

THESIS

MODULAR MODELING AND ITS APPLICATIONS IN STUDIES OF GRAZING
EFFECTS

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ABSTRACT

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Grazing is an important ecosystem process that can affect the grazing system at different levels. Overall grazing effect can be a combination of various direct and indirect effects. It is difficult to study grazing with all of the effects considered. To have a better knowledge of grazing effects and animal-plant interactions, modeling is one important pathway to achieve this goal. People usually use a diversity of approaches when modeling grazing based on different objectives, which makes model evaluations and comparisons difficult. With modular modeling, where different model components are regarded as separate and standardized modules, this situation can be changed. An example model is developed using a modular approach. It included most of the grazing effects and switches that can turn these effects on and off. This model was designed to be capable for applications with different hypothesis and objectives. It is expected to be clearer for people who are not familiar to models to make comparisons and evaluations of grazing effects. To test the feasibility of the model, a theoretical experiment on compensatory behavior in grassland production and a realistic simulation on plant-animal interactions in Qinghai-Tibetan plateau, China, are conducted. The results of these two applications demonstrate the benefits of using modular modeling in studies of grazing effects.

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TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
1 INTRODUCTION	1
2 OVERVIEW OF GRASSLAND SYSTEM MODELING	4
2.1 INTRODUCTION	4
2.2 GENERAL STRUCTURES OF GRASSLAND MODELS	6
2.3 GRAZING COMPONENTS	11
2.3.1 GRAZING PROCESS	11
2.3.2 GRAZING EFFECTS	14
2.4 THE INCONSISTENCY OF MODELING	16
2.5 MODULAR MODELING	17
3 MODULAR MODELING APPLICATION IN GRAZING EFFECTS MODELING ..	21
3.1 INTRODUCTION	21
3.2 MODEL BUILD UP	23
3.2.1 PLANT GROWTH	24
3.2.2 GRAZING COMPONENTS	27
3.2.3 COMBINED EFFECTS	41
3.2.4 OUTPUT	44
3.3 THEORETICAL OVERCOMPENSATION EXPERIMENTS	44
3.3.1 BACKGROUND	44
3.3.2 MODEL SET UP	47
3.3.3 RESULTS	50
3.4 DISCUSSION	52
3.4.1 MODULAR MODELING	52
3.4.2 GRASSLAND SYSTEM MODELING	54
4 REALISTIC APPLICATION OF A EXAMPLE MODULAR GRAZING EFFECTS MODEL ON THE ALPINE REGION OF THE QINGHAI-TIBETAN PLATEAU ...	55
4.1 INTRODUCTION	55
4.2 EXPERIMENTAL SITE	57
4.3 EXPERIMENT RESULTS	57
4.4 MODEL SETUP	59
4.4.1 REASONING FOR MODULE STATUS	62
4.4.2 FUNCTIONS AND VARIABLES	63
4.4.3 SIMULATION OUTPUTS	66
4.5 SIMULATION RESULTS	67
4.5.1 ONE-YEAR SIMULATION	67
4.5.2 TEN-YEAR SIMULATION	67
4.6 DISCUSSION	70
4.6.1 SIMULATION RESULTS	70
4.6.2 MODULAR MODELING	70

5 CONCLUSION.....	72
REFERENCE.....	74

CHAPTER 1

INTRODUCTION

Studies on grazing are fundamental in ecology (Belsky et al., 1993), because of its importance to most ecosystems, especially grassland ecosystems (Stiling, 2002). For decades grazing was conceived as a simple defoliation process (Belsky, 1986), which only had detrimental effects on system production (Briske et al., 2008). However, system production can increase under certain grazing conditions (e.g. De Mazancourt et al., 1999), which is known as the Grazing (Herbivore) Optimization Hypothesis (McNaughton, 1979). It indicates that grazing may be a much more complicated process than it was thought to be (McNaughton, 1986).

Grazing can influence systems in different ways and levels (Ares et al., 2003), where system production dynamics, community structures, and species diversity can be directly affected (McNaughton, 1986; Young et al., 2013). Grazing can also affect the system indirectly through light availability (Knapp et al., 2012), water cycling (Mohtar et al., 1997), nutrient cycling (Lebon et al., 2014), etc. The mechanisms behind grazing effects are usually hard to observe (Leriche et al., 2001). However, comprehensive understanding of grazing process and effects is important to grassland ecosystem management. Grasslands occupy over 40 % of terrestrial land on Earth, and support most of the livestock (Suttie et al., 2005). In addition, combined effects from climate change and land degradation on grasslands make the study of grazing effects critical (Zhang et al., 2015). To study grassland systems and grazing, modeling is one of the methods.

Modeling of grassland system with grazing started in the 1960s (Wright and Dent, 1969), and has been robustly developed since then (Thornley, 1998). However, there is a large diversity in the approaches used in grazing process and grazing effects modeling

(Tietjen and Jeltsch, 2007). For example, grazing can be modeled as either a simple defoliation process with a fixed rate (Parton et al., 1992) or a complicated process that is determined by animal population dynamics, species specific selection, etc. (Ascough et al., 2001; Moore et al., 1997). When modeling grazing effects, the variety can range from effects on nutrient cycling to effects on plant carrying capacity (Hunt et al., 1991; Gillet, 2008; Leriche et al., 2001). No two models share the same grazing process and grazing effects parameterization, which makes it difficult to make comparisons and evaluations of grazing effects (Lebon et al., 2014), especially when the reasons for the different approaches taken are usually unclear. One can not compare different models simply by comparing their outputs, because all models are carefully adjusted and calibrated according to specific objectives (Rykiel, 1996). *Modular modeling* can be one pathway that has the possibility to change this situation.

Modular modeling comes from the two widely applied programming paradigms: Object-Oriented Programming and Modular Programming. With modular modeling, different components of a model are treated as separate modules, which have standardized inputs and outputs, and can be developed independently (Babb and Lee, 2012). In addition, model development is divided into basic structural development and module development, where model structure builders focus on the extensibility of the structure, and module builders focus on the portability and how much their modules represent the observed processes. Modular modeling also enables parallel and collaborative efforts, such as open source approaches, which can largely change the whole modeling development process (Laurent, 2008). What is more important is that with modular approaches, grazing effects can be studied, examined, and compared separately, and it is possible to include all grazing effects into one model structure as long as the inputs and outputs are well standardized. And this can be beneficial to grazing effects studies because most grazing effects are indirect, which means they are difficult to observe, measure, and thus simulate (Lebon et al., 2014). By comparing diff-

erent effects one by one, people may have a better understanding of the mechanisms behind these effects.

In this project, the focus was on application of modular modeling to simulate grazing effects. In the second chapter, there is an overview of current major grassland models with animal-plant interactions, which shows the diversity of modeling approaches, and provides a clearer view of the difficulties of making comparisons and evaluations of different models, especially regarding grazing process and grazing effects. The idea of modular modeling was further discussed, and its potential advantages over traditional linear models were represented. In the third chapter, an example model using the modular approach was developed. It was designed to include as many as grazing effects as possible, which enabled it to be applied to different study objectives, and to make comparisons of grazing effects. A theoretical experiment on overcompensation response in grassland was conducted to demonstrate the utility of modular modeling in studies of grazing effects. In the fourth chapter, a simulation was set up using the example model developed in the third chapter based on real data from the alpine region of the Qinghai-Tibetan plateau. It was meant to give an example of using modularized grazing models in real model studies. A brief conclusion then summarizes the work.

CHAPTER 2

OVERVIEW OF GRASSLAND SYSTEM MODELING

2.1 INTRODUCTION

Grassland is one of the most important ecosystems on Earth, and it occupies over 30% of the Earth's land surface (Sivakumar et al., 2005). Grassland utilization and management can have profound impacts (either positive or negative) on many ecosystem attributes (Watkinson and Ormerod, 2001), because grazing can have both positive and negative effects on grassland production and species diversity, although mechanisms behind these effects are sometimes unclear (Leriche et al., 2001; Young et al., 2013). In addition, combined effects from climate changes and land degradation are making problems in system management more complicated (Dore, 2005), with additional interrelated system affecting variables besides grazing (Zhang et al., 2015). It is thus important to have comprehensive knowledge and to be able to make reliable predictions about future trends of grasslands and possible consequences of different management practices. Modeling is one pathway that enables users to understand the system abstractly and sometimes mechanistically (Tietjen and Jeltsch, 2007).

Modeling of grassland system with animal-plant interactions started in the 1960s (Wright and Dent, 1969). Generally, there are three development directions: 1) theoretical models; 2) decision support systems (DSS); and 3) simulation models. Theoretical models, such as the plant-herbivore model by Lebon et al. (2014), are focused on general patterns and analytical analysis. Usually they are not as detailed as the other two kinds of models, the parameters are not specified, and they are not commonly applied to practical uses. DSS are mainly used for farmland management and quality assessment (Ascough et al., 2001).

Most DSS models are very complicated because they have to give farmland owners and companies an understandable, usable, and economically reasonable output, and usually, they rely on basic simulation models (Moore et al., 1997). Simulation models are developed for both research and management purposes, and are relatively more widely used (Day et al., 1997). They are either detailed or simple based on different objectives and hypotheses of ecosystem processes. Because of the number of choices, model comparison and evaluation become an important issue in making decisions on the usage of existing models.

Models are developed in various ways, especially when modeling components like grazing processes and grazing effects. For example, some models may have no differences in grazing management regimen, or in animal diet selection, such that grazing is simulated as a simple defoliation process (Parton et al., 1992). Some don't have nutrient recycling from animal waste (Day et al., 1997). Some models can have extremely explicit animal submodels where population dynamics and diet selection are species specific (Moore et al., 1997), and different age and sex groups are modeled (Ascough et al., 2001).

With regard to grazing effects, some models have effects on nutrient cycling where grazing animals directly participate in system nutrient cycling (Hunt et al., 1991); some have effects on water availability (Mohtar et al., 1997); some models have physical effects from grazing animals such as trampling and detachment (Day et al., 1997); some have specified the effects on leaf area index (Bondeau et al., 2007); and some even have effects on system carrying capacity (Gillet, 2008). There are also models that don't have any direct effects on plant production from grazing (Ascough et al., 2001).

The inconsistency of grassland system modeling makes it difficult for users and analysts to make comparisons and evaluations of different models. It can be overwhelming to review the many kinds of models and make choices among these approaches, because of the variety of approaches and almost all approaches are specifically parameterized to apply to different study areas. In this paper, 21 models (mostly simulation models) with grazing and plant-animal interaction components have been reviewed. The purpose is to summarize these

models and their different attributes, especially in grazing process and grazing effects, and discuss whether there could be a way to change current modeling efforts so that grassland system modeling can be more efficient, and easier to be compared and evaluated.

2.2 GENERAL STRUCTURES OF GRASSLAND MODELS

The 21 models that have been reviewed (Table 2.1) include three theoretical models, three DSS models, and fifteen simulation models. From the Objectives column we can see that, except for the three DSS models and CENTURY, almost all models were developed specifically to study plant population, community dynamics, and plant-animal interactions. However, the subjects are very different from model to model. They range from specific species (Paruelo et al., 2008) to general grassland systems (Bondeau et al., 2007). Based on different objectives and study subjects, the time step, animal complexity, vegetation complexity, and spatial and temporal scales are also different. Most of the models have daily time steps and use cattle or sheep as the main domestic grazing animal species. With respect to vegetation, many models use “grass, shrub, and tree” to represent vegetation classes (Coughenour, 1994; Day et al., 1997). Sometimes there may also be annual and perennial (Hacker et al., 1991), and C3 and C4 differences in vegetation (Bondeau et al., 2007).

Although most of the models are calibrated to specific study situations, there are still similarities in the structures. Generally, climate data/submodels, water and soil submodels, and nutrient cycle submodels are used to generate growth conditions. Plant submodels simulate plant growth and population dynamics based on the growth conditions, and are partly controlled by animal/harvesting submodels. Grazing process (the way how plant biomass is taken by grazing) is usually modeled in animal/harvesting submodels, and grazing effects can be found in all of these submodels.

Table 2.1: General model comparisons

Models	Model type	Subject	Objectives	Time step	Animal complexity	Vegetation complexity	Spatial scale	Temporal scale
GRASP (Day et al., 1997)	Empirical simulation model	Native pasture growth	The processes of above-ground vegetation dynamics and plant-animal interactions including detachment and decomposition	Daily	Domestic live stock and other herbivore animals	Grass, shrub, and tree covers	Regional	Short term (seasonal and yearly)
BAHUDE (Bachelet et al., 1989)	Mechanistic simulation model	Annual vegetation dynamics	Annual vegetation dynamics and the effect herbivory on productivity and nutrient cycling	Daily	Nematodes, grasshoppers, chewing insects, and cattle	Annual vegetation, mainly blue grama	Field and regional scale	Short term (years)
CENTURY (Parton et al., 1992)	Hybrid* simulation model	General plant-soil nutrient cycling	Carbon and nutrient dynamics for different plant systems	Monthly	General herbivore animals (mostly ungulates)	Grassland/crop system (grass, wheat, corn, etc) forest system (deciduous or evergreen forest)savanna system (tree-grass system)	Large scale	Long term (minimum time scale one year)
COIRON (Paruelo et al., 2008)	Mechanistic simulation model	Grass steppes dominated by <i>Festuca. palleescens</i>	Vegetation dynamics	Annual	Sheep	<i>Festuca. palleescens</i> and other species that are not specified	Local or tussock level to patch or landscape unit level	Long term (decades)
GEM-1 (Hunt et al., 1991)	Mechanistic simulation model	Shortgrass steppes	Vegetation (esp. primary producers) dynamics, nutrient cycle, and the effect of CO2 level and climate change on these dynamics (grassland responses to climate changes)	Daily to monthly (variable based when necessary)	Microbe and other fauna (below- and aboveground herbivore, aboveground predators)	Blue grama and wheatgrass	Regional	Short term (seasonal and yearly)

(Continued)

(Table 2.1. continued)

Models	Model type	Subject	Objectives	Time step	Animal complexity	Vegetation complexity	Spatial scale	Temporal scale
GPFARM (rangeland component) (Ascough et al., 2001; Adiku et al., 2010)	DSS with mechanistic simulation model	Farm lands in Great Plains of the United States and livestock production	Vegetation and animal dynamics under varying soil and environmental conditions	Daily	Cows at different ages and states	C3 and C4 grasses, legumes, shrubs, and forbs	Farmland scale to regional	Long term
GRASIM (El-Awar et al., 2007; Mohtar et al., 1997)	Mechanistic simulation model	Semi-arid grassland	Vegetation dynamic where grazing is a primary forage source with intensive rotational grazing management (esp. during the grass growing season)	Daily	General domestic livestock	General grass species	Farm level	Short term (mainly seasonal)
GRAZPLAN (Moore et al., 1997)	DSS with hybrid simulation model	Grazing industry of temperate southern Australia	General use DSS across the full range of environments and management systems in southern Australia	Daily	Wethers, ewes, steers, and beef cows	Annual and perennial grass and forbs	Farm land scale to regional	Short term (years)
Hurley (Thornley, 1998)	Theoretical model	General grassland	Nutrient cycling and its role in plant-animal-soil system	Daily	Ruminant grazing animals	General vegetative grass crop	Regional	Short term (years)
IMAGES (Hacker et al., 1991)	DSS with mechanistic simulation model	Rangeland grazing system in arid, winter rainfall pastoral region of Western Australia	Vegetation and animal dynamics and the economic performance	4 month	Sheep	Annual and perennial grass and shrubs	Farm land scale (property level)	Long term
LPJml (Bondeau et al., 2007)	Mechanistic simulation model	General arable and managed grassland ecosystem	Vegetation dynamics under CO ₂ increase and climate change.	Annual	General domestic livestock	C3 and C4 grasses	Regional to global scale	Long term

(Continued)

(Table 2.1. continued)

Models	Model type	Subject	Objectives	Time step	Animal complexity	Vegetation complexity	Spatial scale	Temporal scale
MSL (Milchunas et al., 1988; Cingolani et al., 2005)	Theoretical model	Grazing effect studies	Vegetation dynamics and plant-animal interactions along gradients of precipitation and evolutionary history of grazing	No	Generalist ungulate	Climatically determined, nonanthropogenic grasslands (including savanna, and shrub steppes)	Global-regional areas	Short term to long term
PEPSEE (Leriche et al., 2001)	Hybrid simulation model	African grasslands (tropical grassland)	Seasonal variations in soil water availability and vegetation dynamics	Daily	General herbivore animals	C4 grasses	Regional	Short term
PHYGROW (Stuth et al., 2003)	Hybrid simulation model	General grassland	Vegetation dynamics of different species subject to selective grazing	Daily	General herbivore animals (can be specified into different species by changing parameters)	General grassland plants (can be specified into different species by changing parameters)	Regional to global scale	Long term
Plant-Herbivore Model (Lebon et al., 2014)	Theoretical model	General grassland where direct compensation is assumed to exist	Study of overcompensation effect	No	General herbivore animals	General plants	-	-
SAVANNA (Coughenour, 1994)	Mechanistic simulation model	Extensive ecosystems occupied by ungulate herbivores	Vegetation dynamics under different changes	Weekly	General ungulates in different age/sex classes and wolf predation	Tree, shrub, and herbaceous	Regional	Annual to decades
SESS (Díaz-Solis et al., 2003)	Hybrid simulation model	Semi-arid grazing lands of northeastern Mexico and southern Texas	Vegetation dynamics, plant-animal interactions and sustainable stocking rate with respect to time	Monthly	Cattle	General forage plants	Regional or single farm	Long term

(Continued)

(Table 2.1. continued)

Models	Model type	Subject	Objectives	Time step	Animal complexity	Vegetation complexity	Spatial scale	Temporal scale
SimSAGS (Illius et al., 1996)	Hybrid simulation model	Semi-arid grazing systems	Animal response to variation in rainfall and stocking rate, and the effects of animal types and vegetation conditions on system performance	Daily	Cattle and goat with different sex and age classes	Perennial grasses and woody browse	Regional	Long term (hundreds of years)
SPUR (Wight, 1983)	Mechanistic simulation model	General rangeland	Rangeland ecosystem function and ecosystem response to changing determinants and various management practices	Daily	Insects, livestock (cattle and its equivalent), and wildlife	General grassland plants (can be specified into different species by changing parameters)	Pasture to basin	Long term
WoodPAM (Gillet, 2008)	Mechanistic simulation model	Silvopastoral ecosystems	The consequences of hierarchically organized ecological interactions of vegetation and animal habitat use	Annual	Cattle	Herb, shrub, and tree	Local patches to global scale	Long term (hundreds of years)
WWR (Glasscock et al., 2005)	Mechanistic simulation model	Grassland in south Texas	Seasonal and successional changes in vegetation and animal dynamics in response to different management practices	Monthly	Cattle, white-tailed deer, and coyote	Herbaceous community (grasses and forms) and woody plant community (brush)	Regional	Long term (decades)

* Uses both empirical and mechanistic models.

2.3 GRAZING COMPONENTS

2.3.1 GRAZING PROCESS

From the models reviewed (Table 2.2), grazing is generally regarded as a defoliation process. It removes vegetation from both aboveground live and dead tissues (Parton et al., 1992). Sometimes there may also be underground grazing (Hunt et al., 1991), but it is not common. Models most differ in the defoliation or grazing rate calculations. Some models use a preset and fixed grazing rate throughout the simulation or calculations (Leriche et al., 2001), where grazing is regarded as a simple defoliation process (Bondeau et al., 2007). Some models use external factors to determine this rate. For example, in GPFARM, grazing is limited by carrying capacity (Ascough et al., 2001); in IMAGES, grazing is determined by season, pasture type, and water quality (Hacker et al., 1991); and in GRASIM, grazing is based on different management regimes that include rotational grazing or fixed grazing intensity (El-Awar et al., 2007). Similarly, there also are models using variables such as animal species-specific energy requirements (Bachelet et al., 1989). Many models have selection variables or functions, such as diet selections and site selections, that are more suitable for small scale models with various plant species and site differences. There are three main ways to model diet selection: 1) different preference classes of plants species (Stuth et al., 2003); 2) automatically select tissues with a higher than average nutrient content (Hunt et al., 1991); and 3) selection based on potential bite-size (Illius et al., 1996). Grazing site selection can be calculated by forage abundance (Paruelo et al., 2008) and relative distance to fresh water (Wight, 1983).

Table 2.2: Comparisons of grazing processes and grazing effects

Models	How do they simulate grazing process?	Diet and site selection	Trampling and detachment	What's affected by grazing.
GRASP (Day et al., 1997)	Animal intake rate is a function of stocking rate,	No	Yes	Plant growth, nutrient uptakes, root-to-shoot ratio, sensitivity to soil water deficit
BAHUDE (Bachelet et al., 1989)	Animal consumption is based on observed population size and energy requirements, different species of animals have different intake rate and diet preference	Yes	No	Root-to-shoot ratio, nutrient cycle
CENTURY (Parton et al., 1992)	Defoliation and a fixed removal rate	No	No	Root-to-shoot ratio, nutrient content (grazing effects are set to three levels or 7 levels in later versions)
COIRON (Paruelo et al., 2008)	Defoliation based on selection, scale, energy requirement and different grazing regimes	Yes	No	Plant growth, individual based attributes, system water cycle
GEM-1 (Hunt et al., 1991)	Defoliation based on selection and nutrient requirement	Yes	No	Plant growth, root-to-shoot ratio, soil water content, nutrient cycling, evapotranspiration
GPFARM (rangeland component) (Ascough et al., 2001)	Forage feeding based on carrying capacity and overgrazing does not occur	No	No	Soil compactness, respiration
GRASIM (El-Awar et al., 2007; Mohtar et al., 1997)	Defoliation process with rotational grazing management (management rules: minimum and maximum allowable biomass, grazing cycle, and resting period or fixed time rotation), and uniform grazing/harvest rate	No	No	Plant growth, LAI, protein and fiber content, soil water content, nutrient cycle
GRAZPLAN (Moore et al., 1997)	Simple defoliation process	No	No	Plant growth
Hurley (Thornley, 1998)	Defoliation based on nutrient fluxes, LAI, animal requirements, and management	No	No	Plant growth, LAI, nutrient cycle, evapotranspiration, rainfall interception
IMAGES (Hacker et al., 1991)	Defoliation based on season, pasture type, and water quality	No	No	Plant growth with seasonal conditions, seedling survival rate, plant mortality rate

(Continued)

(Table 2.2. continued)

Models	How do they simulate grazing process?	Diet and site selection	Trampling and detachment	What's affected by grazing.
LPJml (Bondeau et al., 2007)	Simple defoliation process	No	No	Plant growth and LAI
MSL (Milchunas et al., 1988)	Defoliation periodically or with a fixed rate	No	No	Plant growth based on grazing history and moisture, community structure
PEPSEE (Leriche et al., 2001)	Defoliation as a function of nutrient quality (N%)	No	No	Plant growth, root-to-shoot ratio, LAI, nutrient cycling
PHYGROW (Stuth et al., 2003)	Consumption based on diet selection, management, and seasonal difference	Yes	No	Plant growth, root-to-shoot ratio, LAI
Plant-Herbivore Model (Lebon et al., 2014)	Use grazing density as a variable in plant growth rate function and response function	No	No	Plant growth
SAVANNA (Coughenour, 1994)	Defoliation based on diet selection, forage abundance, forage quality, and snow cover	Yes	No	Plant growth, plant nitrogen uptake and loss
SESS (Díaz-Solis et al., 2003)	Defoliation based on diet selection	Yes	Yes	Plant growth and general rangeland condition which mostly assesses rangeland production
SimSAGS (Illius et al., 1996)	Defoliation based on diet selection, daily energy intake and net energy costs of foraging	Yes	No	Plant growth
SPUR (Wight, 1983)	Defoliation based on diet selection and grazing site preference	Yes	Yes	Plant growth survival rates
WoodPAM (Gillet, 2008)	Defoliation based on diet selection, and carrying capacity	Yes	Yes	Plant growth, tree sapling survival rate, grazing carrying capacity
WWR (Glasscock et al., 2005)	Defoliation based on diet and site selection	Yes	Yes	Plant growth, senescence, decomposition

2.3.2 GRAZING EFFECTS

For grazing effects, there are differences in modeling as well, because grazing can affect the system in many different ways. These effects are usually indirect (such as grazing-caused changes in system nutrient cycling, and its effect on plant growth), which means it is difficult to specifically model these effects. Besides direct detrimental effects on plant production, there are six other main ways that grazing can affect systems:

i) Light condition modification Grazing can reduce plant leaf area index (LAI) (Leriche et al., 2001). And, some light dominant species can be preferred by grazers, and the living condition (for example available light) for species that are less competitive may be changed (Center et al., 2005). In addition, grazing can also help to remove litter and old, less photosynthetically active plant tissue (Knapp et al., 2012), which can help improve light conditions and photosynthetic rates.

ii) Water condition modification Grazing can have negative effects on water availability by defoliation when grazing intensity is severe, because of the increase in soil evaporation (Mohtar et al., 1997). Defoliation can also reduce system evapotranspiration which, under moderate grazing conditions, helps to reduce water loss and water stress of the system (Leriche et al., 2001).

iii) Nutrient condition modification The most discussed indirect effect from grazing is on nutrient cycling. Besides soil fertilization by animal waste, plant nitrogen uptake rate can be increased (Leriche et al., 2001). In addition, under grazing, N mineralization will be increased (Austrheim et al., 2014), and related nutrient turnover can also stimulate system nutrient cycling (Lebon et al., 2014). On the other hand, although plant carbon reallocation can be stimulated by grazing (Lebon et al., 2014), system C supply may decrease because of herbivore consumption (Bachelet et al., 1989).

iv) Plant physiology modification The effect from grazing on plant physiology can be represented though changed primary metabolism rate. Plant root-to-shoot ratio can be

changed (Leriche et al., 2001), and photosynthetic rate can also be stimulated (Lebon et al., 2014).

v) Soil condition modification Trampling is one of the most important physical effect from herbivory, especially by ungulates. Under heavy grazing, trampling can sometimes increase soil compactness, and thus impede plant growth and reduce soil water availability (Adiku et al., 2010).

vi) Community structure modification Finally, grazing can also have effects on community structure. Grazing can either help to improve community balance when dominant species are preferred by herbivores, or lessened where less competitive species are preferred (Austrheim et al., 2014).

For grazing effects modeling, direct effects, such as animal consumption, are usually easier to simulate because they are usually measurable and thus quantifiable, and almost every model with grazing components has animal consumption calculations. However, one important direct effect that's not widely modeled is the effect on physical conditions that usually comes from trampling and detachment (Day et al., 1997). Trampling can not only affect plant production directly, but can also have impacts on soil conditions, which may have further indirect effects on plant growth (Adiku et al., 2010). As for indirect effects, they can be confusing because it is difficult to directly measure these effects. But some indirect effects have already been modeled. For example, indirect effects on plants from changes in nutrient cycle caused by grazing are commonly modeled. Grazing can increase nitrogen availability in the soil coming from animal waste, and carbon conversion can be decreased because of the consumption by grazers (Bachelet et al., 1989). Effects on root-to-shoot ratio (Parton et al., 1992), LAI calculation (Bondeau et al., 2007), and overall carrying capacity (Gillet, 2008) can also be seen in many models. The model called PEPSEE created by Leriche et al. (2001) does not have many direct effects modeled except for a fixed daily rate of defoliation and nutrient return at certain percentages. Plant growth patterns can still be greatly affected by grazing. In PEPSEE, system N cycling is accelerated because aboveground N concentration

is decreased by grazing, which can have positive effects on plant growth (especially when root-to-shoot ratio or plant conversion rate and light absorption efficiency are set to be nitrogen dependent in the model). In addition, grazing also alters soil water balance by decreasing evapotranspiration in the simulation. Under certain circumstances, there can even be overcompensation in plant growth. This model gives an example that even if when grazing effects are not modeled in detail, as long as other submodels (in PEPSEE, the water balance, nutrient cycle, and plant growth submodels) are well developed and connected to each other, there can still be indirect effects from grazing represented.

2.4 THE INCONSISTENCY OF MODELING

The diversity of grassland system models indicates the robustness of this area of research and management. However, one of the downsides of this diversity is the difficulty for users to make evaluations of each model. Since almost all models are carefully calibrated to specific study situations, it can be problematic to compare two models simply by their outputs. From Table 2.1, even though the basic structures of different models can be similar, no two models have the same setups for ‘Model type’, ‘Model subject’, ‘Model objectives’, ‘Time step’, ‘Animal and vegetation complexity’, and ‘Spatial and temporal scale’, let alone the grazing components and the functions used in the models. To make decisions on modelling, there can be three main methods: 1) to review existing models and find one with modelling attributes (‘Model type’, ‘Model subject’, etc.) that match the user’s needs, which can sometimes be extremely time-consuming given the number of existing models and related literatures; 2) to develop a new model to fit current study situations with functions from experimental and observational studies, which can also be inefficient because data and functions from these studies need to be re-calibrated, and it ignores the value of other modeling studies; 3) try to combine and modify the efforts put into other models for tasks at hand, which is comparatively more efficient. If the use of a model is limited to its own study objectives and subjects, the value of the model can also be limited. However, the efforts made by different modelers can be useful (if correctly used) when combined with each other. One

example of combining efforts is PHYGROW. In addition to functions developed by its own group, it also uses functions from CREAMS, GLEAMS, EPIC, WEPP, SPUR, CENTURY, and ERHYM-II (Stuth et al., 2003). It has extended the usage of these models. But the reason why PHYGROW uses functions from these specific models is mostly unclear in related literatures, which is not rare in grassland system modeling (Hunt et al., 1991; Wight, 1983). This can cause confusion for users and modelers when making evaluations of models with combined efforts.

The relative efficiency of combining efforts depends on the availability and relevance of each component from existing models. If no related components can be found in existing models, one can either abandon including this component into the model or create the component, which requires extra studies. For example, from Table 2.2, despite the comprehensive efforts, there still are some effects that are not modeled well in any of these reviewed models, such as grazing effects on plant species competition and available light. Modelers can not understand all the mechanisms in a given system, and trying to include all different kinds of processes and effects in one model can be inefficient. But no one knows how valuable including these effects may be until they are actually realized.

2.5 MODULAR MODELING

One way of thinking differently about the problem and a potential solution is through modular modeling. This idea comes from modular programming and object-oriented programming. In modular programming, a widely applied programming logic in computer science, modules have standardized inputs and outputs, and the use of modules can help to clarify the structure of a program (Babb and Lee, 2012). Object-oriented Programming treats different program components as single, sometimes standalone, objects that can usually be debugged and reused independently from the main program process, and thus largely increases the efficiency of programming (Kindler and Krivy, 2011). These methods are beneficial for programmers to make improvements and evaluations (Basten et al., 2015). Similarly, modular models may be separated into modules and base model structures, where system

processes are treated as independent and portable modules with standardized inputs and outputs, and the extensible base model structures are used to hold the modules. This can make the whole modelling procedure more flexible. For example in Figure 2.1, there are four ways to get from ‘step 1’ to ‘step 2’ (base model structure): through ‘module 1’, or ‘module 2’, or both, or neither one of the two modules. In an ecological context, plant photosynthesis can be regarded as an independent module. The input to the module is solar radiation, and the output from the module is the amount of carbon converted through this process. This module can be used in a plant growth model structure that uses quantity of carbon converted as one of its input. When the module is not applied, the model structure can simply set this input to a constant value or use other modules that have the same output as carbon conversion amount. In modular modeling, a model structure maker’s job is to focus on developing a base model structure (‘step 1’ and ‘step 2’) and its extensibility (how much inputs should be included), and a module maker’s job is to focus on developing modules in their specific areas and the portability of their modules (the usability of module outputs and inputs). The entire parallel and collaborative work can be relatively more efficient compared to traditional model development.

What is the difference between modular modeling and building a new model directly from existing experiment and observation studies? Basically, modules are functions too. The procedure of modular modeling is similar to traditional modeling procedures: making general model structures, finding suitable functions for each component, and trying to make all necessary components work as a whole process. The main difference between modular modeling and traditional modeling is the way functions and general structure are combined (runtime pathways). In traditional model development, the procedure to create or use functions from other studies is usually linear (*linear modeling*) (Ascough et al., 2001). In linear modeling (Figure 2.2), there is no way to go from ‘step 1’ to ‘step 2’ other than going through ‘function 1’. Users may feel confused if there is not enough information on the reason why ‘function 1’ is chosen to be in between ‘step 1’ and ‘step 2’. In addition, there can be ‘func-

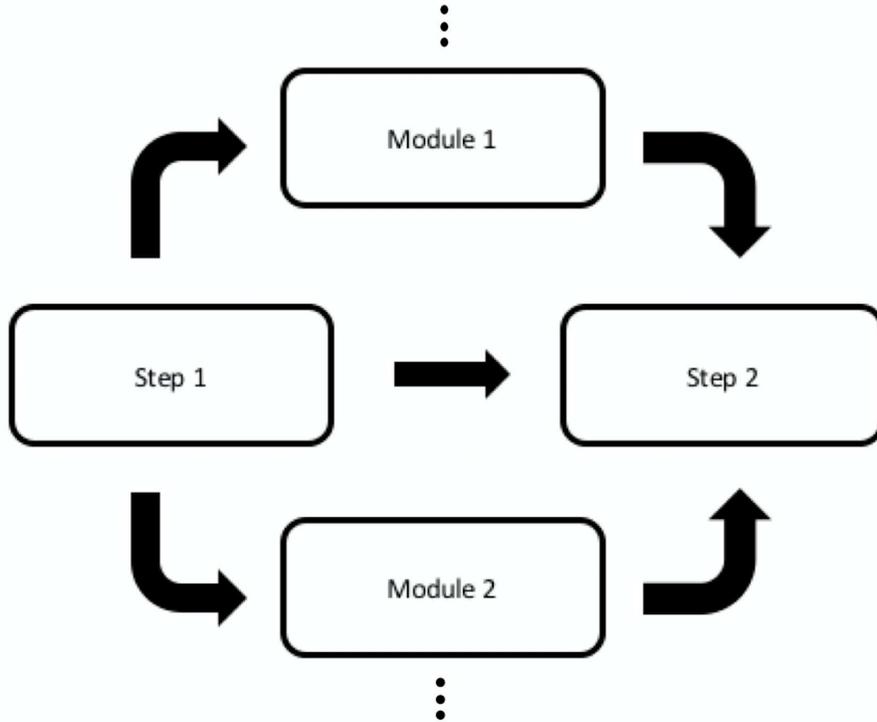


Figure 2.1: Modular modeling

tion 2’, ‘function 3’, ‘function 4’, etc. that also fit between ‘step 1’ and ‘step 2’. When better modeling pathways are discovered, traditional models are hard to improve because of their linear nature. Whereas in modular modeling, modules can be developed to fit in anywhere appropriate (portability), and the basic structure of a model, (‘step 1’ and ‘step 2’) can use all available modules (extensibility). In this case, modelers don’t have to worry about whether their choices on different components are perfect, because the components can always be modified and improved. With well standardized model structure, an open source community development can be encouraged. An active open source community is beneficial to modeling studies, where everyone in the community can participate in the development, make contributions and improvements in many different ways (Laurent, 2008).

Another benefit of modular modeling is that different modules can be studied and compared separately. For example, in grassland system modeling, there are many direct and indirect effects from grazing, and it is difficult to include all of the effects into a single model. Traditional modelers can either ignore some of the effects based on study assumptions, or

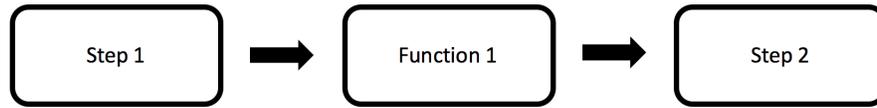


Figure 2.2: Linear modelling

try to make different versions of linear models, compare the output from the versions, and make decisions based on the outcome. With modular modeling, people can test the output simply by using different modules in a basic model structure. If different grazing effects can be regarded as different grazing effect modules, by making ‘switches’ to turn these modules on and off (switching route in Figure 2.1), the grazing effect comparison studies can be done more efficiently.

Modular modeling is collaborative, efficient, and flexible. It can be a modern way of modeling as long as the advantages and conductivity are proved. In addition, more study focusing on modeling methods and modeling efficiency need to be done in addition to pure modeling studies, which could be beneficial because these studies can provide modelers new ways of thinking.

CHAPTER 3

MODULAR MODELING APPLICATION IN GRAZING EFFECTS MODELING

3.1 INTRODUCTION

As an important agent in ecosystem processes, grazing has been widely studied. It can affect the system at different levels and in different ways (Ares et al., 2003). Besides defoliation, there are many other ways (including both direct effects and indirect effects on the plant itself or on the environment) that grazing may affect grassland ecosystems, either positively or negatively (Leriche et al., 2001). For example, under certain circumstances, grazing can promote plant production according to the Grazing (Herbivore) Optimization Hypothesis (McNaughton, 1979). To have a comprehensive understanding of grazing process and effects is necessary to grassland system studies and management (Dore, 2005). And grassland system modeling is an important method for these purposes. (Tietjen and Jeltsch, 2007).

Modeling approaches can help people understand the system abstractly and mechanistically. However, grassland system model development can be inconsistent, especially in grazing process and grazing effect modeling. For example, grazing process can be regarded as a simple defoliation process without any concern for animal diet selection, grazing management regimes, etc. (Parton et al., 1992). Whether there is nutrient recycling from animal waste or explicit animal population dynamics also differs with different models (Day et al., 1997; Moore et al., 1997). With regard to grazing effects, different models include different effects such as effects on system nutrient cycling, water availability, system carrying capacity, etc. (Hunt et al., 1991; Mohtar et al., 1997; Gillet, 2008). No two models have exactly the same parameterization and model setups (Miao, Chapter 2).

The variety of approaches to grassland system modeling makes it difficult for comparisons and evaluations of different models (Leriche et al., 2001; Lebon et al., 2014). Simply comparing the output from different models can be insufficient because most models are specifically calibrated to sites. Besides different study objectives and subjects, the reason for this variety in approaches is usually unclear, which can cause confusion when tracking the choices made by different modelers on grazing effects, and the possibility of effects that are not included. A model with standardized inputs and outputs containing most of the grazing effects that can be invoked as needed may help researchers to clarify their reasons of choosing different grazing effects, and thus improve model comparison and evaluation procedures.

Modular modeling can be useful to achieve this. In modular modeling, different components of a model are treated as separate modules, and model development is divided into two parts, module development, and basic structural development. Model development can become parallel and collaborative. Different modules can be studied and compared separately. In grassland system modeling, people can test the output simply by using different modules as components of a basic model structure. By setting up ‘switches’ to turn these modules on and off, grazing effect comparison studies can be done more efficiently.

This study focuses on applying modular modeling of grazing effects modeling to give an example of a general model with most of the grazing effects included, and test the utility of modular modeling in grassland system simulation, especially in grazing process and grazing effects. An example model written in FORTRAN is developed in this study. In this model, grazing processes and grazing effects are regarded as modules, and a general basic model structure with a simple plant growth process is designed to hold the modules. Switches are added to each module, which can turn these modules on and off to show the independence feature of modular modeling and its enhanced value in comparison and evaluation of effects. The last part is an example experiment on grassland overcompensation behavior in a hypothetical setting using the example model developed in this study, which shows the benefits of modular modeling to grassland system studies.

3.2 MODEL BUILD UP

The example model is written in FORTRAN. FORTRAN is mainly a procedural language with some limited object-oriented features (Allen, 1981), which means it may not be naturally suitable for modular modeling, where most code components are better to be treated as ‘objects’ that include object-specific data and standardized inputs and outputs (Kindler and Krivy, 2011). However, creating the model in FORTRAN demonstrates the ability to apply modular modeling to most modern computer programming languages.

The model development is focused on grazing process and grazing effects, the two most inconsistently modeled components in grassland system modeling (Leriche et al., 2001). The base model contains a simple plant growth process and a general structure that can hold grazing effect modules. Basic work-flow of the model is shown in Figure 3.1. The first step is plant growth calculation. It includes ‘annual rainfall’, ‘plant growth days’, and ‘plant biomass’ calculations. This section is based on Fryxell et al. (2005) to simulate a simple plant growth process.

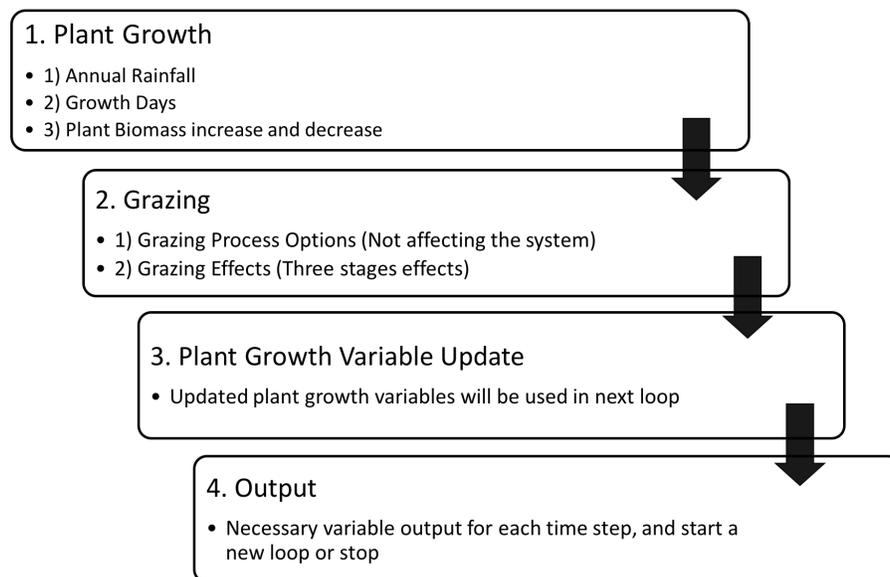


Figure 3.1: Basic model structure

The second step is grazing, where grazing options and grazing effects are included. The grazing options modules determine how grazing is simulated; in other words, how plant biomass is removed. Grazing effects modules run after grazing options modules. There are three stages of grazing effects in this step, simulating most of the direct and indirect effects from grazing. Switches are added to every module in this step, so they can be invoked as needed.

The third step is plant growth variable update. In this step, plant growth variables used in the first step are updated based on outputs from the last step. Indirect grazing effects, most of which come from plant growth variable changes caused by grazing, are produced through this process. In the last step, necessary variables, such as plant biomass, are output for further analysis, and a new loop is started, or the simulation process may be stopped.

Modules are similar to functions used in traditional grassland system models except that the runtime structure for modules is not linear. In this study, most modules come from existing models. Since the objective of building this model is to give an example of modeling grazing effects with modular modeling, the basic standard of choosing functions is simplicity. Referenced models are: GPFARM (Ascough et al., 2001), GRASP (Day et al., 1997), IMAGE (Hacker et al., 1991), HURLEY (Thornley, 1998), PEPSEE (Leriche et al., 2001), and PHYGROW (Stuth et al., 2003).

3.2.1 PLANT GROWTH

The base model is generally based on the simple plant growth process in Fryxell et al. (2005). It is grid based with daily time steps. Spatial variables (dimensions and cell area) can be set up by users as needed. The plant growth process structure is shown in Figure 3.2. Plant growth is solely based on annual rainfall, which is calculated based on average annual rainfall of each row of the grid space. The average annual rainfall values for the northernmost and southernmost rows are set up by users. Average annual rainfall for the intermediate rows are linearly interpolated between the values in northernmost and southernmost rows. Annual

rainfall for each cell is normally distributed with a coefficient of variation of the local mean, which is set by users, and it is spatially autocorrelated.

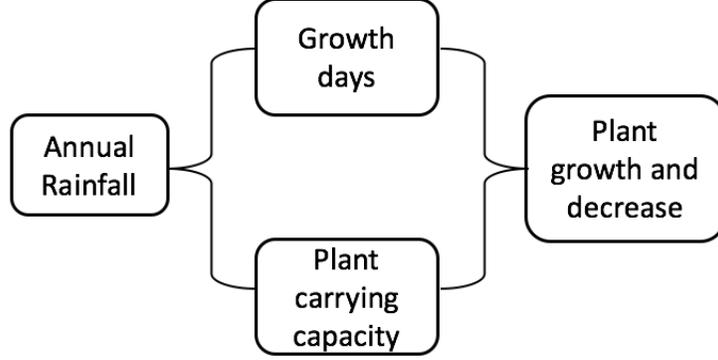


Figure 3.2: Base model structure

In the base model, there are two seasons, growing season and dry season. The length of growing season is determined by grow days, which is calculated from annual rainfall in each cell (Function 3.1):

$$GD = a_{GD} + \frac{b_{GD} \cdot e^{c_{GD} \cdot AN}}{e^{c_{GD} \cdot AN} + e^{d_{GD}}} \quad (3.1)$$

where GD (days) is grow days, AN (mm) is annual rainfall in each cell, a_{GD} , b_{GD} , c_{GD} , and d_{GD} are approximation parameters which can be set by users (Fryxell et al., 2005).

Plant biomass carrying capacity is calculated from annual rainfall and growth days (Function 3.2):

$$\begin{cases} K = \Psi \cdot RPD \\ RPD = \frac{AN}{365} \end{cases} \quad (3.2)$$

where K (g) is species specific plant carrying capacity, and RPD (mm) is average rain fall per day. Carrying capacity coefficient Ψ which can be set by users to represent different plant species (Fryxell et al., 2005).

In growth season, the plant growth function is (Function 3.3):

$$\frac{dB}{dt} = R_{MAX}[B + K]\left[1 - \frac{B + K}{2K}\right] \quad (3.3)$$

where B (g) is plant biomass, and R_{MAX} (g/dt) is maximum plant growth rate based on different plant species. During the dry season, plant biomass would not increase, and declines at a fixed rate (D) (Fryxell et al., 2005).

To make the example model more flexible for theoretical experiments, values for most of the variables in the functions are not set up by default, and can be changed based on different plant species and actual conditions. In addition, since most of the indirect grazing effects come from plant growth variables that are affected by the changes of plant biomass and available nutrients, for example changes in photosynthesis rate caused by the change of plant biomass from grazing can have indirect effects on plant growth (Thornley, 1998). To have indirect grazing effects demonstrated with this simple plant growth process, effects coefficients are calculated with variables in grazing modules by functions that shows basic plant growth variable relationships (Function 3.4). Since this study is focused on grazing modeling, these plant growth variable relationships are not based on any observational or experimental studies.

$$\left\{ \begin{array}{l} CO_{GD} = \frac{0.4}{1 + e^{-1.5 \cdot \alpha_{GD}}} + 0.8 \\ CO_K = \frac{3}{2 + e^{-0.7 \cdot \alpha_K}} \\ CO_{RG} = \frac{2}{1 + e^{\alpha_{RG}}} \\ CO_D = \frac{2}{1 + e^{-0.5 \cdot \alpha_D}} \end{array} \right. \quad (3.4)$$

where $CO_{GD}, CO_K, CO_{RG}, CO_D$ are effects coefficients for growth days, carrying capacity, growth rate, and biomass death rate. $\alpha_{GD}, \alpha_K, \alpha_{RG}, \alpha_D$ are combined effect variables for each effects coefficient that are calculated from related grazing effects. They are discussed

in the ‘Combined effects’ section. With these coefficients, the growth variables are modified (Function 3.5).

$$\left\{ \begin{array}{l} GD = CO_{GD} \cdot GD \\ K = CO_K \cdot K \\ R_{MAX} = CO_{RG} \cdot R_{MAX} \\ D = CO_D \cdot D \end{array} \right. \quad (3.5)$$

These modification functions are also controlled by corresponding switches. Since the same variables are on both sides of these equations, when the switches are off, these variables are not modified.

3.2.2 GRAZING COMPONENTS

Grazing is separated into four sections: grazing options; first stage effects, second stage effects, and third stage effects, each of which has its own modules (Figure 3.3). The first section determines how grazing is simulated. Three modules are included: Difference options, Grazing rate options, and Selection options. In difference options, users can decide whether there are seasonal differences, management grazing differences, and animal species differences and competition. Grazing rate options determine whether grazing rate is based on fixed rate or on animal stocking density, and whether grazing rate is limited by plant biomass. Selection options determine whether there are diet selection and site selection.

The first stage effects are mainly direct effects on the system from grazing animals, containing defoliation, trampling and detachment, and soil compaction changes. Indirect relationships are included in second stage and third stage effects. Second stage effects include LAI calculation, plant respiration calculation, soil available nitrogen modification, and changes in litter pool addition. Third stage effects calculate plant system variables that depend on variables calculated in the second stage.

These are the four sections of base model structure. They are interrelated but can be run independently as well. Values for variables calculated in each section will be passed to

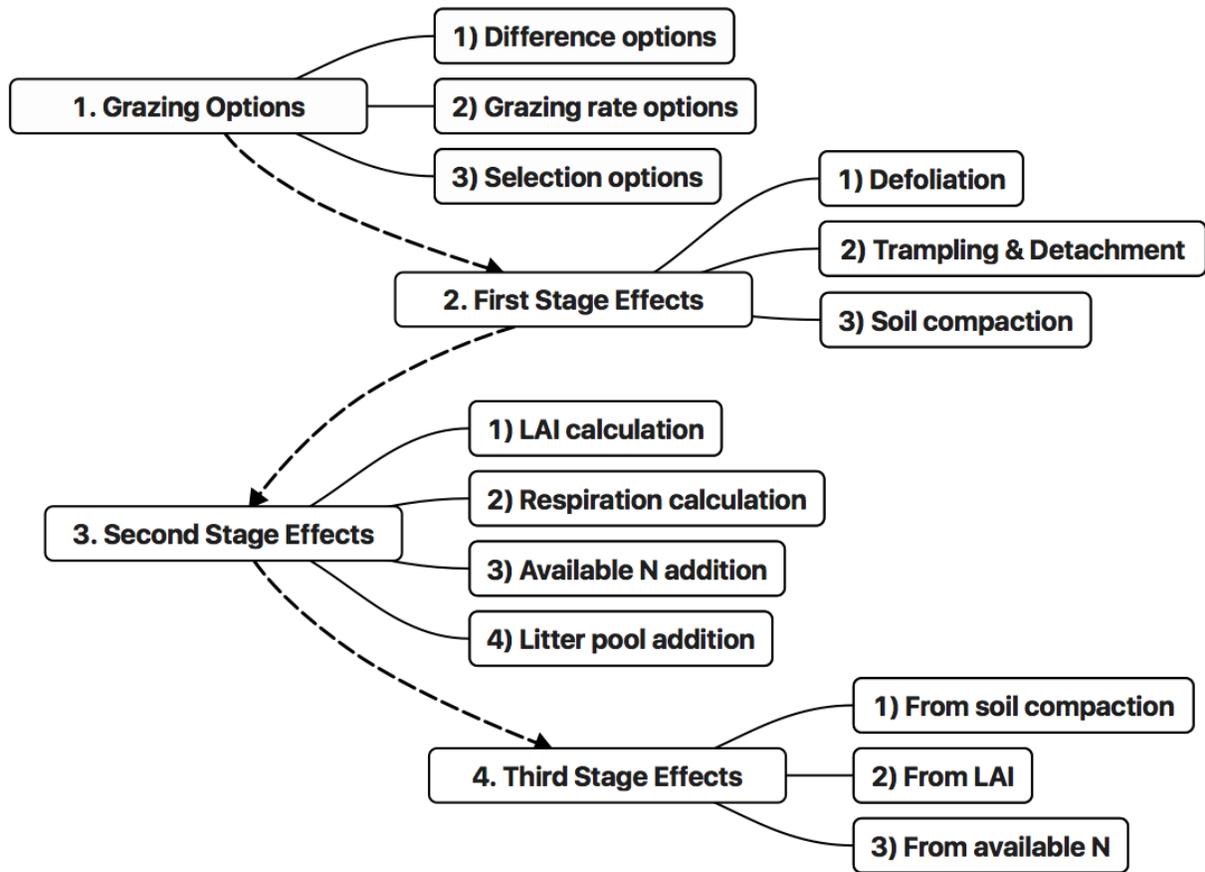


Figure 3.3: Grazing components

the next section for further calculations. If no modules are turned on in these sections, their subsequent sections use default values for necessary variables.

Configuration files used for setting up module variables are separated into annual configurations, where variables are kept the same throughout the year, and seasonal configurations, where values for variables can vary based on different seasons if seasonal difference exists. In both configurations, variables can have multiple values based on the number of animal and plant species represented. A switch file is used to determine whether to read different variables and run corresponding modules (Figure 3.4).

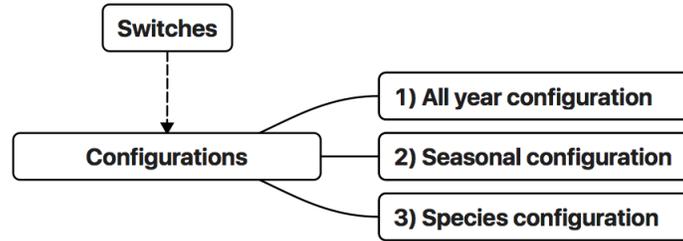


Figure 3.4: Configuration structure

3.2.2.1 GRAZING OPTIONS

The grazing options section is the most important section of the grazing components, because it affects the entire processing of the model. Modules included in this section are shown in Figure 3.5.

1) *Difference options*

i) Seasonal difference When this module is in effect, there can be seasonal differences in grazing behavior. By examining seasonal check points, the model can recognize the current season (Figure 3.6), and pass the season value to modules that have seasonal configurations. When this module is off, there is only be one season for grazing, and there will not be seasonally different variables for grazing modules.

There are two ways to set up seasonal differences. The first way is by manually setting the number of seasons and the values of seasonal check points in the all-year configuration files. The other way is by using values from other modules or base models. For example, in this model, there are two seasons (growing and non-growing) whose lengths are determined by grow days, which can be used as grazing season check points as well. In this case, grazing seasonal differences are directly related to plant seasonal difference.

ii) Management differences There are three sub-modules in this module: rotational grazing, maximum allowable grazing amount, and minimum assigned grazing amount. The process of setting up rotational grazing is similar to the way season check points are set up. The number of rotation periods and rotation period check points are set by users. By examining the check points, the model can decide whether it is grazing period or resting

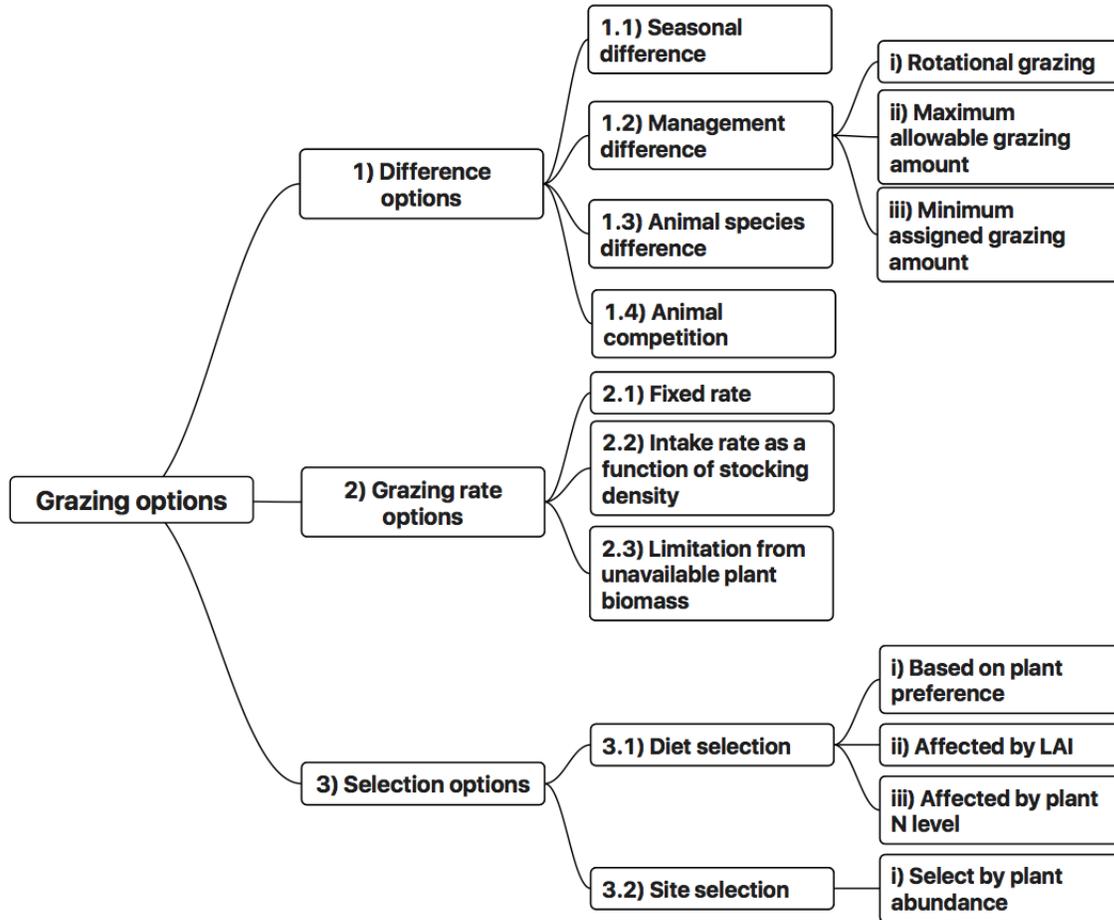


Figure 3.5: Grazing option modules

period. When this module is off, there is only one grazing period, where grazing will not stop.

Maximum allowable and minimum assigned grazing amount are upper and lower grazing amount limits set by users to simulate similar grazing management behavior. Thus these limits are different from natural limits, which are determined by system resources. These two limits can be seasonally different. When these two modules are off, there will be no grazing limits set by humans.

iii) Animal species differences and competition These two modules determine whether there are animal species differences and competition. The animal species number is decided by the user, and this number determines the number of values of animal species different variables. When this module is off, animal species number is set to 1. Since the study is

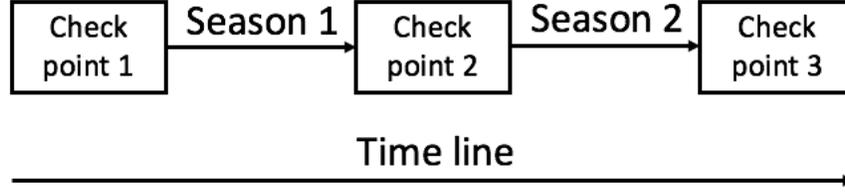


Figure 3.6: Seasonal check point work flow

on grazing effects, the animal competition module is simplified. This module uses a variable called *animal competition factor* to determine the percentage of resources one species of animal can acquire (Function 3.6).

$$AB_{AV} = B_{AV} \cdot F_{COMP} \quad (3.6)$$

where AB_{AV} (g) is available plant biomass for each animal species, B_{AV} (g) is total available plant biomass, and F_{COMP} is competition factor. The values of the factors are set by users. When this module is off, the resource is evenly distributed ($F_{COMP} = 1/\text{animal species number}$). Both animal species number and animal competition factor can both be seasonally different.

2) Grazing rate options

From this section, animal total demand for the time step (in this model, it is daily total demand) is calculated either by fixed grazing rate or a function of stocking density. Fixed grazing rate module and stocking density module can not be turned on at the same time because these two modules calculate the same variable.

i) Fixed grazing rate This module calculates animal total demand from a fixed rate set by users (Function 3.7).

$$TD = AB_{AV} \cdot GR_{FIX} \quad (3.7)$$

where TD (g) is total demand in each time step, GR_{FIX} is fixed grazing rate. This rate can be seasonally different based on different animal species. When this module is off, and stocking density module is not turned on, animal total demand is zero.

ii) As a function of stocking density The function used in this module comes from PHYGROW (Stuth et al., 2003). Animal stocking density is calculated from a maximum and minimum stocking density, plant biomass, and plant carrying capacity (Function 3.8)

$$SD = \frac{AB_{AV}}{K - B_{UAV}} \cdot (SD_{MAX} - SD_{MIN}) + SD_{MIN} \quad (3.8)$$

where SD (animal/m²) is animal stocking density, B_{UAV} (g) is unavailable biomass, SD_{MAX} (animal/m²) is maximum stocking density, and SD_{MIN} (animal/m²) is minimum stocking density.

Total demand is calculated from total animal number and the maximum intake rate, which is set by users (Function 3.9):

$$TD = AN \cdot INT_{MAX} \quad (3.9)$$

where AN is animal number, and INT_{MAX} (g) is the maximum intake rate based on different animal species. When this section is off and fixed grazing rate module is not turned on, animal total demand is zero.

iii) Limitation from unavailable plant biomass This module calculates total unavailable plant biomass (B_{UAV}), and thus total available biomass (B_{AV}). In reality, animals can not eat all of the plant. For example, grazing can be limited by the height of plants (Glasscock et al., 2005). In this module, the limitation is calculated as percentage of plant carrying capacity (Function 3.10).

$$B_{UAV} = K \cdot R_{UAV} \quad (3.10)$$

where R_{UAV} is unavailable rate. When this module is off, $R_{UAV} = 0$.

3) Selection options

Actual grazed forage amount is calculated in this module section.

i) Diet selection Diet selection is determined by three submodules, plant preference selection, LAI modification, and plant nitrogen level modification. The plant preference selection module has three plant preference classes: preferred class, less preferred class, and un-preferred class. This module is used to calculate forage fractions of different plant species (if present). Functions used to calculate these fractions are (Function 3.11):

$$\begin{cases} FRAC_P = 1 - e^{-a_{FP} \cdot \frac{AB_{AV}}{B_{AV}}} \\ FRAC_L = 1 - FRAC_P - FRAC_U \\ FRAC_U = a_{FU} \cdot e^{b_{FU} \cdot \frac{AB_{AV}}{B_{AV}}} \end{cases} \quad (3.11)$$

where $FRAC_P$ is diet fraction for preferred class, $FRAC_L$ is diet fraction for less preferred class, and $FRAC_U$ is diet fraction for un-preferred class. a_{FP} , a_{FU} , and b_{FU} are fraction factors set by users (Stuth et al., 2003). When this module is off, every plant species is evenly grazed.

Forage amount can also be affected by plant LAI, and nitrogen level (Function 3.12).

$$\begin{cases} F = \frac{LAI^3}{LAI^3 + 1} \cdot F \\ F = a_{FN} \cdot CON_N \cdot F + b_{FN} \quad (CON_N \leq 0.0104) \end{cases} \quad (3.12)$$

where F (g) is grazed forage amount based on time step, LAI is leaf area index, CON_N (gN/g) is plant nitrogen concentration, a_{FN} and b_{FN} are the slope and the intercept set by users. (Thornley, 1998; Leriche et al., 2001). F appears on both of sides of the equation which means it is modified when these modules are on. Otherwise, F is not modified.

ii) Site selection Site selection is based on discrete scoring and check points (Figure 3.7). Every cell in the model has a set of site selection attributes. The values of these attributes

give the cell a site preference score (score 1 or score 2 in Figure 3.7) based on check points. A final preference score is calculated by summing up the preference scores of each attributes. By examining the final score, the model can decide which site preference class the cell is in based on score points. Grazing will start from the most preferred cells to the least preferred cells. The number of site preference classes and check points for scoring are set by users. In this example model there is one site selection attribute, plant abundance, which is the ratio between total plant biomass in one cell and cell area. When this module is off, there is only one site preference class.

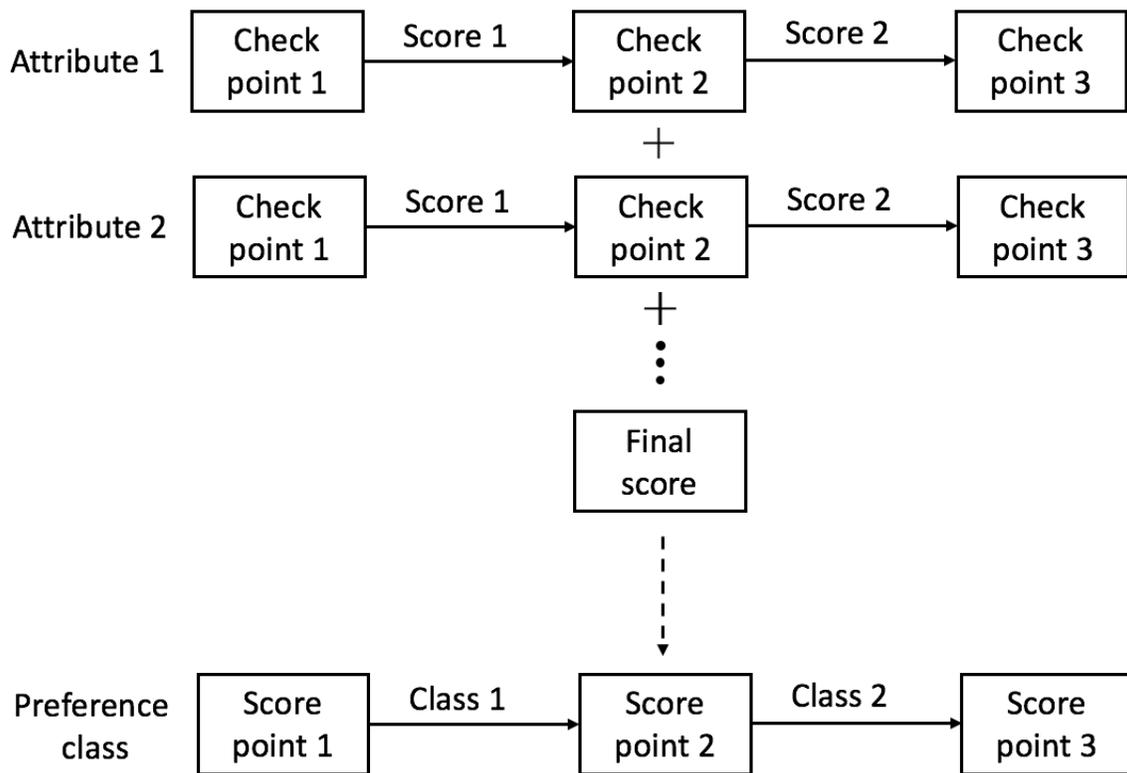


Figure 3.7: Site preference class work flow

3.2.2.2 FIRST STAGE EFFECTS

Actual grazing happens in this section, where direct grazing effects are simulated (Figure 3.8). In addition, starting from this section, all variables used in module functions can be seasonally different and species specific.

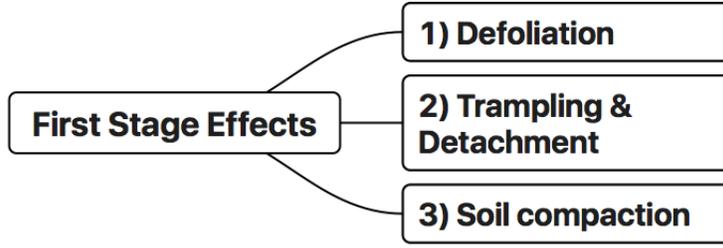


Figure 3.8: First stage effects components

1) *Defoliation*

This module subtracts the grazed forage amount calculated from the last section from total biomass (B). If this module is off, even when forage amount is calculated, total biomass is not subtracted.

2) *Trampling and detachment*

In this module, detached biomass is subtracted from total biomass. Detached biomass is the amount of dead plant biomass caused by animal trampling or other physical contacts with animals besides grazing (Day et al., 1997). This value is calculated from stocking density. Detached biomass equals to forage amount times animal species specific detachment rate (Function 3.13).

$$DET = F \cdot R_{DET} \quad (3.13)$$

where DET (g) is detached amount of biomass, R_{DET} is detachment rate (Day et al., 1997). When this module is off, $DET = 0$.

3) *Soil compaction*

This module calculates the change in soil compaction caused by grazing animals. Soil compaction is a function of stocking density (Function 3.14), and can be used to calculate its indirect effects on plant growth as lands are under grazing.

$$\begin{cases} \Delta SC = a_{SC} \cdot (SD_{MAX} \cdot \frac{AF}{TF} + SD_{MIN}) \\ TSC = SC_0 + \Delta SC \end{cases} \quad (3.14)$$

where ΔSC (Bulkdensity/0 – 0.15 m) is the change of soil compaction. a_{SC} is the slope of the relationship set by users, AF (g) is grazed forage amount from each animal species, TF (g) is total grazed forage amount from all animal species, TSC (Bulkdensity/0 – 0.15 m) is total soil compactness, and SC_0 (Bulkdensity/0 – 0.15 m) is soil compaction when there is no grazing animal (Ascough et al., 2001). When this module is off, $\Delta SC = 0$.

3.2.2.3 SECOND STAGE EFFECTS

Second stage effects come from first stage effects. In this section, plant growth variables that are related to biomass are calculated (Figure 3.9). From this section, when modules are turned off, related variables are set to default values set by users.

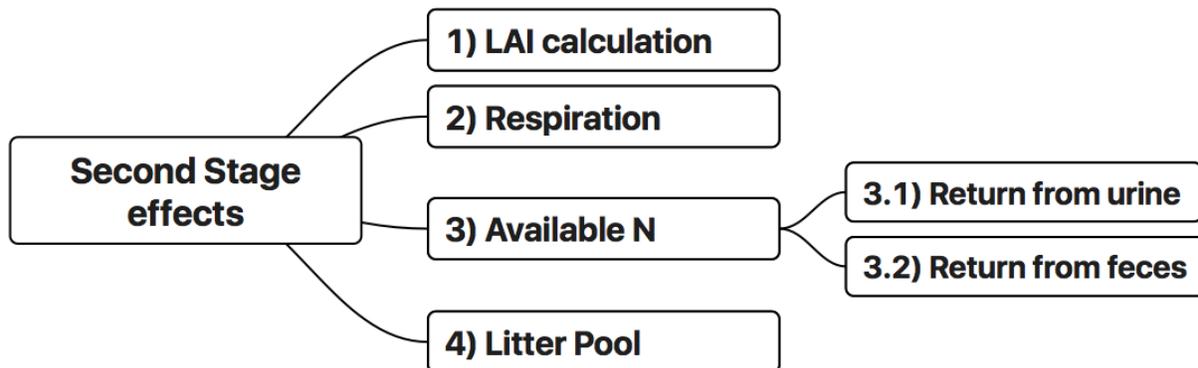


Figure 3.9: Second stage effects components

1) *LAI calculation*

LAI is calculated from plant biomass (Function 3.15):

$$LAI = SLA_{AVG} \cdot FRAC_{LAM} \cdot B \quad (3.15)$$

where SLA_{AVG} (m^2/g) is average specific leaf area given by the users, $FRAC_{LAM}$ is plant growth fraction to leaf given by the users (Thornley, 1998). When this module is off, LAI is set to default value.

2) *Plant respiration*

This module is used to calculate plant respiration amount based on plant biomass (Function 3.16):

$$RES = R_{RES} \cdot B \quad (3.16)$$

where RES (gC) is respiration amount, and R_{RES} (gC/g) is respiration rate (Andales et al., 2005). When this module is off, RES is set to default value.

3) *Soil available N*

There are two submodules in this module calculating nitrogen return from urine and feces, which are affected by plant C to N ratio (Function 3.17):

$$\left\{ \begin{array}{l} NRET_{TOT} = R_{NRET} \cdot F \cdot CON_N \\ NRET_{URI} = NRET_{TOT} \cdot FRAC_{URI} \\ NRET_{FEC} = NRET_{TOT} \cdot (1 - FRAC_{URI}) \\ FRAC_{URI} = -a_{URI} \cdot \left(\frac{R_{C:N} - c_{URI}}{d_{URI}} \right) + b_{URI} \end{array} \right. \quad (3.17)$$

where $NRET_{TOT}$ (gN) is the total N return from animals, $NRET_{URI}$ (gN) is N return from urine, $NRET_{FEC}$ (gN) is N return from feces, R_{NRET} is N return rate given by the users, $FRAC_{URI}$ is fraction of N return from urine, and $R_{C:N}$ is plant C to N ratio given by the

users. a_{URI} and b_{URI} are the slope and intercept of the function, which can be set by users, and c_{URI} d_{URI} are function coefficients. (Thornley, 1998). N returned from urine is directly added to soil available the N pool, and N returned from feces is added to the soil organic N pool (Hunt et al., 1991). When neither one of the submodules are on, $NRET_{TOT} = 0$.

4) Change in the litter pool addition

This section calculates the change of the addition to litter pool caused by detachment from grazing. The addition amount equals the amount of detachment (DET) (Day et al., 1997). When this module is off, there is no litter pool addition change.

3.2.2.4 THIRD STAGE EFFECTS

This section further calculates plant growth variables affected by variables from the last sections, and these variables influence indirect grazing effects (Figure 3.10).

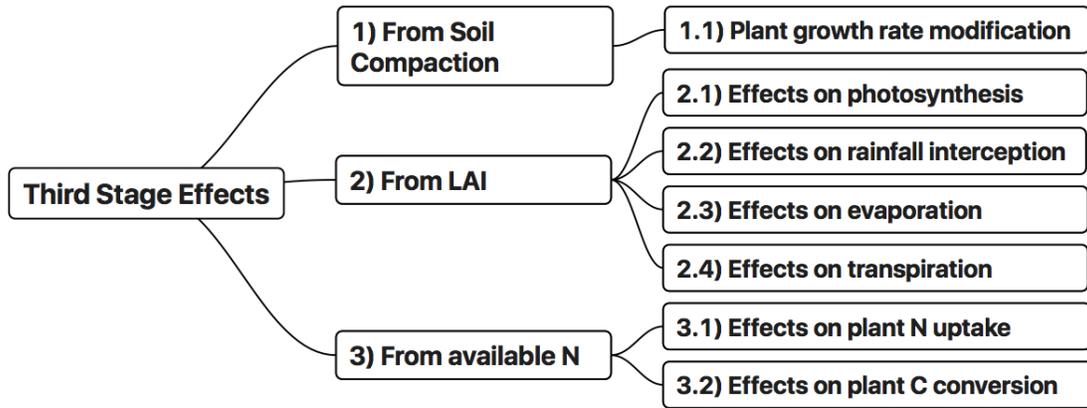


Figure 3.10: Third stage effects components

1) Soil compaction and plant growth rate

From the change of soil compaction, plant growth rate can be modified (Function 3.18):

$$\begin{cases} R_{MAX} = R_{MAX} + \Delta R_{MAX} \\ \Delta R_{MAX} = -a_{RG} \cdot \Delta SC - b_{RG} \end{cases} \quad (3.18)$$

where ΔR_{MAX} (g/dt) is the change in maximum plant growth rate, a_{RG} is the slope, and the b_{RG} is the intercept set by users (Ascough et al., 2001). When this module is off, R_{MAX} is not affected by soil compaction.

2) Effects from LAI

There are three submodules in this module. All of them depend on the change in LAI calculated in the last section.

i) Photosynthesis In this module, the photosynthesis rate is modified by LAI (Function 3.19):

$$PS = \frac{PS_{MAX} \cdot LAI}{a_{PS} + LAI} \quad (3.19)$$

where PS (gC/m² · dt) is photosynthesis rate for the time step, PS_{MAX} (gC/m² · dt) is maximum photosynthesis rate set by users, and a_{PS} is the half saturation constant (Thornley, 1998). When this module is off, PS is set to a default value.

ii) Rainfall Interception This section uses LAI to calculate plant rainfall interception (Function 3.20). Rainfall interception is the percent of rainfall that is intercepted by leaf material.

$$RI = 1 - e^{-CO_{RI} \cdot LAI} \quad (3.20)$$

where RI is the fraction of rainfall that is intercepted by plants, and CO_{RI} (m² Ground/m² Leaf) is canopy extinction (Thornley, 1998). When this module is off, RI is set to a default value.

iii) Evapotranspiration Potential system evaporation and plant transpiration are calculated in this module (Function 3.21):

$$\left\{ \begin{array}{l} ETP_{POT} = a_{ETP} \cdot RAD \cdot \left[1 - \frac{b_{ETP} \cdot (1 - e^{-c_{ETP} \cdot (B + \Delta LIT) + d_{ETP} \cdot ALB})}{e_{ETP}} \right] \\ EV P_{POT} = ETP_{POT} \cdot e^{-a_{EVP} \cdot LAI_{AVG}} \\ TRP_{POT} = ETP_{POT} \cdot \frac{LAI}{3} \quad (LAI \leq 3) \\ TRP_{POT} = ETP_{POT} \quad (LAI > 3) \end{array} \right. \quad (3.21)$$

where $EV P_{POT}$ (cm) is system potential evapotranspiration, RAD (Langleys) is average solar radiation given by users, ΔLIT (g) is litter pool change calculated in the last section, ALB (0 – 0.1 m) is average soil albedo given by users, $EV P_{POT}$ (cm) is system potential evaporation, LAI_{AVG} is average LAI, and TRP_{POT} is potential transpiration. a_{ETP} , b_{ETP} , c_{ETP} , d_{ETP} , e_{ETP} , and a_{EVP} are related water dynamic variables that can be set by users (Stuth et al., 2003). When these modules are off, relative variables are set to default values.

3) Effects from available N

Two submodules are included in this module, which calculates changes in plant N uptake and C conversion into plant material.

i) Changes in plant N uptake The change in plant N uptake is calculated from the changes in the soil available N pool, which is the N return from grazing animals (Function 3.22):

$$\Delta NUP = \frac{NUP_{MAX} \cdot \Delta NRET_S}{a_{NUP} + \Delta NRET_S} \quad (3.22)$$

where ΔNUP (gN/m²·dt) is the change in plant N uptake on time step basis, NUP_{MAX} (gN/m²·dt) is maximum plant N uptake, $\Delta NRET_S$ is the change in soil available N pool, and a_{NUP} is half saturation constant (Hunt et al., 1991). When this module is off, NUP is set to a default value.

ii) *C conversion* This module calculates plant C conversion from plant N concentration, which is affected by plant N uptake (Function 3.23):

$$\begin{cases} CC = a_{CC} \cdot CON_N + b_{CC} \\ CON_N = CON_N + 0.5 \cdot \Delta NUP \end{cases} \quad (3.23)$$

where CC (g/MJ) is plant C conversion rate, a_{CC} is the slope, and b_{CC} is the intercept (Leriche et al., 2001). When this module is off, CC is set to a default value. Plant nitrogen concentration (CON_N) is also updated in this module.

3.2.3 COMBINED EFFECTS

Since plant growth variables are only calculated in stage effects sections, there can not be indirect grazing effects represented in final production outputs if the plant growth process components don't have corresponding relationships with these variables. For example, the simple plant growth processed referenced in this study do not have relationships between plant production and plant photosynthesis. To have fundamental indirect effects shown in the model outputs, basic plant growth variable relationships are introduced into this model. In the 'plant growth' section, growth variable coefficients are discussed, and here is how combined effects variables ($\alpha_{GD}, \alpha_K, \alpha_{RG}, \alpha_D$) are calculated (Function 3.24. and Function 3.25):

$$\begin{cases} \alpha_{GD} = PE(\Delta NRET) + NPE_1(SC) + NPE_2(\Delta LIT) \\ \alpha_K = PE(\Delta NRET) + NPE_1(SC) + NPE_2(\Delta LIT) \\ \alpha_{RG} = PE(RES, \Delta NRET, PS, TRP_{POT}, \Delta NUP, CC) \\ \quad + NE(RI, EVP_{POT}) + NPE_2(\Delta LIT) \\ \alpha_D = PE(RES, \Delta LIT, RI, EVP_{POT}, TRP_{POT}) \\ \quad + NE(\Delta NRET, PS, \Delta NUP) - NPE_1(SC) \end{cases} \quad (3.24)$$

$$\left\{ \begin{array}{l} PE(X_1, \dots, X_n) = \sum_{i=X_1}^{X_n} -\frac{1}{i+1} + 1 \\ NE(X_1, \dots, X_n) = \sum_{i=X_1}^{X_n} \frac{1}{i+1} - 1 \\ NPE_1(X_1, \dots, X_n) = \sum_{i=X_1}^{X_n} \frac{2}{e^{(0.8 \cdot i - 1.5)^2}} - 1 \\ NPE_2(X_1, \dots, X_n) = \sum_{i=X_1}^{X_n} \frac{2 \cdot e - 2}{e - 2 + e^{(2 \cdot i - 1)^2}} - 1 \end{array} \right. \quad (3.25)$$

where $\Delta NRET$ is the change of available N caused by N return from grazing animals, $PE(X)$ is positive effects, $NE(X)$ is negative effects, and $NPE_1(X)$ and $NPE_2(X)$ are both positive and negative effects. The trends of these four functions are shown in Figure 3.25. Positive value represents positive effects, and negative value represents negative effects. All of these functions are limited to either 1 or -1 for simple effects behavior.

Effects on plant grow days and carrying capacity are theoretically the same effects because carrying capacity is determined by grow days. However, in this model, grow days and plant carrying capacity are used nonlinearly in different functions, (Fryxell et al., 2005), thus effects on these two variables are separated for potentially clearer comparisons of effects. Grow days is affected by changes in soil compaction, system litter pool, and change in system available N. When soil compaction is either at a relatively low level or high level, it has negative effects on plant grow days (Figure 3.25 (c)). Only when soil compaction is at an intermediate level can it have positive effect on grow days. The change in the system litter pool addition has positive effects on grow days when it is at relatively low level, and has negative effects on grow days when there is too much litter added into the system (Figure 3.25 (d)). The change in N return from grazing animals has positive effects on grow days. Combined effects in plant carrying capacity has exactly the same set up as grow days.

Plant respiration, N return, photosynthesis, transpiration, N uptake, and C conversion have positive effects on plant growth rate. Rainfall interception and evaporation have neg-

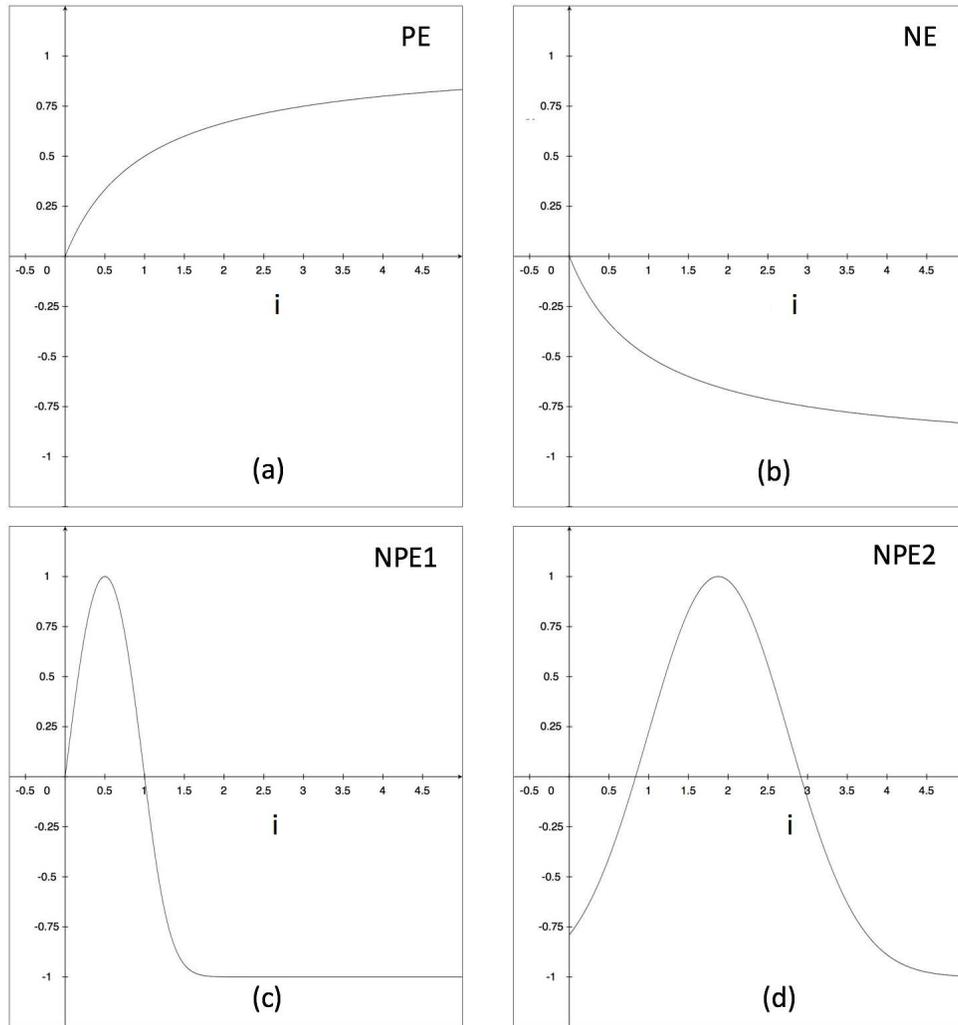


Figure 3.11: Effect functions

ative effects on plant growth rate. Change in litter pool addition has both positive and negative effects. Plant respiration, litter pool, rainfall interception, and evapotranspiration have positive effects on the plant death rate. N return, plant photosynthesis, N uptake, and C conversion have negative effects on plant death rate. Soil compaction has both positive and negative effects on plant death rate, and the sign is reversed, which means it starts with positive effects, than negative effects, and ends up with positive effects again.

3.2.4 OUTPUT

The working process of modular modeling is parallel (Figure 3.12). To go from ‘step 1’ to ‘step 2’ there can be four pathways: through ‘module 1’, or ‘module 2’, or both, or neither one of the two modules.

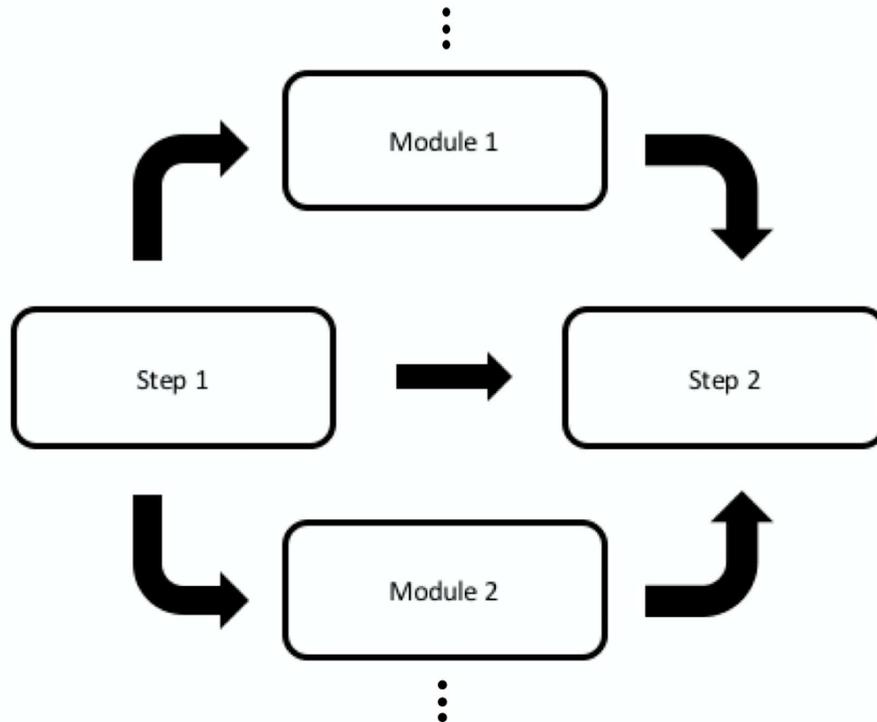


Figure 3.12: Modular modeling

Similarly, when modular modeling is realized in grazing effects models, there can be multiple ways to get model outputs. From Figure 3.13, to have outputs, the model can either go through processes with defoliation effects, or through detachment effects, or no effects, or through both defoliation and detachment effects. With modular modeling, comparisons and evaluations of effects become more straightforward. And this can be beneficial to grassland system studies.

3.3 THEORETICAL OVERCOMPENSATION EXPERIMENTS

3.3.1 BACKGROUND

Grazing can affect the system at different levels in different ways (Ares et al., 2003). Under certain circumstances, grazing can promote plant production according to the Graz-

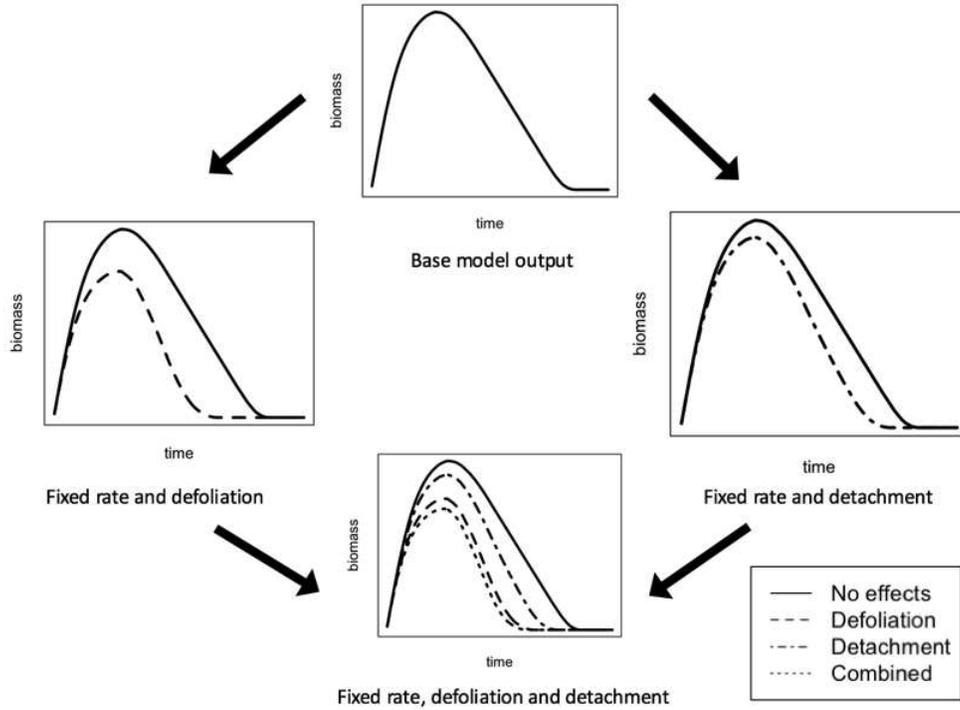


Figure 3.13: Modular output Example

ing (Herbivore) Optimization Hypothesis (overcompensation behavior) (McNaughton, 1979). Overcompensation is defined in Belsky et al. (1993) as positive response in plant growth to grazing. This effect has been debated over decades, although there is evidence supporting Grazing Optimization Hypothesis and overcompensation growth by both experiment data and simulation models (McNaughton, 1986; De Mazancourt et al., 1999).

Being able to explain the mechanisms of overcompensation is important to understanding of grazing system. However, the difference between effects on growth variables and effects on net biomass production is often unclear. For example one study argues that the growth rate can increase after grazing while net production doesn't (Hilbert et al., 1981). Although the study is trying to contradict the idea of overcompensation, increased growth rate could also be regarded as a positive response to grazing.

In Lebon et al. (2014), the difference between grazing effect on growth rate and net biomass production is clarified as direct compensation and apparent compensation:

- Direct compensation: the basic positive response of plants to herbivores, which is measured in terms of growth and/or fitness;
- Apparent compensation: the net result of the whole plant-herbivore interaction, which is measured as the overall effect of herbivores on plant biomass

This clarification is helpful in testing positive effect (direct compensation) from grazing when no apparent compensation effect is observed, so that grazing effects can be better and more comprehensively evaluated. However, with traditional experimental and observational studies, these two compensations can not be easily separated (Patton et al., 2007; Adiku et al., 2010). Modeling becomes a choice of pathway in this kind of study.

In modeling studies that focus on compensatory behavior, grazing effects are usually linearly dependent to the whole model. For example, the calculation of grazing effects on plant photosynthesis cannot be run and studied independently. In addition the choices as to the inclusion of different grazing effects into models are different, which makes it difficult to evaluate and compare different models (Leriche et al., 2001; Adiku et al., 2010; Lebon et al., 2014). With modular modeling and the possibility of including all of the grazing effects into one model with switches that can turn these effects on and off, these problems can be relieved. In this section, experiments are done to show the benefits of modular modeling in overcompensation studies.

3.3.2 MODEL SET UP

In this experiment, a ten year simulation is conducted in a 4×4 grid space, with cell area of 10 m^2 . The coefficient of variation for annual rainfall is set to 25 %. There are no seasonal, management and species differences in grazing. Also there is no site and diet selection. The values for variables that require user input are shown in Table 3.1:

Table 3.1: Variable Values

Variable	Values	Unit	Explanation	Reference
AR_N	671	mm	Annual rainfall for the northernmost row	Fryxell et al. (2005)
AR_S	529	mm	Annual rainfall for the southernmost row	Fryxell et al. (2005)
a_{GD}	65	-	Approximation parameter in Function 3.1	Fryxell et al. (2005)
b_{GD}	300	-	Approximation parameter in Function 3.1	Fryxell et al. (2005)
c_{GD}	0.01	-	Approximation parameter in Function 3.1	Fryxell et al. (2005)
d_{GD}	6.25	-	Approximation parameter in Function 3.1	Fryxell et al. (2005)
Ψ	80.872	-	Carrying capacity coefficient	Fryxell et al. (2005)
R_{MAX}	0.039	g/dt	Plant growth rate	Fryxell et al. (2005)
D	1.79	g/dt	Plant death rate	Fryxell et al. (2005)
SD_{MAX}	0.03	head/m ²	Maximum stocking density	Stuth et al. (2003)
SD_{MIN}	0.005	head/m ²	Minimum stocking density	Stuth et al. (2003)

(Continued)

(Table 3.1. continued)

Variable	Values	Unit	Explanation	Reference
INT_{MAX}	10	kg/head · day	Maximum intake per animal per day	Stuth et al. (2003)
R_{UAV}	0.03	-	Unavailable plant rate	Glasscock et al. (2005)
a_{FP}	3.65	-	Fraction factor in Function 3.11	Stuth et al. (2003)
a_{FU}	0.031917	-	Fraction factor in Function 3.11	Stuth et al. (2003)
b_{FU}	2.89	-	Fraction factor in Function 3.11	Stuth et al. (2003)
a_F	0.964	-	Slope in Function 3.12	Leriche et al. (2001)
b_F	1.5	-	Intercept in Function 3.12	Leriche et al. (2001)
R_{DET}	0.33	-	Detachment rate	Day et al. (1997)
a_{SC}	0.125	-	Slope in 3.14	Ascough et al. (2001)
SC_0	1.6	bulk density (0 – 0.15 m)	soil compaction when there is no grazing	Ascough et al. (2001)
SLA_{AVG}	0.35	m ² /g	Average specific leaf area	Thornley (1998)
$FRAC_{LAM}$	0.7	-	Growth fraction to leaf	Thornley (1998)
CON_N	0.02	gN/g	Initial plant nitrogen concentration	Thornley (1998)
R_{NRET}	0.99	-	Nitrogen return rate from animal	Thornley (1998)
a_{URI}	0.1	-	Slope in Function 3.17	Thornley (1998)
b_{URI}	0.8	-	Intercept in Function 3.17	Thornley (1998)
c_{URI}	12	-	Coefficient in Function 3.17	Thornley (1998)
d_{URI}	13	-	Coefficient in Function 3.17	Thornley (1998)
$R_{C:N}$	25	-	Plant C to N ratio	Thornley (1998)

(Continued)

(Table 3.1. continued)

Variable	Values	Unit	Explanation	Reference
a_{RG}	1.42	-	Slope in Function 3.18	Ascough et al. (2001)
b_{SC}	2.29	-	Intercept in Function 3.18	Ascough et al. (2001)
PS_{MAX}	10	$\text{gC}/\text{m}^2 \cdot \text{dt}$	Maximum photosynthesis rate	Thornley (1998)
a_{PS}	2	-	Half saturation point in Function 3.19	Thornley (1998)
CO_{RI}	0.5	$\text{m}^2\text{Ground}/\text{m}^2\text{Leaf}$	Canopy extinction	Thornley (1998)
a_{ETP}	0.128	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
b_{ETP}	0.23	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
c_{ETP}	$2.9 \cdot 10^{-6}$	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
d_{ETP}	0.24	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
e_{ETP}	58.3	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
a_{EVP}	0.4	-	Water dynamic variable in Function 3.21	Stuth et al. (2003)
RAD	12	Langleys	Average solar radiation	Stuth et al. (2003)
ALB	0.08	0 – 0.1m	Average soil albedo in 0 to 0.1m	Stuth et al. (2003)
NUP_{MAX}	1	$\text{gN}/\text{m}^2 \cdot \text{dt}$	Maximum plant N uptake	Hunt et al. (1991)
a_{NUP}	1	-	Half saturation point in Function 3.22	Hunt et al. (1991)
a_{CC}	0.44	-	Slope in Function 3.23	Leriche et al. (2001)
b_{CC}	0.92	-	Intercept in Function 3.23	Leriche et al. (2001)

3.3.3 RESULTS

From Figure 3.14, three simulations were executed, one with no grazing, one with only first stage grazing effects, defoliation and detachment, and one with all of the grazing effects. When all the grazing effects modules are turned on, apparent positive effects from grazing can be observed. But what exactly caused the positive effects is unknown and hard to tell in traditional studies. With modular modeling, it is possible to compare different effects.

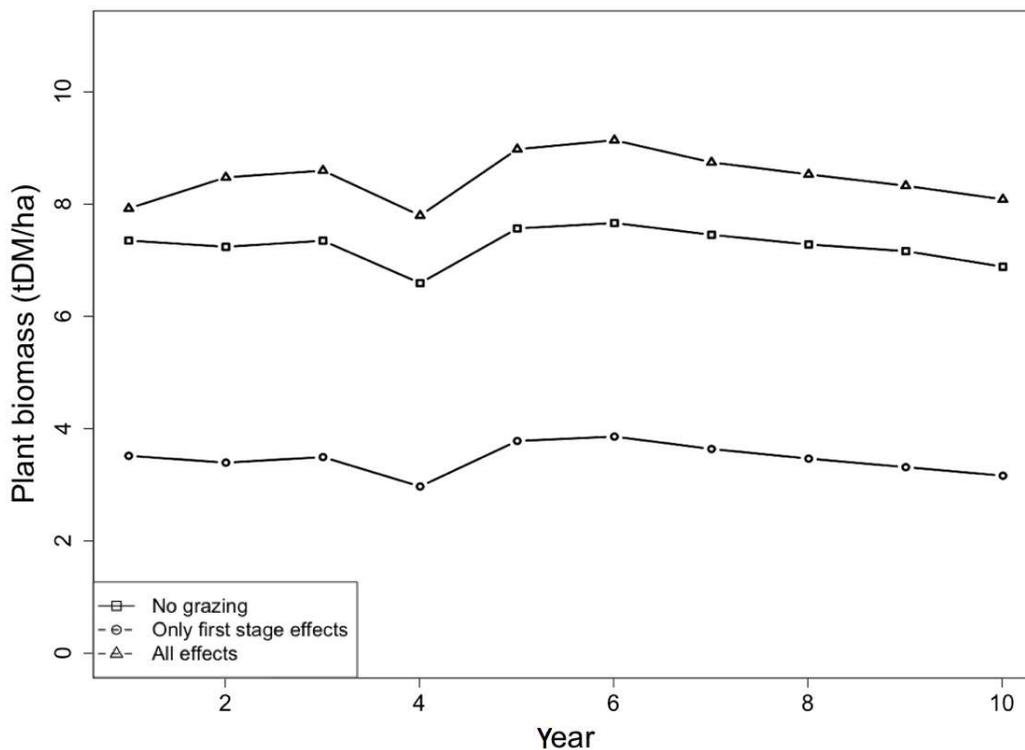


Figure 3.14: Positive effects and simple first stage effects

In Figure 3.15, indirect grazing effects are assessed one by one. Lines above the first stage grazing effects line (soil compaction, plant respiration, N return, litter pool, photosynthesis, and N uptake or C conversion) represent direct positive effects. Lines below the first stage grazing effects line (rainfall interception and evaporation or transpiration) represent direct negative effects. In addition to sorting these effects into direct positive and negative effects, the degree to which these effects are affecting the system can also be quantified.

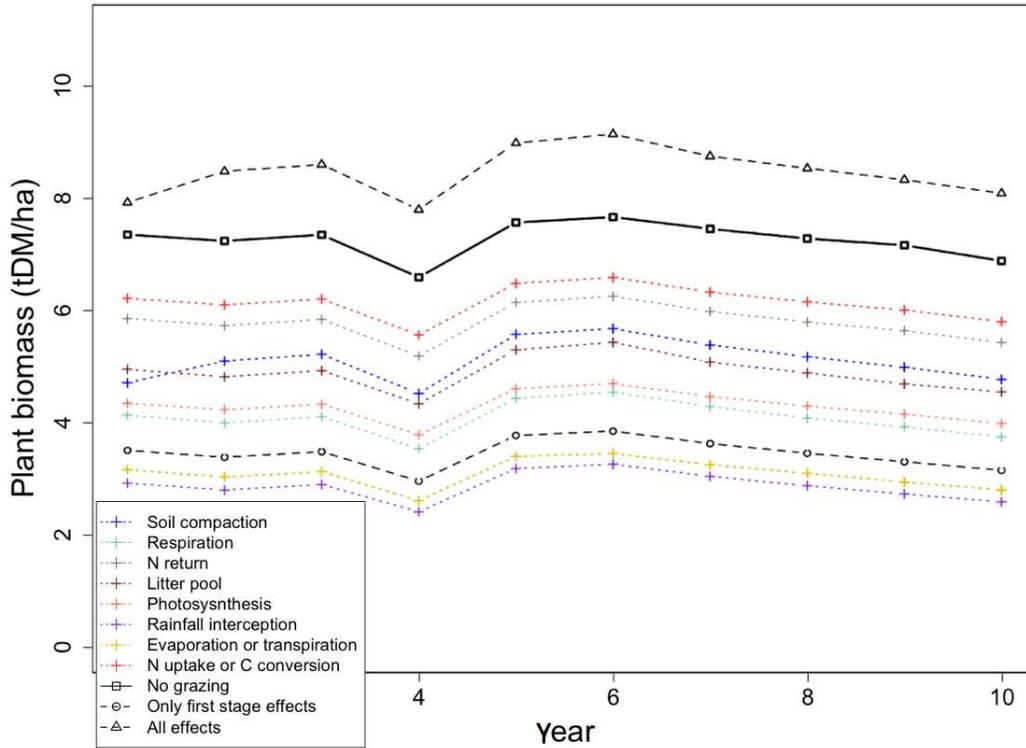


Figure 3.15: Effects comparison

For example, in Figure 3.15, the higher the effect line, the more positive it is to the system. Changes in plant N uptake and C conversion caused by animal N return give the system the largest positive effects compared to the other positive effects in this example model, while plant rainfall interception has the largest negative effect on the system. The whole grazing effect is a combination of all of these single grazing effects. When negative direct effects are large enough to offset the direct positive effects, there may be no apparent positive effects shown in the final result. But this doesn't mean grazing is always detrimental to plant growth. Only by studying and comparing effects one by one can people make a comprehensive conclusion about the relationships between grazing and grassland dynamics.

The base model structure of the example model can also allow comparisons of effects coming from the changes in basic variables such as grow days, carrying capacity, growth rate, and death rate (Figure 3.16). Differences in the results shows effects from carrying capacity and growth rate are positive, and effects from grow days and death rate are negative

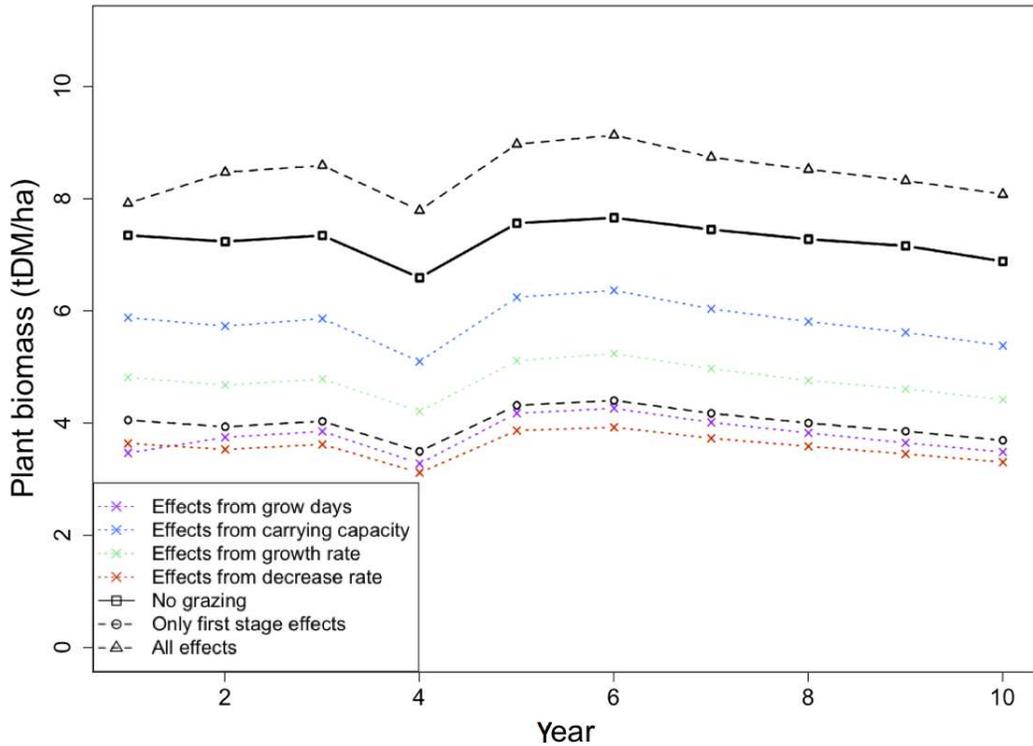


Figure 3.16: Effects from plant growth variables comparison

This is an example of how modular modeling works in overcompensation studies. Although the combined effects functions used in this example model is theoretical in nature, using modules with real functions that are based on observational and experimental studies may have more informative results than traditional methods.

3.4 DISCUSSION

3.4.1 MODULAR MODELING

A great deal of background knowledge on components used in simulation is necessary in traditional model development. If exist components that are beyond a traditional modeler's knowledge, these components are most likely to be ignored (Ascough et al., 2001). Trying to have a solid understanding of all the system processes is almost impossible for most of us. However, including as many system processes as possible, for example grazing effects, is critical in some studies, because informations behind these processes are not always obvious in field studies. Modular modeling makes it possible to include a diversity of processes as options that can be enabled or disabled.

In the ‘Model buildup’ section, the possibility to include most of the grazing effects with modular modeling is demonstrated. By treating different grazing effects as modules, they can be put together and work independently as long as the base model structure is flexible enough to hold these modules. For example, if the base model structure (plant growth process) doesn’t have functions about the interaction between photosynthesis and plant growth, the inclusion of the photosynthesis calculation module can not have any effects on the system production output. This is why basic combined effects functions are included in the example model. The plant growth components can also be regarded as modules, although it is not the objective of this study. A fully modularized model can be a goal for future studies.

By separating the model development work into ‘model structure development’ and ‘module development’, where model structure developers focus on the extensibility of the structure, and module developers focus on the portability and specialty of their modules, the simulation model development can be more efficient and flexible. The structure development is critical to the whole development process. In this study, grazing has four interrelated sections, grazing options, first stage effects, second stage effects, and third stage effects. In traditional model structures, grazing options and first stage effects are usually regarded as one section, the second stage effects and the third stage effects are not regarded as grazing effects sections but plant growth components, or simply are ignored. This can be confusing for grazing effects studies, because most of the indirect grazing effects come from the interactions between the change in plant biomass caused by grazing and related plant growth processes. However, simply by putting these process calculation modules to grazing sections still does not solve the problem completely, because these calculations usually don’t have direct grazing components. How to balance their roles in plant growth and grazing effects is the work of the base model structure development. It represents the way system modelers see the structure of the system.

The work of modular development is different. Besides the portability of modules, how close the functions are to real processes and how general they can be is the main focus. However, system processes are all interrelated. For example, one can not simply study the relationships between photosynthesis and plant biomass without referencing other system processes, such as plant nitrogen uptake, carbon conversion rate, etc. (Thornley, 1998). But these sub-processes should not become the focus of photosynthesis-biomass module development. If everything is modularized, there can be modules (either sub-modules or main modules) for plant nitrogen uptake and carbon conversion rate to be used for photosynthesis-biomass module. This submodule, module, and base model structure relationship is on the basis of Modular Programming and Object-Oriented Programming (Babb and Lee, 2012; Kindler and Krivy, 2011), and is similar to the relationship of software dependency, software, and operating system.

3.4.2 GRASSLAND SYSTEM MODELING

In the experiment section, the benefits of modular modeling is partly demonstrated. By sectioning grazing effects into independent modules, the comparisons and evaluations of effects become much easier. This is meaningful to grassland system studies, especially when the mechanisms are usually indirect and hard to observe, measure, and thus simulate, such as compensatory behavior. With modular approaches, modelers don't have to fully understand the mechanisms of indirect effects before the development of models, and the model output can show the mechanisms behind outcomes, if properly parameterized.

Sometimes, based on study objectives, there is no need to include all of the grazing effects into one model, which would require too much computational power, especially in large-scale and long-term modeling efforts (Boone et al., 2011). In this case, modular modeling is still appropriate because it does not force users to include all possible system processes or grazing effects. It is theoretically flexible in most of the modeling study cases. The flexibility needs more studies to be proved. But in general, by manipulating modules, the indirect mechanisms can be clarified to further our understanding of the whole system and its interactions.

CHAPTER 4

REALISTIC APPLICATION OF A EXAMPLE MODULAR GRAZING EFFECTS MODEL ON THE ALPINE REGION OF THE QINGHAI-TIBETAN PLATEAU

4.1 INTRODUCTION

Grazing is one of the most important processes in grassland ecosystem, which can affect the system in different ways and levels (Ares et al., 2003), either positively or negatively (Leriche et al., 2001), such as grazing effects on system community structures, and system production dynamics (McNaughton, 1986). To further the understanding to the mechanisms behind grazing and their relationships with the system, one important method is modeling, which allows users to study the system abstractly and mechanistically (Tietjen and Jeltsch, 2007).

Modeling of grassland systems with grazing started in the 1960s (Wright and Dent, 1969). Since then, it has been developed using various approaches (Tietjen and Jeltsch, 2007), especially when modeling components like grazing processes and grazing effects, which can range from simple defoliation process without any indirect effects considered to complicated grazing processes that can be determined by multiple animal population dynamic variables and selection components and a number of indirect grazing effects through light availability, water cycling, nutrient cycling, etc. (Miao, Chapter 2). The variability of grassland system modeling approaches makes it difficult for users and analysts to make comparisons and evaluations of different models (Leriche et al., 2001; Lebon et al., 2014). It can be overwhelming to review the many kinds of models and make choices among these approaches, because of the number of approaches, and almost all of them are specifically parameterized into different study areas. Simply comparing the outputs from different models can be misleading because of their different objectives, subjects, and calibrations (Rykiel, 1996). In addition, the reason to the variability of different modeling approaches is sometimes unclear.

To improve this situation, modular modeling can be one of the pathways, which focuses on the extensibility of base model structures and portability of modules, inputs and outputs standards, and modular applications in ecosystem modeling.

Modular modeling comes from the idea of Object-Oriented Programming and Modular Programming, the two widely applied programming paradigms, which can help to improve the development efficiency, and clarify the coding structure (Basten et al., 2015). Different components of a model are treated as separate modules, and model development is divided into two parts, module development, and basic structure development. Model development becomes parallel and collaborative, which can theoretically allow open source community development (Laurent, 2008). And different modules can be independently developed. In Miao (Chapter 3), an example modular model, which focuses on modularizing grazing effects, was developed. This model enables users to use, study, and compare different grazing effects separately. The utility of including grazing effects into one model with modular modeling and its modular feature are demonstrated. However, most of the time, it is not necessary to include all grazing effects into one single study, and the values or functions used in different study situations can vary based on specific study objectives. The flexibility and generality of standardized models from modular modeling remains to be shown in a real-world setting.

In this study, the example modular grazing model is applied to real grazing experimental results from a simple plant-grazing interaction study (Dong et al., 2004) in Qinhai-Tibetan plateau, China, in a general system production simulation. The main purpose is to show the flexibility and generality of using modular modeling approaches in grassland and grazing modeling studies. Values for parameters used in the model were derived from data in the experiment. With calibrated functions, a ten year simulation was done, comparing the system production under different grazing intensities.

4.2 EXPERIMENTAL SITE

The experimental site is at the Alpine Grassland Station of Gansu Agricultural University in the Jingqinghe Region ($37^{\circ}40'N$, $103^{\circ}32'E$, 2960 m above sea level) at the north-eastern end of Qinghai-Tibetan Plateau. There were four plant species used in the experiment: *Bromus inermis*, *Clinelymus nutans*, *Elymus nutansm*, and *Agropyron cristatum*.

Weather data were collected from the nearest weather station from 1998 to 2000. The average total annual rainfall was 416 mm, with an additional 200 mm snowfall in the winter. Rainfall mostly occurs in July, August, and September. Plant growing season is from early May to mid-September.

The experiment units were 10 m \times 15 m fenced plots. Grazing was rotationally managed from July 1st to September 15th, with three five-day grazing periods, and a twenty-day resting period after each grazing period. There was no grazing outside these periods. Grazing animals were five to six months old Tibetan sheep. Four different grazing intensities (GI), the intake proportion to total plant biomass, were applied by changing the number of grazing animals, which were: no grazing (NG, GI=0), light grazing (LG,GI=0.3), medium grazing (MG, GI=0.5), and high grazing (HG, GI=0.7). Plant measurements were taken in July 25th and September 15th. Grazing stopped around 7, 5, and 3cm sward height in LG, MG, and HG respectively. The experiment started in 1998, and all data were collected in 2000 (Dong et al., 2004).

4.3 EXPERIMENT RESULTS

Results from the experiment showed plant biomass (tDM/ha), leaf area index (LAI), and plant photosynthesis rate ($\mu\text{molCO}_2/\text{m}^2\cdot\text{s}$) decreased with grazing intensity, while plant tiller density increased with grazing intensity. Plant specific leaf area (SLA (cm^2/g)) was relatively constant throughout the experiment. LAI was directly affected by plant biomass and SLA, and affected photosynthesis rate. The increase of tiller density indicates the increase of plant growth rate when biomass had decreased (Figure 4.1).

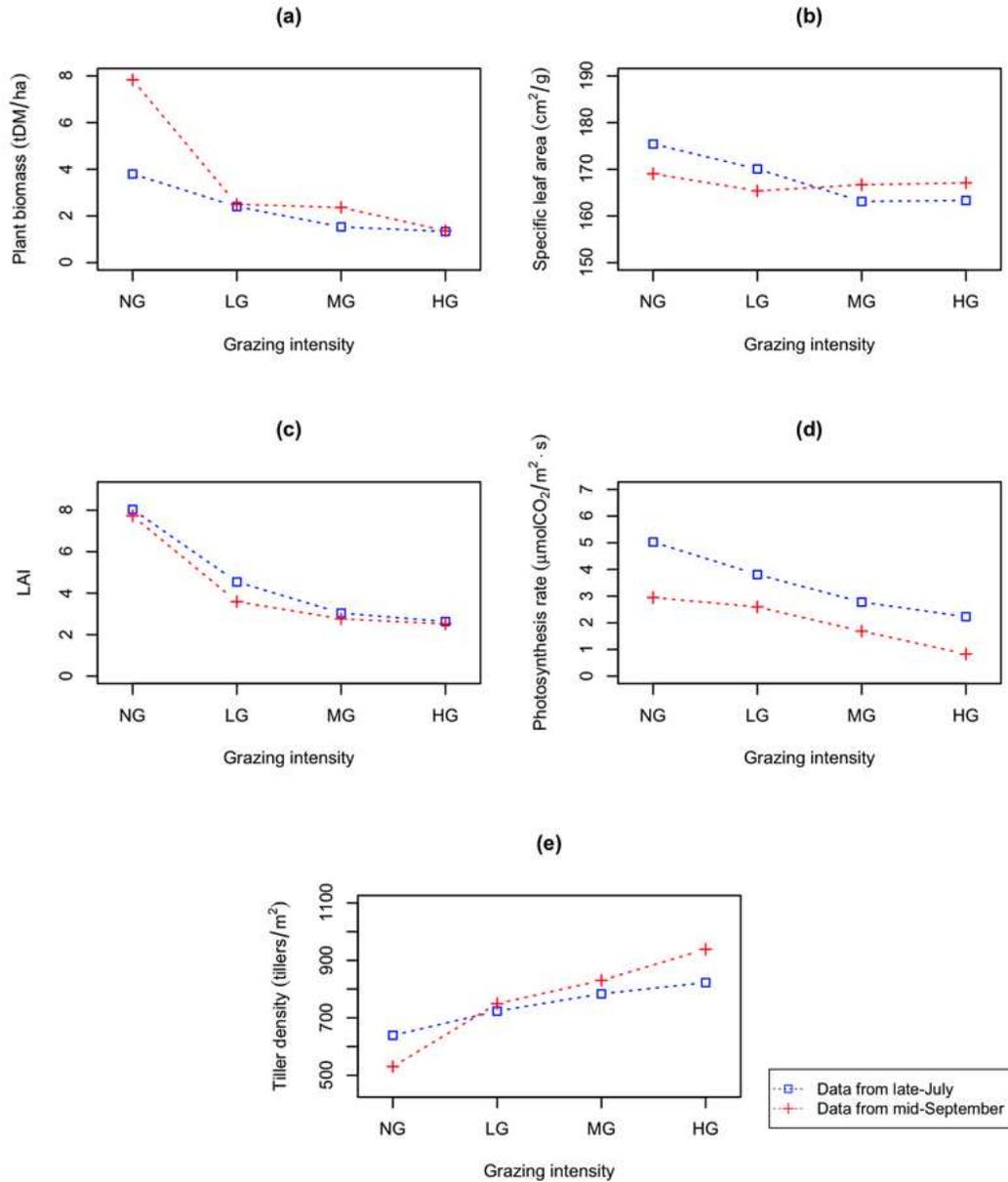


Figure 4.1: Results from the experimental study in Qinghai-Tibetan Plateau. (a) is the relationship between plant biomass and grazing intensity; (b) is the relationship between average plant specific leaf area and grazing intensity; (c) is the relationship between average plant LAI and grazing intensity; (d) is the relationship between average plant photosynthesis and grazing intensity; and (e) is the relationship between average plant tiller density and grazing intensity (Dong et al., 2004).

In the original study (Dong et al., 2004), there are data showing the plant species relative abundance changes in different plant species mixtures according to the changes in grazing intensity. However, the difference in plant mixture did not affect the total system production or other plant variables, such as specific leaf area, LAI, photosynthesis rate, and average tiller density. So in this study, the difference in plant mixture is not considered.

4.4 MODEL SETUP

The example modular grazing model was built with its foundation being a simple plant growth model from Fryxell et al. (2005), which doesn't have plant species differences represented, and is regarded here as the base model structure. Grazing and grazing effects were built as modules with functions from existing grassland models: GPFARM (Ascough et al., 2001), GRASP (Day et al., 1997), IMAGE (Hacker et al., 1991), HURLEY (Thornley, 1998), PEPSEE (Leriche et al., 2001), and PHYGROW (Stuth et al., 2003). Grazing modules are separated into four sections: grazing process options, first stage grazing effects, second stage grazing effects, and third stage grazing effects (Figure 4.2). Grazing process options are used to determine how grazing is simulated, which include animal species differences, animal competition, seasonal and management differences, diet and site selection, and grazing rate as a fixed rate or a function of stocking density. First stage effects use outputs from grazing processes to calculate defoliation, detachment, and effects on system soil compaction. Second stage effects use the change in plant biomass and animal intake to calculate updated LAI, plant respiration, nutrient return, and litter pool changes. Third stage effects use output from second stage effects to calculate changes come from the changes in soil compaction, LAI, and available N, which include photosynthesis calculations, leaf rainfall interception, evapotranspiration, plant N uptake, and C conversion. All of the available effect modules and their status in this study can be found in Table 4.1.

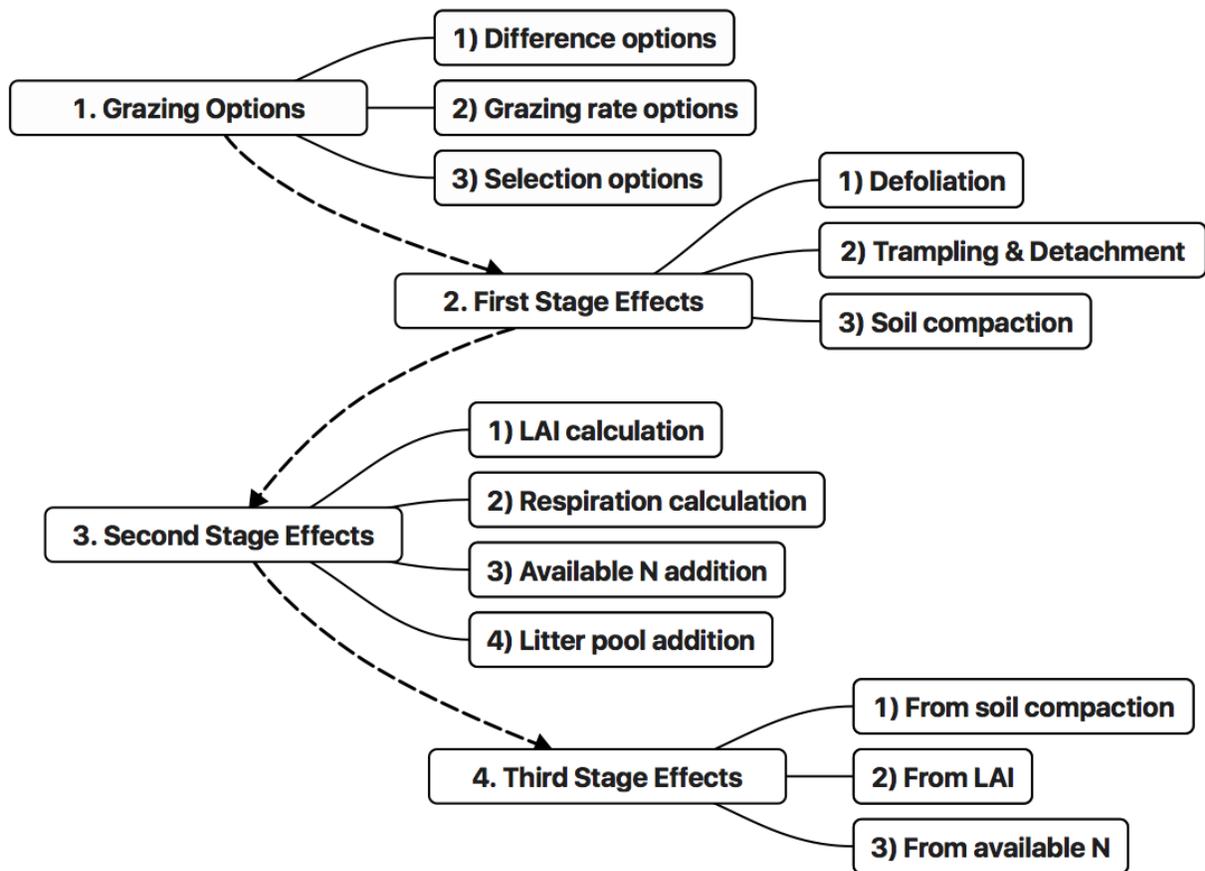


Figure 4.2: Grazing components

Table 4.1: Module setup

Modules	On/Off
Grazing process options	
Animal differences	Off
Animal competition	Off
Seasonal differences	Off
Management differences:	
1) Rotational grazing	On
2) Maximum allowable grazing amount	On
3) Minimum assigned grazing amount	Off
Diet selection:	
1) Plant species preference	Off
2) Diet selection based on LAI	Off
1) Diet selection based on plant N%	Off
Site selection	Off
Grazing rate options	
1) Fixed grazing rate	Off
2) Grazing rate calculated from stocking density	On
3) Naturally unavailable biomass	Off
First stage effects	
Defoliation	On
Detachment	On
Effects on soil compaction	Off
Second stage effects	
Effects on LAI	On
Effects on respiration	Off
Effects on nitrogen return:	
1) Return from urine	Off
2) Return from feces	Off
Effects on litter pool	Off

(Continued)

(Table 4.1. continued)

Modules	On/Off
Third stage effects	
Effects from soil compaction on plant growth	Off
Effects from LAI	
1) Plant photosynthesis	On
2) Plant rainfall interception	Off
3) System evaporation	Off
4) Plant transpiration	Off
Effects from nitrogen return and litter pool	
1) Plant nitrogen uptake	Off
2) Plant carbon conversion	Off

4.4.1 REASONING FOR MODULE STATUS

In the grazing process options, animal differences and animal competition modules are turned off because there is only one grazing animal (Tibetan sheep) in the experiment site. There are no seasonal differences because grazing only happens between July and September, which is the growing season of the system. In management differences, there is rotational grazing, and maximum allowable grazing amount according to the original study. Minimum assigned grazing amount is turned off since there is no related information. In the original study, the authors believe that there was no diet and site selections in the experiments. In addition, in this study, only average system production is considered, so the diet selection and site selection modules are turned off. Grazing rate calculation uses stocking density instead of a fixed grazing rate so users can have a better understanding on how different number of animals changes grazing intensity.

In the first stage effects, defoliation and detachment are turned on, and total grazing intensity is calculated from both of these two modules. Soil compaction is not a consideration in this study, and so it is turned off. In the second and third stage effects, only LAI, and photosynthesis calculations are turned on because only these two variables were studied in the original study (Dong et al., 2004).

4.4.2 FUNCTIONS AND VARIABLES

4.4.2.1 GENERAL STRUCTURE

The model is grid based with a daily time step. In this study, the spatial dimension is set to a 1×1 grid space with cell area of $10 \text{ m} \times 15 \text{ m}$, which is the same as the plots in the original study. There were no plant species differences, and so the production output from the model refers to the average system production. Most values of the parameters used in functions are derived from original data.

4.4.2.2 PLANT GROWTH

Plant growth depends on grow days and annual rainfall (Fryxell et al., 2005). In this study, there is only one cell, so there is no variance in annual rainfall, which equals 436 mm, where 416 mm is from rainfall, and 20 mm is from melted snowfall (Dong et al., 2004). Grow days is calculated from Function 4.1:

$$\begin{cases} GD = 65 + \frac{300 \cdot e^{0.01 \cdot AN}}{e^{0.01 \cdot AN} + e^{6.25}} \\ AN = 436 \end{cases} \quad (4.1)$$

where GD (days) is grow days, and AN (mm) is annual rainfall in each cell.

Vegetation carrying capacity is calculated from annual rainfall and growth days (Function 4.2):

$$\begin{cases} K = \Psi \cdot RPD \\ \Psi = 285 \end{cases} \quad (4.2)$$

where K (g) is species different plant carrying capacity. Ψ is carrying capacity coefficient which equals to 285 derived from the original data.

In growing season, the plant growth function is (Function 4.3):

$$\begin{cases} \frac{dDM}{dt} = R_{MAX} \cdot [DM + 0.07 \cdot K] \cdot \left[1 - \frac{DM + 0.07 \cdot K}{1.07 \cdot K}\right] \\ R_{MAX} = 0.03 \end{cases} \quad (4.3)$$

where DM (g) is aboveground dry plant biomass (model output will convert the unit to t/ha), R_{MAX} (g/dt) is maximum plant growth rate based on different plant species, and it equals to 0.03 in this study. In Fryxell et al. (2005), the plant growth functions are affected by annual rainfall, and the effects are represented as the carrying capacity components (function of rainfall) in Function 4.3. To reduce the rainfall effects on plant growth, the parameters before K in the function are reduced to 0.07, and 1.07 in this study. During dry season, plant biomass would not increase, and declines at a fixed rate (D). Since the original study does not have information on natural plant decrease rate, D was set to 1.79 g as it is in Fryxell et al. (2005).

4.4.2.3 GRAZING MANAGEMENT

According to the original study, grazing was rotationally managed, and grazing stopped at 7, 5, and 3 cm sward height under LG, MG, and HG. Rotational grazing starts at day = 181 (July 1st) with three 5-days grazing periods, and a 20-day resting period following each grazing period. The third grazing period stops at day = 237 (August 24th). After this, there is no grazing, because the whole grazing management stops at September 15th, which is the resting period after August 24th. Three stopping points of sward height were converted in to biomass, which were 1.87, 1.33, and 0.8 tDM/ha.

4.4.2.4 GRAZING AND DETACHMENT

Grazing rate is calculated from stocking density. The stocking density function comes from PHYGROW (Stuth et al., 2003). Animal stocking density is calculated from maximum and minimum stocking density, plant biomass, and plant carrying capacity (Function 4.4):

$$\left\{ \begin{array}{l} SD = \frac{DM_{AV}}{K - DM_{UAV}} \cdot (SD_{MAX} - SD_{MIN}) + SD_{MIN} \\ DM_{AV} = DM - DM_{UAV}, \quad DM_{UAV} = 1.87, 1.33, 0.8 \\ SD_{MAX} = 0, 0.07, 0.13, 0.19 \quad SD_{MIN} = 0 \end{array} \right. \quad (4.4)$$

where SD (animal/m²) is animal stocking density, DM_{AV} (g) is available aboveground biomass, DM_{UAV} (g) is unavailable aboveground biomass that is the stopping points for grazing, SD_{MAX} (animal/m²) is maximum stocking density, which are 0, 0.07, 0.13, and 0.19 (animal/m²) for NG, LG, MG, and HG respectively, and SD_{MIN} (animal/m²) is minimum stocking density, which is set to zero.

Total demand is calculated from the total animal number and maximum intake rate (Function 4.5):

$$\left\{ \begin{array}{l} TD = AN \cdot INT_{MAX} \\ INT_{MAX} = 1000 \end{array} \right. \quad (4.5)$$

where AN is animal number, and INT_{MAX} (g) is maximum intake rate, and is set to 1000 g for Tibetan sheep according to data from Thornley (1998).

Grazing intake equals TD in this study, and detachment amount equals 0.3 TD (Day et al., 1997). Both of these two values are subtracted from plant aboveground biomass. The ratios between the sum of grazing intake and detachment amount after one grazing period and plant biomass at the start of that period is the final grazing intensity, which are approximately 0, 0.3, 0.5, and 0.7 for NG, LG, MG, and HG.

4.4.2.5 LAI AND PHOTOSYNTHESIS

LAI is calculated from plant biomass (Thornley (1998), Function 4.6):

$$\left\{ \begin{array}{l} LAI = SLA_{AVG} \cdot FRAC_{LAM} \cdot DM \\ SLA_{AVG} = 0.017, \quad FRAC_{LAM} = 1 \end{array} \right. \quad (4.6)$$

where SLA_{AVG} (m^2/g) is average specific leaf area, which is 0.017 (m^2/g) according to the original study, $FRAC_{LAM}$ is plant growth fraction to leaf. This value is set to 1 because DM is aboveground biomass, and most of the aboveground biomass of the plants in the experiment is leaf material.

Photosynthesis rate is calculated from LAI with a diminishing-return curve (Thornley (1998), Function 4.7):

$$\begin{cases} PS = \frac{a \cdot (LAI + d)}{b + c \cdot (LAI + d)} + e \\ a = 9, \quad b = 2.5, \quad c = 1.5, \quad d = 2, \quad e = 0.2 \end{cases} \quad (4.7)$$

where PS ($\mu molCO_2/m^2 \cdot s$) is photosynthesis rate on a time step basis, a , b , c , d , e are regression parameters derived the original data (Dong et al., 2004).

4.4.3 SIMULATION OUTPUTS

Two simulations were done in this study: a one-year simulation for comparisons with the origin data, and a ten-year simulation for showing the general patterns of the responses of plant biomass production to different grazing intensities. In the one-year simulation, simulated data were output on day=206 (late-July), and day=258 (mid-September). Since the model doesn't have modules for tiller density calculation, growth ratio (the ratio between the actual growth rate under grazing and no grazing on the same day) was simulated to show the changes in plant growth. In the ten-year simulation, biomass production was recorded on a daily step for ten years from 2000 to 2009.

4.5 SIMULATION RESULTS

4.5.1 ONE-YEAR SIMULATION

From Figure 4.3 the general patterns of the simulated data agree with the observed data. Plant biomass, LAI, and photosynthesis rate decrease with increasing grazing intensity, and plant growth increases largely with increasing grazing intensity and decreasing plant biomass. There are some inconsistencies between the simulation results and observations on LAI and photosynthesis. In the model, LAI and photosynthesis rate have positive relationships with plant biomass. However, in the observation data, especially in data for NG, there can sometimes be non-positive relationships. For example, under NG condition, in late-July, the plot has 3.8 tDM/ha of plant biomass with LAI of 8.04 and photosynthesis rate of $5.02 \mu\text{molCO}_2/\text{m}^2 \cdot \text{s}$, while in mid-September, plant biomass is 7.83 tDM/ha with LAI of 7.73 and photosynthesis rate of $2.94 \mu\text{molCO}_2/\text{m}^2 \cdot \text{s}$ (Dong et al., 2004). Plots with very different plant biomass can have relatively similar LAI, and more plant biomass will have photosynthesis rate in this situation. These relationships are not discussed in the original study, which can be caused by complicated plant growing mechanisms, or simply by measurement errors.

4.5.2 TEN-YEAR SIMULATION

With the current parameterization of the model, a ten year simulation was done under different grazing intensity conditions (Figure 4.4). From the results, the most sustainable grazing intensity was LG with a five-day intake proportion of 0.3, which never touched the grazing stop point (1.87 tDM/ha) throughout the simulation, and is consistent with the conclusions in the original study. Results from MG and HG are close to each other. The minimum biomass under both grazing intensities hit the grazing stopping points, 1.33 tDM/ha and 0.8 tDM/ha respectively, which can be detrimental to the system's ability to recover in real world conditions if there is no grazing management controlling the maximum grazing amount.

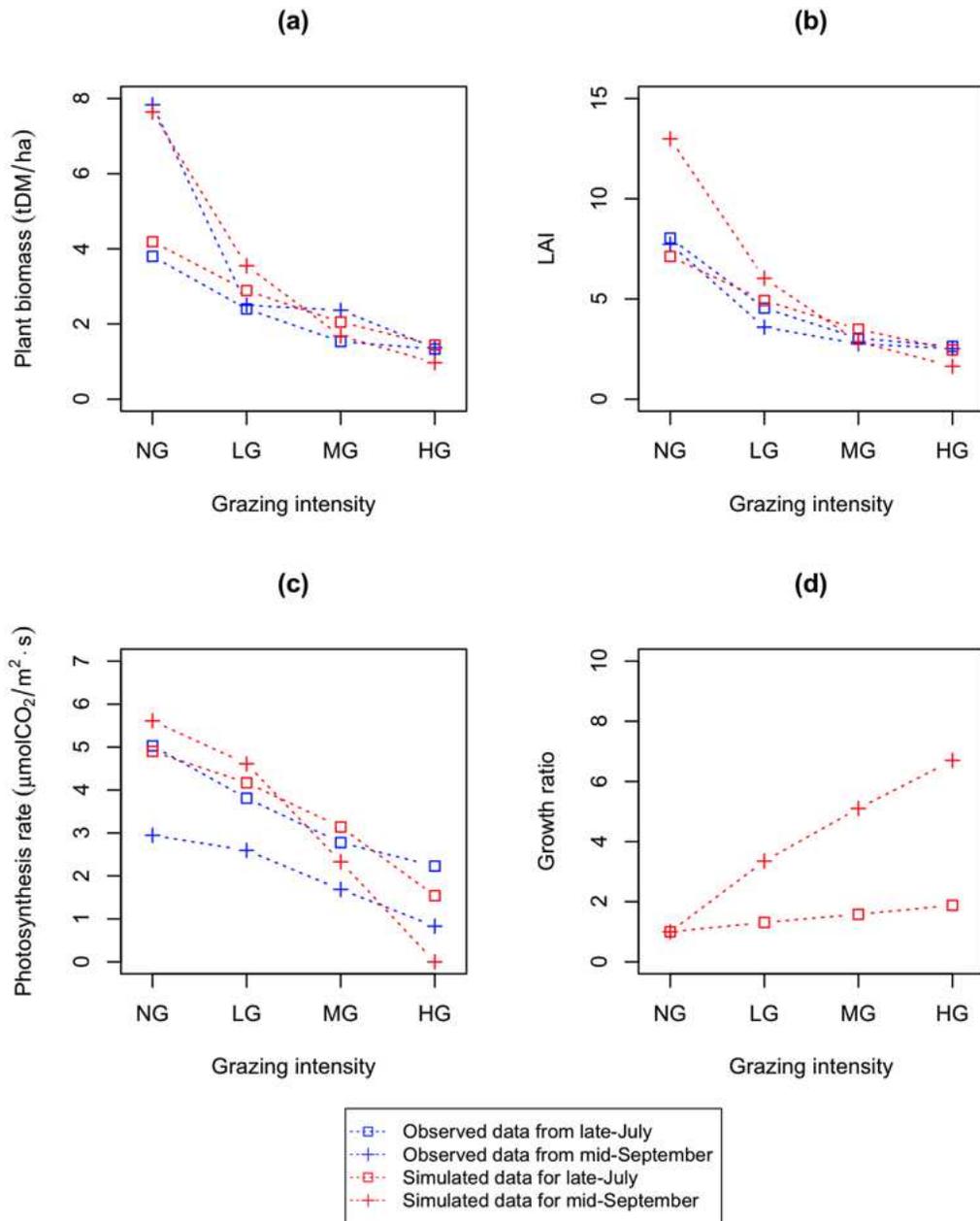


Figure 4.3: Results from the one-year simulation. (a) is the relationship between plant biomass and grazing intensity; (b) is the relationship between average plant LAI and grazing intensity; (c) is the relationship between average plant photosynthesis and grazing intensity; and (d) is the relationship between average plant growth ratio (the ratio between the actual growth rate under grazing and no grazing on the same day) and grazing intensity. Observed data are from Dong et al. (2004).

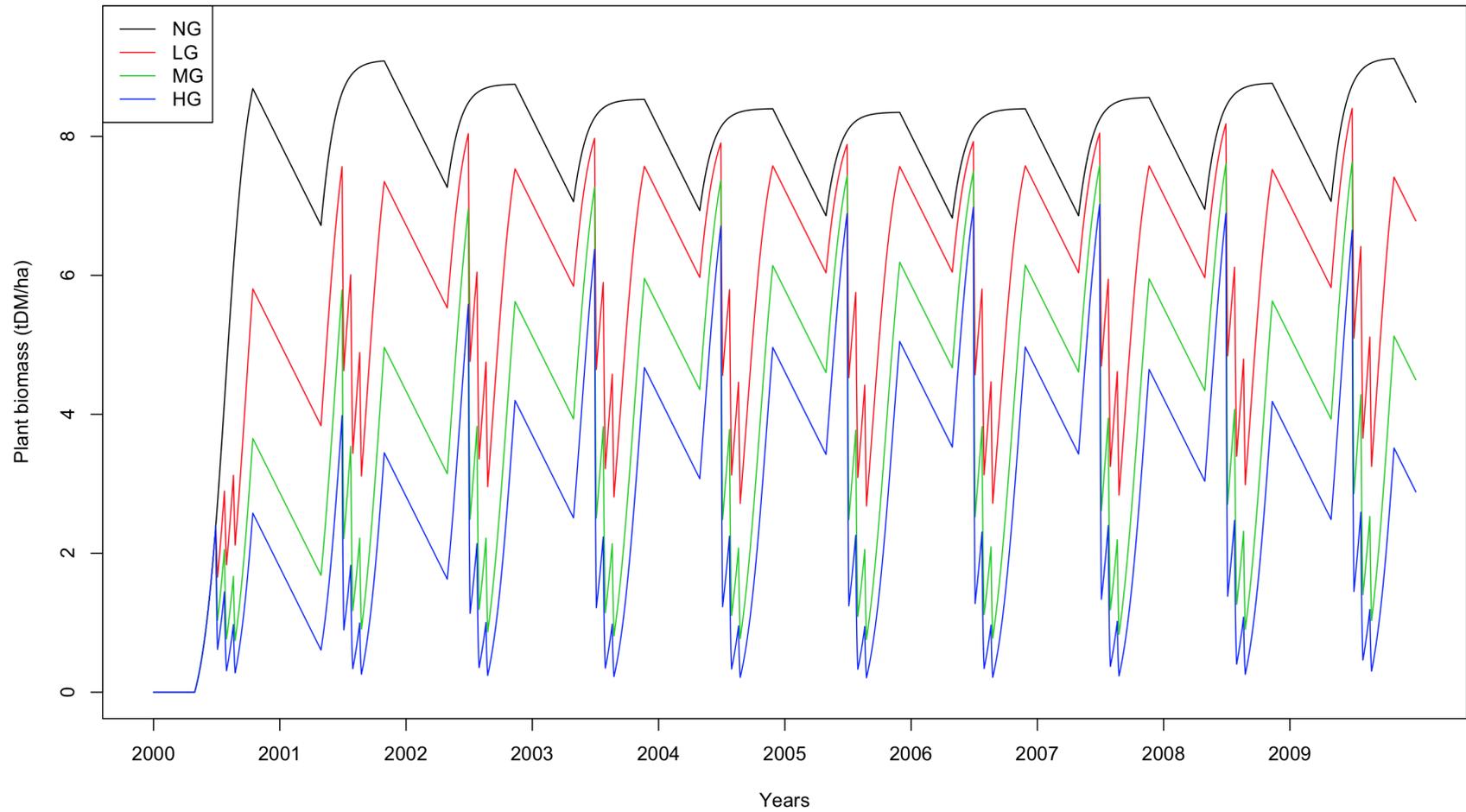


Figure 4.4: Results from the ten-year simulation.

4.6 DISCUSSION

4.6.1 SIMULATION RESULTS

In Tibet, the grassland is constantly under high grazing intensity, which can be harmful to the system (Dong et al., 2004). Studies have suggested that to keep a sustainable grassland system in Qinghai-Tibetan plateau, the maximum of intake proportion should be less than 0.5 (Zhu et al., 1994). Long term high grazing intensity can cause grassland degradation (Li et al., 2001), which can further cause landslides, dust storms, and unbalance in system nutrient cycling (Dong et al., 2012). The detrimental effects of high grazing intensity to grassland ecosystem is represented by the simulation results through plant biomass. Although most of the grazing effects are not included in this study, which can potentially change the simulation outputs, the results are informative for the use as reference in grassland management. In addition, the utility of modular modeling in basic modeling studies is also demonstrated by the two simulations.

4.6.2 MODULAR MODELING

For the challenges in synthesizing grassland modeling studies, a general modeling approach, modular modeling, and an example model with most of grazing effects included using this approach was developed (Miao, Chapter 3). The possibility to include all grazing effects as independent modules with standardized inputs and outputs was demonstrated (Miao, Chapter 3), and it makes this approach promising. Model development processes can be potentially more efficient with the parallel and independent features of modular modeling (Basten et al., 2015), and modeling studies can be more flexible, where users can study different grazing effects separately, and open source community development can be allowed (Laurent, 2008). However, not all of the modeling studies need to include all grazing effects or compare them separately. Under this situation, can modular modeling still be useful? For example, in this study, users may only want to simulate the general patterns of the responses from plants to different levels of grazing intensity with some simple outputs of LAI and photosynthesis rate for management reference. This can be done with standardized modular

models as generally shown in this study. By turning modules on and off, modelers can choose which modules they want to include in the study, and calibrate functions and variable values used in different modules. The results show that although many grazing effects are not included, the model can still generate enough information for users to reference.

What are the benefits of using modular modeling models compared to traditional modeling studies? First the model building processes can be more transparent to users. In traditional modeling studies, people build different models with various approaches and insights. For example, in grazing effects components modeling, there can be many different approaches, ranging from simple defoliation effects to multiple levels of grazing effects (Leriche et al., 2001). Most of the time, the reason for this variability is not clearly discussed in modeling studies. Users can always assume these differences are caused by different study subjects, objectives, hypotheses, etc. But the diversity itself causes confusion. Users don't have standards to make comparisons and evaluations, and may not have enough knowledge as to why the models on hand are setup differently. With standardized modular models, model developers are forced to explain their module setups based on specific study objectives, and subjects. In most cases, including all available modules is unnecessary, and thus the unused modules need to be turned off intentionally with explanations. For example, in the 'Reasoning for module status' section, the status of different grazing related modules are briefly explained, which gives users a basic idea of the reasons why some effects are included and others are not. This clarifies model development processes to both modelers and users.

The flexibility of modular modeling in traditional modeling studies is represented by to the benefits of modular programming from the independent feature of modules (Babb and Lee, 2012). In this study, LAI, and photosynthesis rate calculation are independent to plant growth calculation. When the calculation of these two variables are not concerned, users can turn these two modules off. So the program only has to simulate general plant growth, which can theoretically save computational resources in large scale simulations.

CHAPTER 5

CONCLUSION

From the second chapter, the diversity of current grazing models is generally discussed. With the number of various approaches, it can be overwhelming to make model comparisons and evaluations. Reviewing all of the existing models is time consuming and sometimes unnecessary. Finding a way to make this procedure easier and clearer is thus crucial. Modular modeling can be one of the pathways. Although most modelers have already applied the idea of modularity in structuring their code, such as CENTURY and G-RANGE, to improve the clarity and general programming efficiency of their models (Parton et al., 1992; Boone et al., 2011), treating modular modeling as the basic modeling logic, where single module can be compared and developed separately based on various study objectives has rarely been done. Modular modeling is a small step forward from traditional modeling with modular programming paradigm. It emphasizes the generality and extensibility of base model structures, and the portability of modules. This not only helps people to clarify the structures of models, which makes it easier to conduct comparisons and evaluations, but also promotes the introduction of open source community development to model development. Open source community has been largely beneficial to software developments under certain circumstances (Laurent, 2008). I expect it can also benefit ecosystem modeling in the same way.

To demonstrate the benefits of modular modeling in grazing effects studies, an example model using modular approach was developed in the third chapter. With standardized inputs and outputs, it is possible to include all possible grazing effects into one model, which is meaningful to grazing effects studies when most of the effects are indirect, and the mechanisms behind these effects are usually unclear. By comparing different effects

independently, people can have a better understanding on how much these effects are affecting the system, and potentially add clarity to the relative mechanisms.

In the fourth chapter, a simulation using the example model developed in the third chapter was conducted based on real data. It demonstrates the utility of a large modular model, when most of the modules are unnecessary. Under this situation, the advantage of using standardized models developed with modular modeling is that it can make the model development process more transparent to users. By turning unrelated modules off, the whole model can work just as other traditional models do, and developers and users do not need to parameterize unnecessary elements. However, developers may have to consider discuss the reasons why some modules are turned off and others are not. This helps both developers and users to understand the model much better.

This project is mainly focused on grazing effects modeling. In future studies, a more general application of modular modeling may be done, where the inputs and outputs of an ecosystem model have been generally standardized, which can promote the open source development, another important issue in modular modeling. If there can be a mature and active ecosystem development community working on the same standardized modular model, it is possible that the model will be better than most of existing ecosystem models.

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