasonal grazing acceptance: $GR.5 \in \left[cont = 1.0, spr = 1.5, sum = 0.6, wint = 0.3\right]$

cont   continuous grazing all year round

spr   all biomass is removed in spring

sum   all grazed biomass is removed during summer or autumn

wint   all grazed biomass is removed during winter

Generating a criterion for sustainable management — As the variability in tussock density and other variables is high in ecosystems with strongly fluctuating environmental factors, I tested different criteria to estimate long-term sustainable stocking rates. The idea was to define a stocking rate threshold for a key variable, e.g. tussock density, and to test if this variable did not fall below the threshold after long term simulations (100 years) with a probability of say 90%, including parameter and climatic uncertainty. Or, in other words, I searched the stocking rate, which with 90% probability leads to a long term tussock density higher than the defined threshold. This approach would both minimize stocking rates which are allowed on the long-term under a specific climate sequence or under a specific parameter combination (i.e. the biological assumptions), and thus represents a conservative management approach.

The derivation of the sustainable stocking rate for a given scenario includes the following steps: At first, I defined the threshold, under which tussock density should not fall below with a probability of 90%. I decided to take a tussock density (TD_S) of 3.3 (is approx. equivalent to a *F. pallescens* cover of 30%) as the threshold value which is regarded as a lower limit for a slightly degraded *Festuca* steppe (Bertiller and Defossé 1993). To derive the correspondent sustainable stocking rate, I calculated the 10th percentile for tussock density for each simulated stocking rate for each included model parameterisation and its results for 100 repetitions with stochastic climates. Each stocking rate is evaluated as a valid stocking rate for long term grazing, from which all the 10th percentile-values of tussock density for all parameterisations lead to a higher tussock density than the threshold tussock density Td_S. Hence, I took the highest stocking rate which lead with at least 90% probability for all included parameterisations to a tussock density with higher values than the threshold.

Secondly, I introduced a criterion to avoid unrealistically high sensitivity to grazing. In Chapter 4 I introduced a criterion to avoid parameterisations which were unrealistically robust to grazing. At this step it was necessary to define a lower limit for sensitivity to grazing, because it was possible that model parameterisations were unrealistically sensitive to grazing, leading to erroneous ecological recommendations. It is evident that grazing reduces *F. pallescens* tussock density (Bertiller 1996), but a model parameterisation which would indicate e.g., a complete loss of *F. pallescens* cover at very low stocking rates of Stock = 0.1 sheep / ha is unrealistic.

The only empirical support for defining this criterion is the notion from Bertiller (1996) that 25 years of grazing with stocking rates of 1.5 sheep / ha might have lead to approx. 50% reduction of cover from 60% to 30% in plain uplands. Grazing in this case occurred during 8 months a year, from May to December (mid autumn to begin of summer). This is roughly equivalent to 1.0 sheep / ha continuous grazing all the year round. Starting from this notion I defined the lower limit for sensitivity to grazing as follows: after 25 years of grazing the cover should remain at 30% or higher (or tussock density $Td_S \geq 3.3$) if half of the stocking rate mentioned above is applied (stock = 0.5 sheep / ha). As I simulated stocking rates in intervals of 0.3 sheep / ha, I applied this criterion to the stocking rate of Stock = 0.6.

Qualitative Model understanding – To understand the combined effect of grazing and stochastic climate on the dynamics of *F. pallescens* I compared concrete simulations with one specific climate and different stocking rates (Non- vs. Highly selective, continuous grazing) and compared the change due to precipitation with that due to grazing. This separation is possible if I use always the same precipitation time series and vary only one parameter; the stocking rate. The reference model parameterisation for this analysis was the model parameterisation estimated by the field experts (P_S). I used the expert parameterisation because it yielded good accordance between the simulated and the observed patterns (compare Chapter 3).

Additional simulations were run without any variation of precipitation, using only the mean annual precipitation (MAP = 375 mm) and different stocking rates. These simulations show the effect of grazing alone on the model system.

Time series analysis. — An interesting question is how precipitation and the (grazing) history of the paddock affect the dynamics of *F. pallescens*. To investigate this question I studied the temporal correlation of some response variables with themselves and with precipitation. To test temporal correlation between response variables and precipitation I ran one simulation with the standard parameterisation (no grazing) over 1.000 time steps, memorizing the response variables every time step. I calculated the Spearman's rank correlation of precipitation at the actual time step with the variables at the actual time step. As primarily simulations showed, the model takes at maximum 20 years to equilibrate from initial conditions, so their effect is negligible.

In a next step I ran several simulations for 150 time steps with the standard model parameterisation (P_S), one with no grazing, and one with heavy grazing (1.5 sheep / ha), using the last 130 time steps for analysis. For these simulations I calculated for tussock density and for selected variables (for no grazing, and stock = 1.5 sheep / ha) the temporal auto- and the cross correlations with precipitation and those between grazed and un-grazed tussock density. This to detect effects of precipitation history on important response variables. The time series analysis was performed with the statistical software *R* (Version 1.8.1, R Development Core Team 2003). An estimate of the effect of the precipitation history is essential if one wants to understand how grazing and stochastic act on the long term.

5.3 RESULTS

5.3.1 Impact of grazing under stochastic climate and parameter uncertainty

Inherent uncertainty. — The inherent model uncertainty is very low and does not exceed a coefficient of variation CV of 0.6 % (CV = standard deviation / mean) for important response variables (see Fig. III.1, Appendix III). Thus, for the further presentation of the results the inherent uncertainty can be neglected. This result indicates that the chosen grid size is sufficiently large to ensure that stochastic effects have no large impact on the results.
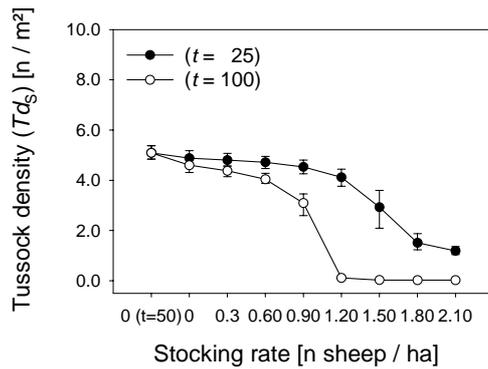
Fig. 5.3: Effect of climatic variability and grazing on tussock density at different time steps.
Shown are the median and the $10^{th}/90^{th}$ percentiles for one model parameterisation, repeated with 100 different stochastic rainfall sequences, after 25 years (t) of grazing (black dots) and 100 years (white dots). The initial value (Stocking rate = 0 (t= 50) acts as a reference, as the model was run 50 time steps without grazing). The variability is at highest when the decrease of tussock density due to grazing begins to increase (Stocking rate = 0.9 at t = 25 years of grazing and Stocking rate = 1.5 after 100 years of grazing). Foraging scenario was the highly selective foraging, continuous grazing all the year round.

Climatic uncertainty. — The variability of important response variables such as tussock density Td_S or mean tussock annual productivity *mean prod* have a CV of approx. 20% and are thus of the same magnitude as the CV of the long-term precipitation (Fig. III.2, Appendix III). Fig. 5.3 shows the effect of stochastic rainfall on the variability of tussock density. The variability is highest when the slope of the decrease of tussock density due to grazing is maximal (Stock = 1.5 after 25 years of grazing or Stock = 0.9 after 100 years of grazing).
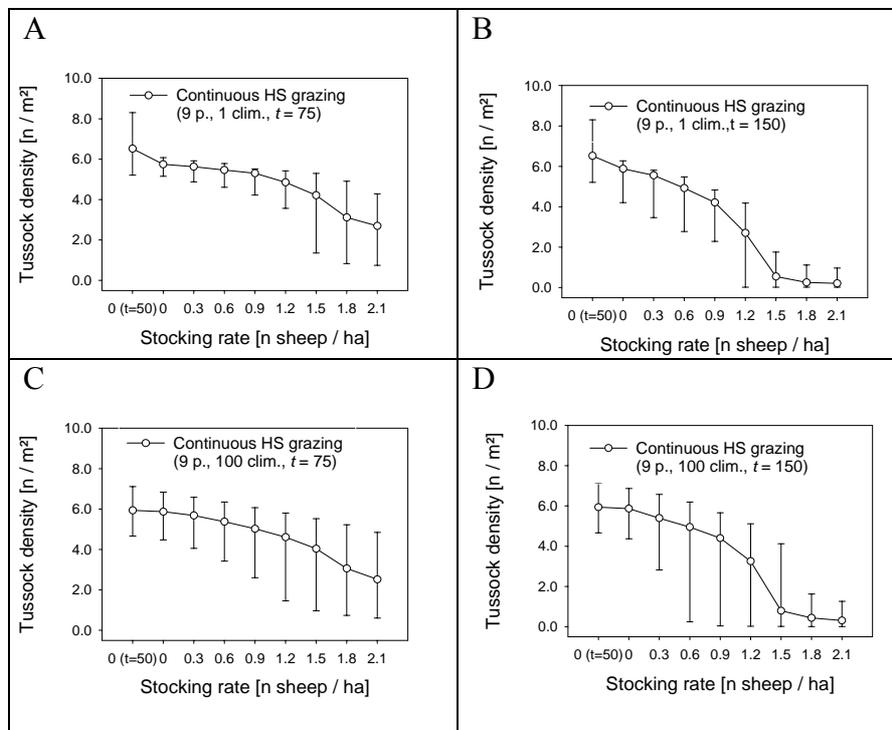
Fig. 5.4: Effect of climatic and parameter uncertainty on tussock density under grazing.
Shown are simulation results for the 9 accepted parameterisations for the scenario Highly selective continuous grazing and **A-B)** one stochastic climate repetition, after **A)** 25 years, and **B)** 100 years of grazing, and **C-D)** 100 stochastic climate repetitions, after **C)** 25, and **D)** 100 years of grazing. Note: For all runs the value for time step (t) = 50 is plotted as a reference.

Parameter uncertainty. — Parameter uncertainty is considerably higher than climatic uncertainty (Fig. 5.4). This result shows that degradation effects can be strongly masked due to the remaining uncertainty about biological processes and parameters. Although the median at high stocking rates (Stock > 1.5 sheep / ha, after 25 grazing years) indicates increasing or strong reduction in tussock density, the variation is high. For 100 years of grazing, a misleading interpretation due to the uncertainty could be that a stocking rate of 1.2 sheep / ha leads to a reasonably high tussock density of approximately 3 tussocks / m². For a sustainable management a precautious strategy seems to be adequate facing such strong uncertainties.

5.3.2 Quantitative estimation of a grazing threshold

The quantitative analysis for estimating a threshold for the effect of grazing on tussock density was performed with a standard logistic curve with four parameters (see eqn. 5.1). The simulation data used for analysis were based on the experts parameter estimation which is used as standard parameterisation (P_S), run with one (Fig. 5.5 A) and 100 climates (Fig. 5.5 B). Furthermore I included parameter uncertainty by using the 9 accepted parameterisations from Calibration (Chapter 4) combining them with one (Fig. 5.5 C) and 100 climates (Fig. 5.5 D).
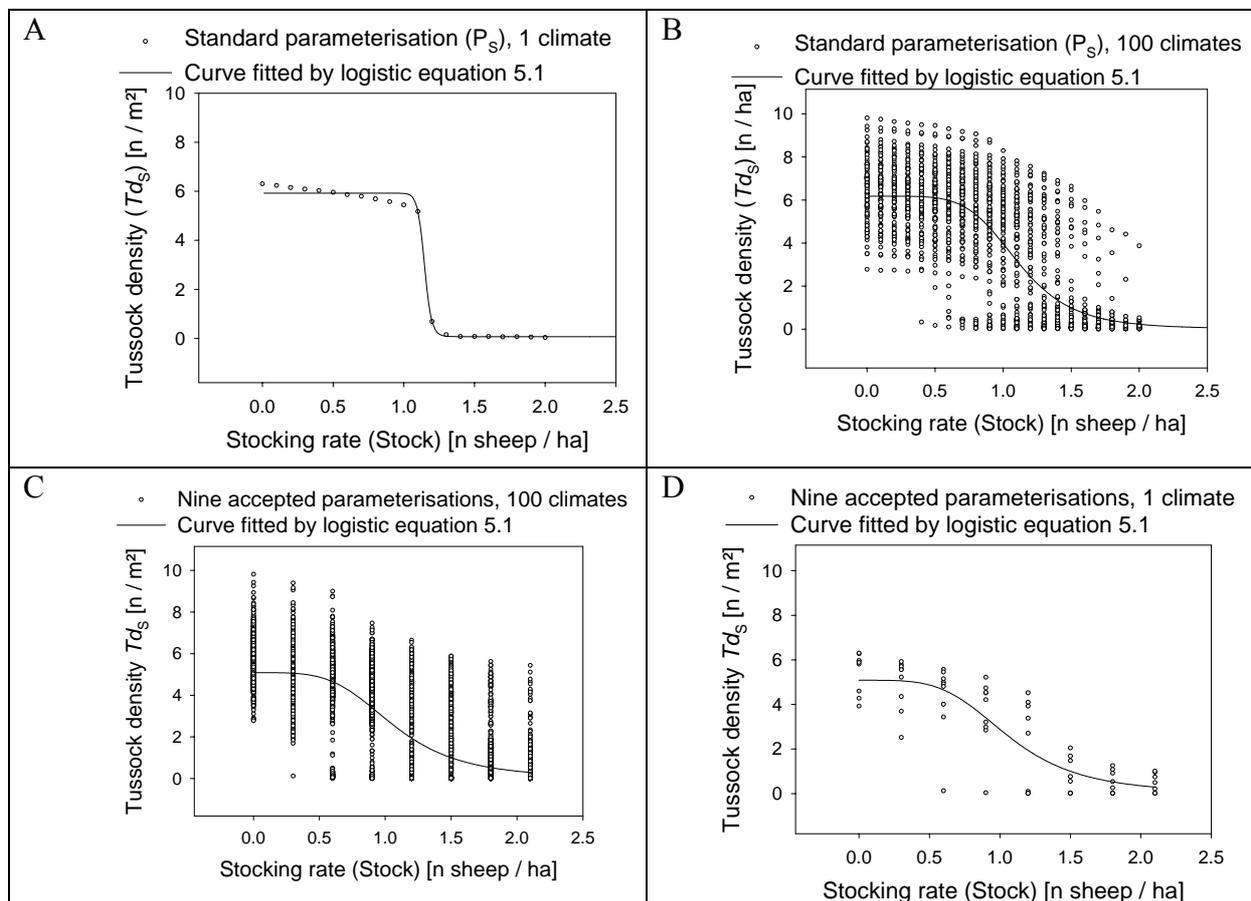
Fig. 5.5: Quantitative threshold estimation under climatic and parameter uncertainty.
   A) Nonlinear regression for the standard model parameterisation (P_S, expert estimation) and one climate, simulation for 150 time steps, grazing during time steps 51-150 and 21 stocking rate intervals; **B**) same as A, but including 100 stochastic climates; **C**) Same as A, but including the remaining parameter uncertainty by including the 9 accepted parameterisations (see Chapter 4), run for eight stocking rates with intervals á 0.3 sheep / ha; **D**) as in B, but showing only remaining parameter uncertainty as in C due to a run with only one rainfall scenario.

Tab. 5.1: Grazing threshold estimation for four climatic and parameter combinations with logistic fit.
R^2: Quality of fit; Parameters are explained in Fig. 5.1 and eqn. 5.1.

Estimated parameters	Coefficient	Standard parameterisation (P_S)		Nine accepted parameterisations (includes P_S)	
		1 climate	100 climates	1 climate	100 climates
R^2	Quality of fit	**0.995**	**0.571**	**0.707**	**0.585**
Max	Parameter estimate	5.9	6.2	5.1	5.4
	Std.-error Coeff.	0.1	0.1	0.3	0.0
	T-value	93.0	87.5	132.1	17.3
	Significance level	<0.0001	<0.0001	<0.0001	<0.0001
Min	Parameter estimate	0.1	0.0	0.0	0.0
	Std.-error Coeff.	0.1	0.2	0.7	0.1
	T-value	1.0	0.0	0.0	0.0
	Significance level	0.3464 (n.s.)	1.00	1.00	1.00
EC50 (grazing threshold)	Parameter estimate	1.1	1.1	1.1	1.1
	Std.-error Coeff.	0.0	0.0	0.1	0.0
	T-value	179.1	64.0	49.4	10.0
	Significance level	<0.0001	<0.0001	<0.0001	<0.0001
Slope	Parameter estimate	46.2	5.5	4.1	3.2
	Std.-error Coeff.	5.9	0.4	1.5	0.2
	T-value	7.9	12.9	19.6	2.7
	Significance level	<0.0001	<0.0001	<0.0001	0.0089

Threshold behaviour for the standard parameterisation. — The simulations using only the standard parameterisation and one climate (Fig. 5.5 A) reveal a strong threshold behaviour at Stock = 1.15 (Tab. 5.1, 3rd column). The estimated threshold coincides with the qualitative estimation derived from Fig. 2.6 (Chapter 2). The estimated slope is very high in comparison to the following estimates (Tab. 5.1). The interpretation of the slope is as follows: The higher the estimate the narrower is the span of stocking rates within the decrease of tussock density between nearly no degradation and nearly complete degradation takes place. (tussock density < 1.1, cover < 10%)

Repeating the simulations for the standard parameterisation (P_S) with 100 stochastic precipitation time series of 150 years with 100 years of grazing (Fig. 5.5 B) it becomes evident that climatic uncertainty has a strong effect on the slope: it decreases from *slope* = 46.2 to *slope* = 5.53 (Tab. 5.1). However, the grazing threshold and the maximum and minimum estimates for tussock density remain nearly unchanged, but the percentage of the variation explained by the logistic function is strongly reduced (Tab. 5.1). The interpretation of this result is that with a stocking rate of 1.1 sheep / ha one might be on the 'safe side' without strong degradation. Since future precipitation is an unknown factor, we have to be aware that a decrease of tussock density may begin at even lower stocking rates (approx. 0.7 sheep / ha). This value can be estimated, considering climatic uncertainty, determining the point at which tussock density begins to decrease (Fig. 5.5 B).

Threshold behaviour under inclusion of parameter uncertainty. — The inclusion of the remaining parameter uncertainty into simulations including climatic uncertainty increases the effect shown for the inclusion of climatic uncertainty (Fig. 5.5 C, Tab. 5.1): The slope decreases, and additionally the tussock density maximum estimate decreases.

Unexpected change of non-liner to linear behaviour. — Inclusion of parameter and climatic uncertainty yields an almost paradoxical result: the distinct threshold behaviour – non-linear behaviour – resulting out of the simulation of one parameterisation with one climate (Fig. 5.5 A) is smoothed to a nearly linearly behaviour, if both uncertainties are included (Fig. 5.5 C). To some extent, threshold behaviour of the model is not surprising, as the tussock mortality parameters due to plant available soil

water include threshold values. The change from non-linear to linear behaviour, thus getting a 'simpler' solution if we include much more complexity into the output by including climatic and parameter uncertainty, seems to be an unexpected result and a paradox, because it returns almost the contrary, as one might expect intuitively, i.e. a more complex result, if the data to analyse are more complex.

Finally, if I remove again climatic uncertainty but leave parameter uncertainty (Fig. 5.5 D), the threshold behaviour becomes clearer again. At least the logistic fit is slightly better than the linear one ($R^2_{logistic}$ = 0.707 (Tab. 5.1) > R^2_{linear} = 0.694 (data not shown)). Thus, the simultaneous consideration of climatic and parameter uncertainty masks the non-linear behaviour observed for individual simulation runs. One could name this the 'uncertainty paradox'. Quantitative threshold behaviour is evident for each parameterisation, as seen from the median values out of 100 climate repetitions of tussock density for each accepted parameterisation after calibration (Fig. 4.8, Chapter 4). Thus, I expected threshold behaviour for almost all parameterisations under all precipitation sequences. As I firstly analysed all simulations together the threshold behaviour of tussock density decline becomes blurred/indistinct by inclusion of climatic and/or parameter uncertainty. As a next step of analysis, it would be interesting to analyse each specific precipitation sequence and each parameterisation alone and analyse the distribution of the fitted parameter values. This step could not yet be performed during this thesis due to the lack of time capacities.
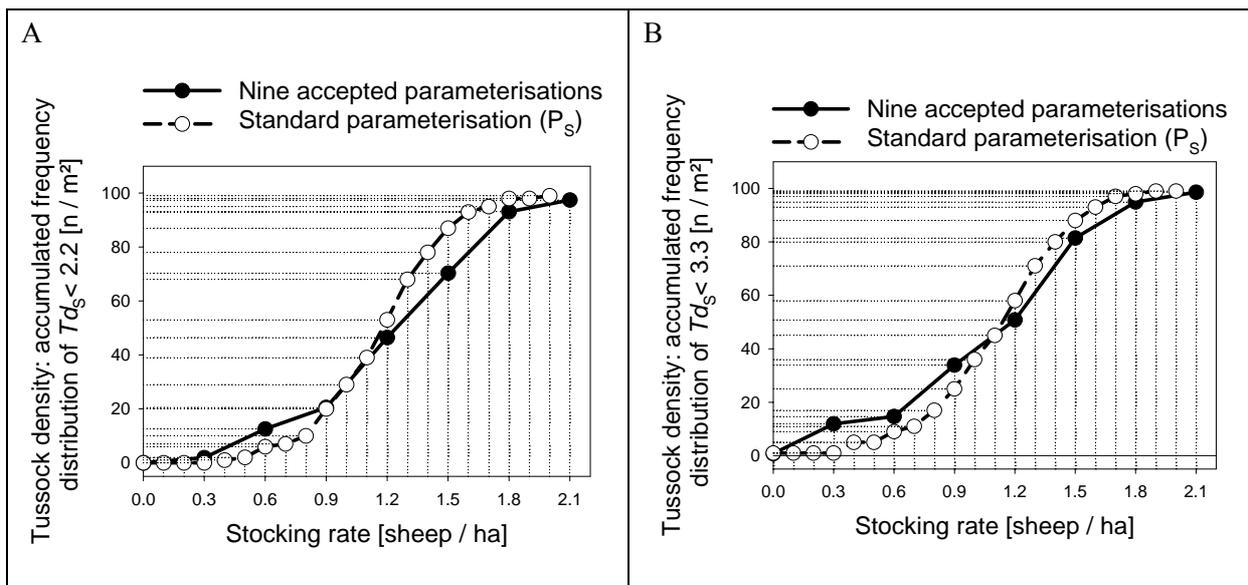
Fig. 5.6: Accumulated frequency distributions for long-term tussock density thresholds.
Shown are the accumulated tussock density frequency distributions over the stocking rate gradient for the 9 accepted parameterisations and the standard parameterisation.
A) Probability of tussock density occurrence up to $Td_S < 2.2$ (tussock density below the regeneration threshold under constant grazing (Chapter 2), Festuca cover max. 20%); **B)** idem for $Td_S < 3.3$ (tussock density above the regeneration threshold under constant grazing (Chapter 2), Festuca cover max. 30%).

Quantifying degradation risk. — The second important result of inclusion of both parameter and climatic uncertainty is that tussock density starts to reduce already at a low stocking rate of approx. 0.3 sheep / ha (Fig. 5.5 C, begin of the curve decline). For a risk averse management strategy this would imply, to reduce even more the constant stocking rate than if only climatic uncertainty was considered (compare with Fig. 5.5 B. To analyse and to quantify the 'degradation risk' more accurately, I plotted the frequency distributions of the data used for Fig. 5.5 C, including specific tussock density thresholds, i.e. Fig. 5.6 shows the frequency of simulations which on the long term

ranged below tussock density = 2.2 (Fig. 5.6 A), which is below the regeneration threshold of 2.5 under constant grazing (Chapter 2), or above this threshold (tussock density 3.3, Fig. 5.6 B). Fig. 5.6 enables me to quantify the probability that tussock density drops for a specific stocking rate below a certain defined threshold. For example, applying a stocking rate of 0.9 sheep / ha, including parameter uncertainty, leads to a 20% probability that the system would degrade and reach a tussock density below 2.2 (Fig. 5.6 A). For the same situation, the probability to reach a sustainable tussock cover (tussock density > 3.3, Fig. 5.6 B) is approx. 70%. The threshold for a potentially sustainable tussock density of 3.3 is a rough estimate, including an approx. 30% buffer on the regeneration threshold of tussock density = 2.5. Thus, Fig. 5.6 allows to quantify the degradation risk for the complete stocking rate gradient and a given tussock density threshold.

Interpretation of the threshold behaviour. — How can we understand the threshold behaviour? This is a prerequisite for interpreting the result described above. I expected threshold behaviour at least for the high selective continuous scenario due to <u>two positive feedbacks.</u> These feedback mechanisms could explain the grazing impact on vegetation and additionally an interaction of grazing, of the dynamics of *F. pallescens*, and of the rainfall sequence with each other.

The first positive feedback occurs due to selective grazing: tussocks with increasing fraction of dead biomass are rejected with a probability which increases non-linearly. As a consequence, each tussock which was once accepted for grazing remains with reduced green biomass. Thus, there is less green biomass which can become senescent and will die in the following time step. Therefore the dead biomass fraction will be reduced during the next time step. This reduction increases the probability of the tussock being accepted for grazing and so on.

The second feed back is related to recruitment and interacts with the feed back function of forage selection. Recruitment declines under reduced tussock density, caused by a high mortality in the anterior year. Mortality occurs mainly during dry years, and only for tussocks in the lowest vitality class. Grazing can reduce vitality and so weaken the tussocks. Seedling survival during the second and third year is linearly related to the mean grazing intensity (*M*). This rule assumes that seedlings are preferred by sheep because they do not yet include any dead material. The same assumption holds for young tussocks which recruited at the actual time step. Thus, forage selection and recruitment interact at least for three time steps. It is possible that the interaction of tussock life stage, grazing and forage selection also impacts the next stage cohorts (2 year old tussocks and so on).

Grazing and the stochastic rainfall sequence interact with the two feedback processes described above. During drier years the realized relative grazing intensity (*M real*) is higher than for humid years, tussocks are reduced in vitality, mortality is higher, seedling and sapling survival is reduced. These mechanisms are strongly reinforced when two dry years occur in sequence. If several years of high tussock mortality occurred due to a prolonged drought, and are then followed by 'good' humid years, seedling survival will remain low, due to a reduced germination within a higher frequency of larger bare patches. Heavy grazing will reinforce this process and will lead to the inhibition of the regeneration process of *F. pallescens* and thus of the *Festuca* steppe.

Though these model assumptions are strong, they are biologically reasonable and plausible. The possible feedbacks between forage selection, recruitment, effect of grazing on vitality and indirectly on tussock density and the effect of unpredictable droughts make threshold behaviour expectable.

Which are the practical implications of these results? On the one hand, it is evident that range management should done with caution. The definition of a 'sustainable' threshold on the base of one parameterisation and one climate might lead to a misleading expectation of long-term sustainable vegetation under a certain stocking rate. A rough estimation could be that a third of the stocking rate,

which was calculated as the stocking rate threshold for the presented results, might have some chance to lead to a low degradation of the *Festuca* steppe.

A further, more detailed quantitative analysis could try to derive a threshold, which determines the stocking rate at which tussock density begins to decrease. A threshold criterion for the second derivative of the used logistic equation could possibly help to determine this stocking rate.

5.3.4 Time scales of degradation

Fig. 5.7 shows time scales for the effect of different stocking rates on tussock density (P_S, 100 climates). If I take climatic uncertainty into account, a clear decrease of tussock density is only visible after very long time scales of say 100 years although the effect on individual runs with concrete rainfall scenarios may become evident earlier (compare with Fig. 2.6). Whereas at the stocking rate Stock = 0.6 sheep / ha no degradation trend, at Stock = 0.9 sheep / ha a clear effect on tussock density is evident. As the variability due to the climatic stochasticity is strong, the effect is masked. This effect might lead to a delay in the detection of degradation in the field, i.e. of a reduction in tussock density. Though the stocking rate 1.2 sheep / ha shows clear temporal threshold behaviour, a detection of this effect could be masked by climatic uncertainty. Only at a stocking rate of 1.5 sheep / ha the threshold effect is significant after 50 years of grazing.
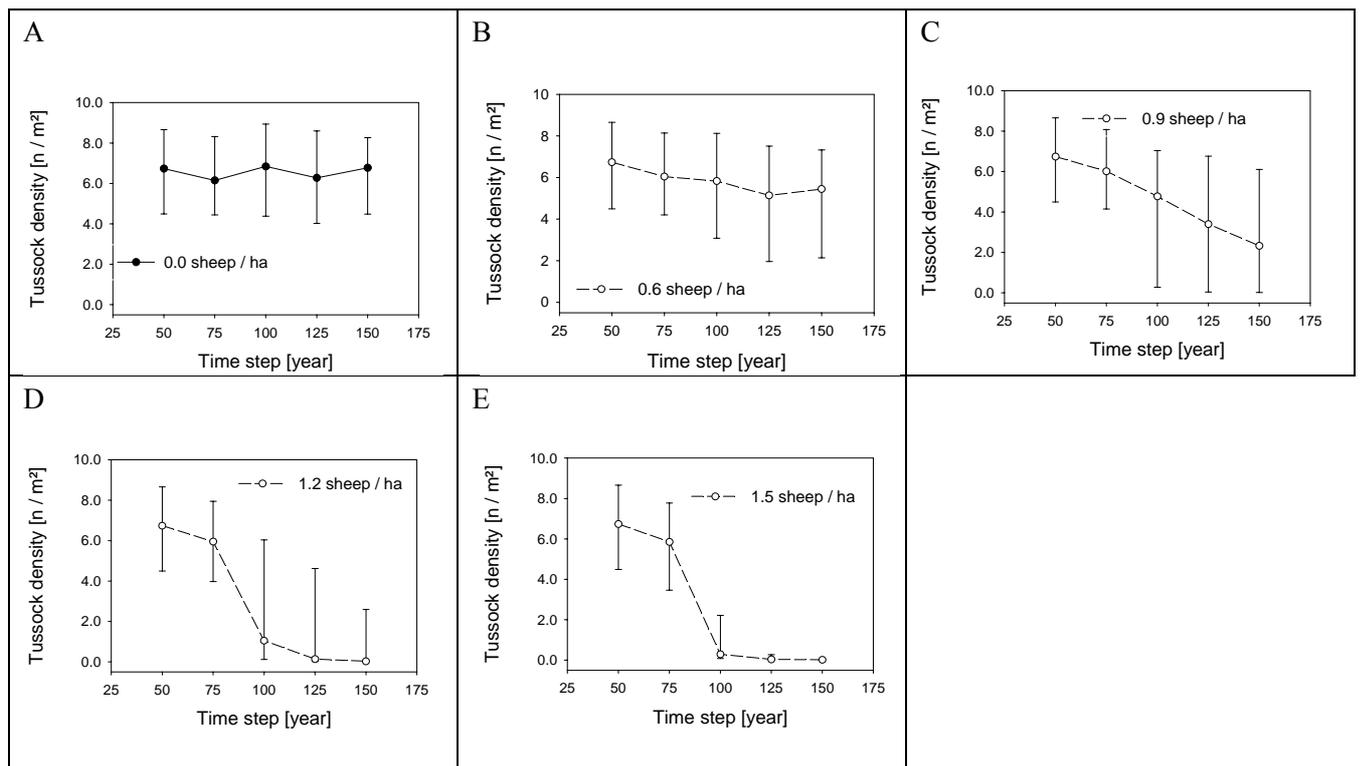
Fig. 5.7: Time scales of degradation.
Shown are simulation results for the standard parameterisation and 100 climate repetitions, comparing the results for tussock density (median and $10^{th}/90^{th}$ percentiles) of no grazing with different stocking rates**: A)** Stock = 0.6; **B)** Stock = 0.9, **C)** Stock = 1.2; **D)** Stock = 1.5. For Stock = 0.6 there is no significant difference evident. For Stock = 0.9 a clear linear reduction in tussock density is evident, but it is still shaded by climatic stochasticity.

5.3.5 Different grazing managements

Forage selectivity. — One option to improve tussock density under grazing is to adopt different grazing management schemes. One option would be to reduce forage selectivity by creating smaller paddocks. This would force sheep to use more green biomass within a shorter time scale and thus would disrupt the feedback mechanism caused be the high amount of dead biomass. Creating smaller paddocks would force sheep to graze less selective. The effect of selectivity is evident especially on the long term (Fig. 5.8) for both shown variables, the tussock density (Td_S) and mean consumed forage per time step during the grazing period (*mean C*). Tussock density declines linearly when grazing is non-selective and relatively higher stocking rates than for high selective continuous grazing seem to be viable on the long term. Clearly, decreasing paddock size needs new fences, which needs economic input. One interesting option would be to test if fencing might be economically successful on the long term.
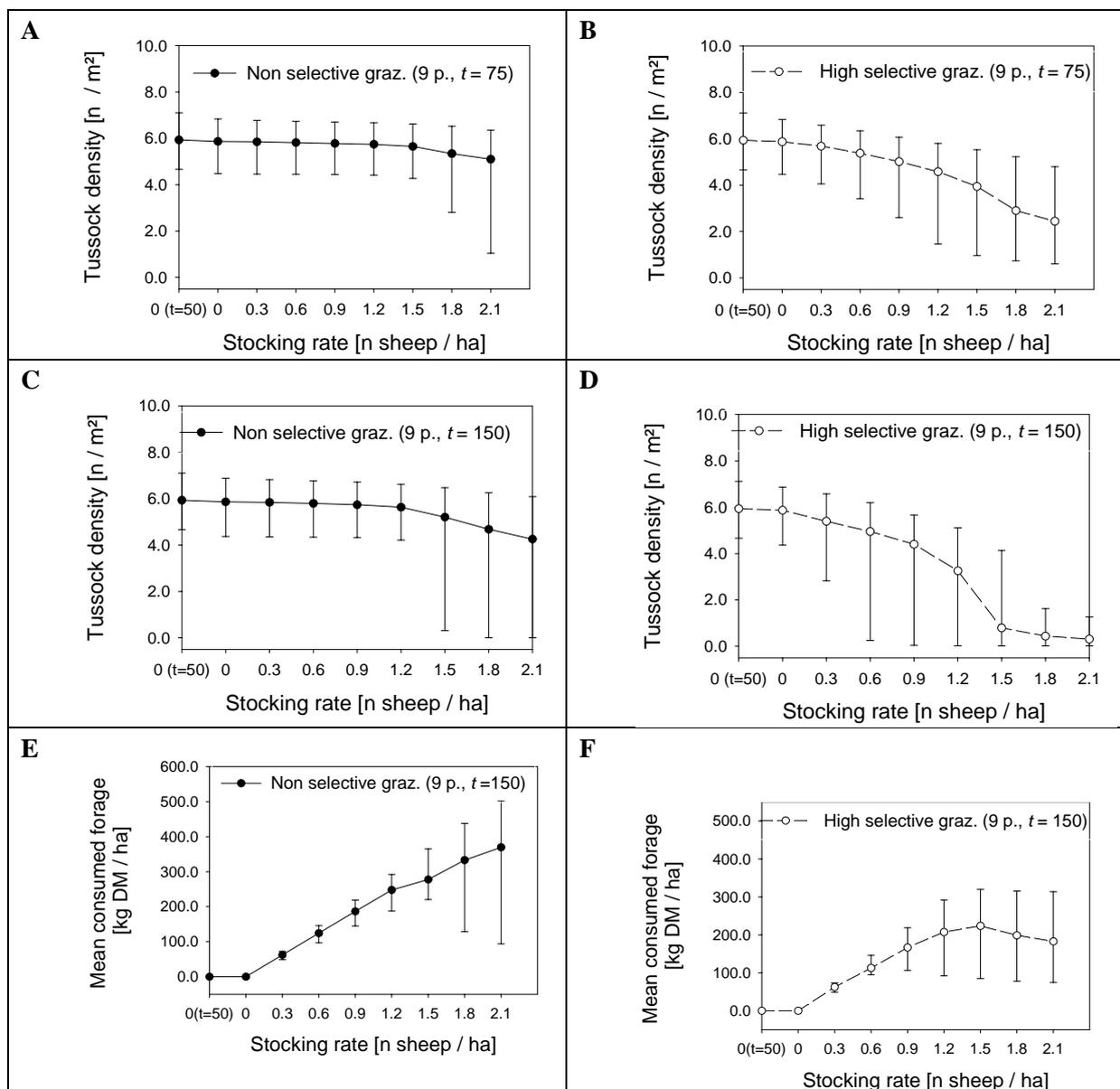
Fig. 5.8: Comparing Non-selective with Highly selective grazing.
Shown are the results for the 9 accepted parameterisations and 100 climate repetitions. Tussock density (Td_S): **A-D)**, Mean consumed forage (*mean C*) per time step t: **E-F)**: **A, C)** 25 time steps of grazing; **B, D-F)** 100 time steps of grazing.

Seasonal grazing: Spring grazing. — Another option to improve the grazing management is to restrict grazing to specific seasons and to introduce rotational grazing. I tested the effect of grazing during i) spring, during ii) summer and/or autumn, and iii) during winter. For spring grazing I expected a stronger negative effect than for the reference scenario (i.e, high selective continuous grazing). This expectation is based on the stronger selectivity of sheep due to the relatively higher availability of fresh produced biomass; additionally, the negative effect of spring grazing on reproductive success might be higher.

The results, including both parameter and climatic uncertainty, indicated no substantial differences between spring and continuous grazing (data not shown). It is not clear why both scenarios behave similar since the herbivore selectivity was theoretically 50% higher. One explanation is that the selectivity of the continuous grazing is already high, and that a higher selectivity will only lead to marginal changes. This finding should be analysed in more detail. A second explanation is that the different scenarios have no effect on the reproductive success of *F. pallescens*. Reproduction is indirectly included into the model: the survival of seedlings depending on tussock density. Thus, no rules are included into the model that might reflect a potentially stronger negative feedback between the high removal of biomass in spring and reproduction. This might be a shortcoming of the actual model version. On the other hand, I could not yet develop a hypothesis to explain differences in reproductive success between spring and continuous grazing.
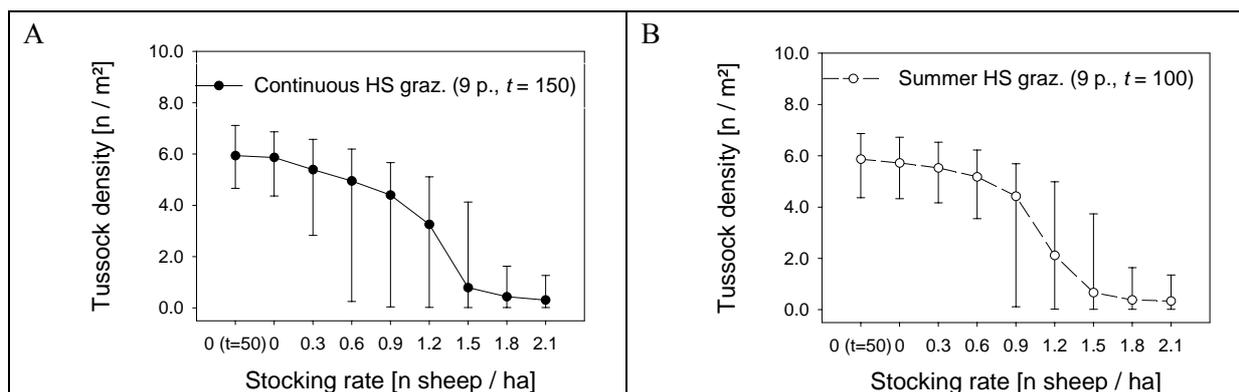
Fig. 5.9: Comparing seasonal different grazing: continuous vs. grazing in summer.
Shown are simulations including both parameter and climatic uncertainty after 100 years of grazing: **A)** Highly selective (HS) continuous grazing, **B)** Highly selective grazing in summer.

Summer grazing. — Summer grazing yields only slight differences compared to continuous grazing (Fig. 5.9). I do not show the data for the mean consumed forage, because the differences are even lower than for tussock density. After 25 years of grazing the median values of tussock density differ between both scenarios, but the differences would not be significant, including all uncertainties (data not shown). For a specific rain scenario and a specific parameterisation the difference might be significant. After the long term simulation (100 years of grazing, Fig. 5.9) the differences are still small, only the median values for the stocking rate 1.2 sheep / ha differ qualitatively. Consequently, summer grazing seems to offer no alternative. This result was expected. During early summer the supply of green biomass remains relatively high, the highest senescence rates occurs during fructification in the mid and end of summer. Forage selectivity can be expected to reduce consecutively, if the amount of green biomass is significantly reduced and replaced by dry biomass. So the implemented low reduction of forage selectivity (GR.5 = 0.6 for summer/autumn grazing vs. GR.5 = 1.0 for continuous grazing) leads to no significant change. A shortcoming of the model at this

point is the lack of separation between the summer and autumn seasons. Forage selection is probably further reduced in late summer after seed dispersal (February / March) and during autumn, when senescence has lead to a stronger reduction of green biomass. On the other hand, another peak in productivity occurs in autumn which should also be considered. For the actual restricted knowledge of how forage selection changes with the season, the applied aggregated approach was justified, but an improvement of the hypothesis and notions about these processes is desirable.

Winter grazing. — For winter grazing I expected a significant result, at least for the response of tussock density. During this scenario, I reduced the forage selectivity strongly (GR.5 = 0.3), so this scenario resembles more the non-selective than the high selective continuous grazing scenario. The median values clearly differ (Fig. 5.10) after 25 and 100 years of grazing, despite the 10th and the 90th percentiles still overlap for both variables and all stocking rates. I consider these differences as qualitatively significant. The results for winter grazing are very similar to the ones for the non-selective grazing (Fig. 5.8), though the long-term decrease of tussock density is evidently higher at winter grazing for high stocking rates and seems to follow a non-linear rather than a linear decrease (Compare Fig. 5.8 C and Fig. 5.10 B).

The results indicate that applying winter grazing would allow higher stocking without increasing the effect on vegetation (see Fig. 5.10 B). It is difficult to decide, whether e.g. a stocking rate of 1.5 sheep / ha would be sustainable for winter grazing on a longer term than 100 years, because variability is considerably high. An economical-ecological trade-off is also evident for winter grazing: if one would apply the stocking rate which returns the highest benefit, measured e.g. with the mean consumed forage (Fig. 5.10 C), tussock density would decrease strongly to values of $Td_S \sim 2.0$, which is equivalent to strong degradation.

There are two restrictions I have to take into account regarding these results: First, the forage selection rule for winter grazing does not take into account the change of forage quality, which might be of higher importance during winter. Dry biomass has a lower quality and this would possibly lead to a higher daily intake by sheep during winter. Secondly, parts of the *Festuca* steppe lie at altitudes affected by snowfall during winter and thus are not available during the whole winter for grazing.
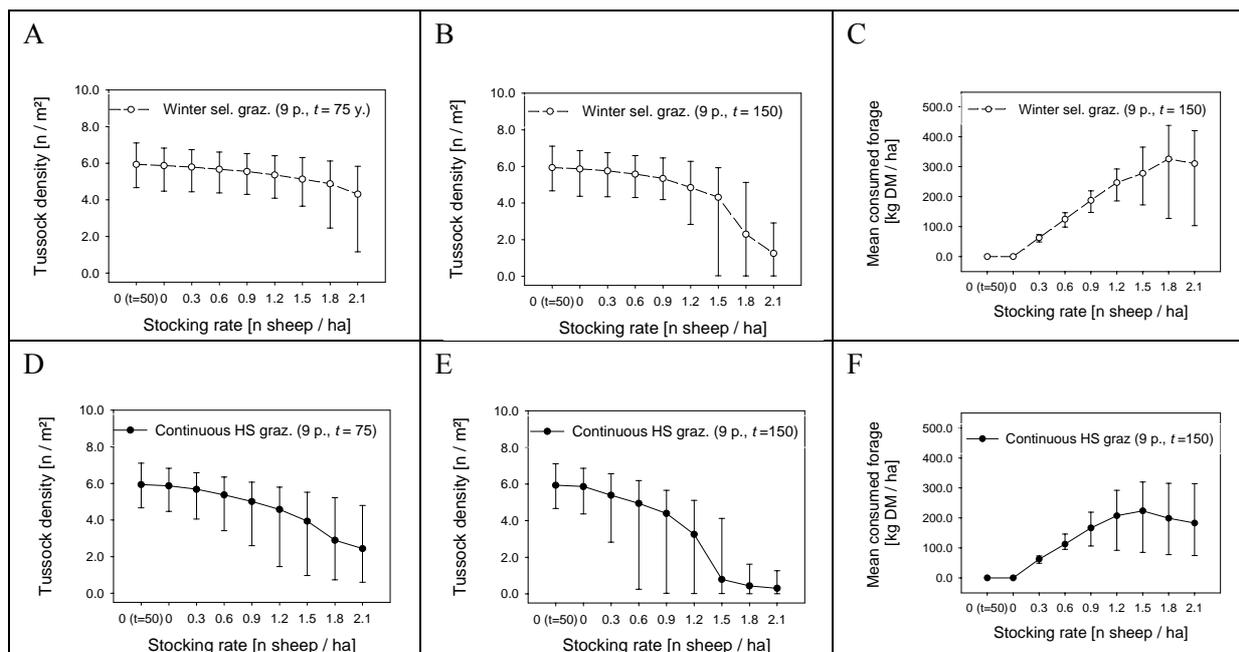
Fig. 5.10: Comparing highly selective continuous with winter grazing.
shown are results out of the 9 accepted parameterisations and 100 climate repetitions. **A-D)** Tussock density, **D-E)** mean consumed forage; **A-B)** 25 years, and **C-F)** 100 years of grazing.

5.3.6 Generating a criterion for sustainable management

Fig. 5.11 shows the results for minimizing the risk of long-term degradation, for the scenarios high-selective continuous grazing and non-selective grazing. I chose 30% cover of perennial tussock grasses of F. pallescens as threshold criterion for a sustainable grazing management. 30% cover is equivalent to a tussock density (Td_S) of 3.3 tussocks / m². This criterion should be fulfilled with a probability of 90%, considering the results of each parameterisation and its 100 repetitions with different stochastic climates. One parameterisation was rejected, due to its unrealistically high sensitivity to grazing.

Potentially sustainable stocking rate leading with 90% probability to at maximum slight degradation *of F. pallescens* (cover ≥ 30 %)
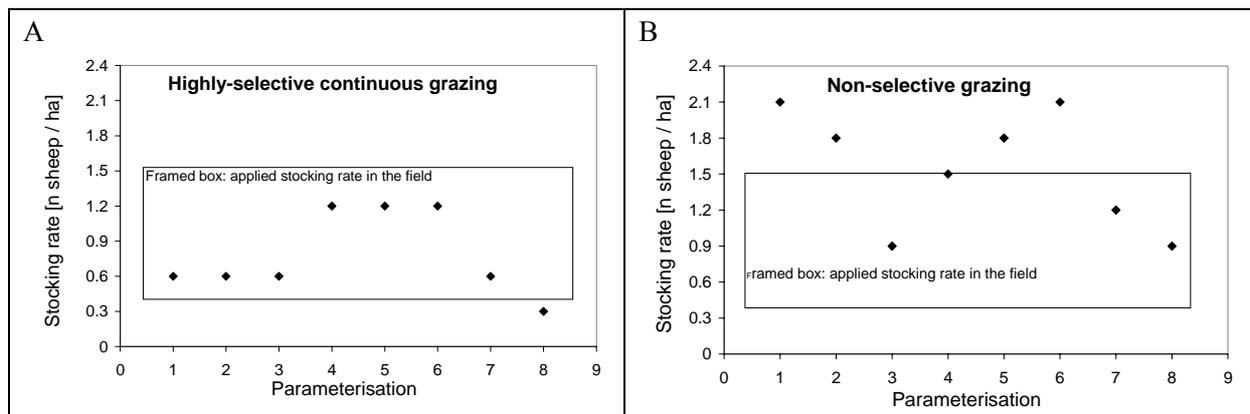
Fig. 5.11: A criterion for long term sustainable grazing.
> Shown are for **A)** Highly selective continuous, and for **B)** Non-selective grazing the stocking rate for each parameterisation, at which long term grazing (100 years) is potentially sustainable. A stocking rate was potentially sustainable, if it lead with a probability of 90% to at maximum to a slight degradation *of F. pallescens* (cover ≥ 30 %, tussock density Td_S ≥ 3.3). The minimum of the stocking rate out of the investigated parameterisations is proposed as the potentially sustainable stocking rate. Grey shaded area: applied stocking rate range in the field (0.3 sheep / ha for highly selective grazing and 0.9 sheep / ha for non-selective grazing).

Regarding the remaining eight parameterisations, the result for the high selective grazing is, that a stocking rate of 0.3 sheep / ha would be a long-term sustainable stocking rate, considering climatic and the remaining parameter uncertainty. Thus, a stocking rate of 0.6 is the upper limit, where the risk is slightly higher than the threshold (or level of risk) I defined. Due to the relatively coarse resolution of my simulations I cannot give a more precise estimate of this grazing threshold. The interpretation for farmers, who try to maximize their income, would be that a stocking rate below 0.6 / sheep might be sustainable, e.g. a stocking rate (Stock) of approximately 0.5 sheep / ha; the ecological interpretation would recommend not to exceed 0.3 sheep / ha. Simulations with stocking rates between both levels would be required to solve the question after the exact sustainable stocking rate under the given conditions and the actual available knowledge.

Non-selective grazing. — The same analysis for the non-selective grazing scenario leads to the result that a stocking rate of Stock = 0.9 sheep / ha might be sustainable on a long term. This is nearly a two- to threefold higher stocking rate than under the normally applied high selective continuous grazing scenario (compare Fig. 5.11 A and B).

5.3.7 Understanding the combined effect of grazing and stochastic precipitation on vegetation

In this section I present results which will contribute to a general understanding of how grazing and the stochastic climate interact and how this interplay affects the dynamics of *F. pallescens*. Improving understanding of these processes is of general interest for semi-arid and arid regions.

During this section

- I present the effect of grazing on tussock density under constant rainfall.
- I analyse the temporal correlation of rainfall with selected variables of vegetation dynamics.
- I analyse selected time series to discuss the combined effect of grazing and rainfall on important response variables qualitatively.
- I show the combined effect of grazing and precipitation on the annual change of important response variables
- I show time series, which separate the specific contributions of precipitation and grazing to the net change of important response variables.
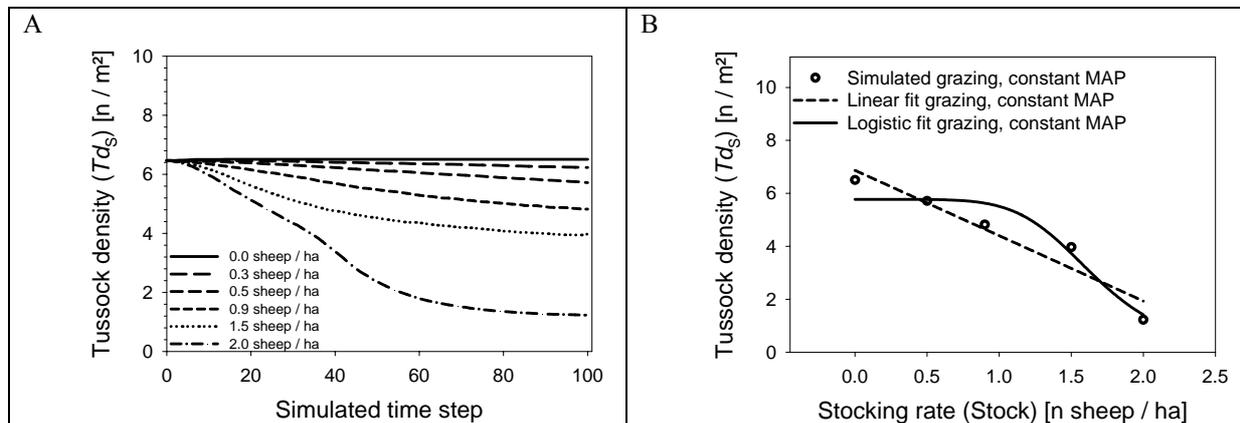
Fig. 5.12: Grazing effect on tussock density under constant mean annual precipitation.
A) Shown are the effect of different stocking rates on tussock density under constant mean annual precipitation (MAP = 375 mm rain / year). I used the standard parameterisation (P_S) and the standard initial conditions. The grazing scenario is the highly selective continuous grazing; **B)** linear and non-linear fit (see eqn. 5.1) of the response of tussock density on the grazing gradient under constant MAP after 100 years of grazing. The linear fit has a higher quality (linear $R^2 = 0.89$ (adjusted) than the non-linear one $R^2 = 0.69$ (adj.). The slope for the linear fit is significant, whereas the *slope* = 6.00 and EC50 = 1.66 (= stocking rate threshold) for the non-linear fit were not significant (Details see Tab. III.1, Appendix III).

Grazing under constant climate — The effect of grazing on tussock density, excluding the stochasticity of rainfall, can be roughly described as a linear negative one (Fig. 5.12). But the negative effect of grazing on tussock density under constant mean annual precipitation for the Media Luna Ranch (MAP = 375 mm) is lower than the negative effect of grazing under stochastic climate (compare Fig. 5.12 with Fig. 5.10 E, in the latter the median values for tussock density ~ 1.0 for Stock = 1.5, vs. Td_S ~ 4.0 for constant rain). The conclusion to draw out of this comparison is that the combined effect of grazing and stochastic rain is clearly more negative than grazing in isolation.

Correlations between precipitation and response variables. — An interesting question is how precipitation affects the dynamics of *F. pallescens*. The Spearman's rank correlation between the actual precipitation and the response variables reveals interesting insights (Fig. 5.13). Tussock density and tussock recruitment are weakly correlated to rainfall, whereas tussock mortality and seedling

survival (1st year) are strongly correlated and respond instantaneously to actual rainfall. This indicates that the response of tussock density to rainfall is more complex and may include a memory effect. Mean vitality, which is important in order to explain both tussock mortality and productivity, is highly correlated to rainfall. This high correlation is probably due to the strong correlation of vitality at *dfrac*-class 3 tussocks (40-60% fraction of dead biomass). As expected, annual tussock productivity is strongly correlated to rainfall, but tussock biomass after senescence and total standing green biomass (before senescence, representing available forage) are weaker correlated with rainfall, which reflects the history of tussock density, too. As expected, mean *dfrac* is negative correlated to rainfall. If rainfall is high, productivity is high and the relative *dfrac* is reduced. Surprising is the result, that the proportion of tussocks in *dfrac*-class 3 and 4 (with 40-60% and 60-80% dead biomass fraction) are inversely correlated to rainfall.
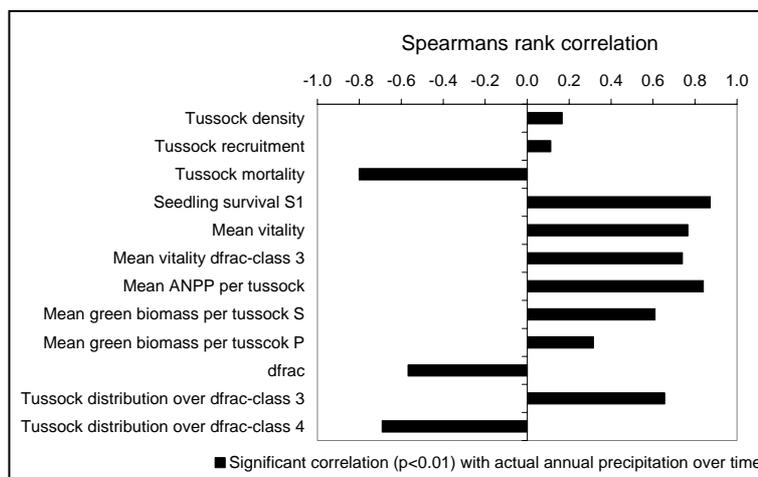
Fig. 5.13: Correlations between this year's precipitation with exemplar response variables.
Shown are the significant correlations (Spearman's rank correlation coefficient, $p < 0.01$) between the responses variables and this year's precipitation out of one run of 1.000 time steps with stochastic rainfall (standard parameterisation, no grazing).

Temporal autocorrelations. — The temporal autocorrelations (Fig. 5.14) for the variables tussock density (Td_S), including grazing with Stock = 1.5 sheep / ha, and excluding grazing, mean dead biomass fraction (*dfrac*) and the landscape annual net primary production (*ANPP*) provide interesting insights into the model behaviour. Tussock density Td_S (without grazing) is significantly autocorrelated 12 years for the given scenario (Fig. 5.14 B). I interpret this result in the way that the initial conditions or the state of a paddock would affect the results at least 12 years, if no grazing takes place. However, if grazing takes place, the temporal autocorrelation increases and is significant during 20 years and more (Fig. 5.14 H). This is because the system responds under grazing to a lesser extent to differences in rainfall. This result is supported by the lack of autocorrelation of Td_S (Stock = 1.5 sheep / ha) with precipitation, whereas tussock density Td_S without grazing is significantly correlated to the four years preceding the actual time step (Fig. 5.14 A).

The significant cross-correlation between *tussock density* without grazing and the four years of preceding precipitation (Fig. 5.14 A) is a highly interesting finding. It proves that the system includes a second memory, in addition to the initial conditions of the vegetation mentioned above. An interpretation is that the precipitation is the main cause for this memory. Precipitation determines seedling survival which takes place three years before tussock recruitment. Somewhat surprising is it that the actual precipitation (lag = 0) is not significant, though tussock mortality depends partly on
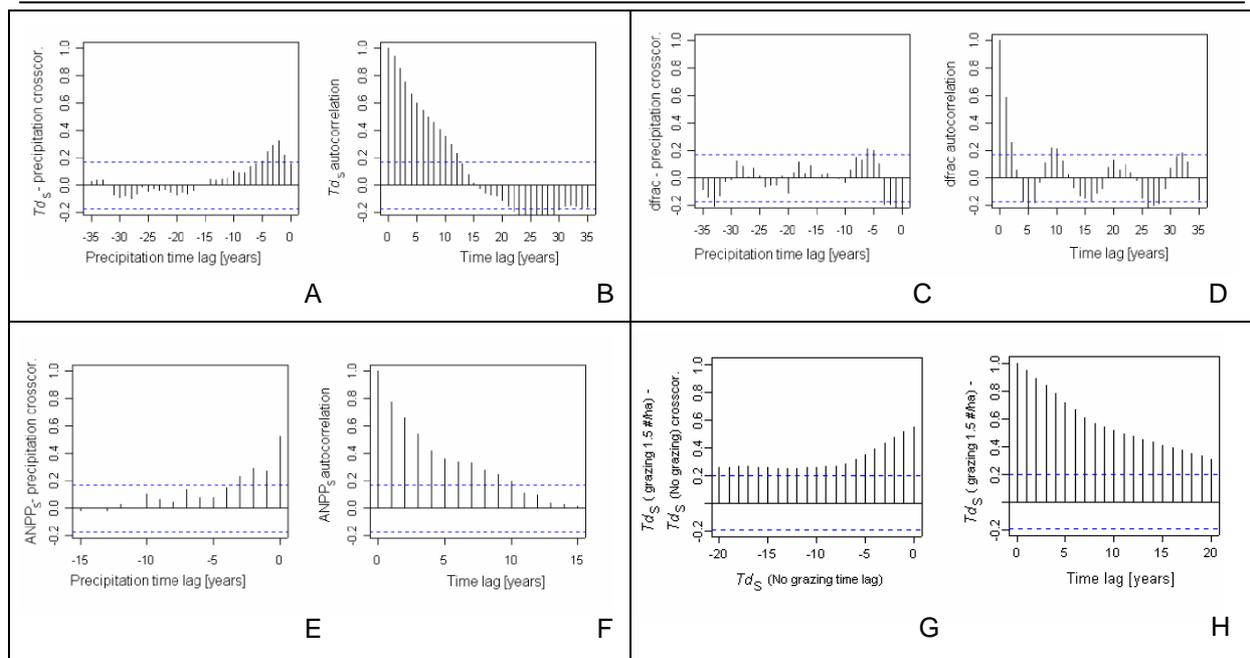
Fig. 5.14: Temporal auto- and cross-correlation for exemplar response variables.
Shown are exemplar results from simulations over 150 time steps over the whole grazing gradient (standard parameterisation, one climate repetition, time step 1-50 without grazing, time steps 51-150 analysed). Fig. A-F) No grazing; Fig. G) cross-correlation of heavy grazing with no grazing; Fig. H) heavy grazing; Fig. A, C, E show the cross-correlation between the response variable and the correspondent precipitation time lag; Fig. B, D, F, H show the temporal autocorrelation of each variable with itself; A, B): Tussock density; C, D): dead fraction of biomass (*dfrac*); E, F) landscape-level *ANPP* per year; G, H) Tussock density, heavy grazing. The dashed line indicates the confidence interval.

precipitation of the actual year. But it also depends on precipitation of the three years before, because precipitation has effects on tussock vitality. Interestingly, precipitation (lag = - 4 years) is significantly correlated to Td_S (Stock = 0.0 sheep / ha) and the time lag = 5 years correlation is as strong as lag = 0. This result indicates that the memory might last longer than one cycle of complete tussock recruitment.

The four years lasting significant cross-correlation between precipitation and tussock density indicates that the *F. pallescens* population 'memorises' not only the last recruitment event or vitality change, but also the earlier events and that these events may have significant effect on the actual tussock density.

Dead biomass fraction autocorrelation. – The dead biomass fraction *dfrac* shows a different temporal pattern. Its significant autocorrelation lasts only 2 years (Fig. 5.14 D) and it shows a cyclical behaviour of alternating negative and positive autocorrelations. This pattern is surprising. I did expect significant autocorrelation during more years than the result indicates but without a clear pattern at higher time lags. The cyclical dynamics of *dfrac*-autocorrelation could be related to a precipitation pattern or to patterns of tussock recruitment. Tussock recruitment reduces *dfrac* due to the assumption that recently recruited tussocks include only green biomass during their first year. I did not detect any autocorrelation within precipitation, though I observed a trend to a significant negative autocorrelation at lag = -3 (see Chapter 2). Possibly, this slight pattern in autocorrelation might affect *dfrac*-dynamics. As *dfrac*-dynamics are assumed to be an important characteristic for forage selection, this aspect is worth further investigation.

Annual net primary production autocorrelation. – Finally, annual productivity of the simulated patch (*ANPP*) behaves similar as Td_S without grazing (Fig. 5.14 E-F). The significant

autocorrelation of *ANPP* lasts nearly 10 years (Fig. 5.14 F), and its cross-correlation with precipitation is strong up to lag = - 3 (Fig. 5.14 E), whereas the cross-correlation with lag = 0 is the highest one, as expected. Thus, at least four years of rainfall have a relevant effect on *ANPP*. This results indicates, that the memory effect resulting from the seedling survival at lag = - 3 directly affects the history and development of annual net primary production *ANPP*.

Combined effect of grazing and precipitation on vegetation. — Fig. 5.15 shows the combined effect of grazing and stochastic precipitation on tussock density (ungrazed ($Td_{S0.0}$) and at Stock = 1.5 sheep / ha, $Td_{S1.5}$), the net change for Td_S between grazed (Stock = 1.5 sheep / ha) and ungrazed per time step, and how precipitation and grazing contribute to the change in tussock density, the mean vitality (*mean vit$_S$*), tussock recruitment and tussock mortality.

The time series comparing the tussock density Td_S (grazed and ungrazed, Fig. 5.15 A) shows the following: $Td_{S0.0}$ shows a certain delay in reacting on precipitation, and thus shows certain constancy. A single more humid year (e.g. $t = 4$ or $t = 14/15$) does not lead to a rapid change in $Td_{S0.0}$. An increase in $Td_{S0.0}$ occurs after a series of average and/or humid years. Normally, three years without a dry year might lead to an increase in $Td_{S0.0}$ ($t = 6$ or $t = 10$), but one dry year in between can be compensated by humid years (e.g. $t = 16$ or $t = 21$). $Td_{S0.0}$ reacts more directly to dry years with decrease due to mortality, whereas reduction of $Td_{S0.0}$ can be masked by a high recruitment during the same time step (e.g. $t = 6$).

Td_S reacts similar under grazing ($Td_{S1.5}$) as $Td_{S0.0}$, but shows essentially two differences: Firstly, the mortality due to drier years might be higher ($t = 6$, Fig. 5.15 F) and tussock recruitment does not compensate mortality during drier years ($t = 6$, Fig. 5.15 E). A higher negative change of tussock density (Fig. 5.15 B) due to grazing can occur due to additional mortality (Fig. 5.15 F) or due to the lack of compensation by tussock recruitment (Fig. 5.15 E). Additional tussock mortality due to grazing contributes with a certain constancy but with small amounts (Fig. 5.15 F) to the net change between no grazing and the heavy grazing scenario. The most catastrophic events for both tussock densities occur during a second dry year (see Fig. 5.15 F). But only the non grazed vegetation is on the long term able to regenerate with recruitment, responding to a series of average and humid years (Fig. 5.15 E). This result is a very important one, because it may explain important characteristics of the observed dynamics for *F. pallescens*.

Lack of recruitment causes decrease in density. — The higher reduction of $Td_{S1.5}$ is mainly caused by lower tussock recruitment on the long term. This means that $Td_{S1.5}$ is not able to regenerate as strongly as $Td_{S0.0}$ after a series of average or good years. Thus, under heavy grazing the ability to respond with recruitment to average or good climatic conditions is lacking. When $Td_{S1.5}$ decreases under a certain threshold ($Td_S = 2.5$, compare Chapter 2) $Td_{S1.5}$ is not able to respond with tussock recruitment to average or good conditions any more. The net differences between $Td_{S0.0}$ and $Td_{S1.5}$ (Fig. 5.15 B) reflect these findings: the greatest difference between both variables occurs in years, where $Td_{S0.0}$ increases, but $Td_{S1.5}$ is unable to follow. Fig 5.15 B shows that the difference between $Td_{S0.0}$ and $Td_{S1.5}$ may stay constant during five or ten years.

The contributions of precipitation and grazing to Td_S-change depend also on the climatic context (Fig. 5.15 C). If Td_S decreases strongly due to mortality the dominant contributions comes from precipitation ($t = 1$, $t = 13$). The contribution of heavy grazing to change in tussock density varies over time (Fig. 5.15 F): At the onset of grazing it contributes more to additional mortality (Fig. 5.15 F, $t = 6$), after 16 years the lack of recruitment triggers the increasing tussock density change. From time step 16 on $Td_{S1.5}$ compensates all large tussock recruitment events completely, which demonstrates the lack of the ability to respond to favourable conditions.
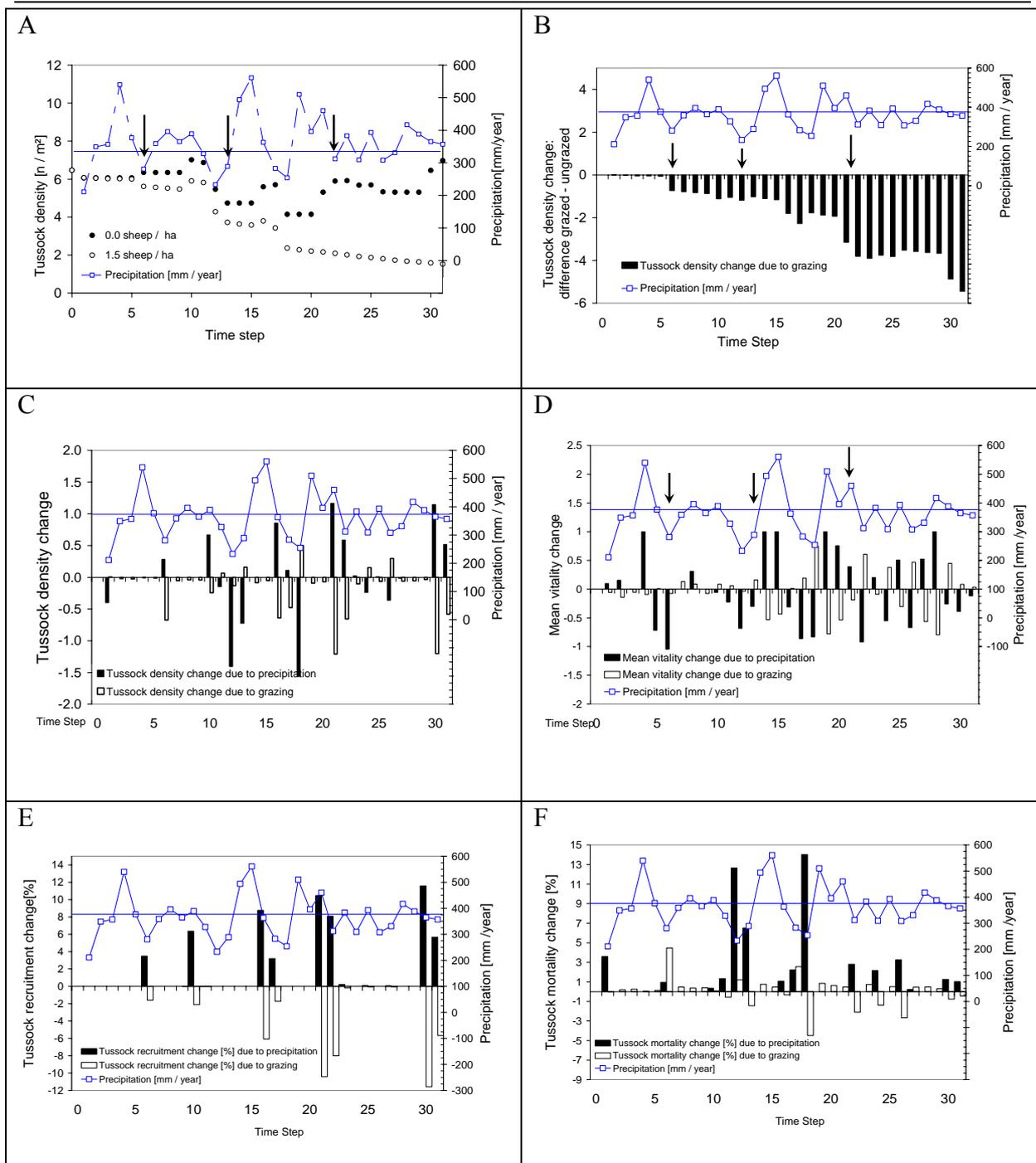
Fig. 5.15: Combined effect of grazing and stochastic rainfall on tussock density
    Shown are the relative contributions of stochastic rainfall and heavy grazing (1.5 sheep / ha) on tussock density change. **A**) First 30 time steps of a simulated time series for tussock density Td_S without grazing and $Stock = 1.5$, and the effect of annual precipitation on both (Note for Fig. 5.15 A-C: 100% *Festuca* cover equals to $Td_S = 11.1$); **B**) Net difference for Td_S at time step i between grazed and ungrazed simulation; **C**) contributions of precipitation and grazing to annual changes in tussock density per time step. **D**) Net mean vitality change due to precipitation and grazing; **E**) Tussock recruitment change [%] due to precipitation (without grazing) and due to grazing (1.5 sheep / ha, difference between no grazing and grazing); **F**) Tussock mortality change [%] due to precipitation (without grazing) and due to grazing (1.5 sheep / ha, difference between no grazing and grazing).

During some time steps, grazing seems to contribute positively to tussock density change (Fig. 5.15 C, D, and F). This might be an artefact, which is caused by the reduced response of $Td_{S1.5}$ to precipitation. The reduced response would be a consequence of the already reduced tussock density and the reduced absolute number of dying tussocks relative to $Td_{S0.0}$ (Fig. 5.15 F). The contributions of precipitation and grazing to mean vitality change show a similar pattern as the tussock density changes (Fig. 5.15 D). During the first 13 years, grazing does not contribute much to the mean vitality change, and then the contributions increase considerably. The virtually positive contributions of grazing are interpreted as a lack of response to precipitation, because vitality is already reduced to low values.

5.4 DISCUSSION

During the discussion I resume how I answered the questions raised at the beginning of chapter 5 and I place my results in the context of the following issues: degradation and desertification, the interaction between unpredictable rainfall and grazing, state and transition model vs. rangeland model, threshold effects in land use, and management.

I used a spatial explicit, individual based simulation model which was constructed and analysed with a pattern oriented approach. The simulation model was calibrated and validated against all available field data (see Chapter 4) and the remaining model parameterisations, which represented the reasonable range of model dynamics, were used for the simulation experiments. The general aim of this chapter was to understand the mechanisms which cause degradation of the *Festuca* steppe under climatic uncertainty, considering the remaining parameter uncertainty. The simulation experiments included different scenarios of seasonal or continuous grazing, and a grazing gradient ranging from mean stocking rates of 0 to 2.0 sheep / ha. All simulations were repeated for 100 stochastic climates and run over 150 yearly time steps. The first 50 years were simulated without grazing to facilitate adaptation of the simulated steppe to the initial conditions. Additionally, several single simulations were run with the standard parameterisation (based on the expert estimation) to illustrate the specific development of the vegetation dynamics. I addressed the following questions and will shortly resume the most important results.

1) How does grazing affect vegetation under stochastic climate, considering parameter uncertainty?
Grazing affects vegetation negatively on the long-term and tussock density shows threshold behaviour in respect to stocking rate. Parameter and climatic uncertainty change the slope of the tussock density response to grazing as well as the initial equilibrium value and mask the threshold behaviour to an important extent. Because of climatic uncertainty, negative effects of grazing on vegetation may not be detectable early in the field. Additionally, parameter uncertainty leads to uncertainties in the estimation of a sustainable stocking rate threshold.
1 b) How does grazing affect vegetation under different time scales, different types of forage selection and different grazing regimes?
The detection of a significant vegetation changes requires often time scales of more than 50 years, due to the mentioned uncertainties. If grazing would be non-selective, stocking rates could be higher than under continuous grazing all the year round, or grazing only in spring, or summer/autumn. Winter grazing also reduces selectivity and allows for higher sustainable stocking rates.
2) I derived a criterion for long-term sustainable grazing management under stochastic climate conditions and parameter uncertainty.
The proposed criterion for a long-term sustainable grazing management requires that, at a given stocking rate, tussock density remains above 30% of the original level with a 90% probability,

considering additionally climatic and parameter uncertainty. I found that the sustainable stocking rate ranges for continuous highly selective grazing between $0.3 < \text{Stock} \leq 0.9$ sheep / ha, and for non-selective grazing it may reach $\text{Stock} \leq 0.9$ sheep / ha.

3) **I provide an understanding of how grazing and stochastic climate interact and how this interplay affects the dynamics of *F. pallescens*.**

The time series of several important response variables show significant correlations to the rainfall time series (tussock density and annual net primary production at the patch level *ANPP*). Two memory effects were found: the first memory is the memory to the initial condition. The duration of this memory increases under grazing. This indicates that the non grazed vegetation is stronger coupled to climate than under grazing. This is because without grazing both recruitment and mortality events change tussock density, whereas recruitment events are strongly reduced under heavy grazing. The second memory effect is a delay in vegetation response to precipitation, which may last for tussock density or *ANPP* up to five years. This finding is explained by the three year development time a seedling needs to become a mature tussock.

Grazing and stochastic climate in combination have stronger effects on vegetation than grazing under a constant average climate. Two mechanisms explain this finding. A series of two (or more) consecutive dry years can cause higher tussock mortality than would occur under constant climate. Grazing leads to additional mortality, but more important is that grazing causes the vegetation to loose its ability to produce sufficient recruitment after a series of average and more humid years. Additionally, vitality of tussock is reduced during dry years. Thus, the differences in tussock density occur between a non-grazed and a heavy grazed patch especially after a large tussock recruitment event at the not grazed patch.

The duration of tussock recruitment and the impact of grazing on two and three year old saplings are critical biological assumptions for these results and should be tested in the field. Additionally, the conditions for a safe site for seedlings recruitment are unknown and the assumption that larger bare patches ($\geq$ 90 x 120 cm) lead to reduced seedling survival should be tested. Further the details of tussock mortality are highly uncertain. I assume that grazing affects tussock vitality and tussock mortality, a hypothesis which is well founded by general observations (see Chapter 2), but should be investigated more in detail. It is important to have these assumptions in mind for later discussion.

5.4.1 Understanding the grazing effect in combination with stochastic rainfall

Understanding how stochastic rainfall and grazing interact together is one of the great challenges in modelling grazing in semi-arid regions. Due to the high variability in vegetation dynamics, which is caused by rainfall variability, it is difficult to separate long-term effects from short-term effects (Pickup 1996). Several studies have dealt with the effect of grazing under stochastic rainfall on vegetation (Ellis and Swift 1988, Ellis 1994, Wiegand and Milton 1996, Jeltsch et al. 1997, Stafford Smith and McKeon 1998, Stephan et al. 1998, Weber et al. 1998, Weber et al. 2000, Illius and O'Connor 2000, Janssen et al. 2004). The novel contribution of the present study is the quantitative separation of the contribution from anthropogenic (grazing) and natural effects (rainfall). Simulation models offer the option of performing controlled experiments even under stochastically fluctuating conditions. Hence I was able to identify the proportion of demographic processes such as tussock recruitment or mortality caused by either rainfall or grazing.

To my knowledge such a separation of grazing and rainfall effects has not yet been done, at least for studies the grazing impact on vegetation under stochastic rainfall. None of the simulation

studies mentioned above analysed a time series in such detail (but see Wiegand et al. 1995; Jeltsch et al. 1999).

My results confirm the results of a simulation model developed by Stephan et al. (1998), which analysed the sustainability of a management strategy based on resting a part of the paddocks during wet years. This strategy which was empirically derived by the farmer H.A. Breiting seems to work very similar to my finding. The justification of this strategy is that regeneration would be impossible during dry years and that therefore resting will be in vain. But in humid years regeneration is possible and could be promoted by resting a part of the paddocks. If a paddock is rested during a humid year it has the chance to rebuild plant cover by recruitment and to regenerate the vitality of existing tussocks. However, substantial differences between the *Festuca* steppe and the desert ecosystem studied by Stephan et al. (1998) may exist. Therefore it is unclear if similar or different processes lead to similar results. This would be an interesting point for further investigation.

Empirical data on the interaction between grazing and stochastic climate are rare. I could find some studies which are related to this topic: Kelly and Walker (1976) in Illius and O'Connor (1999), Danckwerts and Stuart-Hill (1988), O'Connor (1994), Fynn and O'Connor (2000), Fuhlendorf et al. (2001), Teague et al. (2004). Illius and O'Connor (1999) state that during droughts heavy grazing has negative effects on vegetation, as do Fuhlendorf et al. (2001). These studies report that higher mortality occurs during a dry year under heavy grazing. They hypothesize that higher mortality is due to the additional stress which is exerted by grazing on the plants. Fynn and O'Connor (2000) and Teague et al. (2004) found significant interactions between grazing and year (i.e. rainfall variability). But these studies do not specify how this interaction works. O'Connor (1994) states, that the tussock grass *Themeda triandra* is markedly reduced during drought and heavy grazing. This perennial South African tussock grass reproduces strictly from seeds and is comparable to *F. pallescens* in Patagonia. Danckwerts and Stuart-Hill (1988) observed that decreaser species like *Themeda triandra* do badly regenerate under grazing after a drought occurred. This aggregated finding parallels my finding that limited recruitment after dry years might be decisive for the fate of a grazed paddock.

5.4.2 State and transition

In rangeland ecology the equilibrium versus non-equilibrium debate referred to earlier (Chapter 2.5.6) is paralleled by a more applied discussion, namely the debate over the Range succession Model versus the State and transition model. The range succession model (Clements 1916) assumes that grazing and drought act similar on vegetation, and that negative effects of grazing or drought are reversible since succession will always compensate for negative effects. Several authors argued that this approach is unsuitable for semi-arid grasslands because the response of vegetation to rainfall and grazing is discontinuous (e.g., Westoby et al. 1989, Walker 1993). Sutherland (1974) introduced a theoretical concept of multiple stable states describing vegetation dynamics as a non-linear set of alternative stable states which differ markedly and are separated by abrupt transitions in space or time.

Though many state-and-transition concepts exist for specific systems (Bertiller and Defossé 1993, Walker 1997, Milton et al. 1998, Stringham et al. 2003), experimental validation of this concept is difficult. Wiegand et al. (1995) pointed with a simulation model for the Karoo shrubland two reasons why proving such state transition in the field is fraught with difficulties: recruitment events are rare because they depend not only on rainfall conditions, but also on the availability of safe sites for germination. Therefore, correct formulation of states and transitions would require observation times much larger than usual observation times. Not surprisingly, empirical studies on this topic are rare (Oliva et al. 1998) because they require long-term vegetation monitoring.

In the following I will interpret my results within the context of the state-and-transition model. As discussed above (Fig. 5.15 A and B), tussock density reacts with a temporal delay to precipitation. Changes in tussock density occur mostly discontinuously (Fig. 5.15 A and B) and in between tussock density remains unchanged for two or more years. These changes do not represent different stable states neither for the no grazing nor for the grazing scenario. Interestingly, the differences between a not grazed and a grazed patch remain stable for a longer time, often 5 years or even up to 10 years (Fig. 5.15 B). I suggest that for management such 'transient or medium-term stable states' are relevant and should be included into rangeland monitoring. The reason is that the proposed stable states for the *Festuca* steppes are very coarse (Bertiller and Defossé 1993): They demand for State I (optimal condition) a total cover of 60-90% and a *Festuca* cover of 30-50%, for State II (slight degradation) a total cover of 30-60%, with a *Festuca* cover of 10-40%.

One problem of the state and transition models is that they are conceptual models and do not give time horizons for vegetation change and refer only to clearly visible changes in vegetation. Thus, it is difficult to recognize these transient or medium-term stable states and more subtle changes using this concept.

My results show that with a tussock density of approximately $Td_S = 2.5$ (cover $\sim 23\%$) regeneration might already be inhibited in an irreversible way under constant grazing. Under the assumption that the simulation model works for all palatable tussock grasses of the *Festuca* steppe in a similar way, my estimates for State I would be: 55-85% and for State 2: 15-50%. Thus, there is a real danger that a classification into State II (slightly to moderately degraded) is already near or even below the limit of the regeneration ability of the tussock grass population. These results show that management of relatively complex systems such as the *Festuca* steppe require a more sophisticated approach for range management than provided by the state-and-transition concept.

Management options related to state and transition monitoring. – I suggest to use the 'medium-term stable states', which are stable during a series of years, for range assessment and to monitor the difference e.g. in tussock density between a non-grazed reference and the grazed paddock (Fig. 5.15 B). Comparing changes in tussock density between a grazed and a non grazed situation showed that the difference changed discontinuously and tended to be stable for 5 to 10 years (Fig. 5.15 B). Medium-term time scales are relevant for management (Bertiller and Defossé 1993). After critical negative or positive events, e.g. one or more dry years or a series of at least two average or humid years, a monitoring comparing tussock density in a grazed and an ungrazed paddock should reveal if discontinuous behaviour occurred. And one would detect the cause for the change, if it would be caused by grazing. In theory, after the first discontinuous negative change occurred, the farmer would be able to react and consider changes in management. Necessary for such a monitoring system is the creation of representative exclosures and their continuous monitoring. The costs for exclosures should be paid off by the benefit of a better knowledge of vegetation dynamics which could be used for appropriate management.

Obviously there are several problems to be solved before this approach could be applied in practice. One problem might be that the *Festuca* steppe could have evolved under low grazing (M.B. Bertiller, pers. comm.). Thus, the optimal reference would be a lightly grazed exclosure, similar to sporadically grazing e.g. by guanacos. Thus a not yet quantified amount of grazing might be necessary to maintain the *Festuca* steppe as it evolved.

Consideration of scale. — Another problem one has to consider for a comparison between a reference and a grazed situation is the scale problem. I simulated on a small scale which is representative only for homogeneous parts of a larger paddock. As paddocks in Patagonia are 1.000 ha and more in size, larger scale patterns due to landscape characteristics (e.g. slope), distance to water

places, fences etc. will occur. These larger scale effects on grazing and its effect on vegetation would be important to study in a following project.

A pragmatic approach would be to select referenced plots for grazing and no grazing at areas of the paddock which are similar in important landscape characteristics, e.g. altitude, slope, exposition, soil and position within the paddock. Another problem which might masks the detection of change is the spatial variability of tussock density. In a first rough estimate given in Chapter 3, Fig. 3.9 the spatial variability of tussocks density reaches approx. 20% in exclosures. Spatial variability of tussock density should be investigated more in detail. Another interesting question is, if a systematic pairwise comparison would work for also for patches which are already in a certain state of degradation and hence not initiated from the assumed natural state as the simulation results presented here.

Additional focus variables: dead biomass fraction. — An additional option for a response variable which would be suitable to detect grazing effects is the dead biomass fraction *dfrac*. *Dfrac* has a low temporal autocorrelation and a low cross-correlation with precipitation (Fig. 5.14 C-D). I assume that the low autocorrelation in time leads to a faster detection of the grazing impact. The time series of *dfrac* for a grazed and an ungrazed situation revealed a typical pattern for both scenarios (see Fig. III.4 A, Appendix III): without grazing *dfrac* shows a pattern of rapid increase at some years. I assume that this is mostly caused by recruitment events, but could also be caused by high mortality events. This would be an interesting point for further investigation. *Dfrac* shows under grazing no extreme changes, and when grazing is completely coupled to vegetation, the variability of *dfrac* is strongly reduced (Fig. III. 4 A, time step 19). But this finding would indicate an already degraded state with low probability of regeneration (compare with Fig. 5.15 A).

Conclusion. — The qualitative approach I presented might help to detect early warning signals of conditional changes using time series data, which represents one of the outstanding challenges in ecosystem studies (see Scheffer and Carpenter 2003).

5.4.3 Threshold behaviour

The non-linear response of tussock density to stocking rate showed clear threshold behaviour (Fig. 5.5) behind grazing under stochastic climate. Threshold behaviour under grazing was detected in previous studies for the phenomenon of shrub encroachment in semi-arid savannas in Southern Africa (Jeltsch et al. 1997, Weber et al. 1998, Weber et al. 2000), and is a phenomenon which is found and discussed widely in ecology (see van de Koppel et al. 1997, Scheffer et al. 2001, Cousins et al. 2003, Scheffer and Carpenter 2003, Schwinning et al. 2004). Simulation models about grazing, which detected grazing thresholds, are rare (but see Jeltsch et al. 1997, Weber et al. 1998, Weber et al. 2000) and have a coarser resolution than the presented model (30 cm x 30 cm vs. 5 m x 5 m). Thus, the *Festuca* model is the first simulation model which includes realistic small-scale processes at the individual tuft level which shows threshold behaviour. One of the most important findings of my study is that that the slope of the threshold-response curve to grazing depends both on the specific precipitation time series and on the biological or parameter uncertainty (see Fig. 5.5).

This finding has important implications for management. First, in regions with highly variable rainfall the threshold value itself is of little use as reference for sustainable grazing management. This is because the essential feature of the threshold-response curve in relation to sustainability is the slope, not the threshold. Thus, under unpredictable rainfall one should be aware that the slope will depend on the specific sequence of rainfall events. A precautionary management recommendation (derived from simulation studies) should define a sustainable stocking rate as the stocking rate where the slope of the fitted tussock density-stocking curve becomes negative. This finding has important practical consequences. For the *Festuca* steppe, the estimated threshold, which proved to be very robust over

139

the biologically and climatologically uncertainty, lies at approx. 1.0-1.1 sheep / ha (Fig. 5.5). If I consider both uncertainties, the point of inflexion is shifted to a stocking rate of approx. 0.3 sheep / ha, which is a third or fourth of this threshold. This estimate is in good agreement with the other qualitative estimate for a sustainable management (Fig. 5.11 A, for continuous high selective grazing), which demands a stocking rate lower than 0.6 sheep / ha to be sustainable.

Conclusion. — The results presented here are an important advance to quantify a risk level that is acceptable for a given time scale, as postulated by Jeltsch et al. (1997).

5.4.4 The criterion for sustainable management and the effect of grazing on biodiversity.

In Chapter 5.3.6 I proposed a criterion for a long-term sustainable stocking rate for the *F. pallescens* steppe. The criterion uses a cover threshold of 30% *F. pallescens* cover. This threshold lies at the transition between the best state of a *F. pallescens* steppe and a state where the steppe might show slight signs of degradation. Due to the lack of field data the limit cannot be determined sharply (see Bertiller and Defossé 1993). The proposed threshold limit is reasonable because I assumed a threshold which is above the regeneration threshold for constant grazing (cover ~ 23%, see Chapter 2), including a 30% buffer. The proposed 30% cover only for *F. pallescens* lies within the *Festuca* state showing slight signs of degradation (Bertiller and Defossé 1993), but also at the lower limit for the optimal state. Thus, additional variables would define the exact state, as e.g. the total plant cover. One shortcoming of the model is that it does not include other species, as other palatable tussock grasses. However, most of the plants, which contribute to additional plant cover of the *Festuca* steppe, are tussock grass species, too. Thus, it is reasonable to assume that they are prown to similar processes as *F. pallescens*. Considering this simplifying assumption, the 30% threshold would already be at the lower limit of the second state of the *F. pallescens*, as proposed by Bertiller and Defossé (1993). Despite I do not know the exact regeneration threshold for *F. pallescens* under constant grazing under the presence of further species, my result is a reasonable first approximation assuming similar dynamics for other tussock grass species integrating the *Festuca* steppe. The proposed threshold is reasonable from a farmers point of view, but would it also the case from an ecological point of view?

Sustainable grazing threshold and biodiversity. — From an ecological point of view, one of the decisive questions related to grazing management is if biodiversity is conserved sufficiently under the proposed grazing threshold. The knowledge about the relation between grazing and its effect on biodiversity is scarce for the *F. pallescens* steppe. Reviewing the available literature concerning this topic (León and Aguiar 1985, Facelli and León 1986) suggest that if *Festuca* cover is reduced to 30% a low reduction seems to occur. But this topic requires more detailed investigation.

Facelli and León (1986) provided the only data and analysis I could find related to this topic. They studied 43 paddocks differing in the visible impact of grazing. They ordered the samples after their inequality, which is assumed to be correlated with the grazing impact. They derived a linear regression function, which indicates that the paddocks in the best states contained 34 species, which declines to approx. 20 species at the other end of the axis. León and Aguiar (1985) fitted a curve for *F. pallescens* cover following the same order of paddocks. This curve shows that *F. pallescens* cover declines exponentially along the paddocks order. Transferring this finding on the data given by Facelli and León (1986) the species reduction might reach approx. 4 species at average, when *F. pallescens* is reduced to 30% cover. Using this estimation, the suggested cover threshold leads to a low reduction in biodiversity. But I do not know if species composition changes occur already at the transition between the good and the slightly degraded state. León and Aguiar (1985) list the cover for *F. pallescens* along the ordered gradient and discuss some species which seem to decline along the 'grazing impact axis'. A qualitative assessment of *F. pallescens* cover and its correlation with the 'grazing impact axis'

shows neither a clear correlation of the *Festuca* steppe at 30% cover with the ordering axis nor with the species group, which seems to decline along the axis. So a question if a proposed threshold cover of 30% for *F. pallescens* is sufficient for conserving biodiversity at the *Festuca* steppe is subject to further studies and discussions.

5.4.5 Temporal Memory

As I showed with Fig. 5.14, tussock density Td_S and annual net primary productivity *ANPP* are significantly correlated with precipitation 4 and 3 years before the actual time step, respectively. Hence the system shows a considerable memory. I explain this memory mainly with the seedling dynamics implemented into the model. After seedling survival there are two years of juvenile state. As seedling survival is an important parameter for the population dynamics (see Chapter 4.3.2, Tab. 4.6, parameters ColWS0 and ColS0p), it is no surprise that precipitation which occurs three years before the actual tussock recruitment is significant correlated with tussock density Td_S. An additionally explanation for the relation of previous precipitation to tussock density could be the effect of precipitation on vitality, which will have delayed effects on the actual tussock mortality since only tussocks in the lowest vitality class die. A series of good years improves the vitality of tussocks, so mortality is reduced when a dry year follows. A future task would be to separate the relative contributions of both effects. The critical point considering this finding seems to be the dynamics of juveniles. The dynamic of juveniles is highly uncertain. Field data exist only for survival of seedlings for a maximum of approx. one year (Defossé et al. 1997a, Defossé et al. 1997b). The majority of seedlings emerge in autumn and the following summer is critical for survival.

Thus, a seedlings dynamics of at least 2 years is empirically justified. At the end of the summer seedlings grow up to one tiller, but its fate from this stage is unknown. Sapling states lasting several years has been observed (M.B. Bertiller and J.M. Paruelo, pers. comm.). Thus we included an additional saplings state. It is also reasonable to assume a higher grazing impact on young tussocks and saplings. The reproductive contribution by two years old tussocks and their susceptibility to drought is not known. These assumptions should be tested carefully in the field or in glasshouse experiments.

There are few studies which report memory effects. Oesterheld et al. (2001) and O'Connor et al. (2001) found that the previous year ANPP helped to explain a higher proportion of variability of the actual ANPP. Wiegand et al. (2004c) developed a regression model which integrates a memory index for precipitation to predict ANPP. They hypothesized that the layer from which grasses provide themselves with water accounts for the memory effect. If this is the case for adult *Festuca* tussocks, is actually not known. Wiegand et al. (2004c) discuss further effects which may cause a memory of previous precipitation events. In some cases the soil can act as 'capacitor', when water is transferred from one year to the other. Features of plant population dynamics (e.g. a seed bank, establishment of a cohort of perennial plants, initiation of buds, Goward and Prince (1995) in Wiegand et al. 2004c) or plant structural factors to changes in biomass, storage organs, or cover (see Gibbens and Beck 1988, Anderson and Inouye 2001, both in Wiegand et al. 2004c) may explain memory effects within a system. Paruelo et al. (2005, i.e. Chapter 3) discuss different memory time scales for different variables.

For *F. pallescens* it is probable that several effects contribute to the found memory effect. The most important I assume will be the recruitment of cohorts (plant population dynamics effect); a structural effect, expressed as the memory incorporated into the vitality change dynamics is relevant. Carry over of plant available soil water to the next year, was neglected within this model. We do not

know further detail about this topic, but to date there is no evidence that *F. pallescens* is able to gain water from deeper soil levels.

If memory effects can indeed explain important fractions of actual annual productivity, theoretical models of multiple stable states (van de Koppel, et al. 1997, van de Koppel and Rietkerk 2000) should be revised, because the pathway of attraction starting from an unstable equilibrium will be influenced by history.

5.4.6 Grazing scenarios and implications for management.

My results showed that continuous grazing leads to heavy overgrazing and cover loss if the stocking rate exceeds a certain threshold. Continuous, highly selective grazing with high stocking rates is similar to an opportunistic, exploitative strategy, a so called 'trial and error'-strategy (Golluscio and Paruelo 1998), which tries to maximize the economic output on a short term. On the long term it will lead to a reduction of tussock density and for high stocking rates tussock density will fall below the regeneration threshold. A constant stocking rate implies that during dry years, if natural forage supply is deficient, supplementary feeding is applied. Such an approach might increase the negative effects of grazing in comparison to a natural herbivore dynamics. For a natural herbivore dynamics one can expect that after a series of dry years the population is weakened by drought, and there will be a certain delay in the recovery of the herbivore population which provides the vegetation a rest. So the grazing effects under natural herbivore dynamics should be less severe than under constant grazing at or over the threshold limit. Below alterative management scenarios are discussed further. These include non-selective grazing, adaptive stocking and precautionary constant low stocking.

Non-selective grazing management. — My results showed that grazing scenarios, involving less selective grazing (winter grazing and non-selective scenarios), lead to a more sustainable use of the *F. pallescens* steppes. The best method to force sheep to graze non-selectively is to create smaller paddocks by fencing. Then each small paddock would be grazed for a shorter time, and the resting time for each paddock will be longer. The ecological and economic sustainability of this strategy is supported by simulation studies (Stephan et al. 1998, Beukes et al. 2002). The question remains whether this will hold true in the low productive system of Patagonia where farmers are reluctant to investing in additional fencing (Stafford Smith and Foran 1992).

Adaptive stocking. — Adaptive stocking management is poorly documented and a controversial topic (Stafford Smith and Foran 1992, Stafford Smith and McKeon 1998, Weber et al. 1998, Weber and Jeltsch 2000, Weber et al. 2000, Janssen 2004). Weber et al. (2000) found that adaptive stocking rates are more sustainable than constant stocking rates. Stafford Smith and Foran (1992) report, that destocking of 20% of livestock, after one dry year, and destocking of 40% for longer dry periods, was economically valid. Stafford Smith and McKeon (1998) compare a reactor strategy, which aims to graze at a constant relative grazing intensity, with a constant stocking rate strategy with a long-term simulation study. The reactor strategy showed a high variability of income, but was approximately as valuable as the constant strategy. None of the studies addressed how the resource develops on the long-term. Stafford Smith and McKeon (1998) pointed to an important economic problem of an adaptive stocking rate: the high variability of income within years. Beukes et al. (2002) criticize adaptive stocking rates, because it is probable that the farmer gets low prices if he sells parts of his stock during bad years (because all other farmer will do the same), and might pay high prises when he wants to restock. The assumption behind this argument is that if many farmers start to de-stock, when a drought begins, prises will fall. When those farmers want to restock after drought has broken, prises will rise due to the synchronized higher demand. Additionally the decision when to destock and to what extent is not an easy one (Stafford Smith and Foran 1992).

My results add a biological constraint to these economical problems. As I showed, high stocking rates have a negative impact on tussock recruitment, which should occur after a series of good years. Higher mortality during dry years caused by high stocking rates occurred only at the beginning of a specific grazing history of a patch (Fig. 5.15 F). The failure of regeneration is the more important impact on the long term. So restocking after drought might have a similar negative impact on recruitment, than a constant high stocking rate and might fail to reach a long-term sustainable management. So the topic of adaptive management stays controversial and should be investigated further.

Conservative constant, but low stocking mangement. — The final strategy involves constant stocking at very low rates. Janssen et al. (2004) recommend such a cautious management strategy for grazing in highly variable environments, where stocking rates should be lower than for a low or constant climatic variability. They compared optimal stocking rate strategies under constant and highly variable climate. My results suggest that a low constant stocking rate, which should reach only approximately a third or a fourth of the stocking rate estimated stocking rate threshold, has a chance to be sustainable on the long-term. The advantage of such a strategy would be economically the low cost, which is an important factor in low productive systems. A natural herbivore dynamics could be allowed to a limited extent, because during a series of dry years, reproduction of sheep might be reduced, which lead to a delay in herbivore increase, if a series of average or more humid years follow. Natural reproduction would allow the higher forage supply to be exploited to some extend during periods of average to humid years. On the other hand, grazing itself may create structural changes within vegetation, which may create positive feedbacks between vegetation heterogeneity and grazing, which may create patch dynamics consisting out of strongly used and avoided patches (Posse et al. 2000). If such feedbacks contribute significantly to vegetation dynamics in the Festuca steppe, was not yet investigated. All these aspects and relationships should be tested in detail by additional simulations, because the effects will depend on the applied mean grazing intensity relative to available forage.

The main disadvantage of conservative low constant stocking rates is that excess forage available during good years is difficult to utilise. Options may exist for using this as dry forage in subsequent dry years. The results of the *Festuca* simulation model suggest a long-term viable *F. pallescens* population requires the following conditions: tussock density should be maintained at a high level to avoid permanent degradation, vitality or potential productivity of plants should not decrease significantly in comparison to an ungrazed or slightly grazed system and recruitment should be possible. Further investigation is necessary to test if a simple strategy can be derived which is sustainable on the long term and makes a better use of resources during humid years. From an ecological point of view, low constant stocking strategies seem to be feasible. Low stocking rates might have a low negative effect on biodiversity and could also improve quality of the products Golluscio et al. (1998).

Golluscio et al. (1998) discuss three factors which might be responsible for ecosystem degradation: 1) overestimation of carrying capacity of the rangelands, 2) inadequate distribution of animals in very large, heterogeneous paddocks, and 3) year-long continuous grazing. My results show that point 2) and 3) could be improved by non-selective grazing and probably even would allow higher stocking rates. The overestimation of the carrying capacity could be a consequence of an underestimation of forage selection by sheep which might lead to a higher loss of green biomass due to senescence as otherwise would be the case or of an underestimation of senescence (see Chapter 4).

Summary. — The discussion of the most important results leads to the following conclusion: I presented a simulation model which integrates an individual-based description of the grazing process (as an interaction between the individual plant resource and herbivores) with the development of a

framework, where both grazing and climate act upon essential demographic processes such as seedling survival, tussock recruitment and mortality, or biomass production and vitality. I provide an understanding of how uncertainty about the degradation process is affected by the stochasticity of the climate and the remaining biological uncertainties, represented by parameter uncertainty. This understanding is directly translated into quantification of risk levels for specific time-scales, which might be acceptable on the long-term. I presented two independent methods to estimate long-term sustainable stocking rates under the given conditions for Patagonian Ranches (i.e. grazing all-year round in paddocks of tenths of km², which leads to high selective grazing). I quantified the effect of a management, which would force herbivores to non-selective grazing by creating smaller paddocks. This method was shown to be effective by other simulation models. My contribution was to study these management methods under biologically more realistic conditions, because the forage selection models are based on a biologically plausible foraging hypothesis and not from theoretical models or aggregated assumptions.

I separated the relative effects of stochastic climate and grazing on the demographic processes of a dominant forage species for a semi-arid ecosystem; a task which is especially difficult in ecosystems with stochastic rainfall (Pickup 1996). I derived a hypothesis how stochastic rainfall and grazing interact and provided a quantified understanding of this process. I detected significant correlations between the precipitation of the past and essential response variables of *F. pallescens* population dynamics, as tussock density or *ANPP*. Thus, the investigated systems show an important memory component for its own precipitation history. A similar memory was found by Wiegand et al. (2004c). Wiegand et al. (2004c) detected the memory effect via regression analysis which included an abstract memory parameter, whereas within my model the memory is an emergent characteristic of the implemented demographic processes. The remaining biological uncertainties should be studied further. I improved the quantitative understanding of the degradation process and showed a threshold which leads to a long-term degradation due to the loss of regeneration ability. This type of multiple stable states were already predicted by theoretical models (compare van de Koppel and Rietkerk 2000), but if one wants to face the global problem of desertification and degradation, one has to fill the theoretical models with biology, using concrete stocking rates, time scales of degradation and so on, if they should be of more than intellectual and academic use. The finding of memory of the *F. pallescens* for its own history might have important consequences for equilibrium models and might be worth of further investigation.

6 GENERAL DISCUSSION WITH RESPECT TO UPSCALING

I will discuss the results of my thesis with respect to the upscaling issue which was raised in Chapter 1. Grazing generates heterogeneities on several scales (Golluscio et al. 1998, Parsons and Dumont 2003). While individual defoliation event takes place on the scale of individual tussocks, herbivores may take grazing decisions at the landscape scale. For example, their decision about the next grazing location may depend on the distance from a watering point and on the relative attractiveness of one patch relative to the accessible neighbouring patches. Thus, which patch will be grazed by an individual sheep or flock, when and at with which average intensity throughout the year, will depend on several larger scale factors. These factors may include the size of the paddock, the composition of the patch, its actual state and that of the neighbouring patches.

The model presented and analyzed in this thesis cannot address such larger-scale effects which are nevertheless important for an understanding of the degradation process and for management (management units comprise typically thousands of hectares). The thesis provided an understanding of the small-scale grazing process within the investigated ecosystem and the hypothesized grazing model. However, the construction and analysis of the small-scale model was always done with view to the next step; an upscaling of the small-scale model to the landscape scale. A natural continuation of this thesis would be therefore a project 'Impact of Grazing and Drought on the Vegetation Dynamics of the semi-arid Steppe in western Patagonia' that aims to assess the impact of grazing on vegetation at the next larger scale, the landscape scale for development of sustainable management strategies.

Aims and Questions of the general discussion: — In this chapter I will discuss several issues which have to be consider before an upscaling procedure can be started. First, it would be necessary to develop the model at a landscape scale and to simulate at least entire paddocks with several thousands of hectares, as they are used in Patagonia, or, even better, to simulate an entire Ranch with up to 250.000 hectares (2500 km² = approximately 3 times the area of Berlin/Germany). Because the vegetation units are not uniform at this scale, it might be necessary to include other dominant ecosystem types such as shrub-grass steppe or humid meadows. However, I will not discuss this issue here in detail because it would take one entire chapter. A first basic concept I presented at the IAVS conference in Porto Alegre in 2002.

Second, there are several possibilities to upscale a model and to integrate it into a larger scale model. I briefly discuss the advantages and disadvantages of different upscaling methods used in the literature and evaluate the results of this thesis with respect to its possibilities to derive an upscaled model. Both points are addressed at the end of the chapter.

The third issue to decide on is about the temporal scale at which the upscaling should be done. Finally, it is important to define the objectives and questions to be addressed with a larger-scale model because they will determine technical details of the upscaling procedure. The importance of this task is illustrated with the discussion on the appropriate temporal scale to be used for upscaling.

6.1. TEMPORAL SCALING

A central decision to be taken is definition of the time scale (or time step) of the upscaled model. The higher the temporal resolution, the higher the number of state variables and parameters are which have to be memorised. If the temporal resolution is one year, which makes sense for a grazing model, it would be necessary to track the survival of seedlings, and the different saplings stages, due to its susceptibility to stochastic rainfall. Using a temporal resolution of e.g., five years one would not need to track seedlings and saplings but use instead a probability distribution (or a functional relationship) of recruitment (and mortality) events resulting out of simulations crossing the factors precipitation time series, grazing intensity, patch history, and the remaining biological uncertainty. In

practice, generation of the probability distribution would require repeated simulations with systematic variation of the different factors to derive a probability for each combination of factors which may occur. The factors precipitation time series, grazing intensity, patch history, and the remaining biological uncertainty are the minimum factors which have to be considered separately for upscaling of the *F. pallescens* simulation model. The results of the thesis, shown in Chapter 2 (Fig. 2.4, Fig 2.5), and Chapter 5 (Fig. 5.5, 5.6, 5.14, 5.15) provide information on the relative importance of the different factors.

For a larger time step, e.g. 20 years, it might be possible to separate the 'parameter' history of the patch into the components 'initial state of the patch', which may include grazing history or not, and the memory of the grazing history of the last 20 years. As the analysis of the temporal autocorrelations and the analysis of the interaction between grazing and precipitation showed, the memory of a given patch changes depending on grazing intensity and grazing duration. But these effects were detectable only on a longer time scale of approximately 20 years. To upscale the model at a larger time scale, it would be necessary to derive a probability distribution (or a functional relationship) between time, grazing intensity, grazing duration and structural response of the vegetation. A first guess would be a linear increase of the memory (see Fig. 5.14) with increasing grazing intensity in comparison to the no grazing scenario. A second guess would be an exponential decay of the memory of the patch for itself, as it is generally discussed within this issue (see Wiegand et al. 2004c and there for further citations).

6.2 PERSPECTIVES FOR AN UPSCALING PROCEDURE

The discussion of the temporal scale shows that an upscaling procedure implies two further essential questions: What is the objective of the upscaled model and how aggregated should the upscaled model (or its results) be? The approach used for upscaling depends on the aim of the upscaled model. If the aim of the upscaled model is to gain a general understanding of the development of a patch under different conditions, an aggregated measure (such as a probability distributions) could be used to describe the state transitions from one vegetation state to another (see Tab. II.1) as a function of time, initial state, included biological uncertainty, grazing intensity and grazing duration. A similar approach was performed by Acevedo et al. (2001). However, if the upscaled model should be used for more applied questions in management it might be necessary to include some detail on the precipitation time series e.g. to investigate what happens after series of dry, average, or humid years. This requires more effort because different types of precipitation time series need to be considered rather than pooling completely different stochastic time series.

Upscaling using the state and transition concept. — One coarse upscaling approach is to perform repeated simulations to generate a probability distribution for the transition matrix from one state to another, similar to the approach performed by Acevedo et al. (2001). This approach neglects details of the answer of the vegetation to the short term precipitation regime and generalizes the behaviour of the system only at a specific time scale. This approach assumes that specific states of vegetation are discernible. For the *F. pallescens* steppe (Bertiller and Defosse 1993, Bertiller et al. 1998, Tab. II.1) exists a classification according to the state and transition concept, but the classification includes considerably overlaps between states, which complicates a separation of distinct degradation states.

Upscaling by extrapolation by expected value. — An upscaling approach which retains more detail of the small-scale model is to produce a "model of the model" which predicts the average behaviour of the small-scale model by integrating the outcome of the relevant small-scale spatial dynamics of the small-scale simulation model. This approach can be called 'Explicit upscaling by

extrapolation by expected value' (Bugmann et al. 2000) and tries to derive the joint frequency distributions of the variables describing landscape heterogeneity. The complete small-scale simulation model would be applied for all possible combinations of factors and parameter ranges necessary to cover both the small-scale heterogeneities and the heterogeneity imposed by the landscape scale model. For example, grazing intensity higher than the average stocking rate, which may temporally arise due to an actual higher preference of the simulated patch, need to be included. This approach requires a high simulation effort because it uses the whole 30-paraemter model. Bugmann et al. (2000) argue that this approach is only feasible if it would be possible to obtain an analytical expression for the joint frequency distribution. Since the *F. pallescens* simulation model reacts in a non-linear way to the grazing gradient and since discontinuous structural changes may occur, an analytical approach would be difficult for the *F. pallescens* model. To the knowledge of Bugmann et al. (2000) and mine, this approach has not been successfully implemented, at least for an ecosystem with focus on vegetation.

Upscaling by analytical integration. — A similar approach to the extrapolation with expected value would be the 'explicit upscaling by extrapolation with analytical integration' (Bugmann et al. 2000). Bugmann et al. (2000) argue that this method is not feasible in most cases because closed analytical expressions cannot be found for many ecological models, including all gap models where the state transition functions are based on an algorithmic approach rather than on differential or difference equations. But there exists at least one example where analytical integration was performed successfully. Moorcroft et al. (2001) upscaled an individual based forest gap model and derived a set of partial difference equations (PDEs), which represents the upscaled model. They included important smaller-scale spatial relations, which are missing in "mean-field" approximation, by additionally including the second-moment equations which describe spatial effects in a first approximation. They used some simplifying assumptions for the gap-dynamics of one patch and derived a model with a reduced number of terms, which essentially contribute to the upscaled dynamics. However, this approach has at least two major problems. First, Moorcroft et al. (2001) did not show that the upscaled model is indeed simpler than the original individual based gap model. Second, the mathematical derivation of the upscaled model is complex and incommunicable to most field ecologist and biologists concerned with applied questions.

Explicit upscaling by model abstraction and extrapolation by expected value. — As an alternative to approaches discussed above, I suggest an approach which combines elements of the different approaches. My interest is in deriving an upscaled model which is able to predict structural changes in more detail than possible with the state and transition concept. My idea is to first simplify the original small-scale model based on the results of my sensitivity analysis, retaining only those parameters and processes which are essential for generating the small-scale model dynamics and then to statistically summarize the simplified model. This combined approach is in accordance with Levin (1992), who asked to include only necessary details into a large scale model and it integrates elements of the approaches used by Bugmann et al. (2000) and Moorcroft et al. (2001). In practice, the upscaling will be done by numerical simulation of the simplified model using the method of the extrapolation with an expected value, as proposed by Bugmann et al. (2000), rather than by generating an analytical solution as proposed by Moorcroft et al. (2001). The difference to the approach of Bugmann et al. (2000) is that a model with reduced complexity is used (instead of the full model) which will (hopefully) reduce the former complexity of the initial model. This approach could be called 'Explicit upscaling by model abstraction and extrapolation by expected value'.

6.3 DISCUSSION OF THE THESIS' RESULTS AS A BASIS FOR UPSCALING

Potential of the Festuca model processes to be abstracted/upscaled.. — I now will evaluate the processes and parameters of the *F. pallescens* model based on the results obtained in my thesis and ask if they need to be integrated into an upscaled model. The important task here is to identify the essential ingredients and the necessary detail of the small-scale model which should be included into an upscaled model (Levin 1992). The discussion follows systematically the order of implemented processes (Fig. 2.3).

Initialisation. — The autocorrelation analysis showed (Fig. 5.14) that the initial distribution has an important impact on the dynamic of the steppe. The most simple approach would be to define a vector which includes only mean values, e.g. for tussock density, mean tussock vitality, seedlings survival memory and e.g. for saplings survival memory. A more sophisticated approach would be to use for each state variable would a specific distribution, e.g. a normal distribution of vitality values. Another possibility is to start with an artificial initial condition and simulate the model over longer time spans until an equilibrium is reached and use simulated "snapshots" which correspond to defined conditions.

Biomass carry over. — This 'process' is a technical one which memories the remaining biomass from the past simulated time step and thus is not relevant here.

Global water input. — As precipitation is one of the essential external drivers contributing to heterogeneity and variability it is essentially to include it to the upscaled model. The spatial distribution of precipitation might be highly heterogeneous on a larger scale. As a consequence, the dynamics of the different patches may become desynchronised and thus differentially attractive for livestock. As global water input was homogeneous for the small-scale model, no change would be necessary here.

Water redistribution. — An important question for the upscaling procedure is if the effect of local heterogeneities of water redistribution needs to be integrated into a upscaled model. Otherwise one could use a much simpler non-spatial model of *Festuca* dynamics, which would probably be similar to the classical models of population dynamics (Wissel 1989). To remember, the local water redistribution includes a trade-off. On the one hand, a high use of lateral plant available soil water helps to compensate grazing effects due to higher productivity of adult tussocks (Fig. 4.6), but on the other hand it leads to asymmetric competition (Weiner 1990) and to endogenous limitation of recruitment (see Colonization, eqn. I.23-I.25). For example, bare patches may create non-linear feedbacks and create localized drought conditions even if global rainfall is sufficient. Such small-scale effects would be difficult to describe with classical "mean field" approximation.

Indeed, the results of the sensitivity analysis (see Tab. 4.6-4.7, Fig. 4.4-4.6) highlighted the potential strong overall positive effect of lateral water uptake on *F. pallescens*. A detailed analysis of the effect of water redistribution on recruitment inhibition is still lacking. But, as it is empirically indicated (Defossé et al 1997a, b), I argue that it would be necessary to include this small-scale effect into the upscaled model. Here one should have in mind, that the empirically estimation of the parameter lacks to date. Possibly it might be useful o separate both effects from each other – the positive effect on adult tussocks, and the negative on recruitment – and to integrate both separately into the upscaled model. This task is interesting enough to devote one complete chapter or publication to this topic. An important challenge is the question how to upscale the small-scale water redistribution. One feasible option seems to be, to generate the frequency distributions under an exemplary range of initial conditions, including tussock vitality distribution, eventually including extreme scenarios of spatial configurations of the tussocks, and the whole range of precipitation scenarios. That implies that all possible initial distributions which might occur under the complete scenario-parameter space (precipitation x grazing intensity x initial distribution x (grazing duration) x

parameter uncertainty) are included into this simulation. Thus, a certain discretisation of the central state variable, the *F. pallescens* vegetation structure (here tussock density) is necessary.

Water induced vitality change. — The state variable 'vitality of a tussock' (vit) strongly influenced the *ANPP* of a tussock (*mean prod* see Tab. 4.8). The four parameters describing the water related vitality dynamics were of different importance, depending on grazing (see Tab. 4.6-4.7) but one of them was the most important one. For an upscaled model, the simplest approach would be to use one parameter for increasing, and one for decreasing vitality, possible using the same parameter and reversing its sign.

Plant production. — Only the basic parameter for productivity (PG.1/ProdV1) resulted to be essential for absolute maximum productivity, and the second parameter for plant productivity might be neglected. Additionally the non-linear Michaelis-Menten equation could be reduced to a linear relationship, but without abstracting one parameter and this is feasible only, if the temporal resolution will be kept.

Defoliation. — Within the defoliation process the stocking rate is the most importnat parameter, and has to be included into an upscaled model. Additionally, as a theoretical interesting option, it would be possible to include the grazing shape parameter Gshape/GR.4, which modifies the grazing acceptance of a tussock. The analysis of the grazing model for upscaling would be mainly related to the probability of grazing acceptance (eqn. I.16). An alternative approach would be to estimate the dead biomass fraction (*dfrac*) as a non spatial average value out of dead and living biomass. However, such an approach might miss just the objective for which the simulation model was developed and would work only for the non-selective forage selection scenario. A better options would be to calculate the average of the dead biomass fraction *dfrac* out of an biomass frequency distribution derived from the multiplication of the productivity parameter with a generated vitality frequency distribution. But this approach would also fail because it cannot memorize the grazing history. Thus, I assume that it is necessary to derive a frequency distributions for the dead biomass fraction (*dfrac*) under different conditions. As this approach requires the covering all possible scenarios of initial conditions x grazing intensities x precipitations x prior *dfrac* distribution this could be a challenging task also.

Colonization. — The results of Chapter 5 showed that recruitment comprises several aspects, which make scaling to the possibly most complicated process. Within this process the interaction between grazing and climate is most important and includes a highly relevant memory effect. This memory effect is a result from tussock recruitment which lasts several years over with one seedling and two sapling stages. Sensitivity analysis showed that the most important parameter was the water related germination parameter ColWS0/CO.1. Thus, a simplifying model might be including a submodel for saplings survival, which includes mainly the germination parameter plus the effect of precipitation and grazing and an exponential decay of saplings survival, triggered by seedlings survival and the time lag to tussock recruitment. Such an approach should be tested, if it captures the essential characteristics of the interaction between grazing and precipitation, as it was analysed within Chapter 5. Otherwise, an explicit scaling of each seedling and sapling stage might be necessary, which would complicate the scaling approach considerably.

Grazing induced vitality change. — As this sub-process includes only one free parameter, the others are related to it relatively and apply to different seasonal grazing scenarios, this parameter should be left included, as it is reasonable to assume a sub-lethal negative effect of grazing on tussocks.

Senescence and littering. — Both parameters involved in senescence and littering proved to be essential antagonists to stocking rate. Therefore they have to be included into an upscaled model.

Since they do not contain direct small-scale variability they might be translated directly into the new model. Similar to the local water redistribution, this parameters are not yet estimated in the field.

Mortality. — Mortality is obviously an essential process, and proved also to interact with the precipitation time series, but less with grazing. Similarly to vitality dynamics, one mortality parameter (Mort.W1/ MortW1) was the most sensitive one (Tab. 4.6 and Tab. III.4). This offers another option for simplification. The two grazing related mortality parameters were also less important, due to the inherent dynamics of the model system, which was unknown before starting this analysis.

Conclusion. — As the detailed analysis of the model processes show, there are several options for model simplification and upscaling. To find out which of these approaches are most appropriate to upscale the small-scale grazing process to patch level vegetation dynamics, accurately averaged under grazing and stochastic climate, is a highly interesting challenge and task. Such an upscaled model could be integrated into a larger scale model, which incorporates drivers and relevant factors at the larger scale (heterogeneous precipitation regime, herbivore large scale site selection, states of neighbouring patches, and long distance dispersal). It would also provide a highly interesting tool for analysing and learning about grazing impacts on a larger scale under stochastic precipitation. The presented simulation model, the model calibration and sensitivity analysis, as well as the gained understanding about the interaction and memory effects of grazing and precipitation, were necessary steps and will facilitate an upscaling for the presented ecosystem. Thus, the presented thesis, despite the numerous single interesting and novel results, contributes to an understanding of the complex and challenging problem of crossing different scales, which are regarded as the some of the most important challenges in ecology (Levin 1992).

7 SUMMARY AND CONCLUSION

7.1 SUMMARY

The presented PhD thesis presents a simulation model, which was developed to gain an improved understanding for the causes of desertification and degradation of vegetation. Despite degradation of drylands has occurred on a global scale, and the problem is discussed since decades, the details of the degradation process are poorly understood. It is generally accepted, that grazing and highly variable rainfall interact together and may lead to discontinuous shifts in vegetation. But highly variable rainfall masks the effect of grazing and makes it difficult to separate the natural from the man-induced effects which lead to degradation of vegetation.

The general aim of this thesis is to obtain an understanding of the small-scale processes involved in degradation, especially the interaction between grazing and highly variable rainfall. I used an individual based, spatially explicit simulation model to separate the natural from the anthropogenic effects. The gained new understanding of the degradation process may lead to a further development of long term sustainable management strategies.

Individual and rule based, spatially explicit simulation models are ideal tools to investigate such a problem, because they are able to bridge several time and spatial scales. Further, they are able to integrate 'soft knowledge', for example expert knowledge about the system, as rules into the simulation model.

As study system I used the cold temperate, semi-arid *Festuca pallescens* grass steppe in North West Patagonia, Argentina. The *Festuca* steppe is suitable to investigate degradation because detailed empirical knowledge about the system was available, a biologically plausible grazing model could be developed, and the system consists mainly out of the eudominant species *F. pallescens*, which provides at least two third of the vegetation cover and up to 90% of the aerial biomass. Thus, this ecosystem can be abstracted in a first approximation to a one species system.

The general philosophy of the model – integrating both essential drivers, grazing and precipitation with the main demographic processes of *F. pallescens* on the level of individual plants – requires the implementation of a medium complex model with 30 parameters, which could not be estimated in the field or in the literature.

The implementation of such a complex simulation model requires considerable efforts of model calibration which was done by comparison of the output of the simulation with the available field data. Thus, this PhD thesis has additionally a methodically focus, which is represented within the investigated questions:

- What type of vegetation dynamics shows the *Festuca* steppe in terms of equilibrium vs. non-equilibrium dynamics? (Chapter 2)
- How well do the results of the standard parameterisation, estimated by the field ecologists, coincide with the available field data? (Chapter 3)
- Can we validate some basic assumptions of the simulation model with available field data? (Chapter 3)
- Can we calibrate a medium complex simulation model with 30 uncertain parameters despite of a strongly limited amount of field data? (Chapter 4)
- Which biological processes or parameters have a large impact on the results of the calibrated simulation model, and determine the remaining biological uncertainty? (Chapter 4)
- Does the change in vegetation structure show threshold behaviour against a grazing gradient, and is that threshold affected by biological and climatic uncertainty? (Chapter 5)

- Is it possible to derive management options out of the analysis of the relation between vegetation structure change and the grazing gradient, which may lead to long term sustainable dynamics of *F. pallescens*? (Chapter 5)
- Can we detect memory effects or time lags which affects the vegetation dynamics of *F. pallescens* ? (Chapter 5)
- How do grazing and highly variable rainfall interact, how do they affect vegetation, and which are the relative contributions of both drivers to the specific demographic events of *F. pallescens* and to the total change in the temporal change of vegetation structure? (Chapter 5)

The main results of the presented PhD thesis are:

The investigated system shows an event-driven behaviour, which is demonstrated with the demographic behaviour of *F. pallescens*. Grazing modifies the event-driven behaviour both gradually and qualitatively (Chapter 2). The medium complex simulation model was calibrated successfully, applying and further developing the indirect pattern oriented calibration method, conceptualised by Wiegand et al. (2003), despite the low amount of available field data. (Chapter 4)

The results of the sensitivity analysis highlight that the senescence rate, the littering rate and the local soil water redistribution are important processes within the investigated system (Chapter 4). The change in vegetation structure shows threshold behaviour against the grazing gradient (Chapter 5). I demonstrated that the stocking rate at which vegetation starts to decrease in the model depends on remaining biological and climatic uncertainty (Chapter 5). Based on the results characterising the long term behaviour of vegetation structure a criterion for a long term sustainable grazing management was proposed, which contains a risk level of degradation for each grazing level (Chapter 5).

Further the modelled system shows memory effects involving its own history and for approximately five years that of precipitation history. Finally I demonstrated that a separation of natural and anthropogenic effects is possible. I found that that the interaction of grazing and stochastic rainfall leads to a lack of regeneration during a series of favourable years of precipitation, and not, as conventionally assumed, that higher mortality during drought leads to degradation of the vegetation. Finally the results of this PhD thesis are discussed with respect to scaling issues (Chapter 6).

7.2 CONCLUSION

The presented PhD-thesis analyses both short-term and long-term effects of grazing on a semi-arid *Festuca pallescens* grass steppe over a range of stocking rates and considers the remaining biological and climatic uncertainty. The presented analyses of the results demonstrated the non-linear behaviour of vegetation structure changes due to grazing, they provide new insights and understanding of the interaction of grazing with stochastic rainfall in semi-arid ecosystems, and they provide a criterion for a long term sustainable grazing management considering the remaining uncertainties. Furthermore the presented indirect multi-criterial pattern oriented calibration method helps to bridge the gap between theoretical and empirical ecology as it enables us to gain strong confidence into simulation models even if we dispose only over scarce evidence from empirics. This PhD-thesis enhances our understanding of the complex dynamics of semi-arid systems significantly and improves methods for comparison of results of simulation models with field data.

Both aspects lead to a better understanding of ecosystems, which are endangered by land use and strongly affected by stochastic environmental processes. This helps to understand and to manage better such ecosystems with inherent uncertainties over several spatial and temporal scales, and to bridge the gaps between theory and empirics. The methodological aspect of this PhD-thesis is of general interest for simulation models facing a high degree of uncertainty because the presented method allows tying the model closely to the data, i.e. ensuring a biologically reasonable behaviour and parameter values.

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DEUTSCHE ZUSAMMENFASSUNG

Die vorliegende Doktorarbeit untersucht mit Hilfe eines Simulationsmodells für ein konkretes System die Ursachen für das globale Problem der Degradation und Desertifikation von semiariden und ariden Ökosystem unter dem Einfluss menschlicher Landnutzung und Übernutzung im Zusammenspiel mit komplexen natürlichen Einflussfaktoren (Schlesinger 1990). Semiaride und aride Ökosysteme sind häufig unter dem Einfluss räumlich und/oder zeitlich zufällig stark schwankenden Umwelteinflüssen vor allem des Klimas unterworfen, wie zum Beispiel stark schwankenden jährlichen Niederschlagsmengen. Solche stochastischen Effekte erschweren es den Einfluss anthropogener Landnutzung sowohl kurz- als auch langfristig von den Effekten stark schwankender natürlicher Umweltfaktoren zu trennen (Pickup 1996).

Das Hauptziel dieser Doktorarbeit ist es, an diesem Problem anzusetzen und mittels eines individuenbasierten, räumlich expliziten regelbasierten Simulationsmodells die anthropogenen und natürlichen Einflussfaktoren auf die Vegetation voneinander zu trennen und somit ein tieferes Verständnis der Interaktion zwischen menschlich verursachten und natürlichen Einflussfaktoren zu gewinnen. Dieses neu gewonnene Verständnis soll dazu beitragen, langfristig nachhaltige Bewirtschaftungsstrategien in semiariden Weidegebieten zu entwickeln

Räumlich explizite, individuenbasierte Simulationsmodelle sind dafür die ideale Untersuchungsmethode, da hiermit sowohl die räumliche als auch die zeitlich langfristige Entwicklung des Ökosystems untersucht werden kann, wobei sämtliches Wissen über das Ökosystem – auch so genanntes, weiches Wissen', wie Expertenwissen – mit Hilfe von Regeln im Simulationsmodell Verwendung findet.

Das untersuchte Ökosystem ist die kalt temperierte semiaride *Festuca pallescens* Grassteppe (Golluscio 1982) in Nord-West Patagonien, Argentinien. Sie stellt ein ideales Untersuchungsobjekt dar, da bereits umfangreiche Kenntnisse über das System vorhanden waren, ein biologisch plausibles Beweidungsmodell formuliert werden konnte und die eudominante Art *Festuca pallescens* (St. Yves) Parodi ca. 2/3 der Pflanzendecke und bis zu 90% der oberirdischen Biomasse produziert, so dass das Modell in erster Näherung als ein Ein-Art System modelliert werden kann.

Das Grundkonzept dieser Arbeit, nämlich den Einfluss von Beweidung und stochastischem Niederschlag auf Individuenebene zu simulieren, erfordert die Implementierung eines komplexen Modells mit 30 freien, nicht im Feld oder aus der Literatur schätzbaren Parametern. Das Modell ist derart komplex, da jeder demographische Prozess explizit modelliert wird und sowohl Parameter enthält, die den Einfluss des schwankenden Niederschlags enthalten, als auch Parameter, die den Beweidungseinfluss repräsentieren Diese Komplexität stellt hohe methodische Anforderungen an die Kalibrierung des Modells mittels der verfügbarer Daten aus dem Freiland. Aus diesem Grund hat diese Arbeit über die inhaltliche Ausrichtung hinaus einen starken methodischen Schwerpunkt, der sich in den **untersuchten Fragen** ausdrückt:

- Welche Art der Vegetationsdynamik im Sinne einer Gleichgewichts- oder einer ereignisgesteuerten Vegetationsdynamik zeigt das entwickelte Simulationsmodell und damit das hiermit untersuchte Ökosystem? (Kapitel 2)
- Wie gut stimmen die simulierten Ergebnisse des Simulationsmodells bei Nutzung des durch Experten geschätzten Parametersatzes mit den verfügbaren Felddaten überein?
- Können einige zentrale Annahmen des Simulationsmodells durch Daten, die im Feld genommen wurden, unterstützt werden? (beide Kapitel 3)
- Kann ein komplexes Simulationsmodell mit 30 freien Parametern mit Hilfe der indirekten multivariablen musterorientierten Modellierung anhand einer geringen Menge verfügbarer Felddaten so kalibriert werden, dass die kalibrierten Parametersätze ein biologisch plausibles Verhalten zeigen und somit ein hohes Vertrauen in das Simulationsmodell gesetzt werden kann?

- Welche biologischen Prozesse und/oder Parameter haben innerhalb der kalibrierten Parametersätze einen hohen Einfluss auf die Ergebnisse des Simulationsmodells und können damit als besonders bedeutsam bewertet werden? (beide Kapitel 4)
- Zeigt Beweidung unter zufällig schwankendem Niederschlag ein Schwellenwertverhalten bezüglich des Verlaufs der Vegetationsstruktur und wird dieser Schwellenwert durch die biologische oder durch die klimatische Unsicherheit beeinflusst?
- Können aus der Analyse des Schwellenwertverhaltens Managementempfehlungen abgeleitet werden, die zu langfristig nachhaltiger Beweidung führen könnten?
- Spielen Gedächtniseffekte eine Rolle für die zeitliche Entwicklung der Vegetationsstruktur?
- Wie wirken Beweidung und die jährlich zufällig schwankenden Niederschläge zusammen auf die Vegetation ein und welche relativen Effekte haben beide Einflussfaktoren jeweils auf die demographischen Ereignisse und in ihrer Summe auf die zeitliche Änderung der Vegetationsstruktur? (alle Kapitel 5)

Die wichtigsten Ergebnisse dieser Doktorarbeit sind: Das untersuchte System zeigt in seiner Demographie ein von den schwankenden Niederschlägen bestimmtes ereignisgesteuertes Verhalten. Beweidung modifiziert dieses Verhalten sowohl graduell als auch qualitativ (Kap.2). Anhand des Vergleichs mit Felddaten konnte gezeigt werden, dass sowohl der von Experten geschätzte Parametersatz ein biologisch plausibles Verhalten zeigt als auch die zentralen Modellannahmen (Kap.3). Das von Wiegand et al. (2003, 2004a) entwickelte und von mir angewandte und weiterentwickelte Verfahren der indirekten multikriteriellen musterorientierten Modellkalibrierung konnte erfolgreich auf ein komplexes Modell mit 30 freien Parametern bei schwacher Datenlage übertragen werden.

Die durchgeführte Elastizitätsanalyse zeigte, dass die Seneszenz- und die Dekompositionsrate sowie die lokale nachbarschaftliche Bodenwasserverteilung wichtige Teilprozesse innerhalb des Systems darstellen (Kapitel 4).

Es konnte gezeigt werden, dass das Modellsystem ein Schwellenwertverhalten gegenüber dem Beweidungsgradienten aufweist, und dass der Beginn der negativen Veränderung der Vegetationsstruktur entscheidend von der klimatischen und der verbleibenden biologischen Unsicherheit abhängt. Aus der integrierten Analyse des Schwellenwertverhaltens in Kombination mit der Integration der beiden Unsicherheiten wurde ein Kriterium für die langfristig nachhaltige Bewirtschaftung eines semiariden Weidesystems bei definiertem Risikolevel und stochastisch schwankenden jährlichen Niederschlägen entwickelt.

Das Modellsystem zeigt signifikante Gedächtniseffekte gegenüber seinem früheren Zustand und seiner Niederschlagsgeschichte hinsichtlich bis hin zu fünf Jahre zurückliegender Regenereignissen. Des Weiteren konnte gezeigt werden, dass Beweidung diese Gedächtniseffekte qualitativ verändert, namentlich indem das Gedächtnis gegenüber seinem früheren Zustand erhöht wird und sich damit von der Niederschlagsgeschichte abkoppelt. Schließlich konnte gezeigt werden, dass die Interaktion zwischen Beweidung und schwankenden Niederschlägen zu einem Ausbleiben der Regeneration des Systems während einer Serie niederschlagsreicher Jahre führt und dies die Hauptursache für die Degradation des Systems ist und nicht wie allgemein angenommen, die Beweidung während einer Trockenperiode.

Zusammenfassend lässt sich feststellen, dass die vorliegende Arbeit sowohl methodisch einen entscheidenden Baustein in der Zusammenführung von Theorie und Empirie in der Ökologie beiträgt, da sie zeigen konnte, dass selbst komplexe Modelle bei schlechter Datenlage so gut kalibriert werden können, dass sie als biologisch vertrauenswürdig angesehen werden können. Zweitens trägt diese Arbeit entscheidend zur Verbesserung des Verständnisses der komplexen Zusammenhänge in semiariden Gebieten bei, die durch starke Zufallsschwankungen in den natürlichen Umweltbedingungen geprägt werden.

Populärwissenschaftliche Zusammenfassung
Langfristige Auswirkungen von Beweidung auf Vegetation unter stochastisch schwankendem Klima: Eine Skalenübergreifende Simulationsstudie

Sandro Pütz

Desertifikation und Landdegradation – die langfristige Zerstörung der fruchtbaren Vegetation durch natürliche oder vom Menschen verursachte Prozesse – der empfindlichen halbtrockenen und trockenen Ökosystemen gehören zu den globalen und größten ökologischen Bedrohungen unserer Zeit. Etwa ein Drittel der kontinentalen Erdoberfläche und ein Fünftel der Erdbevölkerung ist von der Degradation dieser Ökosysteme betroffen. Diese Systeme sind in der Regel durch jährlich stark schwankende Niederschläge charakterisiert, die natürliche Trockenheiten verursachen können und es verhindern, das negative Effekte z.B. die durch menschliche Landnutzung sowohl kurz- als auch langfristig erkannt werden können. Es gilt als wissenschaftlich anerkannt, dass die menschliche Landnutzung, wie zum Beispiel extensive Beweidung durch Schafe in Patagonien, mit der zufällig schwankenden Niederschlagsgeschichte zusammenwirkt. Wie die Prozesse im Einzelnen aufeinander einwirken ist weitgehend unbekannt und es ist bislang äußerst schwierig die relativen Beiträge der zur Wüstenbildung führenden natürlichen oder menschlichen Faktoren zu bestimmen.

Ziel der vorliegenden Arbeit ist es, mit Hilfe eines individuenbasierten gitterbasierten Simulationsmodells ein Verständnis für die Zusammenhänge zu gewinnen, wie menschliche Landnutzung und zufällig schwankende Umweltfaktoren zusammenwirken und damit Wüstenbildung und Degradation von Vegetation begünstigen. Ein Simulationsmodell ist ein idealer Ansatzpunkt für das vorliegende Problem, da hiermit verschiedene räumliche und zeitliche Skalen überbrückt werden können, was mit empirischer Arbeit allein nur unter äußerst großem Aufwand zu bewerkstelligen ist. Des weiteren können verschiedene Beweidungsmodelle oder Hypothesen über die Zusammenhänge innerhalb des Ökosystems getestet werden. Als Modellgrundlage diente die semiaride *Festuca pallescens* Grassteppe, im Nordwesten Patagoniens in Argentinien gelegen, für die bereits zahlreiche Untersuchungen, Felddaten und eine gut begründetes Beweidungsmodell vorlagen.

Das Interessante dieses Modellansatzes ergibt sich daraus, dass beide Faktoren, Beweidung und Niederschlag, auf jeden Grashorst einzeln in Abhängigkeit seines Zustandes und seiner Geschichte ein- und auf die einzelnen biologischen Prozesse wie Etablierung, Wachstum oder Tod direkt einwirken und somit die relativen Beiträge beider Faktoren auf die Vegetationsdynamik rekonstruiert werden können. Dieser Ansatz erforderte die Entwicklung eines komplexen Simulationsmodells, was außergewöhnliche methodische Anforderungen an den Vergleich des Modells mit den Felddaten (Kalibrierung) stellte. Durch die Weiterentwicklung der von Wiegand et al. 2003) entwickelten Methode der indirekten musterorientierten Modellkalibrierung konnte das Modell trotz einer geringen Datenlage, wie es in der Ökologie sehr häufig der Fall ist erfolgreich kalibriert werden.

Wichtige Ergebnisse des Modells sind die Erkenntnis, dass die Vegetation nicht linear auf den Beweidungsgradienten reagiert, wobei sowohl die verbleibende biologische Unsicherheit als auch die Unsicherheit in der Niederschlagsgeschichte einen hohen Einfluss auf den Effekt der Beweidung haben. Weiterhin konnte das Zusammenspiel von zufälliger Niederschlagsabfolge und Beweidung und seine Wirkung auf die Vegetationsstruktur aufgeklärt werden und Kriterien für eine langfristig nachhaltige Bewirtschaftung mit definiertem Risiko entwickelt werden.

Die vorliegende Arbeit bringt wesentliche Fortschritte für das Verständnis der ökologischen Zusammenhänge für halbtrockene Ökosysteme wie Steppen, die durch Landnutzung und jährlich zufällig schwankende Niederschläge gekennzeichnet sind. Des Weiteren zeigt sie, dass selbst komplexe Modell bei spärlicher Datenlage erfolgreich kalibriert werden können, womit diese Arbeit eine wichtige Brücke zwischen empirischer und theoretischer Ökologie schlägt.

APPENDIX I

I.I Detailed Model description

Here I present the detailed description of the rule set for the *F. pallescens* simulation model. It describes how precipitation and grazing affect the dynamics of *F. pallescens*. The general approach used to model the effect of precipitation or grazing on biological processes is the inclusion of thresholds, which are combined with probabilities of occurrence. This approach was used for every process, where detailed knowledge is lacking on how one driver affects the process. If certain hypothesis exists about the relation between *F. pallescens* and one of both drivers, a correspondent rule was used and implemented. The processes and equations follow the order given in Fig. 2.2 and Fig. 2.3.

I.1.1 Initialisation

A default initial distribution for *F. pallescens* was used for all simulations presented in this thesis (Tab. I.1). I assumed a hypothesized natural *Festuca* steppe with approx. 58% cover of *Festuca* tussocks and approx. 80% mean dead biomass fraction as the most important characteristic of the *Festuca* steppe. The initial distribution is orientated on field data for exclosure paddocks at the Estancia Media Luna in very good compositional state, which are used in this thesis for model calibration (see Chapter 3 and Chapter 4). In ungrazed uplands total vegetation cover can reach more than 70% (Coronato and Bertiller 1996). Perennial grasses reach 90% of vegetation cover in ungrazed uplands (Bertiller and Aloia 1997), and *F. pallescens* may reach up to 90% of the vegetation cover (Defosse et al. 1990) and up to 90% of the aerial biomass (Defossé et al. 1997a). We ignore the natural state of the *F. pallescens* steppe, due to the overall grazing in Patagonia since decades. So the data for the oldest exclosure for the *F. pallescens* seem to be the best reference. The initial distribution was generated with the simulation model itself by starting the simulation model with a random distribution of tussocks, running it for 20 time steps and saving the distribution if tussock density ranged between 6.0 and 7.0 (approx. between 54% and 63% *Festuca* cover) and cover of dead tussocks was between 3.5 and 8%.

Tab. I.1: Values for selected variables of the *F. pallescens*-model for default initial conditions (t=1) at population level.
Variables are defined in Tab. 2.2.

Variable	Abb.	Unit	Value
Cover live tussocks	cov_F	%	58.2
Tussock density	Td_S	n / m²	6.5
Cover dead tussocks	cov_D	%	8.1
Cover empty cells	cov_E	%	33.7
Mean vitality of tussocks	*mean vit*		2.46
ANPP per grid ($t = 1$)	*ANPP*	kg DM / ha	930
ANPP per tussock ($t = 1$)	*mean prod*	g DM / tussock	14.4
Precipitation use efficiency ($t = 1$)	*mean PUE*	-	0.38
Initial dead biomass	*db*	kg DM / ha	4142
Initial dead biomass fraction	*dfrac*	%	78.0
initial dead biomass fraction CV	$dfrac_{CV}$	%	10.8
Initial % primary forage	*PF*	%	30.0

Tab. I.2: Additional variables of the *Festuca pallescens* simulation model used within the Rule-Set.
Variables are listed, which are used only within the detailed Rule-Set in Appendix I.

State variable	Explanation	Unit	Detailed explanation
			Tussock level
b	Total *F. pallescens* tussock biomass	gb / cell area · year (g DM / 0.09 m² y)	Total biomass of a live tussock ($gb_P + db$)
$dfrac_S$	Seasonal altered $dfrac$	-	Seasonal weighted tussock structure $dfrac$ due to seasonal altered herbivore selectivity
di	Realized local defoliation severity	-	Realized relative local defoliation severity is realized through a random variable
ga	Grazing acceptance decision	-	grazing acceptance decision for actual tussock
$gprob$, $gprob_{GR.5}$	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 $dfrac_i$.
p_C	Colonization probability	-	Conditional colonization probability from $cs = 0$ to seedling states S_i and finally to a fully grown tussock ($cs = 2$)
$p_E \{cs = 0 \vert cs = 1\}$	Transition probability to empty cell from dead tussock	-	Transition probability of a cell with state $cs = 1$ (dead tussock) to $cs = 0$ (bare soil cell)
$p_M\{vit = 0 \vert vit = 1\}$	Probability of tussock mortality	-	Conditional mortality probability of a tussock; a tussock may die only if it has $vit = 1$
$p_{VC}\{vit = i+1$ or $vit\ i - 1 \vert vit = i\}$	vitality change of tussock	-	Probability of vitality change of tussock may depend on soil water w or defoliation severity ds

Tab. I.2 continued			Tussock level
$w'(x, y)$	Plant available soil water after water redistribution	H$_2$O / area (mm / cm²)	Local plant available soil water w for focus cell after first step of local water redistribution step1/ step 2
w_G	soil water before redistribution	H$_2$O / area (mm / cm²)	Soil water before local water redistribution, spatially homogeneous; contains a fraction defined by WI.1 from annual precipitation
			Patch / Landscape level
Bm	Green consumable biomass from all species	kg / ha	Green biomass including *F. pallescens* and / or green biomass from other species
CV$_{dgC}$	*cv of simulated degree of consumption*	-	*Cv of Mean relative consumption degree for patch (grid) and time step t*
DB	Landscape level dead biomass	Kg DM / ha	Landscape level of dead biomass (live tussocks only)
dgC	Simulated degree of consumption	-	Mean relative consumption degree for the whole grid (patch) and time step t
PF	Primary forage	*bm* / area (kg DM / ha)	Forage provided by other species, determined in relation to *F. pallescens*
R	Residual Forage	$\sum gb_P$ / area (g DM / 1500 m² t)	Total residual forage after grazing for total grid
R_S	Precipitation, simulated	H$_2$O / area (mm / cm²)	Spatially homogeneous annual precipitation
TF	Total available forage	*bm* / area (kg DM / ha)	Total available Forage, including other species, which are consumed with higher priority than *Festuca pallescens*

I.1.2 Biomass carry over

Carry over of resting green tussock biomass:

$$gb_{Co}(t) = \quad gb_S(t\text{-}1) \qquad\qquad , \text{ if } cs = 2 \qquad\qquad (I.1)$$

$gb_{Co}(t)$ Residual green biomass of live tussock from time step t-1, which is carried over to actual time step t

$gb_S(t\text{-}1)$ Resting green biomass of live tussock for time step t-1 after senescence,

I.1.3 Global Water input

The first of the three steps of water dynamics, 'Water input' is modelled as global, equal precipitation input for each cell of the grid (compare Chapter 2.2.2). There is no carry-over of plant available soil water from one year to another. Precipitation is implemented after Biomass carry over (see Fig. 2.3). The chosen reference site was 'Media Luna Ranch', because the first exclosure data were provided from there. Statistical description of the available precipitation data are presented in Tab. I.3. The Media Luna time series consists out of 24 years. As this time series is not enough as a input time series for the model, we generated a 10.000 data point precipitation time series, transforming the 68-year data set from the Leleque Ranch which has similar characteristics as 'Media Luna'. We transformed the Leleque data set to the mean and approximately to the CV of 'Media Luna' and generated the time series, using the transformed Leleque precipitation series as the first 68 data points, and then adding to them randomly drawn data points out of the first 68 data points (compare Chapter 2.2.2).

Tab. I.3: Statistical characteristics of the available and generated precipitation time series.
Given are Data from the Ranches Media Luna, Leleque and for the generated time series used as input for the simulation model.

	Leleque	Leleque partial	Media Luna partial	Media Luna	Generated time series
No. of years	67	22	22	24	10.000
Mean rainfall	459	481	385	385	375
Std. dev. Rainfall	118	118	69	66	76
Cv %	26	25	18	17	20
Min. rainfall	173	292	267	267	211
Max. rainfall	715	649	529	529	561
Max. – min. rainfall	542	357	262	262	350
First year	1931	1975	1975	1975	1931
Last year	1998	1997	1997	1999	-
Missing year	1991	1991	1991	1991	-

Fig. I.1 A shows the default precipitation input used for the simulations in this thesis (time steps 1 to 100). The probability of occurrence for a dry year (one standard deviation below mean annual precipitation MAP) is prob.$_{dry}$ = 0.12 and 0.17 for the original 68 data points and the first 100 time steps of the default precipitation scenario respectively. The probability for a humid year (prob.$_{humid}$) = 0.18 for both data sets. Fig. I.1 B shows the accumulated frequencies for the first 150 precipitation data points and for the threshold values for the nine parameters related to precipitation. This figure thus illustrates for a given precipitation how many parameters during this time step lie above or under their threshold and thus affect vegetation in one or the other direction, according to the rules. Thus, approx. 15% of the precipitation data during the first 150 time steps provide optimal conditions, because precipitation is higher than all nine parameter thresholds. Note that this figure holds only for the standard model parameterisation, because for each parameter variation (see
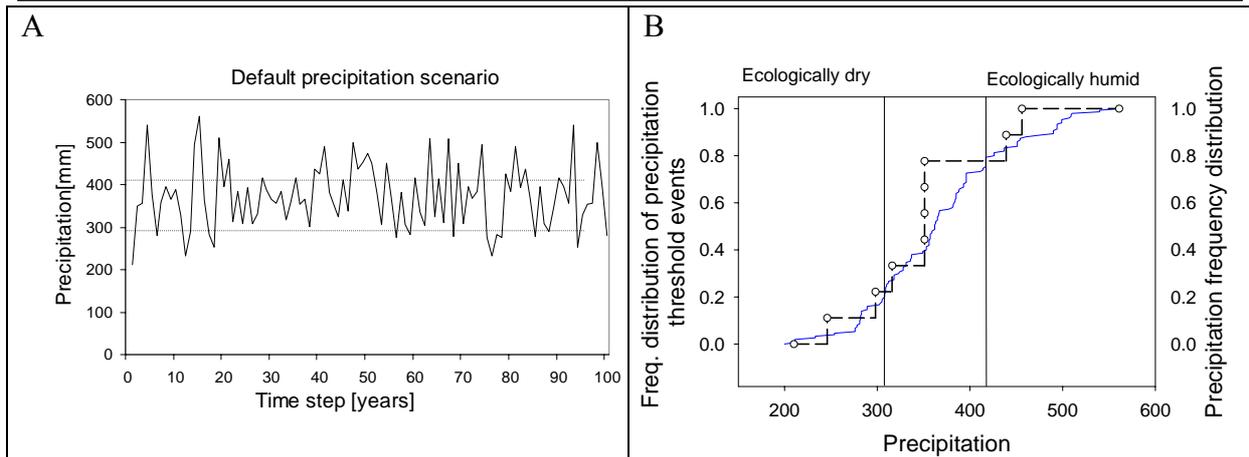
Fig. I.1: Default precipitation scenario and frequency distribution of precipitation related thresholds.
A): Shown are the first 100 years of the transformed Leleque data set to the default 'Media Luna-like' precipitation scenario used for simulations. Precipitation outside one standard deviation (see lines) is assumed to represent dry or humid years respectively. B) shows the accumulated frequencies of annual precipitation events during the first 150 time steps of the default precipitation scenario (straight line) and the accumulated frequencies for the 'decision points' (default threshold values) for the nine precipitation parameters implemented into the model (dashed line). The distribution shows, e.g. if precipitation lies between 300 and 350 mm, six default values for those parameters lie above such a precipitation and thus will show no positive effect on vegetation and three default values for water related parameters lie below this precipitation (frequency = 0.33), so more negative effects of precipitation will result finally on vegetation. The lines indicate an approximate ecological status of the *Festuca* steppe according to the implementation into the simulation model (accumulated frequency for standard model parameterisation and default rain use efficiency).

Chapters 4 and 5) the threshold accumulated frequency changes. Additionally this illustration only holds before local water redistribution. After local water redistribution plant available soil water is heterogeneous on a small scale, so patches may occur which are 'ecologically dry' and patches which might be 'ecologically medium or even humid'.

Global plant available soil water:

$$w_G \quad = \quad R \cdot WI.1 \tag{I.2}$$

w_G Plant available soil water for one time step *t* [year] before local water redistribution
R global annual precipitation [mm] at time step *t*,
$WI.1$ global parameter which defines the relative proportion of precipitation which will be plant available

After global precipitation the local plant available soil water is determined. In a first step the parameter WI.1 = 0.57 (default value, WI.1 = rain use efficiency per tussock), it is calculated which fraction of precipitation is potentially left as plant available soil water. WI.1 summarizes water losses due to evaporation, deep percolation or runoff:

I.1.4 Water redistribution

Local water redistribution includes all spatial or neighbourhood effects implemented into this model. Hence neighbourhood effects are modelled through soil water status exclusively. Live tussocks gain plant available soil water by lateral influx from empty and dead tussock cells in the neighbourhood (Fig. I.2). This rule assumes lateral root spread, which can be expected especially for arid systems (Schenk and Jackson 2002), due to the often relative shallow infiltration of rainfall. Bare soil and dead tussock cells loose plant available soil water due to lateral efflux to live tussock cells in

the neighbourhood. Direct competition between neighbouring living tussocks is not modelled; they behave neutral to each other.

A second algorithm increases water loss for so called 'large bare patches' (Fig. I.3). A large bare patch is a patch of bare soil cells, for which we assume higher water losses due to higher evaporation and/or runoff due to reduced water retention by the lack of vegetation. The higher loss of plant available soil water simulates indirectly the lack of available seeds in 'interspaces' or bare patches between *Festuca* tussocks (Bertiller and Coronato 1994). So the higher loss of plant available soil water is one hypothesis to explain the lack of reproduction of *F. pallescens*, as the reason for this findings are not yet clear (Bertiller 1996, Bertiller and Aloia 1997).

1) Local Water redistribution step 1: Water gain or loss respectively due to number of neighbouring live tussocks:

$$
w'(x, y) \;=\;
\begin{cases}
w_G(x, y) + N_1 \cdot WR.1 & , \text{if } cs(x, y) = 2 \\[2em]
w_G(x, y) - N_2 \cdot WR.1 & , \text{if } cs(x, y) = 0 \text{ or } cs(x, y) = 1
\end{cases}
\tag{I.3}
$$

$w(x, y)$	Local available soil water w for focal cell before local water redistribution
$w'(x, y)$	Local plant available soil water w for focal cell after local water redistribution
N_1	Counter variable: Counts nr. of cells in the Moore neighbourhood which are in the state of live tussock $cs = 0$ or $cs = 1$. The Moore neighbourhood are the eight cells directly neighbouring the focus cell
N_2	Counter variable: Counts nr. of cells in the Moore neighbourhood which are in the state of live tussock $cs = 2$
$WR.1$	Fixed amount of lateral soil water w loss of a empty cell or a dead tussock ($cs_{0/1}$) due to water uptake from a neighbouring live tussock (cs_2) cell or vice versa

2) Step 2 of local water redistribution: water loss due to a large bare patch:

The Algorithm. — The second step of local water redistribution consists out of two parts: First all cells within the grid are scanned, if they are empty cells and if they lost water during 1st step of local water redistribution. If not, they are considered as a cell which potentially lies within a "large bare patch". Second, all cells in the Moore neighbourhood of the focus cell, are scanned for water loss due to neighbouring live tussocks, using the counter variable N_3. The Moore neighbourhood are all eight cells lying within the direct neighbourhood of the focal cell. If there is at least one cell in the Moore neighbourhood, which did not loose water to a neighbouring live tussock, the focal cell gets part of a 'Large Bare Patch (LBP)'. For each cell in the Moore neighbourhood, which did not loose water to a neighbouring live tussock, the water loss of the focal cell is incremented by $WR.2$ due to higher run off or higher evaporation. Thus the smallest LBP consists out of 2 cells, which have incremented water loss by – n * $WR.2$. This minimum sized LBP consists out of empty cells 3 x 4 empty cells or 90 cm x 120 cm (Fig. I.3).

$$
w(x, y) = w'(x, y) - N_3 \cdot WR.2
\tag{I.4}
$$

$w(x, y)$	Final local plant available soil water for focal cell at actual time step t after water loss due to "large bare patch effect" (2nd step of local water redistribution)
$w'(x, y)$	local plant available soil water after 1st step of local water redistribution
N_3	Counter variable: Counts nr. of cells in the Moore neighbourhood which a did not loose plant available soil water during first step of water redistribution: $w'(x, y) = w_G(x, y)$

WR.2	for empty cells within 'large bare patches'; fixed amount of soil water loss, for each empty neighbouring cell in the Moore neighbourhood unaffected by lateral roots water uptake of a live tussock

Definitions of cell state counters in the Moore neighbourhood of a focal cell:

N_1	Counter variable: Counts nr. of cells in the Moore neighbourhood which are in the state of live tussock $cs = 0$ or $cs = 1$
N_2	Counter variable: Counts nr. of cells in the Moore neighbourhood which are in the state of live tussock $cs = 2$
N_3	Counter variable: Counts nr. of cells in the Moore neighbourhood which a did not loose plant available soil water during first step of water redistribution: $w'(x, y) = w_G(x, y)$

□ Empty focal cell loosing water to neighbouring tussocks cell

■ Live tussock

□ Empty cells

→ Lateral water flux to live tussock due to 1st step of local water redistribution
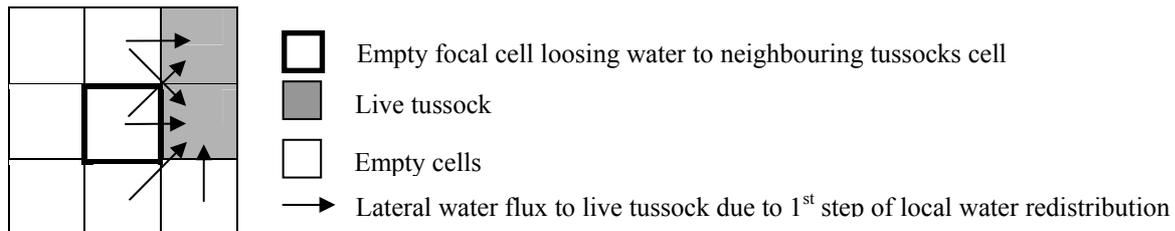
Fig. I.2: Example for water redistribution step 1.
Empty cells loose water to neighbouring live tussocks and vice versa. Empty cells against each other behave neutral, as do neighbouring live tussocks.

■ Focal cell

□ Empty cells in the 1st oore neighbourhood of focus cell

■ Live tussock

□ Empty cell at larger distance

→ Lateral water flux to live tussock due to 1st step of local water redistribution

□ Cell within Moore neighbourhood which does not loose water to a neighbouring live tussock. Forms part of minimum sized 'Large Bare Patch' (LBP) together with focal cell

⌐ Outer boundary of minimum sized „large bare patch"

Fig. I.3: Example for water redistribution step 2: Minimum sized Large Bare Patch (LBP).
Both cells of inner boundary of the Large Bare Patch loose additionally plant available soil water w due to higher evaporation or runoff caused by the large area of open soil.

Consequences of the 'large bare patch' effect. – Consequences for the possible range of the 'large bare patch' effect: The smallest "large bare patch" consists out of two neighbouring cells which neighbours all are unaffected by lateral roots. Each of both cells then looses 1**WR.2* mm of plant available soil water. Both cells are surrounded by ten empty cells. So the smallest 'large bare patch' consists out of 3 x 4 cells or 0.9 m x 1.2 m respectively, considering the grid cell size of this simulation model.

The maximum "large bare patch" effect occurs in a cell which is completely surrounded by cells lacking effect of lateral roots. Based on the Moore neighbourhood, the minimum bare patch size for this maximum effect to occur in its focal cell is a square of five by five empty cells or 1.5 m * 1.5 m in our case. Sites affected by this maximum effect would loose 8 * *WR.2* mm of plant available soil water.

Consequences for the spatial pattern of recruitment:

- Large bare patches are not colonized from central sites, since these are the ecologically most "dry" locations.
- Large bare patches are colonized from their border areas, since these offer better ecological conditions.
- In general, recruitment does not occur at large distances from tussocks. This is an indirect implementation of dispersal limitation.
- Best sites for recruitment are cells which have one live tussock in each direction of the 'second' Von Neumann neighbourhood that means one bare soil cell has to be between the focal cell and the live tussock. Reasons for this pattern of optimal recruitment are the lack of a large bare patch and the lack of water loss to a live tussock in the direct neighbourhood.

I.1.5 Water induced vitality change (vitality dynamics)

Vitality dynamics. – The concept of vitality was introduced in section 2.2.2. It is necessary to integrate sub lethal effects of both precipitation and grazing and to integrate the compositional state of the tussock, both the ability to intercept photosynthetic radiation as the capacity to use below-ground resources. Both precipitation and grazing show their effects on vitality after the respective processes of local water redistribution and defoliation (Fig. 2.3). Vitality changes by water are realised deterministically by threshold parameter (eqn. I.5). Two soil water thresholds are defined for increasing, and two thresholds for decreasing tussock vitality.

$$p_{VC}\{vit + 1|vit = 1\} = \begin{cases} 1 & \text{, if } w > VD.1 \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases} \quad \text{(I.5 a)}$$

$$p_{VC}\{vit + 1|vit = 2 \text{ or } vit = 3\} = \begin{cases} 1 & \text{, if } w > VD.2 \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases} \quad \text{(I.5 b)}$$

Soil water status induced vitality decrement:

$$p_{VC}\{vit - 1|vit = 4\} = \begin{cases} 1 & \text{, if } w > VD.3 \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases} \quad \text{(I.5 c)}$$

$$p_{VC}\{vit - 1|vit = 2 \text{ or } vit = 3\} = \begin{cases} 1 & \text{, if } w > VD.4 \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases} \quad \text{(I.5 d)}$$

p_{VC}	probability of tussock vitality change
$p_{VC}\{vit \text{ n+1}|vit \text{ n}\}$	conditional probability for tussock with vitality state = n to increase by 1
$pVC\{vit \text{ n-1}|vit \text{ n}\}$	conditional probability of tussocks with vitality states n to decrease by 1
w	plant available soil water
VD.1	soil water at which tussock with vit =1 increases vitality
VD.2	soil water at which tussock with vit =2 or 3 increases vitality
VD.3	soil water at which tussock with vit = 4 decreases vitality
VD.4	soil water at which tussock with vit =2 or 3 decrease vitality

I.1.6 Plant production

Total and for grazing available biomass of the *Festuca* steppe consists out of green biomass remaining from time step *t*-1 (eqn. I.1) after the occurrence of the processes grazing, senescence, and tussock mortality, and the annual net primary production of the actual time step. Biomass carry-over (see Fig. I.4) is calculated at the beginning of each time step. The process 'Plant production' simulates annual net primary production of a tussock (*prod*, see variable definitions Tab. 2.2). For production response to soil water – the only resource considered – we assume Michaelis-Menten kinetics (see eqn. I.6 and Fig. I.4). Michaelis-Menten kinetics leads to a saturation of plant growth when the resource reaches its maximum. I assume a plant growth saturation at maximum precipitation, which might be due to density dependence (reduced productivity of tillers of one tussock, due to shading effects of neighbouring tillers, J.M. Paruelo, pers. comm.) or due to inability to use the high offer of the resource. The inclusion of saturation into modelling of resource dependent plant growth is normally used for resources (Passioura 1982, Richter 1985, Richter and Söndgerath 1990, Crawley 1997).

The tussock annual biomass production depends on tussock vitality *vit* (M.B. Bertiller pers. comm.), the local plant available soil water *w*, the plant productivity parameters PG.1, PG.2, which indicate maximum plant productivity per vitality status of the tussock, and the parameter PG.3 (eqn. I.6), which determines the soil water status, at which the tussock reaches 50% of its productivity. The effect of tje productivity increment caused by the tussock vitality increment of *vit* by +1 on plant growth lies within the same range as the productivity increment between minimum and maximum precipitation within one vitality class (Fig. I.4)*.*

Tussock annual net primary production:

$$prod(vit, w) = (PG.1 + (vit - 1) \cdot PG.2) \cdot \frac{w}{w + PG.3} \qquad \text{, if } cs = 2 \qquad (I.6)$$

prod	simulated *ANPP* / year per tussock area [0.09 m²],
vit	*vitality* class for each tussock *vit* = {0, 1, 2, 3, 4},
w	local cell specific plant available soil water
PG.1	annual production at *vitality* 1 (see Tab. 2.3),
PG.2	annual production increment per *vitality* class > 1,
PG.3	half maximum soil water constant for production.
cs(x, y, t)	Possible states of a grid cell (30 cm x 30 cm) at location *x, y* and time step *t*: *cs* = 0 for empty /bare soil cell; 1 for dead tussock; 2 for live tussock.

Tussock total green biomass at actual time step:

$$gb_P = gb_{Co} + prod \qquad \text{, if } cs = 2 \qquad (I.7)$$

gb_P	absolute green biomass of a live tussock after production
gb_{Co}	carry over of resting *gb* (*t* – 1) of a *F. pallescens* tussock
prod	simulated *ANPP* / year per tussock
cs(x, y, t)	Possible states of a grid cell (30 cm x 30 cm) at location *x, y* and time step *t*: *cs* = 0 for empty /bare soil cell; 1 for dead tussock; 2 for live tussock.
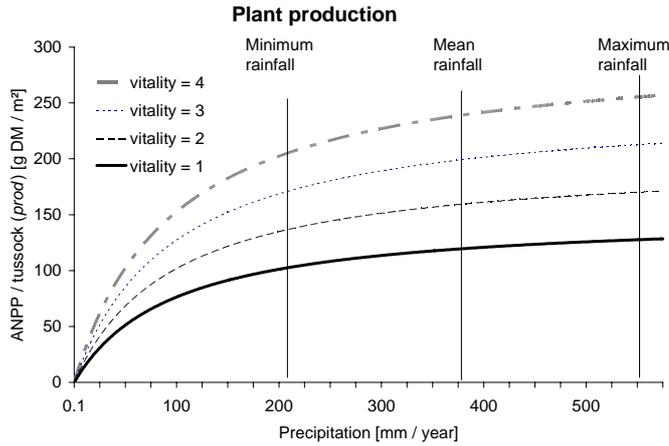
Fig. I.4: Potential tussock productivity.
Plant production depends on rainfall, tussock vitality and default values for parameters PG1.- PG.3. Vertical lines indicate the range and average productivity given by the range of plant available rainfall. Note that productivity increment for vitality increment by +1 lies within the same range as the productivity increment between minimum and maximum precipitation for one vitality class.

During 'plant production' the dead biomass fraction $dfrac_i$ of total biomass of each tussock is calculated (eqn. I.8). $Dfrac_i$ is assumed to be an essential characteristic of the tussock compositional state which decides about forage selection by sheep and thus about defoliation (see eqn. I.10 and I.16-17).

Dead biomass fraction of total biomass:

$$dfrac_i(t) = \frac{db(t-1)}{db(t-1) + gb_P(t)} \qquad \text{, if } cs = 2 \qquad (I.8)$$

$dfrac_i(t)$	dead biomass fraction of total tussock biomass
$db(t\text{-}1)$	absolute dead biomass of a live tussock for time step t-1
$gb_P(t)$	absolute green biomass of a live tussock after production

As a precondition a minimal amount of residual green biomass ($bgmin$) which is not available for grazing is calculated during the process plant production. $Bgmin$ is calculated for each tussock and time step for the high selective forage selection scenario (HS) only (see Chapter 5). For the non-selective grazing scenario (NS) the value bgmin is a fixed parameter value.

Minimum residual green phytomass after grazing

$$gbmin_{HS} \qquad = \qquad gb_P \cdot (1 - dsmax) \qquad \text{, if } cs = 2 \qquad (I.9)$$

$gbmin_{HS}$	minimum residual biomass after grazing for high selective foraging scenario (HS)
gb_P	standing green biomass prior to grazing,
$dsmax$	maximum defoliation severity a tussock can experience at actual time step

The maximum relative defoliation severity $dsmax$ (Fig. I.5) a tussock can experience during one time step depends on the standing dead biomass fraction $dfrac_i$ and the 'defoliation shape parameter' (GR.4). Thus, maximum relative grazing intensity is reduced with increasing dfrac of a tussock and lower values for the 'defoliation shape parameter'. As default I assume a moderate decrease of maximum relative defoliation with increasing $dfrac_i$ ('defoliation shape parameter'

(GR.4) = 0.5). *Dsmax* is calculated once per time step and tussock prior to the grazing routine, that is, *dsmax* is not altered during the grazing process.

Maximum defoliation severity:

$$dsmax = \begin{cases} (GR.3 - dfrac_i)^{GR.4} & \text{, if } dfrac_i < GR.3 \text{ and } cs = 2 \\ 0 & \text{, if } dfrac_i \geq GR.3 \end{cases} \tag{I.10}$$

dsmax	maximum possible defoliation severity at time step *t*
GR.3	defoliation threshold parameter: Sets the minimum limit of *dfrac*, at which tussock is rejected obligatory due to high *dfrac*
dfrac_i	dead fraction of live tussock biomass
GR.4	shape parameter for defoliation intensity: Determines the shape of defoliation severity *ds* as a function of *dfrac*; defines the dynamics of reduced *ds* with increasing *dfrac*.
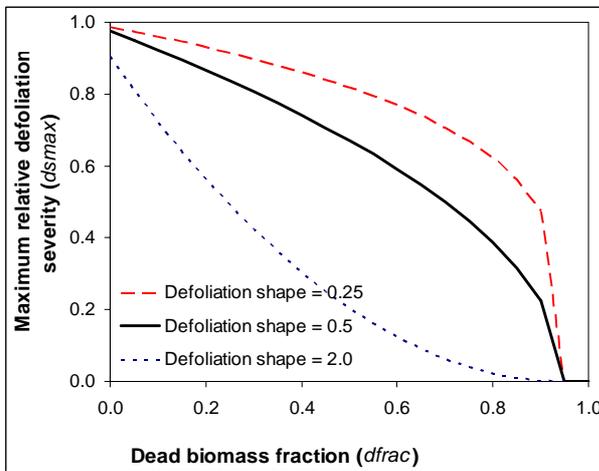
Fig. I.5: Maximum relative defoliation of a tussock during one time step.
Dsmax as a function of the dead biomass fraction of a tussock *dfrac_i* is additionally influenced by the 'defoliation shape parameter (GR.4) given in equation (22). The assumed value for GR.4 = 0.5 (expert estimation). For theoretical reasons I included values for GR.4 < 1. These values lead to enforced selectivity by herbivores, due to a increased rejection of tussocks with higher dead biomass fractions.

I.1.7 Defoliation

Landscape level of grazing. — I distinguish two spatial scales for the grazing process: the local, small-scale or tussock level, and the patch or landscape level scale. The last scale covers the whole area or simulated grid resp. and may represent e.g. an assumed homogeneous paddock, or homogeneous fractions of a paddock. The landscape level mean grazing pressure or "utilization intensity" is defined as the total forage need by livestock over theoretical total forage available. Theoretical means that there might be available forage but it might be rejected by livestock due to its forage selectivity. Total available forage consists out of the living (green) Festuca biomass and the Primary Forage (*PF*). A fixed total annual forage need *FN* (kg ha^{-1}) results from a fixed forage need per capita *GR.2* (1 kg sheep^{-1} day^{-1}) and a fixed stocking rate during one simulation (e.g. 1 sheep / ha, *GR.1* or *Stock*).

Landscape level Forage Need / ha-1:

$$FN = GR.1 \cdot GR.2 \cdot 365 \tag{I.11}$$

FN	total forage need per hectare and year by the applied stocking rate
GR.1	stocking rate / ha
GR.2	fixed forage need per sheep and day

Primary Forage:

$$PF = \begin{cases} 30\,\% & \text{, if} \quad cov > 40\,\% \\ PF.1 + PF.2 \cdot (cov - 10) & \text{, if} \quad 10\,\% \leq cov \leq 40\% \\ PF.1 & \text{, if} \quad cov < 10\,\% \end{cases} \tag{I.12}$$

PF	fraction of *F* covered by other items which as a function of *F. pallescens* cover
cov	actual *F. pallescens* cover
PF.1	minimum relative amount of primarily consumed *forage*
PF.2	increment of *primary forage* proportional to *F. pallescens* cover increment

Primary Forage *PF* summarizes a component of non – *Festuca* species which are consumed with higher priority than *Festuca pallescens* (i.e. forbs and small grasses, Bertiller and Defossé 1993). Biomass of other species may account for 10% to 50% of total production (Defossé et al. 1997a). Primary Forage covers a part of total forage needed by livestock and is not modelled explicitly, but in function of *Festuca* cover. We assumed as a default that *AF* contributes 30% (the average of 10 to 50%) of total forage need, when *Festuca* cover is 40% or more, and its contribution is linearly reduced to 5%, when *Festuca* cover is 10% or less (default values for standard model parameterisation P_S).

I get the *Forage* amount provided by *Festuca* by discounting the relative amount of Primary Forage from total Forage need:

Total forage need from *Festuca*:

$$F = FN - (FN \cdot PF / 100) \tag{I.13}$$

F	total forage need from *F. pallescens*
FN	total forage need per hectare and year by the applied stocking rate
PF	fraction of *FN* covered by other items which as a function of *F. pallescens* cover

The total available *Festuca* forage *AF* (kg ha^{-1}) is the sum of the standing green biomass gb_P from all tussocks.

Total standing forage of actual year:

$$AF = \sum_{x=1}^{m} \sum_{y=1}^{n} gb_P(cs(x,y,t), vit(cs(x,y,t)), w(x,y,t)) \qquad \text{, if } cs(x,y,t) = 2 \tag{I.14}$$

AF	Total available forage of actual time step *t*,
$gb_P((cs(x, y, t), vit(cs(x, y, t)), w(x, y, t))$	Standing green biomass standing per live tussock at time step *t and* grid coordinates *x, y*
cs(x, y, t)	Cell state for cell with grid coordinates *x, y*

Landscape level necessary mean utilization intensity *M* to accomplish needs of stock is given as:

Landscape level mean utilization intensity:

$$M = \begin{cases} F / AF & , \text{if} \quad AF \geq F \\ 1 & , \text{if} \quad AF < F \end{cases} \tag{I.15}$$

M	landscape level necessary mean utilization intensity
F	total forage need from *F. pallescens*
AF	total standing forage of actual time step, if $AF < F$ it is assumed that sheep get additionally supply

The necessary mean utilization intensity M indicates the theoretical utilization intensity. The mean realized defoliation intensity (*Mreal*) might differ from expected M. *Mreal* depends on the realized consumption of the standing green biomass per tussock (gb_P) by livestock. The consumption is realized as a function of forage selectivity depending on the relative amount of dead biomass *dfrac* per tussock (see below).

Local or tussock level of defoliation. — The grazing process is considered as a sequence of local grazing events that continues until the total forage need has been met, no more forage is available or no suitable cell has been found over several consecutive trials. Due to off take restrictions, green biomass might be present without being available for grazing, e.g. a high proportion of tussocks with high fractions of standing dead (high *dfrac*) allowing only limited defoliation severity (*ds*). As a precondition a minimal amount of residual green biomass (*bgmin*) which is not available for grazing is calculated during the process 'Plant production' (eqn. I.9). If the total forage needed from *Festuca* (F) is higher than the available forage (AF) from *F. pallescens*, it is assumed that livestock is supplemented by other sources of food, as population dynamics of herbivores is not modelled explicitly.

Forage selectivity. – The essence of the grazing model is the probability of a tussock to be accepted for grazing (*gprob*), if it is selected by livestock during a random process of tussock selection. The grazing probability depends on the compositional state of the tussock, expressed by its dead biomass fraction ($dfrac_i$) and the expected landscape level mean utilisation intensity (M, see eqn. I.16, Fig. I.6). Although, initially cells are selected at random, this algorithm ensures that tussocks are not grazed randomly but in a highly selective way. With increasing utilization intensity the grazing probability of a tussock with a given composition ($dfrac_i$) increases. In addition maximum defoliation intensity of a grazing event is determined by tussock composition (eqn. I.10). The grazing probability *gprob* decides not about the grazing intensity a tussock has to tolerate, the defoliation severity (*ds*) is modelled later. The presented grazing probability (eqn. I.16) will be used as the default scenario for forage selectivity, which is assumed to apply for continuous grazing all the year round in large, fenced paddocks of ca. 1.000 to 5.000 ha size. Livestock has all the year round the option to select the most attractive tussocks, due to the size of a paddock, but sheep are fenced, so there is a certain probability that a tussock will be regrazed, if forage need increases. I assume that under these conditions livestock prefers tussocks with low dead biomass fraction (*dfrac*, Fig. I.6). Under very low utilization intensity (M close to 0), grazing probability *gprob* shows a close to linear decrease with increasing dead biomass fraction. With increasing utilization intensity M, livestock would increasingly accept tussocks with higher fractions of standing dead (Fig.I.6).

XIII

Tussock grazing acceptance probability for 'high selective forage selectivity' (HS):

$$gprob_{HS} = \begin{cases} (1 - dfrac_i)^{(1-M)} & , \text{if} \quad 0 < M \leq 1 \text{ and } cs = 2 \\ 0 & , \text{else} \end{cases} \qquad (I.16)$$

$gprob$	tussock grazing acceptance probability
$dfrac_i$	dead fraction of live tussock biomass
M	landscape level necessary mean utilization intensity
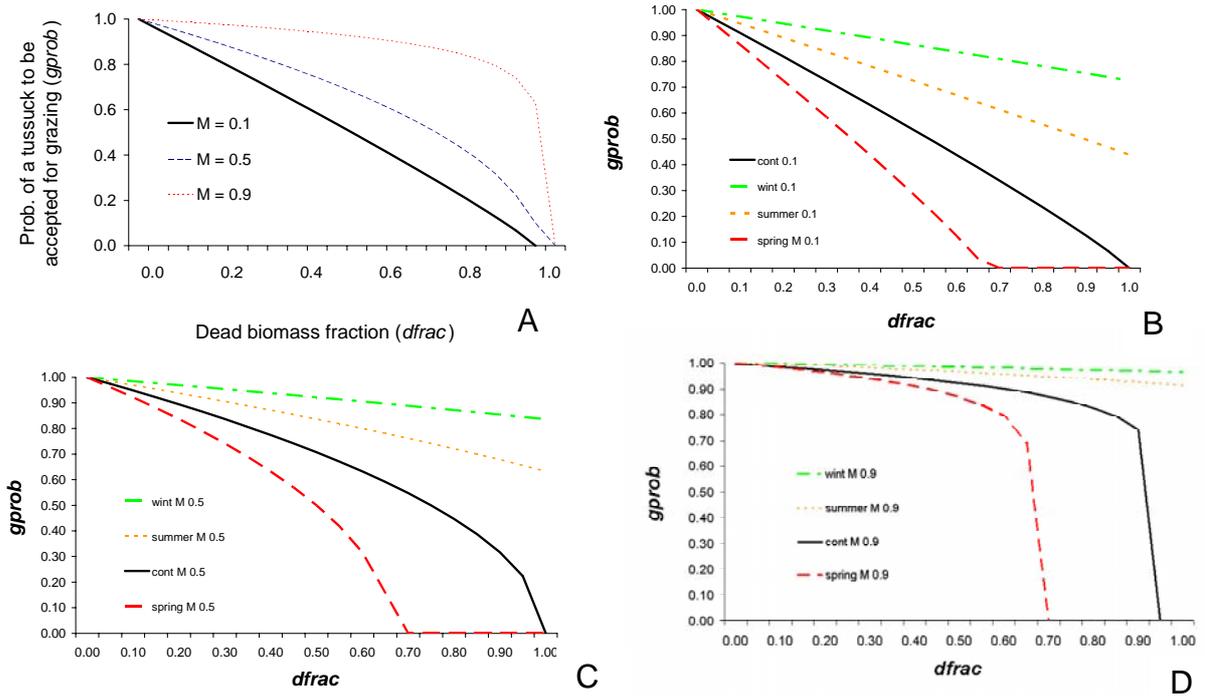
Fig. I.6: Probability of a tussock to be accepted for grazing during the High selective foraging scenario.
Illustration of the probability *gprob* for a live tussock of being accepted for grazing after a random hit (eqn. I.16 – 17) for A) high selective continuous grazing (cont) at different relative grazing intensity levels (*M*). B) - D) grazing probability of a tussock for the different seasonal scenarios and grazing levels. **Legend**: *gprob*: grazing probability of a tussock; *dfrac*: dead biomass fraction per tussock; *M*: expected relative mean utilization intensity as total annual forage need from *Festuca* over total amount of available forage of *Festuca*.

Seasonal altered forage selectivity. – To simulate in a more realistic way different grazing regimes, we introduced different grazing scenarios, defined in terms of a *seasonality* parameter (GR.5, see Tab. 2.3 and eqn. I.17). A seasonal different grazing assumes that livestock forage selectivity is changed relative to the default continuous grazing differently according to the season. 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. 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). In spring selectivity increases, because grasses are in the full vegetative growth and nearly no senescence has occurred. During summer and spring selectivity might already reduced, because important fractions of the green biomass produced during the actual year has already gone senescent, and livestock is forced to forage also on 'less attractive' tussocks. Finally, winter grazing should be less selective, due to the low offer of live biomass production in

winter, and the changed and possible better accessible composition of the dry, recently senescent biomass (see Fig. I.6). The parameter GR.5 affects the probability of a tussock of being accepted for grazing and qualifies the influence of the dead fraction of each tussock (Fig. I.6 B-D). The seasonal altered dfrac ($dfrac_{HS}(S)$) is used in eqn (I.17).

Seasonal altered *dfrac*:

$$dfrac_{HS}(S) = \begin{cases} dfrac_i \cdot GR.5 & \text{, if } dfrac_i \cdot GR.5 \leq 1 \text{ for } GR.5 = \{1.0, 1.5, 0.6, 0.3\} \text{ and } cs = 2 \\ 1 & \text{, if } dfrac_i \cdot GR.5 > 1 \text{ and } cs = 2 \end{cases} \quad (I.17)$$

$dfrac_{HS}(S)$	seasonal altered *dfrac* by weighted herbivore selectivity
$dfrac_i$	dead fraction of a live tussock biomass
$GR.5_i$	seasonal grazing acceptance: $GR.5 = 1.0$ for *cont*, 1.5 for *spr*, 0.6 for *sum*, 0.3 for *wint* (Tab. 2.3)
cont	continuous grazing all year round
spr	all biomass is removed in spring
sum	all grazed biomass is removed during summer or autumn
wint	all grazed biomass is removed during winter

The realisation of a discrete grazing event. A grazing event consists of the selection of a tussock, and its subsequent defoliation. If a selected tussock has not yet been grazed down to its minimum residual green biomass *bgmin* it is accepted for grazing with the probability *gprob* (eqn. I.16-17). Then the local consumption (lc_i) of the selected tussock is calculated for each grazing step (eqn. I.19). Each tussock can be grazed during one time step several times until the tussock biomass is reduced to the minimum residual biomass or the total forage need from *Festuca* was satisfied before or no available biomass is left (eqn. I.21). Up to this decision at the end of grazing during the actual time step after each discrete grazing event the local consumption for the actual tussock is calculated (eqn. I.19), the remaining living biomass is updated (eqn. I.20 a), the dead biomass fraction is determined a new (eqn. I.20 b), and the relative defoliation severity is calculated (eqn. I.22).

Decision algorithm if actual tussock is accepted for grazing:

$$ga_i = \begin{cases} 1 & \text{, if } gb_P - lc_i > gbmin, gprob_S > rp_i \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases} \quad (I.18)$$

ga_i	grazing acceptance decision for actual tussock at grazing event i
gb_P	green biomass of actual tussock before grazing
gbmin	minimum residual green biomass, calculated prior to grazing (eqn I.9)
gprob	grazing prob. of a tussock
rp_i	random probability variable drawn for each tussock to realize grazing decision at each grazing step i
lc_i	Absolute local defoliation intensity after i-th defoliation

A tussock that has been accepted for grazing is defoliated with a local defoliation intensity *di*, with *di* denoting a random variable. Local consumption lc_i in a grazing event is then given by:

Local consumption:

$$lc_i = \begin{cases} di_i \cdot (gb_P - \sum_{i=1}^{i-1} lc_i), \text{ if } di_i \cdot (gb_P - \sum_{i=1}^{i-1} lc_i) > gbmin, \ ga_i = 1 \ cs = 2 \\ \\ 0 \qquad\qquad\qquad\qquad\quad , \text{ else} \end{cases}$$

(I.19)

lc_i	Absolute local defoliation intensity after i-th defoliation
gb_P	local green biomass before grazing
di	local defoliation intensity drawn from a random variable with equal distribution for high selective forage selection scenario
$gbmin$	minimum not grazable, green biomass of a tussock

Update local green tussock biomass after each grazing step:

$$gb_{Gi} = gb_P - (\sum_{i=1}^{i} lc_i) \qquad\qquad , \text{ if } cs = 2$$

(I.20 a)

gb_G	Green tussock biomass after defoliation process for each live tusscock
lc_i	Absolute defoliation intensity for each tussock, grazing event i and time step t
gb_P	Pre-grazing green biomass of distinct tussock

Update of dead fraction of total biomass for each grazing step:

$$dfraci(gb_{Gi}, t) = \frac{db(t-1)}{db(t-1) + gb_{Gi}(t)} \qquad\qquad , \text{ if } cs = 2$$

(I.20 b)

$dfrac_i(gb_{Gi}, t)$	Fraction of dead biomass updated after each grazing hit a tussock receives
$db(t-1)$	Local dead biomass during grazing procedure
$gb_{Gi}(t)$	Local green biomass per tussock, updated after each grazing hit

Decision rule to finish the grazing algorithm:

$$G_E = \begin{cases} 1 & , \text{ if } \quad C < FF \qquad\qquad\qquad \text{ or} \\ 1 & , \text{ if } \quad \sum_{x=1}^{n} \sum_{y=1}^{m} R(x,y) < 100\,g \qquad \text{ or} \\ 1 & , \text{ if } \quad \sum_{x=1}^{n} \sum_{y=1}^{m} (1 - ga_i) > 2500 \qquad \text{ or} \\ 0 & , \text{ else} \end{cases}$$

(I.21)

G_E	end grazing for actual time step
C	total Consumption for actual time step and total grid
x, y	grid coordinates
F	forage needed from *F. pallescens*
R	total residual forage for the whole grid at time step t

Relative local defoliation severity:

$$ds = (\sum_{i=1}^{i} lc_i) / gb_P \qquad\qquad , \text{ if } cs = 2$$

(I.22)

ds	Realised local relative defoliation severity for each tussock and time step
lc_i	Absolute defoliation intensity for each tussock, grazing event i and time step t
gb_P	Pre-grazing green biomass of distinct tussock

Finally, if grazing is finished during the actual time step, consumption related landscape level variables are calculated as e.g. total consumed forage, residual forage and realized relative utilisation intensity (*Mreal*).

I.1.8 Colonization

F. pallescens reproduces exclusively from seeds (Soriano 1960 in Soriano and Sala 1986, Bertiller 1992), and seed distribution is considered to be spatially homogeneous. The latter assumption is a simplified assumption derived from the observation that seedling density declines proportional to vegetation and *Festuca* cover in the steppe (Bertiller 1996, Bertiller et al. 1996). Seed production and distribution are not modelled explicitly. Seedling emergence and survival of the first year occurs only in empty cells, it depends on local plant available water, and *Festuca* cover. Thus seedling emergence depends not directly from grazing, but if *Festuca* cover is reduced by grazing there is an indirect effect of grazing included. Emergence is highest if *Festuca* cover is as high as in an assumed natural state, expressed by parameter *CO.5* (see eqn. I.23). Survival of emerged seedlings is stochastic with a probability set by parameter CO.2 (default CO.2 = 0.3). The survival probability of emerged seedlings $p_C\{S_1|cs = 0\}$ declines linearly and proportional to the ratio between actual cover and assumed cover of a natural state of the *Festuca* steppe (parameter CO.5 = 40% (default)). This rule directly includes the findings of Bertiller (1996) and Bertiller et al. (1996) of a linear decrease of seedling density at reduced cover. A tussock is recruited after a two years sapling stage (M.B. Bertiller, L. Ghermandi, J.M. Paruelo, pers. comm.). Survival probabilities of saplings during the first and the second year depend on plant available soil water threshold (CO.3 and CO.4 respectively, see eqns. I.24-25) and on the mean realized defoliation severity in the current year (*Mreal,* see Fig. I.7). The sensitivity of saplings to drought is considerably reduced in comparison to seedlings, which is in accordance to empirical evidence (Defossé et al. 1997a, Defossé et al. 1997b). They found that one year old seedlings begin to root to more profound soil layers so that they profit from deeper soil layers which fluctuate less in water saturation that shallow soil layers (Defosse et al. 1997a/b). Fig. I.7 illustrates equation I.24. Saplings survival depend on the one hand on plant available soil water, which is modelled as deterministic threshold, and on the other hand it depends on grazing, expressed by the relative grazing intensity *Mreal*.
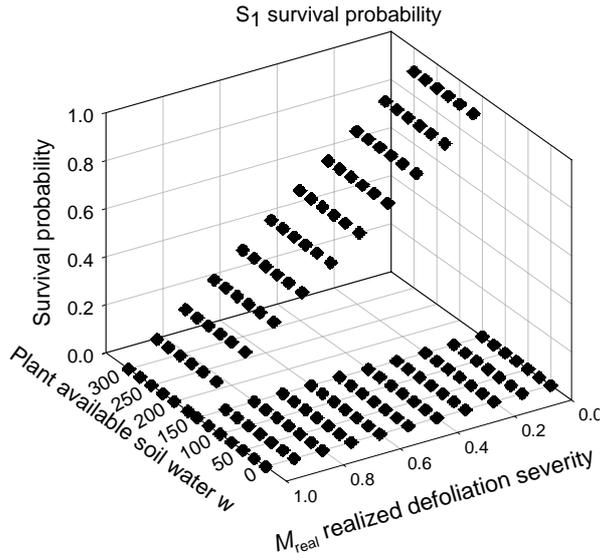
Fig. I.7: Sapling survival probability.

   Shown is the survival of one year old saplings as a function of plant available soil water and mean realized grazing intensity.

1) Emergence of seedlings (survival of the first year):

$$p_C\{S_1|cs = 0\} = \begin{cases} CO.2 & , \text{if } w > CO.1,\ cov > CO.5 \\ CO.2 \cdot (cov\,/\,CO.5) & , \text{if } w > CO.2\ \ cov \le CO.5 \\ 0 & , \text{else} \end{cases} \qquad (I.23)$$

p_C	colonization probability
$p_C\{S_1|cs = 0\}$	survival probability for seedlings S_0 emerged from a empty cell $cs = 0$ into state S_1:
S_i	seedling of state i; i= 0 for recently emerged seedlings; 1 for 1st year seedling; 2 for 2nd year seedling.
$cs(x, y, t)$	possible states of a grid cell (30 cm x 30 cm) at location x, y and time step t: $cs = 0$ for empty /bare soil cell; 1 for dead tussock; 2 for live tussock.
$CO.2$	prob. of emergence at cover > 40 % if soil water $w > CO.1$
w	plant available soil water
$CO.1$	minimum soil water for emergence
cov	actual *F. pallescens* cover,
$CO.5$	minimum *F. pallescens* cover for maximum S_0 survival prob.

2) Survival of one-year-old saplings into the 3rd year:

$$P_C\{S_2|S_1 \text{ and } cs = 0\} = \begin{cases} CO.6 \cdot (1 - Mreal) & , \text{if } w > CO.3 \\ 0 & , \text{else} \end{cases} \qquad (I.24)$$

$P_C\{S_2|S_1 \text{ and } cs = 0\}$	survival probability of seedlings S_1 into 2nd year S_2 seedlings
$CO.6$	minimum soil water for survival of first year seedlings
Mreal	realized mean defoliation severity *ds* over whole grid
w	plant available soil water
$CO.3$	survival prob. for seedling S_1 if $w > CO.3$

3) Tussock recruitment or survival of two year old saplings is given as:

$$p_C\{cs = 2|S_2 \text{ and } cs = 0\} = \begin{cases} CO.6 \cdot (1 - Mreal) & , \text{if } w > CO.4 \\ 0 & , \text{else} \end{cases} \qquad (I.25)$$

$p_C\{cs = 2|S_2 \text{ and } cs = 0\}$ transition probability from seedling S_2 to fully grown live tussock ($cs = 2$)

$CO.6$ survival probability for seedling 2nd year if soil water $w > CO.4$

$Mreal$ realized mean defoliation severity ds over whole grid

w plant available soil water

$CO.4$ minimum soil water for survival of second year seedlings

I.1.9 Grazing induced vitality change (vitality dynamics)

Grazing induced vitality change combines a threshold and a probability of transition. Water thresholds refer to plant available soil water, not to global precipitation. The possible range of plant available soil water is from 0 mm to 360 mm in the range of precipitation from 211 mm - 561 mm (for default precipitation use efficiency WI.1 = 0.57). Grazing induced vitality change refers to relative defoliation severity (ds) in relation to total green biomass of a tussock (Tab. I.4). Vitality change by grazing is applied only in vitality classes 2 to 4, where the higher vitality class is more resistant to grazing (Tab. I.4). Grazing induced vitality change also includes a seasonal effect of grazing (compare process 'defoliation', see eqn. I.26 and Tab. I.4). Defoliation severity which reduces vitality by defoliation is altered depending on season. For example defoliation in severity in winter grazing may be higher than if continuous grazing is allowed. I assume that spring grazing reduces vitality less than continuous grazing, because resting during summer and autumn leaves longer resting times than continuous grazing. The same will occur during summer grazing, but during summer grazing the tussocks will profit fully from the best part of the growing season, in spring.

a) for continuous grazing:

$$p_{VC}\{vit\text{ -}1|vit = 2, 3 \text{ or } 4\} = \begin{cases} VD.6 & , \text{if } ds > (VD.5 + (vit - 2) \cdot 0.1)\, ds > VD.5,\ vit = 2, 3, \\ & \text{or } 4 \text{ and } cs = 2 \\ 0 & , \text{else} \end{cases} \qquad (I.26\text{ a})$$

b) for spring grazing:

$$p_{VC}\{vit\text{ -}1|vit = 2, 3 \text{ or } 4\} = \begin{cases} VD.6 & , \text{if } ds > (VD.5 + 0.1 + (vit - 2) \cdot 0.1) \text{ and } vit = 2, 3, \text{ or} \\ & 4 \text{ and } cs = 2 \\ 0 & , \text{else} \end{cases} \qquad (I.26\text{ b})$$

c) for summer / autumn grazing:

$$p_{VC}\{vit\text{ -}1|vit = 2, 3 \text{ or } 4\} = \begin{cases} VD.6 & , \text{if } ds > (VD.5 + 0.2 + (vit - 2) \cdot 0.1) \text{ and } vit = 2, 3, \text{ or} \\ & 4 \text{ and } cs = 2 \\ 0 & , \text{else} \end{cases} \qquad (I.26\text{ c})$$

d) for winter grazing:

$$p_{VC}\ \{vit\text{-}1|vit = 2, 3 \text{ or } 4\} = \begin{cases} VD.6 & \text{, if } ds > (VD.5 + 0.3 + (vit - 2) \cdot 0.1) \text{ and} \\ & vit = 2, 3, \text{ or } 4 \text{ and } cs = 2 \\ \\ 0 & \text{, else} \end{cases} \qquad \text{(I.26 d)}$$

p_{VC}	probability of tussock vitality change
$p_{VC}\{vit\text{-}1|vit=2, 3 \text{ or } 4\}$	conditional probability vitality decrease by 1 for tussocks with vit = 2, 3 or 4
VD.6	defoliation severity threshold for tussock transition $vit = n \rightarrow vit\ n\text{-}1$ for continuous grazing
ds	defoliation severity
VD.5	prob. of grazing induced vitality transition: if defoliation severity $ds > VD.5 + ((vit - 1)*0.1)$
vit	tussock vitality state

Tab. I.4: Relation between seasonal grazing management and grazing induced vitality change.
Illustration of eqn. I.26. Grazing induced vitality change depending on seasonal grazing management. Vitality is decreased if defoliation severity *ds* exceeds indicated values.

	Decrease vitality *vit* by 1 (for *vit* = 2-4 only), if *ds* [%] is higher than		
Grazing management	vit = 2	vit = 3	vit = 4
Continuous	50	60	70
Spring	60	70	80
Summer / autumn	70	80	90
Winter	80	90	100

I.1.10 Senescence and littering

Senescence rate is 'very low' during early and mid-spring' and 'very high during mid summer' (Bertiller and Defossé 1990a). Bertiller and Defossé 1990b estimated senescence rate on a daily basis with a set of differential equations. Integration on yearly time step was not possible, because not all correspondent data were published. Senescence and littering are modelled after 'Defoliation' and change both biomass variables gb_G or gb_P (if the tussock is not grazed) and *db* of a tussock and thus these processes have impact on the green biomass carry over and grazeable green biomass for the following time step. Senescence and littering rate are fixed for each tussock during one simulation and expressed by the parameters PG.4 (senescence rate) and PG.5 (littering rate). The default values are 60% respectively 40%. During model calibration the whole possible parameter range for both parameters (senescence and littering) was investigated, due to the lack of information about both rates and due to the general relevance of both processes for grazing systems. The senescence rate is higher than the littering rate, which leads to a long-term accumulation of above-ground dead material. Grazing has also an impact on the absolute biomass which goes senescent, intermediated by defoliation severity *ds* (eqn. I.22) on a tussock. The higher the relative defoliation *ds* is, the lower is the subsequent biomass which goes senescent.

The indirect effect of grazing on the absolute biomass which goes senescent might lead to the assumed positive feedback response between grazing intensity and grazing selectivity, i.e. a tussock with a reduced dead biomass fraction *dfrac*– caused by grazing – is highly preferred for grazing to a non-grazed tussock with high fraction of dead biomass.

Senescence and littering of a live tussock:
1) Senescence rate of live biomass and live biomass of live tussock after senescence:

$$gb_S \quad = (1 - (1 - ds) \cdot PG.4) \cdot gb_G \qquad\qquad \text{, if } cs = 2 \qquad\qquad (I.27)$$

gb_S	Final green biomass of live tussock for actual time step t after senescence,
ds	accumulated relative defoliation severity a tussock undergoes per time step t,
$PG.4$	relative annual rate of senescence fixed per parameterisation,
gb_G	Green biomass of live tussock for actual time step t after grazing,

2) Littering rate of dead biomass for a live tussock:

$$db(t) = (1 - PG.5) \cdot db(t-1) + PG.4 \cdot (1 - ds(t)) \cdot gb_G(t) \qquad \text{, if } cs = 2 \qquad (I.28)$$

$db(t)$	dead biomass of live tussock after senescence and littering,
$PG.5$	relative annual rate of littering fixed per parameterisation,
$db(t-1)$	dead biomass of live tussock before senescence and littering,
$PG.4$	relative annual rate of senescence fixed per parameterisation,
$ds(t)$	accumulated relative defoliation severity a tussock undergoes per time step,
$gb_G(t)$	Green biomass of live tussock for actual time step t after grazing.

3) Littering rate of dead tussock:

$$db(cs,t) = (1 - PG.5) \cdot db(cs, t-1) \qquad\qquad \text{, if } cs = 1 \qquad\qquad (I.29)$$

$db(cs=1, t)$	dead biomass of a tussock (dead tussock if cell state $cs = 1$) at time step t,
$PG.5$	relative annual rate of littering fixed per parameterisation.

4) Transition of a dead tussock to an empty / bare soil cell:

$$p_E\{cs = 0 | cs = 1\} \quad = \quad \begin{cases} 1 & \text{, if } db < PG.6 \\ 0 & \text{, else} \end{cases} \qquad\qquad (I.30)$$

$p_E\{cs = 0 | cs = 1\}$	transition probability of a cell with state $cs = 1$ (dead tussock) to $cs = 0$ (empty / bare soil) cell
db	biomass of tussock (dead tussock if cell state $cs = 1$) at time step t,
$PG.6$	fixed threshold below a dead tussock converts to an empty cell (50 g / m²).

A dead tussock converts to an empty cell if the dead biomass db is lower than the value of the fixed parameter 'Standing dead threshold' $PG.6$.

I.1.11 Mortality

Mortality occurs for tussocks in lowest vitality class only. Thus, I assume that mortality only occurs for tussock which are already or still in a weak state, such as tussock which suffered individual heavy grazing for several years, or one or more dry years, or when they recruited just at the actual time step. The mortality probability depends on thresholds related to soil water availability w (MO.1, MO.2) and defoliation severity, ds (MO.5). But I assume that grazing may have effect on tussock mortality. This assumptions assumes, that *F. pallescens* is a **decreaser** species (Snyman 1993), i.e. it is a species, which is preferred by livestock for grazing and losses cover after long-term grazing, as it assumed e.g. for *Themedra triandra* in Southern Africa (O'Connor 1994). The question if grazing has biological feedback on its resource might be an essential one for the debate about the equilibrium dynamics of

semi-arid ecosystems and the interaction between the resource (vegetation) and herbivores as consumers. If a negative biological feedback between herbivore and resource is assumed, it is a grazing system including feedback mechanisms (May 1973, Richter 1985). So one can expect that the total behaviour of the system is changed, depending on the biological assumptions included.

Grazing mortality is realized by a combination of two parameters: one parameter (e.g. MO.1 = 200 mm (default) which corresponds to a relative plant available soil water status of 0.4, regarding the normalized range between 120 mm to 320 mm of total annual plant available soil water at the default annual rain use efficiency per tussock WUE.1 = 0.57 or 57% respectively) represents a discrete threshold of plant available soil water status and the second one which defines the probability of mortality occurrence (e.g. MO.1 = 0.1 or 10%). I defined two pairs of mortality threshold and probability to account for the assumed variability of mortality occurrence. As it is unknown how in detail a summer drought may affect a live tussock, I introduced discrete thresholds of mortality rather than a linear increase of mortality. An introduction of a discrete threshold seems to be a less strong assumption about the relation between annual plant available soil water and tussock mortality than e.g. a linear increase of mortality with increasing drought. Additionally this approach is more accessible for analysis. Mortality is implemented as a combination of two conditions, which must be fulfilled: A threshold for plant available soil water or defoliation severity is combined with a certain probability of occurrence.

Mortality rule:

$$p_M\{vit\text{-}1|vit = 1\} = \begin{cases} MO.3 & \text{, if} \quad w < MO.1 \text{ and } cs = 2 \\ MO.4 & \text{, if} \quad MO.1 \leq w < MO.2 \text{ and } cs = 2 \\ \\ MO.6 & \text{, if} \quad ds > MO.5 \text{ and } cs = 2 \\ 0 & \text{, else} \end{cases}$$

(I.31)

$p_M\{vit\text{-}1|vit = 1\}$	conditional mortality probability of a tussock; a tussock may die only with $vit = 1$
MO.3	prob. of tussock mortality for $w < MO.1$
w	plant available soil water,
MO.1	soil water w induced tussock mortality threshold 1
MO.4	prob. of tussock mortality for $MO.1 \leq w < MO.2$
MO.2	soil water w induced tussock mortality threshold 2
MO.6	prob. of tussock mortality for $ds > MO.5$
ds	defoliation severity,
MO.5	defoliation severity t

Appendix II

Additional Information to Section 3.2.8:

Tab. II.1: Classification of Festuca steppe into degradation states.
Classification was performed after Bertiller and Defossé (1993), with slight modifications. Each number within the table indicates one qualitative *Festuca* steppe state, depending on ANPP and total cover of non-woody plants. These *Festuca* steppe states were used for calibration during calibration step 3.

Festuca - steppe state classification Classification by ANPP X Cover		Cover-states				
		1: overoptimal	2: optimal	3: slight degraded	4: strong	5: near desert
				Cover [%]		
ANPP-states	**ANPP[kg/ha]**	**>90**	**60-90**	**30-60**	**10-30**	**<10**
0 overoptimal	**>2000**	**1**	**7**	**13**	**19**	**25**
1 optimal	**1100-2000**	**2**	**8**	**14**	**20**	**26**
1.5 slightly degraded	**750-1100**	**3**	**9**	**15**	**21**	**27**
2 moderate degraded	**365-750**	**4**	**10**	**16**	**22**	**28**
3 strong degraded	**175-350**	**5**	**11**	**17**	**23**	**29**
4/5 near desert	**<175**	**6**	**12**	**18**	**24**	**30**

Additional Information to Section 3.3.1

Fig. II.1: Effect of different combinations of pattern filter criteria on number of accepted parameterisations
Selectivity of the multicriterial filtering procedure is shown for the Example 'No grazing calibration scenario, parameters independent (NG_i)'. Illustration of the results shown in Tab. 4.5.
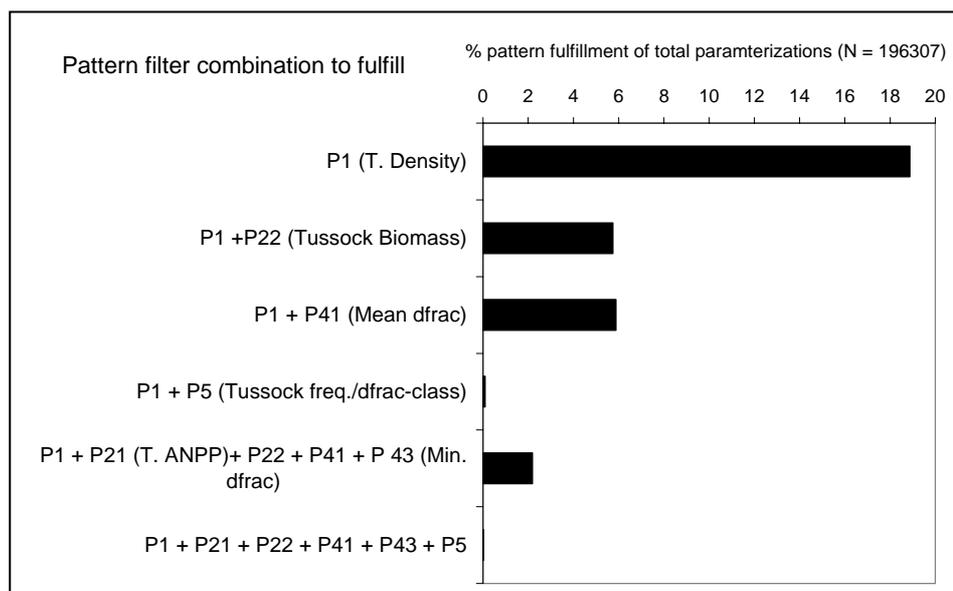
Additional Information to Section 3.2 Sensitivity analysis

Tab. II.2: Calibration scenario NG$_i$: Sensitivity state variables against less correlated parameters.
Shown are those parameters with low mean relative correlation strength (rcs). Definition of parameter and process abbreviations see Tab. 2.3. Definition of variables are given in Tab. 2.2. Shown are significant correlation ± 0.19 (N = 105).

Calibration scenario No Grazing, parameters independent (Ng$_i$), N = 105, Filter: P1 P2 P4 P5	13 MO MO W MortWp1	14 CO CO W ColWS2	15 VD VD G VdecGp	16 VD VD W VdecW1	17 VD VD G VdecG	18 WI - WUE	19 CO CO W ColWS1	20 CO CO D ColS0Cov	21 PG - MMconst	22 WR WR O WredO	23 G G T Gshape	24 CO CO D ColS12p	25 MO MO W MortW2	26 MO MO W MortWp2	27 MO MO G MortG	28 MO MO G MortGp	29 PF - PFmax
Variables	MO.3	CO.4	VD.6	VD.3	VD.5	WI.1	CO.3	CO.5	PG.3	WR.2	GR.4	CO.6	MO.2	MO.4	MO.5	MO.6	PF.1
$Td_S(t=100)$																	
TB_P				0.21					-0.22								
TB_S					0.22												
$dfrac_S$																	
$fT_{Sdfrac1}$							0.23										
$fT_{Sdfrac2}$																	
$fT_{Sdfrac3}$																	
$fT_{Sdfrac4}$																	
$fT_{Sdfrac5}$																	
$mean\ vit_S$	0.28	0.28															
$mean\ vit_{dfrac1}$						0.19											
$mean\ vit_{dfrac2}$			0.24	0.25													
$mean\ vit_{dfrac3}$	0.23		0.26					0.22	-0.20								
$mean\ vit_{dfrac4}$	0.23	0.24															
$mean\ vit_{dfrac5}$																	
$mean\ prod$																	
$min\ prod$																	
$max\ B$				0.20	0.23												
relative correlation strength	0.26	0.25	0.25	0.23	0.21	0.24	0.23	0.22	0.21	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Tab. II.3: Sensitivity analysis of calibration scenario No grazing, grouped parameters

Shown are descriptive statistics and significant correlations between independent parameters and model variables of the calibration scenario No grazing, parameters grouped (NG$_g$). Definition of parameter and process abbreviations see Tab. 2.3. Definition of variables are given in Tab. 2.2. Shown are significant correlation ± 0.179 (N = 122). Parameter groups are ranked after relative correlation strength (*rcs*).

Calibration scenario No Grazing, 15 parameter groups (NG$_g$): N = 122, Filter: P1 p2 p4 p5									Process and sub-process		SEN/LIT SEN	SEN/LIT LIT	MO MO W	PG PG V	WR WR L	VD VD W	CO CO D	WI
Descriptive statistics											**Included parameters**							
Median, upper and lower median confidence (99%) level											SEN	LIT	MortW1, MortW2, Mortp1, Mortp2,	ProdV1, PodincV2-4	WredT	VincW1, VincW2, VdecW1, VdecW2	ColS0Cov, ColS12p	PUE
Variables	Min	lower confidence	Median	upper confidence	Max	Mean	SD	CV			PG.4	PG.5	MO.1 MO.2 MO.3 MO.4	PG.1 PG.2	WR.1	VD.1 VD.2 VD.3 VD.4	CO.5 CO.6	WI.1
Td_S	0.70	1.28	3.56	4.77	5.12	3.29	1.31	40										0.19
$Min\ cov_F$	0.39	0.61	1.12	2.46	3.51	1.33	0.74	55			-0.25			-0.34			0.20	
$Mean\ prod$	6.74	8.60	11.24	15.34	17.75	11.61	2.65	23					**0.45**	**0.80**				0.31
$Mean\ gb_S$	2.68	5.50	16.27	42.21	58.99	19.92	14.45	73			**-0.94**	**-0.75**				0.25	0.26	
$Mean\ gb_P$	9.77	16.12	28.92	56.19	79.25	32.47	15.47	48			**-0.86**	**-0.68**		0.27		0.26	0.24	
$dfrac$	0.39	0.44	0.50	0.54	0.61	0.49	0.05	9								0.26		
$fT_{dfrac\ 1}$	0.00	0.09	0.13	0.26	0.34	0.15	0.07	49			-0.31	-0.40				-0.18		
$fT_{dfrac\ 2}$	0.04	0.07	0.15	0.22	0.31	0.15	0.06	42			**0.41**	0.21					-0.37	
$fT_{dfra\ c3}$	0.04	0.13	0.22	0.37	0.62	0.24	0.11	45			-0.25						0.26	
$fT_{dfra\ c4}$	0.10	0.33	0.49	0.58	0.60	0.46	0.11	23			0.24							
$fT_{dfra\ c5}$	0.00	0.00	0.00	0.00	0.08	0.00	0.02	366				-0.29				0.19	-0.30	
$mean\ vit$	1.00	1.00	1.60	1.90	2.67	1.47	0.45	30					**0.74**			0.28	**-0.58**	
$mean\ vit_{dfrac\ 1}$	1.00	1.00	1.00	1.00	1.14	1.00	0.02	2			-0.29	-0.18	0.33	-0.20		0.22	-0.21	
$mean\ vit_{dfrac\ 2}$	1.00	1.00	1.00	1.43	3.00	1.18	0.47	40			**-0.54**	-0.39	0.22	-0.23		0.27	-0.31	
$mean\ vit_{dfrac\ 3}$	1.00	1.00	1.58	2.45	3.00	1.63	0.64	39			-0.23		**0.67**	-0.19		0.24	**-0.61**	
$mean\ vit_{dfrac\ 4}$	1.00	1.00	1.87	2.05	3.00	1.62	0.57	35					**0.74**			0.22	**-0.63**	
$mean\ vit_{dfrac\ 5}$	0.00	0.00	0.00	0.00	2.00	0.11	0.35	317				-0.28				0.20	-0.30	
$mean\ ANPP$	198	319	482	741	1006	518	179	35					0.18	**0.56**		-0.19		**0.41**
$min\ ANPP$	45	83	145	268	502	171	95	55						0.23				
$max\ ANPP$	629	784	1141	1636	2459	1220	394	32					0.28	**0.68**	-0.31	-0.26		**0.49**
$ANPP$	65	164	439	682	912	430	200	46						0.38				0.33
B_S	40	132	473	1434	2751	656	573	87			**-0.77**	**-0.60**				0.27	0.20	
$max\ B$	309	561	1495	3235	5764	1793	1194	67			**-0.86**	**-0.67**		0.20			0.26	0.24
Relative rank correlation (*rcs*, not all variables listed)											0.25	0.19	0.17	0.15	0.14	0.13	0.11	0.10

Tab. II.3: continued:

Process and sub process	CO CO W	GR GR T	PG PG W	WR WR O	PF	VD VD D	MO MO D
	Included parameters						
	ColWS0, ColS0p, ColWS1, ColWS2	Gshape	MMconst	WredO	Pfmax, Pfinc	VdecG, VdecGp	MortG. MortGp
Variables	CO.1 CO.2 CO.3 CO.4	GR.4	PG.3	WR.2	PF.1 PF.2	VD.5 VD.6	MO.5 MO.6
Td_S					0.19		
$Min\ cov_F$							
$Mean\ prod$	0.20	-0.19	-0.27				
$Mean\ gb_S$							
$Mean\ gb_P$							
$dfrac$							
$fT_{dfrac\ 1}$							
$fT_{dfrac\ 2}$			0.21				
$fT_{dfra\ c3}$							
$fT_{dfra\ c4}$							
$fT_{dfra\ c5}$							
$mean\ vit$		-0.21					
$mean\ vit_{dfrac\ 1}$							
$mean\ vit_{dfrac\ 2}$							
$mean\ vit_{dfrac\ 3}$							
$mean\ vit_{dfrac\ 4}$		-0.21					
$mean\ vit_{dfrac\ 5}$							
$mean\ ANPP$	0.21						
$min\ ANPP$							
$max\ ANPP$	0.28		-0.18				
$ANPP$							
B_S							
$max\ B$							
rcs	0.04	0.02	0.02	0.01	0.01	0.00	0.00

Tab. II.4: Sensitivity analysis of calibration scenario Grazing, independent parameters, less correlated parameters.

Shown are those parameters with low mean relative correlation strength (rcs). Definition of parameter and process abbreviations see Tab. 2.3. Definition of variables are given in Tab. 2.2. Shown are significant correlation ± 0.12 (N = 250).

Scenario G_i	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Process	MO	PF	VD	CO	GR	MO	VD	CO	PF	MO	CO	CO	CO	PG	VD	WR	CO	VD	MO	MO	MO
Sub-process	MO W	-	VD D	CO W	GR T	MO W	VD W	CO W	-	MO D	CO D	CO W	CO W	PG V	VD D	WR O	CO D	VD W	MO W	MO W	MO D
Parameters (1st row: names of Chapter 4, 2nd row: as in other chapters)																					
	MortW1	PFmax	VdecG	ColWS0	Gshape	MortWp1	VdecW1	ColS0p	PFinc	MortGp	ColS0Cov	ColWS2	ColWS1	MMconst	VdecGp	WredO	ColS12p	VIncW1	MortW2	MortWp2	MortG
Variables	MO.1	PF.1	VD.5	CO.1	GR.4	MO.3	VD.3	CO.2	PF.2	MO.6	CO.5	CO.4	CO.3	PG.3	VD.6	WR.2	CO.6	VD.1	MO.2	MO.4	MO.5
Td_S																					
$Min\ cov_F$				0.13			-0.12														
Mean prod	0.17	-0.13			-0.14																
$Mean\ gb_S$						-0.13															
$Mean\ gb_P$					-0.14																
dfrac																					
$fT_{dfrac\ 1}$			-0.17											-0.14							
$fT_{dfrac\ 2}$																					
$fT_{dfrac\ 3}$																					
$fT_{dfrac\ c4}$											-0.14	-0.12									
$fT_{dfrac\ c5}$																					
mean vit	0.22	-0.20	-0.19	0.15									0.12								
$mean\ vit_{dfrac\ 1}$	0.20	-0.21	-0.25	0.15				0.12					0.12								
$mean\ vit_{dfrac\ 2}$	0.20	-0.21	-0.24	0.16				0.14													
$mean\ vit_{dfrac\ 3}$	0.23	-0.15								0.13											
$mean\ vit_{dfrac\ 4}$												-0.14									
$mean\ vit_{dfrac\ 5}$																					
mean ANPP				-0.15		-0.16		-0.13		0.14											
min ANPP						-0.13	-0.18								0.14						
max ANPP								-0.20													
ANPP				-0.13		-0.12															
B_S						-0.15															
max B											0.12										
Relative correlation	0.04	0.04	0.03	0.03	0.03	0.03	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
fT_G		-0.14			0.36																
cov_{EL}														0.17							
cov_{ES}					0.13																
mean PUE																					
C		-0.14			-0.12		-0.18														
Mean C		-0.15			-0.12		-0.18														
Mreal		-0.13					-0.13														

Tab. II. 5 Sensitivity analysis of calibration scenario Grazing grouped parameters.

Shown are descriptive statistics and significant correlations between independent parameters and model variables of the calibration scenario Grazing, parameters grouped (G_g). Definition of parameter and process abbreviations see Tab. 2.3. Definition of variables are given in Tab. 2.2. Shown are significant correlation ± 0.089 (N = 527). Parameter groups are ranked after relative correlation strength (*rcs*).

Calibration scenario Grazing 16 parameter groups (G_g), N = 542 Filter: P1 P3 P4 P5									Process, sub-process	GR GR M	PG PG V	SEN/ LIT SEN	WR WR L	VD VD W	MO MO W	WI -	SEN/ LIT LIT	CO CO W
	Descriptive statistics — Median, upper and lower median confidence (99%) level								Included parameters	Stock	ProdV1, PodincV2-4	SEN	WredT	VincW1, VincW2, VdecW1, VdecW2	MortW1, MortW2, Mortp1, Mortp2,	PUE	LIT	ColWS0, ColS0p, ColWS1, ColWS2
Variables	Min	lower confidence	Median	upper confidence	Max	Mean	SD	CV		GR.1	PG.1 PG.2	PG.4	WR.1	VD.1 VD.2 VD.3 VD.4	MO.1 MO.2 MO.3 MO.4	WI.1	PG.5	CO.1 CO.2 CO.3 CO.4
Td_S	0.46	1.93	3.72	4.47	4.59	3.49	0.85	24.4		**0.57**			0.20					
Mean gb_P	10.85	13.11	17.87	21.90	22.64	17.71	2.88	16.3		0.50	**0.61**	0.35	0.24					
Mean gb_S	10.80	11.14	13.59	19.63	22.68	14.29	2.75	19.3			0.27	**-0.50**						
dfrac	0.29	0.32	0.36	0.40	0.49	0.36	0.03	7.6			0.19	**0.42**						
$fT_{dfrac\,1}$	0.03	0.03	0.06	0.18	0.43	0.08	0.05	65.2										
$fT_{dfrac\,2}$	0.10	0.33	0.52	0.71	0.74	0.52	0.13	24.6			-0.28	**-0.58**						
$fT_{dfra\,c3}$	0.10	0.21	0.41	0.57	0.60	0.40	0.12	29.4			0.24	**0.51**						
$fT_{dfra\,c4}$	0.00	0.00	0.00	0.00	0.29	0.01	0.04	613.2									-0.34	-0.19
mean vit	1.00	1.55	2.78	3.27	3.66	2.62	0.54	20.5		0.36	-0.30		0.20	**-0.53**	**0.42**	-0.20		
mean vit $_{dfrac\,1}$	1.00	1.02	2.54	3.25	3.55	2.35	0.69	29.3		0.33	-0.30		0.24	**-0.49**	0.32	-0.25		0.20
mean vit $_{dfrac\,2}$	1.00	1.31	2.77	3.29	3.68	2.60	0.58	22.4		0.37	-0.30		0.18	**-0.52**	**0.42**	-0.19		
mean vit $_{dfrac\,3}$	1.00	1.63	2.85	3.28	3.99	2.71	0.52	19.2		0.35	-0.28			**-0.53**	**0.45**			
mean vit $_{dfrac\,4}$	0.00	0.00	0.00	2.00	3.00	0.19	0.66	355.0									-0.39	
mean prod	243	479	800	1086	1720	802	193.5	24.1		**0.74**	0.38	0.23		-0.31				
min prod	59	230	548	793	922	535	172.6	32.3		**0.79**		0.21	0.38	-0.27				
max B	496	698	932	1484	3274	994	299.2	30.1			0.36	**-0.55**	-0.38				0.30	-0.21
Relative correlation strength (*rcs*, not all variables listed)										0.30	0.26	0.22	0.20	0.17	0.14	0.12	0.09	0.08

Tab. II.5 continued

Process, sub-process	VD VD D	GR GR T	PG PG W	PF	CO CO D	MO MO D	WR WR O
Included parameters	VdecG, VdecGp	Gshape	MMconst	Pfmax, Pfinc	ColS0Cov, ColS12p	MortG. MortGp	WredO
Variables	VD.5 VD.6	GR.4	PG.3	PF.1 PF.2	CO.5 CO.6	MO.5 MO.6	WR.2
$Td_S(t = 100)$							
τB_P							
τB_S							
$dfrac_S$							
$fT_{Sdfrac1}$							
$fT_{Sdfrac2}$							
$fT_{Sdfrac3}$							
$fT_{Sdfrac4}$							
mean vit_S							
mean vit$_{dfrac1}$							
mean vit$_{dfrac2}$							
mean vit$_{dfrac3}$							
mean vit$_{dfrac4}$							
mean prod							
min prod							
max B							
rcs	0.06	0.04	0.02	0.02	0.01	0.00	0.00

Tab. II. 6: Correlations of parameters for all calibration scenarios.

Shown are all correlations between the independent parameters of the simulation model for all four calibration scenarios: **A)** No grazing, parameters independent (NG$_i$), N = 105, significance level (p<0.05) = ±0.19; **B)**; No grazing, parameters grouped (NG$_g$), N = 122, significance level (p<0.05) = ±0.179; **C)** Grazing, parameters independent (G$_i$), N = 250, significance level (p<0.05) = ±0.12; **D)** Grazing, parameters grouped (G$_g$), N = 527, significance level (p<0.05) = ±0.089. Definition of parameter and process abbreviations see Tab. 2.3. Definition of variables are given in Tab. 2.2. Shown are significant correlation ± 0.179 (N = 122).

Tab. II.6 A

Parameter correlations (calibration scenario		PUE WI.1	WredT WR.1	WredO WR.2	ProdV1 PG.1	Prodinc V2-4 PG.2	MMconst PG.3	SEN PG.4	LIT PG.5	Gshape GR.4	ColWS0 CO.1	ColS0p CO.2	ColWS1 CO.3	ColWS2 CO.4	ColS0Cov CO.5	ColS12p CO.6
PUE	WI.1		**-0.31**	-0.03	-0.03	-0.01	0.13	-0.11	-0.12	-0.03	**0.38**	-0.07	0.17	0.14	0.17	0.03
WredT	WR.1	**-0.31**		0.03	0.06	0.04	-0.12	0.07	0.16	-0.03	-0.05	-0.04	-0.16	-0.03	-0.17	-0.08
WredO	WR.2	-0.03	0.03		-0.05	0.15	0.04	-0.05	-0.01	-0.08	0.14	0.00	-0.02	0.21	0.08	-0.02
ProdV1	PG.1	-0.03	0.06	-0.05		0.16	0.02	0.10	0.12	-0.16	0.09	0.04	0.09	0.07	-0.03	-0.06
ProdincV2-4	PG.2	-0.01	0.04	0.15	0.16		0.12	-0.03	-0.02	0.12	0.02	-0.08	-0.01	0.07	0.04	-0.01
MMconst	PG.3	0.13	-0.12	0.04	0.02	0.12		-0.05	-0.13	-0.10	0.16	0.08	0.00	0.11	-0.09	-0.01
SEN	PG.4	-0.11	0.07	-0.05	0.10	-0.03	-0.05		**0.86**	0.05	-0.18	-0.03	0.03	0.07	0.12	0.06
LIT	PG.5	-0.12	0.16	-0.01	0.12	-0.02	-0.13	**0.86**		0.02	-0.06	**-0.25**	0.03	0.03	0.20	0.03
Gshape	GR.4	-0.03	-0.03	-0.08	-0.16	0.12	-0.10	0.05	0.02		-0.15	-0.02	-0.02	-0.07	0.04	0.05
ColWS0	CO.1	**0.38**	-0.05	0.14	0.09	0.02	0.16	-0.18	-0.06	-0.15		-0.04	-0.01	0.06	0.09	0.00
ColS0p	CO.2	-0.07	-0.04	0.00	0.04	-0.08	0.08	-0.03	**-0.25**	-0.02	-0.04		0.04	0.05	0.06	**-0.26**
ColWS1	CO.3	0.17	-0.16	-0.02	0.09	-0.01	0.00	0.03	0.03	-0.02	-0.01	0.04		0.17	0.01	0.08
ColWS2	CO.4	0.14	-0.03	0.21	0.07	0.07	0.11	0.07	0.03	-0.07	0.06	0.05	0.17		0.07	-0.14
ColS0Cov	CO.5	0.17	-0.17	0.08	-0.03	0.04	-0.09	0.12	0.20	0.04	0.09	0.06	0.01	0.07		0.01
ColS12p	CO.6	0.03	-0.08	-0.02	-0.06	-0.01	-0.01	0.06	0.03	0.05	0.00	**-0.26**	0.08	-0.14	0.01	
VIncW1	VD.1	0.02	-0.13	0.07	0.09	0.08	0.01	0.00	-0.08	0.05	0.00	0.02	0.19	-0.12	-0.04	0.05
VincW2	VD.2	**0.25**	0.02	-0.08	-0.17	0.00	0.07	-0.18	**-0.27**	0.08	0.10	-0.05	-0.13	-0.10	-0.18	-0.02
VdecW2	VD.4	0.05	-0.03	0.09	0.10	0.01	0.11	0.02	0.09	-0.23	0.08	-0.20	0.02	-0.07	-0.14	0.06
VdecW1	VD.3	**0.30**	**0.31**	-0.09	0.10	-0.11	-0.06	0.09	0.07	0.03	-0.01	-0.03	-0.02	0.06	-0.06	0.07
VdecG	VD.5	0.06	-0.01	0.02	0.22	-0.06	0.13	-0.20	-0.18	-0.09	0.18	0.04	0.06	0.12	-0.11	0.03
VdecGp	VD.6	0.13	0.18	0.19	-0.16	-0.11	0.04	-0.15	-0.11	0.04	0.10	0.03	0.01	0.15	-0.12	-0.04
MortW1	MO.1	0.18	**0.26**	-0.13	-0.13	0.01	0.02	0.19	0.21	0.06	-0.04	0.05	0.03	-0.06	0.10	-0.05
MortW2	MO.2	0.08	-0.03	-0.10	0.05	-0.07	-0.11	-0.04	-0.10	0.07	-0.05	0.08	-0.09	0.03	-0.16	0.06
MortWp1	MO.3	0.15	0.08	-0.19	0.06	-0.16	-0.10	**0.26**	**0.28**	0.09	-0.16	-0.08	0.01	-0.01	0.17	0.06
MortWp2	MO.4	0.12	-0.07	-0.09	0.10	0.01	-0.02	0.11	0.02	0.00	0.16	0.00	-0.06	0.10	0.01	0.01
MortG	MO.5	-0.03	-0.02	0.08	-0.05	0.06	-0.07	0.06	0.04	0.07	-0.06	0.05	0.03	-0.08	0.18	-0.02
MortGp	MO.6	-0.05	-0.06	0.00	0.08	-0.03	0.04	-0.04	-0.01	0.05	0.04	-0.06	0.16	0.10	0.07	0.09
PFinc	PF.2	-0.08	0.10	0.07	0.17	0.01	0.01	0.12	0.15	-0.02	-0.05	0.02	-0.02	0.00	0.04	-0.15
PFmax	PF.1	0.20	-0.03	-0.17	-0.04	0.09	0.09	0.05	0.11	0.15	0.02	0.00	0.04	0.01	0.01	-0.07

Tab. II.6 A continued

Parameter correlations (calibration scenario		VIncW1 VD.1	VincW2 VD.2	VdecW2 VD.4	VdecW1 VD.3	VdecG VD.5	VdecGp VD.6	MortW1 MO.1	MortW2 MO.2	MortWp1 MO.3	MortWp2 MO.4	MortG MO.5	MortGp MO.6	PFinc PF.2	PFmax PF.1
PUE	WI.1	0.02	**0.25**	0.05	**0.30**	0.06	0.13	0.18	0.08	0.15	0.12	-0.03	-0.05	-0.08	0.20
WredT	WR.1	-0.13	0.02	-0.03	**0.31**	-0.01	0.18	**0.26**	-0.03	0.08	-0.07	-0.02	-0.06	0.10	-0.03
WredO	WR.2	0.07	-0.08	0.09	-0.09	0.02	0.19	-0.13	-0.10	-0.19	-0.09	0.08	0.00	0.07	-0.17
ProdV1	PG.1	0.09	-0.17	0.10	0.10	0.22	-0.16	-0.13	0.05	0.06	0.10	-0.05	0.08	0.17	-0.04
ProdincV2-4	PG.2	0.08	0.00	0.01	-0.11	-0.06	-0.11	0.01	-0.07	-0.16	0.01	0.06	-0.03	0.01	0.09
MMconst	PG.3	0.01	0.07	0.11	-0.06	0.13	0.04	0.02	-0.11	-0.10	-0.02	-0.07	0.04	0.01	0.09
SEN	PG.4	0.00	-0.18	0.02	0.09	-0.20	-0.15	0.19	-0.04	**0.26**	0.11	0.06	-0.04	0.12	0.05
LIT	PG.5	-0.08	**-0.27**	0.09	0.07	-0.18	-0.11	0.21	-0.10	**0.28**	0.02	0.04	-0.01	0.15	0.11
Gshape	GR.4	0.05	0.08	-0.23	0.03	-0.09	0.04	0.06	0.07	0.09	0.00	0.07	0.05	-0.02	0.15
ColWS0	CO.1	0.00	0.10	0.08	-0.01	0.18	0.10	-0.04	-0.05	-0.16	0.16	-0.06	0.04	-0.05	0.02
ColS0p	CO.2	0.02	-0.05	-0.20	-0.03	0.04	0.03	0.05	0.08	-0.08	0.00	0.05	-0.06	0.02	0.00
ColWS1	CO.3	0.19	-0.13	0.02	-0.02	0.06	0.01	0.03	-0.09	0.01	-0.06	0.03	0.16	-0.02	0.04
ColWS2	CO.4	-0.12	-0.10	-0.07	0.06	0.12	0.15	-0.06	0.03	-0.01	0.10	-0.08	0.10	0.00	0.01
ColS0Cov	CO.5	-0.04	-0.18	-0.14	-0.06	-0.11	-0.12	0.10	-0.16	0.17	0.01	0.18	0.07	0.04	0.01
ColS12p	CO.6	0.05	-0.02	0.06	0.07	0.03	-0.04	0.06	0.06	0.06	0.01	-0.02	0.09	-0.15	-0.07
VIncW1	VD.1	■	-0.08	0.14	-0.24	-0.04	-0.19	-0.06	-0.04	-0.01	0.05	0.03	-0.03	0.10	-0.13
VincW2	VD.2	-0.08	■	0.08	0.04	0.11	0.03	-0.13	0.11	-0.16	0.01	0.07	-0.03	**-0.29**	0.03
VdecW2	VD.4	0.14	0.08	■	-0.01	-0.03	-0.09	-0.18	-0.10	-0.06	-0.03	-0.08	-0.11	-0.08	-0.07
VdecW1	VD.3	-0.24	0.04	-0.01	■	0.06	**0.36**	0.05	0.08	0.02	0.06	-0.09	-0.06	0.05	0.24
VdecG	VD.5	-0.04	0.11	-0.03	0.06	■	0.03	-0.04	0.09	-0.22	0.06	-0.02	0.03	-0.01	-0.10
VdecGp	VD.6	-0.19	0.03	-0.09	**0.36**	0.03	■	0.06	-0.09	-0.09	0.16	-0.01	-0.03	0.00	0.11
MortW1	MO.1	-0.06	-0.13	-0.18	0.05	-0.04	0.06	■	**-0.27**	0.12	**-0.25**	0.07	0.00	**0.27**	0.00
MortW2	MO.2	-0.04	0.11	-0.10	0.08	0.09	-0.09	**-0.27**	■	0.04	0.10	-0.14	-0.06	-0.10	-0.02
MortWp1	MO.3	-0.01	-0.16	-0.06	0.02	-0.22	-0.09	0.12	0.04	■	-0.13	-0.09	-0.13	-0.09	0.17
MortWp2	MO.4	0.05	0.01	-0.03	0.06	0.06	0.16	**-0.25**	0.10	-0.13	■	-0.05	0.03	0.02	0.04
MortG	MO.5	0.03	0.07	-0.08	-0.09	-0.02	-0.01	0.07	-0.14	-0.09	-0.05	■	0.06	0.07	-0.07
MortGp	MO.6	-0.03	-0.03	-0.11	-0.06	0.03	-0.03	0.00	-0.06	-0.13	0.03	0.06	■	0.12	-0.03
PFinc	PF.2	0.10	**-0.29**	-0.08	0.05	-0.01	0.00	**0.27**	-0.10	-0.09	0.02	0.07	0.12	■	-0.09
PFmax	PF.1	-0.13	0.03	-0.07	0.24	-0.10	0.11	0.00	-0.02	0.17	0.04	-0.07	-0.03	-0.09	■

Tab. II.6 B

Correlation of parameters	Process and sub-process	Calibration scenario NG$_g$ / Included parameters / Process and sub-process	WI WUE WI.1	WR WR L WredT WR.1	WR WR O WredO WR.2	PG PG V ProdV1, PodincV2-4 PG.1 PG.2	PG PG W MMconst PG.3	SEN/LIT SEN SEN PG.4	G T Gshape GR.4	G CO W ColWS0, ColS0p, ColWS1, ColWS2 CO.1 CO.2 CO.3 CO.4	CO CO ColS0Cov, ColS12p CO.5 CO.6	VD VD W VincW1, VincW2, VdecW1, VdecW2 VD.1 VD.2 VD.3 VD.4	VD VD D VdecG, VdecGp VD.5 VD.6	MO MO W MortW1, MortW2, Mortp1, Mortp2, MO.1 MO.2 MO.3 MO.4	MO MO G MortG. MortGp MO.5 MO.6	PF Pfmax, Pfinc PF.1 PF.2	SEN/LIT LIT LIT PG.5
WI	WUE	WI.1	■	-0.23	0.10	**0.27**	0.05	0.04	-0.12	**0.54**	0.02	**0.27**	0.13	**0.33**	0.04	0.04	0.00
WR L	WredT	WR.1	-0.23	■	-0.06	-0.13	0.00	-0.20	-0.15	**-0.29**	-0.07	0.24	-0.07	**0.40**	0.01	-0.03	-0.13
WR O	WredO	WR.2	0.10	-0.06	■	-0.03	0.02	0.18	0.01	0.02	-0.16	-0.07	-0.14	0.13	-0.02	0.11	0.10
PG V	ProdV1, PodincV2-4	PG.1 PG.2	**0.27**	-0.13	-0.03	■	-0.12	0.09	-0.04	0.21	-0.08	0.19	0.18	0.02	0.07	-0.11	0.02
PG W	MMconst	PG.3	0.05	0.00	0.02	-0.12	■	-0.10	0.13	0.06	0.00	0.06	-0.04	-0.02	0.05	0.11	-0.08
SEN/LIT SEN	SEN	PG.4	0.04	-0.20	0.18	0.09	-0.10	■	0.10	0.06	**-0.26**	0.00	0.08	0.15	0.02	-0.11	**0.82**
G T	Gshape	GR.4	-0.12	-0.15	0.01	-0.04	0.13	0.10	■	-0.02	0.00	0.05	-0.08	-0.19	-0.14	0.07	0.06
CO W	ColWS0, ColS0p, ColWS1, ColWS2	CO.1 CO.2 CO.3 CO.4	**0.54**	**-0.29**	0.02	0.21	0.06	0.06	-0.02	■	-0.09	0.14	0.17	0.10	-0.12	0.06	0.15
CO G	ColS0Cov, ColS12p	CO.5 CO.6	0.02	-0.07	-0.16	-0.08	0.00	**-0.26**	0.00	-0.09	■	-0.11	0.11	-0.12	0.05	-0.13	0.02
VD W	VincW1, VincW2, VdecW1, VdecW2	VD.1 VD.2 VD.3 VD.4	**0.27**	0.24	-0.07	0.19	0.06	0.00	0.05	0.14	-0.11	■	0.08	-0.20	0.08	-0.04	-0.09
VD D	VdecG, VdecGp	VD.5 VD.6	0.13	-0.07	-0.14	0.18	-0.04	0.08	-0.08	0.17	0.11	0.08	■	0.03	-0.13	0.03	0.04
MO W	MortW1, MortW2, Mortp1, Mortp2,	MO.1 MO.2 MO.3 MO.4	**0.33**	**0.40**	0.13	0.02	-0.02	0.15	-0.19	0.10	-0.12	-0.20	0.03	■	-0.02	-0.08	0.17
MO G	MortG. MortGp	MO.5 MO.6	0.04	0.01	-0.02	0.07	0.05	0.02	-0.14	-0.12	0.05	0.08	-0.13	-0.02	■	-0.13	-0.01
PF	Pfmax, Pfinc	PF.1 PF.2	0.04	-0.03	0.11	-0.11	0.11	-0.11	0.07	0.06	-0.13	-0.04	0.03	-0.08	-0.13	■	-0.13
SEN/LIT LIT	LIT	PG.5	0.00	-0.13	0.10	0.02	-0.08	**0.82**	0.06	0.15	0.02	-0.09	0.04	0.17	-0.01	-0.13	■

Tab. II.6 C

Parameter correlations (calibration scenario G$_i$)		Stock	PUE	WredT	WredO	ProdV1	Prodinc V2-4	MMconst	SEN	LIT	Gshape	ColWS0	ColS0p	ColWS1	ColWS2	ColS0Cov
		GR.1	WI.1	WR.1	WR.2	PG.1	PG.2	PG.3	PG.4	PG.5	GR.4	CO.1	CO.2	CO.3	CO.4	CO.5
Stock	GR.1		0.14	**0.28**	-0.06	0.12	-0.02	0.01	-0.15	**-0.55**	-0.12	0.03	-0.05	0.03	-0.12	0.02
PUE	WI.1	0.14		**-0.38**	0.08	-0.08	0.07	-0.05	-0.15	-0.21	0.03	0.08	-0.18	-0.01	0.00	0.08
WredT	WR.1	**0.28**	-0.38		-0.12	-0.06	-0.04	0.09	**0.26**	0.12	-0.11	-0.04	0.11	0.06	0.01	-0.09
WredO	WR.2	-0.06	0.08	-0.12		-0.11	0.13	-0.07	-0.04	0.05	0.04	-0.08	0.04	-0.05	0.00	0.11
ProdV1	PG.1	0.12	-0.08	-0.06	-0.11		-0.20	0.05	0.12	0.02	-0.06	-0.03	-0.06	-0.03	0.02	0.06
ProdincV2-4	PG.2	-0.02	0.07	-0.04	0.13	-0.20		0.17	0.12	-0.01	0.01	-0.04	-0.10	0.01	0.00	-0.02
MMconst	PG.3	0.01	-0.05	0.09	-0.07	0.05	0.17		-0.06	-0.06	-0.05	0.04	-0.03	0.07	0.00	-0.02
SEN	PG.4	-0.15	-0.15	**0.26**	-0.04	0.12	0.12	-0.06		**0.63**	0.17	0.06	-0.04	0.00	0.05	-0.09
LIT	PG.5	**-0.55**	-0.21	0.12	0.05	0.02	-0.01	-0.06	**0.63**		0.08	0.07	-0.01	-0.03	0.12	-0.08
Gshape	GR.4	-0.12	0.03	-0.11	0.04	-0.06	0.01	-0.05	0.17	0.08		-0.10	0.03	0.08	0.03	0.03
ColWS0	CO.1	0.03	0.08	-0.04	-0.08	-0.03	-0.04	0.04	0.06	0.07	-0.10		-0.01	-0.09	0.01	0.06
ColS0p	CO.2	-0.05	-0.18	0.11	0.04	-0.06	-0.10	-0.03	-0.04	-0.01	0.03	-0.01		0.04	-0.04	0.04
ColWS1	CO.3	0.03	-0.01	0.06	-0.05	-0.03	0.01	0.07	0.00	-0.03	0.08	-0.09	0.04		0.01	0.00
ColWS2	CO.4	-0.12	0.00	0.01	0.00	0.02	0.00	0.00	0.05	0.12	0.03	0.01	-0.04	0.01		0.13
ColS0Cov	CO.5	0.02	0.08	-0.09	0.11	0.06	-0.02	-0.02	-0.09	-0.08	0.03	0.06	0.04	0.00	0.13	
ColS12p	CO.6	-0.01	-0.03	0.12	-0.06	-0.03	0.08	-0.06	-0.04	0.02	-0.02	0.11	-0.08	-0.02	0.05	-0.04
VIncW1	VD.1	-0.05	0.01	0.00	-0.02	0.04	0.00	0.02	0.04	0.03	-0.05	-0.03	-0.06	-0.02	0.00	-0.04
VincW2	VD.2	0.02	0.25	**0.29**	0.05	0.03	0.18	0.07	0.03	-0.09	0.04	-0.05	0.05	-0.07	0.02	0.00
VdecW2	VD.4	-0.01	0.12	0.06	0.02	0.01	0.03	0.06	-0.07	-0.05	0.05	-0.05	0.02	0.01	0.03	0.05
VdecW1	VD.3	-0.16	0.14	0.14	0.03	-0.03	0.07	0.02	0.04	0.12	0.16	-0.06	0.00	0.06	0.04	-0.06
VdecG	VD.5	0.04	0.12	0.14	0.03	0.01	0.04	0.09	0.02	0.02	0.10	0.00	0.05	-0.03	0.00	0.05
VdecGp	VD.6	0.00	-0.05	0.11	0.00	-0.02	0.00	-0.07	0.10	0.08	0.04	-0.05	0.11	0.02	-0.03	-0.07
MortW1	MO.1	0.07	0.02	0.07	-0.06	-0.01	-0.03	-0.01	0.09	0.02	0.05	0.00	-0.04	-0.02	-0.08	0.09
MortW2	MO.2	-0.03	0.17	0.05	0.03	-0.08	0.09	-0.02	0.08	0.01	0.02	0.04	-0.04	0.09	-0.02	-0.14
MortWp1	MO.3	-0.06	0.06	-0.05	0.14	-0.10	0.11	0.12	0.05	0.00	-0.02	0.08	0.05	-0.01	0.01	0.05
MortWp2	MO.4	-0.05	-0.03	0.02	-0.06	0.01	0.04	0.05	0.05	-0.06	0.09	-0.05	-0.02	0.03	-0.01	0.08
MortG	MO.5	-0.01	-0.07	-0.06	0.06	0.14	0.03	0.03	0.01	-0.03	0.08	-0.05	-0.02	0.00	-0.09	-0.02
MortGp	MO.6	0.06	0.07	0.02	0.04	-0.01	0.01	0.00	-0.01	-0.01	-0.06	-0.02	0.07	0.09	-0.01	-0.02
PFinc	PF.2	0.20	0.01	-0.01	0.16	-0.05	-0.03	0.05	-0.06	-0.02	-0.06	0.02	-0.02	0.02	-0.01	-0.01

Tab. II.6 C continued

Parameter correlations (calibration scenario G$_i$)		ColS12p	VIncW1	VincW2	VdecW2	VdecW1	VdecG	VdecGp	MortW1	MortW2	MortWp1	MortWp2	MortG	MortGp	PFinc
		CO.6	VD.1	VD.2	VD.4	VD.3	VD.5	VD.6	MO.1	MO.2	MO.3	MO.4	MO.5	MO.6	PF.2
Stock	GR.1	-0.01	-0.05	0.02	-0.01	-0.16	0.04	0.00	0.07	-0.03	-0.06	-0.05	-0.01	0.06	0.20
PUE	WI.1	-0.03	0.01	0.25	0.12	0.14	0.12	-0.05	0.02	0.17	0.06	-0.03	-0.07	0.07	0.01
WredT	WR.1	0.12	0.00	**0.29**	0.06	0.14	0.14	0.11	0.07	0.05	-0.05	0.02	-0.06	0.02	-0.01
WredO	WR.2	-0.06	-0.02	0.05	0.02	0.03	0.03	0.00	-0.06	0.03	0.14	-0.06	0.06	0.04	0.16
ProdV1	PG.1	-0.03	0.04	0.03	0.01	-0.03	0.01	-0.02	-0.01	-0.08	-0.10	0.01	0.14	-0.01	-0.05
ProdincV2-4	PG.2	0.08	0.00	0.18	0.03	0.07	0.04	0.00	-0.03	0.09	0.11	0.04	0.03	0.01	-0.03
MMconst	PG.3	-0.06	0.02	0.07	0.06	0.02	0.09	-0.07	-0.01	-0.02	0.12	0.05	0.03	0.00	0.05
SEN	PG.4	-0.04	0.04	0.03	-0.07	0.04	0.02	0.10	0.09	0.08	0.05	0.05	0.01	-0.01	-0.06
LIT	PG.5	0.02	0.03	-0.09	-0.05	0.12	0.02	0.08	0.02	0.01	0.00	-0.06	-0.03	-0.01	-0.02
Gshape	GR.4	-0.02	-0.05	0.04	0.05	0.16	0.10	0.04	0.05	0.02	-0.02	0.09	0.08	-0.06	-0.06
ColWS0	CO.1	0.11	-0.03	-0.05	-0.05	-0.06	0.00	-0.05	0.00	0.04	0.08	-0.05	-0.05	-0.02	0.02
ColS0p	CO.2	-0.08	-0.06	0.05	0.02	0.00	0.05	0.11	-0.04	-0.04	0.05	-0.02	-0.02	0.07	-0.02
ColWS1	CO.3	-0.02	-0.02	-0.07	0.01	0.06	-0.03	0.02	-0.02	0.09	-0.01	0.03	0.00	0.09	0.02
ColWS2	CO.4	0.05	0.00	0.02	0.03	0.04	0.00	-0.03	-0.08	-0.02	0.01	-0.01	-0.09	-0.01	-0.01
ColS0Cov	CO.5	-0.04	-0.04	0.00	0.05	-0.06	0.05	-0.07	0.09	-0.14	0.05	0.08	-0.02	-0.02	-0.01
ColS12p	CO.6		-0.02	0.09	-0.02	0.13	-0.08	-0.08	-0.01	0.04	0.01	0.08	0.00	0.01	0.01
VIncW1	VD.1	-0.02		-0.05	0.13	-0.09	-0.06	0.01	-0.04	0.00	0.07	0.01	0.12	0.06	0.03
VincW2	VD.2	0.09	-0.05		0.01	-0.03	0.03	-0.02	-0.01	0.04	0.06	0.00	-0.02	-0.12	-0.12
VdecW2	VD.4	-0.02	0.13	0.01		0.04	-0.12	-0.06	0.00	-0.01	0.01	-0.03	0.09	-0.03	0.02
VdecW1	VD.3	0.13	-0.09	-0.03	0.04		-0.06	-0.04	-0.10	0.15	-0.01	-0.01	-0.06	0.01	0.11
VdecG	VD.5	-0.08	-0.06	0.03	-0.12	-0.06		0.06	-0.12	0.02	-0.01	-0.05	-0.03	0.14	-0.03
VdecGp	VD.6	-0.08	0.01	-0.02	-0.06	-0.04	0.06		0.11	0.02	-0.09	0.01	0.04	0.01	0.00
MortW1	MO.1	-0.01	-0.04	-0.01	0.00	-0.10	-0.12	0.11		-0.24	-0.11	-0.15	-0.02	-0.02	-0.06
MortW2	MO.2	0.04	0.00	0.04	-0.01	0.15	0.02	0.02	-0.24		-0.02	0.07	0.08	-0.02	-0.01
MortWp1	MO.3	0.01	0.07	0.06	0.01	-0.01	-0.01	-0.09	-0.11	-0.02		-0.07	0.04	-0.08	-0.02
MortWp2	MO.4	0.08	0.01	0.00	-0.03	-0.01	-0.05	0.01	-0.15	0.07	-0.07		0.07	-0.13	0.06
MortG	MO.5	0.00	0.12	-0.02	0.09	-0.06	-0.03	0.04	-0.02	0.08	0.04	0.07		-0.07	0.02
MortGp	MO.6	0.01	0.06	-0.12	-0.03	0.01	0.14	0.01	-0.02	-0.02	-0.08	-0.13	-0.07		0.03
PFinc	PF.2	0.01	0.03	-0.12	0.02	0.11	-0.03	0.00	-0.06	-0.01	-0.02	0.06	0.02	0.03	

Tab. II.6 D

Correlation of parameters			GR Stock GR.1	WI WUE WI.1	WR L WredT WR.1	WR O WredO WR.2	PG PG V ProdV1, PodincV2-4 PG.1 PG.2	PG PG W MMconst PG.3	SEN/LIT SEN SEN PG.4	G T Gshape GR.4	G CO W ColWS0, ColS0p, ColWS1, ColWS2 CO.1 CO.2 CO.3 CO.4	CO G ColS0Cov, ColS12p CO.5 CO.6	VD W VincW1, VincW2, VdecW1, VdecW2 VD.1 VD.2 VD.3 VD.4	VD D VdecG, VdecGp VD.5 VD.6	MO MO W MortW1, MortW2, Mortp1, Mortp2, MO.1 MO.2 MO.3 MO.4	MO MO G MortG. MortGp MO.5 MO.6	PF Pfmax, Pfinc PF.1 PF.2	SEN/LIT LIT LIT PG.5
GR	Stock	GR.1	■	0.00	**0.25**	-0.03	0.16	0.06	0.12	0.07	0.01	-0.02	-0.20	0.07	-0.09	-0.07	0.18	**-0.26**
WI	WUE	WI.1	0.00	■	**-0.30**	0.04	-0.04	-0.01	-0.02	0.05	0.11	0.08	**0.33**	0.11	0.22	-0.09	-0.06	-0.16
WR L	WredT	WR.1	**0.25**	**-0.30**	■	0.02	-0.11	0.05	0.03	-0.07	-0.01	-0.04	**0.42**	0.04	0.06	-0.03	0.03	0.12
WR O	WredO	WR.2	-0.03	0.04	0.02	■	-0.03	0.02	-0.01	-0.03	0.02	-0.02	0.02	-0.04	0.05	-0.03	-0.04	0.05
PG V	ProdV1, PodincV2-4	PG.1 PG.2	0.16	-0.04	-0.11	-0.03	■	0.15	0.22	-0.03	-0.16	-0.03	0.14	-0.10	-0.16	0.02	-0.05	-0.03
PG W	MMconst	PG.3	0.06	-0.01	0.05	0.02	0.15	■	-0.05	0.00	-0.05	0.05	-0.05	-0.03	0.05	0.02	-0.05	0.00
SEN/LIT SEN	SEN	PG.4	0.12	-0.02	0.03	-0.01	0.22	-0.05	■	0.18	0.03	0.01	-0.07	0.01	0.06	-0.01	-0.01	**0.25**
G T	Gshape	GR.4	0.07	0.05	-0.07	-0.03	-0.03	0.00	0.18	■	-0.04	0.14	0.04	-0.01	0.11	0.00	0.01	-0.12
CO W	ColWS0, ColS0p, ColWS1, ColWS2	CO.1 CO.2 CO.3 CO.4	0.01	0.11	-0.01	0.02	-0.16	-0.05	0.03	-0.04	■	-0.07	-0.05	-0.05	-0.08	0.01	0.07	0.13
CO G	ColS0Cov, ColS12p	CO.5 CO.6	-0.02	0.08	-0.04	-0.02	-0.03	0.05	0.01	0.14	-0.07	■	0.07	-0.04	0.08	0.01	0.04	-0.04
VD W	VincW1, VincW2, VdecW1, VdecW2	VD.1 VD.2 VD.3 VD.4	-0.20	**0.33**	**0.42**	0.02	0.14	-0.05	-0.07	0.04	-0.05	0.07	■	-0.20	-0.04	-0.05	0.05	-0.03
VD D	VdecG, VdecGp	VD.5 VD.6	0.07	0.11	0.04	-0.04	-0.10	-0.03	0.01	-0.01	-0.05	-0.04	-0.20	■	0.04	-0.02	0.05	0.02
MO W	MortW1, MortW2, Mortp1, Mortp2,	MO.1 MO.2 MO.3 MO.4	-0.09	0.22	0.06	0.05	-0.16	0.05	0.06	0.11	-0.08	0.08	-0.04	0.04	■	0.19	-0.04	-0.10
MO G	MortG. MortGp	MO.5 MO.6	-0.07	-0.09	-0.03	-0.03	0.02	0.02	-0.01	0.00	0.01	0.01	-0.05	-0.02	0.19	■	-0.02	0.00
PF	Pfmax, Pfinc	PF.1 PF.2	0.18	-0.06	0.03	-0.04	-0.05	-0.05	-0.01	0.01	0.07	0.04	0.05	0.05	-0.04	-0.02	■	0.07
SEN/LIT LIT	LIT	PG.5	**-0.26**	-0.16	0.12	0.05	-0.03	0.00	**0.25**	-0.12	0.13	-0.04	-0.03	0.02	-0.10	0.00	0.07	■

Note: Row header hierarchy — "Calibration scanario G_g" / "Included parameters" / "Process and sub-process" appear as stacked labels in the header region.

Appendix III
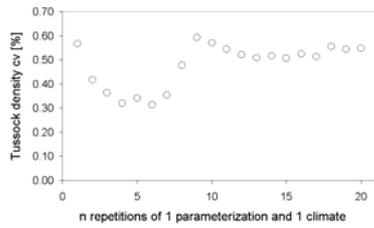
A)   B)
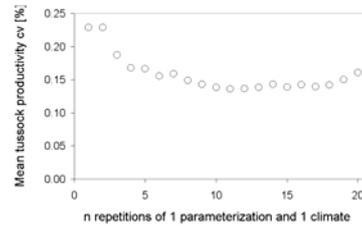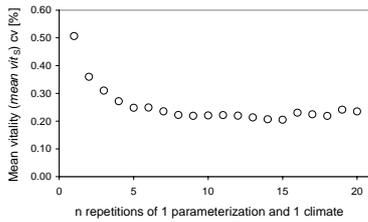
C)   D)
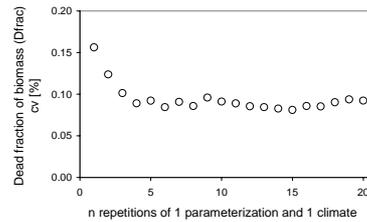
Fig. III.1: Inherent model uncertainty.
Shown are the CV for some important variables for 20 repetitions of the standard parameterisation and one climate: A) Tussock density; B) Mean tussock productivity; C) Mean tussock vitality; D) Mean dead biomass fraction.

A)   B)
Fig. III.2: Effect of 100 different stochastic climate on Cv of response variables.
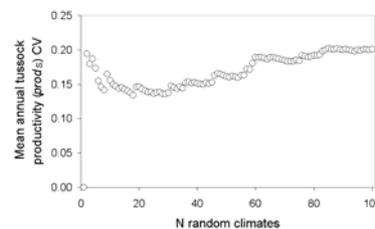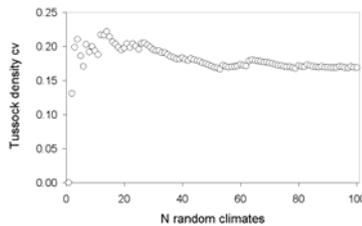
I used the standard parameterisation and 100 different stochastic annual rainfalls: A) CV of tussock density, B) CV of Mean annual tussock annual productivity. As mean tussock productivity (B) increased up to 100 repetitions, it is necessary to include 100 climatic repetitions to estimate the effect of climatological uncertainty.

Tab. III.1: Grazing under constant precipitation: Results for the linear and the non-linear fit
Non linear fit:

R = 0.96032876 R-sqr. = 0.92223132   **Adj. R-sqr. = 0.68892528**

Parameter	Coefficient	Std. Error	T	P
min	0.0000	14.8577	0.0000	1.0000
max	5.7733	0.8313	6.9453	0.0910
EC50	1.6588	1.7094	0.9704	0.5096
slope	6.0082	22.1276	0.2715	0.8312

Linear fit:

R = 0.95955729 R-sqr. = 0.92075019   **Adj. R-sqr. = 0.89433358**

Parameter	Coefficient	Std. Error	T	P
y0	6.8672	0.5054	13.5881	0.0009
a	-2.4676	0.4180	-5.9038	0.0097

A)   B)   C)
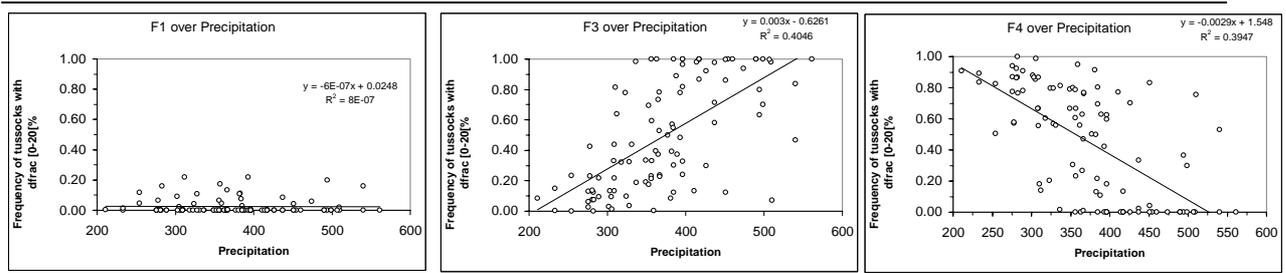
Fig. III.3: Correlation between precipitation and tussock distribution over *dfrac*-classes.
Shown are correlations between the tussock distribution over *dfrac*-classes with precipitation for one simulation with the standard parameterisation over 100 time steps: **A)** *dfrac*-class 1; **B)** *dfrac*-class 3; **C)** *dfrac*-class 4.

A)

B)
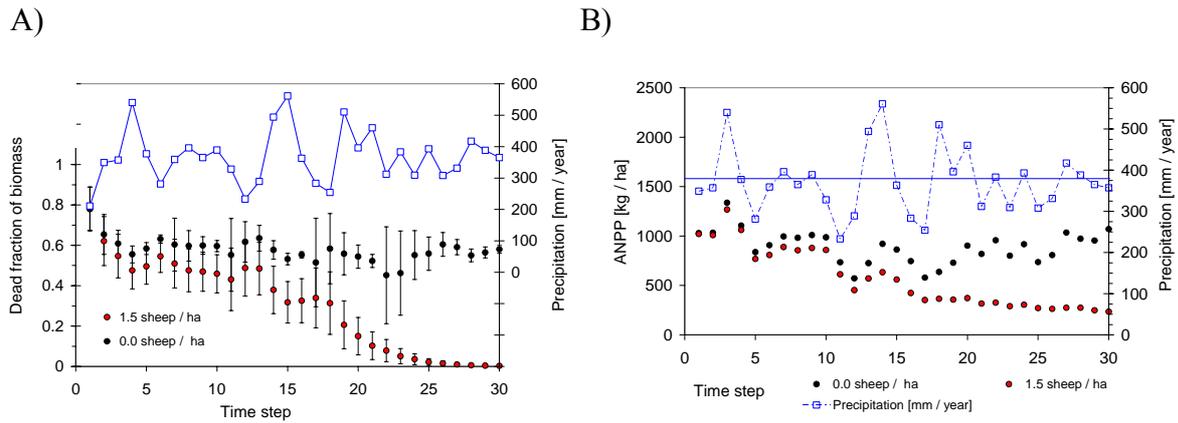
Fig. III.4: Time series for standard parameterisation and additional variables.
A) Dead biomass fraction *dfrac*; B) Simulated annual net primary production *ANPP*.

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Landscape of the *Festuca pallescens* steppe (Foto: Nestor Fernandez).

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Erklärung

Erklärung über die Anfertigung der Dissertationsschrift

Ich, Sandro Pütz, geboren am 15.10. 1967 in Krefeld-Uerdingen, erkläre, dass ich die im September 2005 an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Potsdam, Deutschland, eingereichte Dissertationsschrift selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Die Arbeit wurde an keiner anderen Hochschule eingereicht.

Leipzig, den 5. September 2005,

Sandro Pütz

Zitat / Citation:

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THE END