

# Modeling how herbivores facilitate lawn and bunch grass coexistence: comparing two hypotheses



Masterproject by

Studentnr:

Supervisors:

Research group:

Institute:

Date:

E.R. Veldhuis

s1913298

prof. dr. F.J. Weissing,

dr. J. Bakker

Theoretical Research in Evolutionary Life Sciences (TRÈS)

Groningen Institute for Evolutionary LIFE Sciences (GELIFES)

5/12/2015



## **Summary**

It is generally accepted that herbivores promote lawn grasses and thereby play an important role in the lawn- and bunch- grass coexistence. Whereas lawn grasses are nutrient rich and have a short stature, bunch grasses have a tall erect growth and have high concentrations of unpalatable compounds. Indirect effects of herbivores that promote lawn grasses outweigh direct effects of herbivory that reduce lawn grasses. The mechanism of the indirect effects is controversial and currently two hypotheses exist that explain how herbivores promote lawn grasses. Whereas the nutrient-based hypothesis assumes that herbivores promote lawn grasses by increasing nutrient availability, the water-based hypothesis states that herbivores increase drought stress and lawn grasses are better in the competition for water than bunch grasses. With two models we investigated whether the assumed indirect effects of herbivores of each hypothesis can outweigh the costs of herbivory and thus result in a net benefit for lawn grasses. Our nutrient-limited model shows that herbivores only stimulate the evolution of lawn and bunch grasses when herbivores are externally controlled. Although herbivores increase the nutrient cycling speed, herbivores always suppress lawn grasses because of herbivory. Thus indirect positive effects did not compensate for the direct negative effects. Outcomes of our nutrient-limited model did not correspond with field observations. Our water-limited model shows that herbivores stimulate the evolution of lawn and bunch grasses, regardless of how herbivore numbers are controlled. An increase in the water influx promotes evolution of bunch grasses and bunch patch formation. When competition for light was implemented in our water-limited model herbivores promote lawn grasses. Our water-limited model supports the water-based hypothesis, but only when competition for light was implemented.



## Table of Contents

1.	Introduction .....	1
2.	Overview of the Methods .....	2
	<i>Ecological baseline model</i> .....	2
	<i>Plant competition</i> .....	2
	<i>Invasion analysis</i> .....	3
3.	The model.....	4
	3.1 <i>Nutrient-limited growth</i> .....	4
	3.2 <i>Water-limited growth</i> .....	4
	3.3 <i>Competition for light</i> .....	6
	3.4 <i>Effects of bunchness</i> .....	8
4.	Results.....	9
	4.1 <i>Nutrient-limited model</i> .....	9
	4.2 <i>Nutrient-limited model, incorporating competition for light</i> .....	10
	4.3 <i>Water-limited model</i> .....	10
	4.4 <i>Water-limited model incorporating competition for light</i> .....	10
5.	Discussion.....	12
	<i>Nutrient based hypothesis</i> .....	13
	<i>Water based hypothesis</i> .....	14
	<i>Use other ecosystem</i> .....	Error! Bookmark not defined.
	<i>Robustness of the model</i> .....	15
6.	Bibliography.....	16

## 1. Introduction

In many geographically and climatically separated grazed ecosystems a mosaic pattern of lawn- and bunch grass patches has been found (Howison et al. unpublished). In general, lawn grasses are shorter and invest more in vegetative lateral growth using horizontal stems which make them able to easily invade bare soil. Lawn grasses have higher concentrations of several minerals (Na, N, P, K, Mg and Ca) in their tissues (McNaughton 1983, Stock et al. 2010, Anderson et al. 2013, Veldhuis et al. 2014, Fokkema et al. unpublished) which makes them more drought tolerant (Hasegawa et al. 2000, Munns 2002, Bartlett et al. 2012) but also more attractive to herbivores (Kleynhans et al. 2011). Bunch grasses on the other hand have a tall erect growth form which makes them good light competitors. The accumulation of building compounds (e.g. lignin) makes bunch grasses less palatable.

Herbivores prefer eating lawn above bunch grasses, which suggest that herbivores suppress lawn grass abundances. However, herbivores do promote lawn patches and thereby the coexistence of these two grass types (McNaughton 1984, Van Coller et al. 2013). Apparently, the direct negative effects of herbivory are outweighed by indirect effects of herbivores that promote lawn grasses, resulting in a net benefit for lawn grasses. Currently two hypotheses explain the beneficial effect of herbivores on lawn grasses: a nutrient-based hypothesis and a water-based hypothesis.

The nutrient-based hypothesis states that herbivores increase the nutrient turnover speed and therefore the nutrient availability in grazing lawns (Fig. 1A)(Ruess and McNaughton 1987). Herbivores convert grass into urine and dung which contains nutrients that rapidly become available for plants (McNaughton 1984). Herbivores visit lawn patches more frequently because lawn grasses are more palatable than bunch grasses (McNaughton 1984). Thus herbivores particularly increase nutrient availability in lawn patches giving lawn grasses an advantage over bunch grasses.

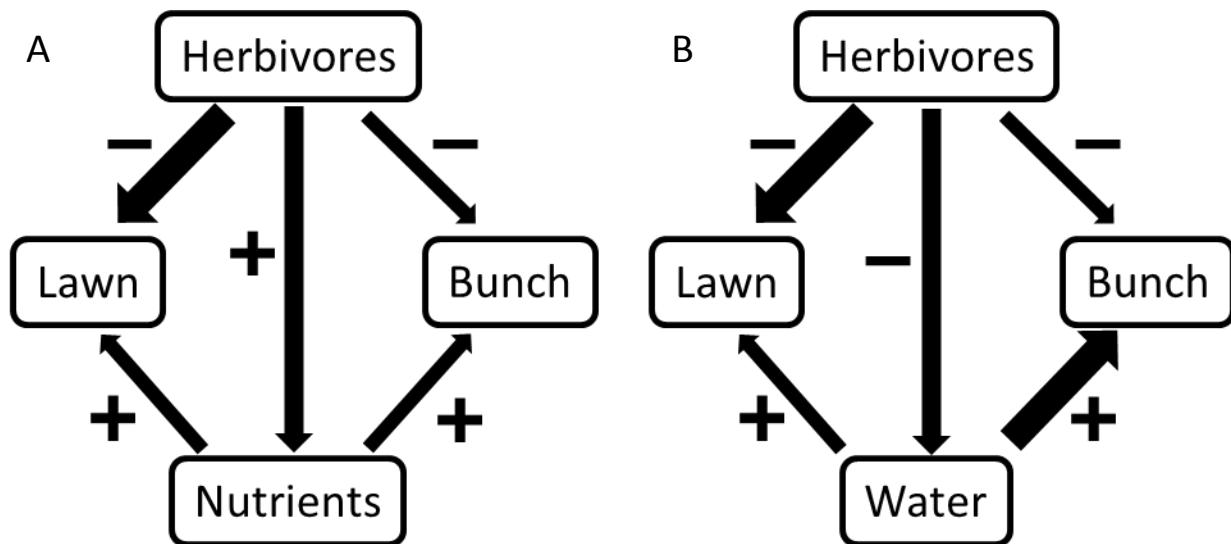


Figure 1. Scheme of the nutrient-based hypothesis (A) and the water-based hypothesis (B).

(A) According to the nutrient-based hypothesis herbivores have a direct negative effect on both grasses through herbivory. The direct negative effect is stronger to lawn grasses since herbivores prefer lawn grasses over bunch grasses. Note that the size of the arrows correspond with the strength of is effect. Indirectly herbivores promote both grasses by increasing the nutrient availability. (B) The water-based hypothesis expects the same negative effects of herbivory on both grasses as the nutrient-based hypothesis. Herbivores indirectly negatively affect both grasses by reducing the water availability through trampling. Water has a strong positive effect on bunch grasses, while lawn grasses are better adapted to drought. Since lawn grasses are better competitors for water, the reduction of water by herbivores result in a net benefit for lawn grasses.

The recently proposed water-based hypothesis states that herbivores create drier environments where only lawn plants can survive (Fig. 1B). Herbivores compact the soil which decreases water infiltration (Abdelmagid et al. 1987) and therefore increases water run-off and soil evaporation (Schrama et al. 2013). Thereby herbivory reduces plant biomass and shading. This leads to an increased soil temperature and wind velocity which in turn will increase the evaporation (Schrama et al. 2012). Because of the low water availability, plants cannot invest in costly anti-herbivore defenses. To increase the water uptake, plants accumulate minerals in their shoots to increase their osmolarity (Veldhuis et al. 2014, Fokkema et al. unpublished) which, as a side effect, makes them more attractive to herbivores as well. Thus due to the stressful conditions only palatable plants are able to survive in these lawn patches.

The aim of this study is to investigate both hypotheses. Since these hypotheses include feedback loops with indirect effects, simple causal reasoning is difficult. Therefore we used a model to investigate these hypotheses. We performed an invasion analysis in order to test these hypotheses from both an evolutionary and ecological perspective.

## 2. Overview of the Methods

### *Ecological baseline model*

For each hypothesis a standard model was made (Fig. 2). Each model contains a system of three ordinary differential equations, one for each of the state variables (plant biomass in terms of the limiting nutrient ( $P$ ), herbivore biomass in terms of the limiting nutrient ( $H$ ) and nutrients ( $N$ ) or water ( $W$ )). Typically a system is in stable state when the variables are equal to  $P^*$ ,  $H^*$  and  $N^*$  or  $W^*$ . In some cases  $H$  was fixed to investigate scenarios where herbivores numbers are externally controlled.

### *Plant competition*

In both models, we compare two plants with different characteristics. Plants differ in their “bunchness”, this means, some of the parameters that describe plant characteristics vary with parameter ‘ $b$ ’.

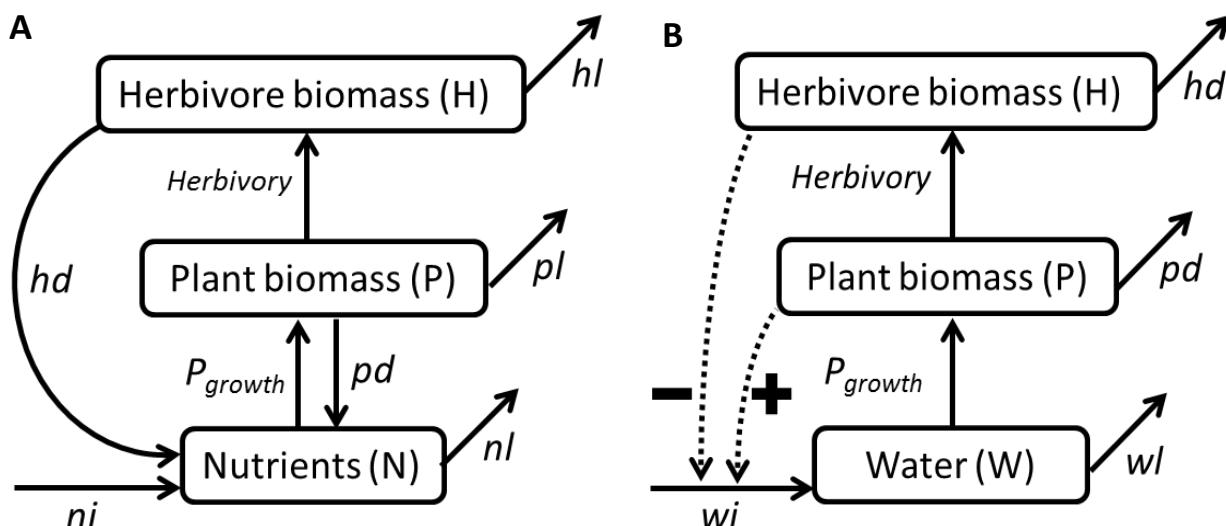


Figure 2. (A) Scheme of the nutrient-limited model. The scheme is identical to the standard plant herbivore model proposed by DeAngelis (1992). (B) Scheme of the water-limited model. Herbivores negatively affect water infiltration whereas plants positively affect water infiltration.

"Bunchness" ( $b$ ) varies from  $b=0$ , a lawn grass, to  $b=1$  a bunch grass. We used a typical resident scenario: one resident plant with bunchness  $b_{res}$  that has reached equilibrium that is confronted with a rare mutant plant with bunchness  $b_{mut} = b_{res} + \epsilon$ . The residential plant has a per capita growth rate of zero; otherwise the system would not be in equilibrium. Therefore the sign of the per capita growth rate of the invader in a population with  $P^*(b_{res})$ ,  $H^*(b_{res})$  and  $N^*(b_{res})$  or  $W^*(b_{res})$  determines whether the invader will grow, and outcompete the resident, or decline and go extinct.

### Invasion analysis

For both models we calculated the per capita growth rate of the rare mutant for each resident and visualized this with a pairwise invasibility plot (PIP; Fig. 3 ; (Geritz et al. 1998)). The horizontal axis represents the bunchness of the residential plant whereas the vertical axis represents the bunchness of the rare mutant. In white areas the per capita growth rate of the mutant is negative, meaning that the mutant will go extinct. In dark green areas the per capita growth rate of the mutant is positive, meaning that the mutant can invade the resident population and will become the new resident. The new resident can again be invaded by another mutant, which will become the new resident etc. A resident that cannot be invaded by any mutant (the per capita growth rate is negative for all mutants) is called an **attractor**, since the bunchness of the plant population will 'walk towards' this one resident with an intermediate bunchness (Fig. 3B). A resident that can be invaded by both mutants with a higher and a lower

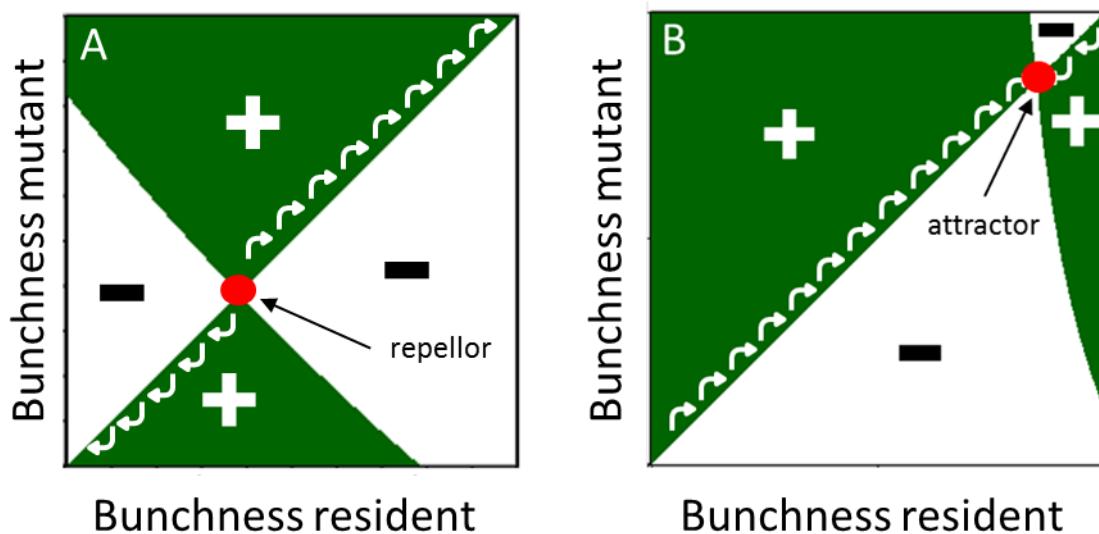


Figure 3. Example of pairwise invasibility plots.

The horizontal and vertical axes show the bunchness of the resident ( $b_{res}$ ) and a rare mutant ( $b_{res} + \epsilon$ ) respectively. Since the system of differential ordinary equations in equilibrium the per capita growth rate of the residential population is zero. APIP shows the sign of the per capita growth rate of rare mutants. The per capita growth rate of mutants is positive in dark green areas and negative in white areas. On the diagonal the bunchness of the mutant and resident are equal, therefore the per capita growth rate of both mutant and resident are zero. In dark green areas, where the per capita growth rate of mutants is positive, mutants can invade the population and become the new resident. This way the bunchness of the population can 'walk across' the diagonal (indicated by the white arrows). Figure 3A shows a repeller, a resident population with a bunchness that can be invaded by both mutants with higher and lower bunchnesses. Bunchness of the population will always 'walk away' from repellers. Depending on the initial conditions invasions can lead to one of two populations: a population with a low bunchness (a lawn grass) or a population with a high bunchness (a bunch grass). Figure 3B shows an attractor, a residential bunchness that cannot be invaded by any mutant. Bunchness of the population will always 'walk towards' attractors. In this case invasions will always lead to a population with the bunchness of the attractor, one intermediate bunchness.

bunchness is called a **repellor**, since selection will ‘walk away’ from this resident (Fig. 3A). Depending on the starting conditions a plant with a low or high bunchness will be selected. In a heterogeneous environment a variety of initial conditions are available, therefore a mosaic pattern of lawn and bunch patches can be formed. When the repellor has a higher bunchness, more to the upper right corner of the figure, there is an increased probability that initial conditions start left from the repellor and lawn patches are formed.

### 3. The model

#### 3.1 Nutrient-limited growth

The nutrient-limited growth model is described by the following system of ordinary differential equations, a modified version of the model of DeAngelis (1992) (Fig 2A):

$$\frac{dP}{dt} = P * \left( r_{max}^P \frac{N}{N + Kn} - d_P - l_P - r_{max}^H \frac{H}{P + Kp} \right) \quad (1)$$

$$\frac{dH}{dt} = H * \left( r_{max}^H \frac{P}{P + Kp} - d_H - l_H \right) \quad (2)$$

$$\frac{dN}{dt} = n_{in} + P * d_P + H * d_H - r_{max}^P * P * \frac{N}{N + Kn} - N * l_N \quad (3)$$

This system reflects the following assumptions:

- Plant growth is described by a Holling type II function depending on nutrient availability with max per capita growth rate of  $r_{max}^P$  and a half saturation constant  $Kn$
- Herbivore growth is described by a Holling type II function depending on plant density with max per capita growth rate of  $r_{max}^H$  and a half saturation constant  $Kp$
- Plants and herbivores have a per capita loss rate by death  $d_P$  or  $d_H$  and leaching  $l_P$  or  $l_H$ , respectively
- Plant loss due to herbivory is equal to the growth of herbivores ( $H * r_{max}^H * \frac{P}{P + Kp}$ )
- Nutrient loss due to plant growth is equal to the plant growth ( $P * r_{max}^P * \frac{N}{N + Kn}$ )
- There is a constant input of nutrients  $n_{in}$
- Part of the plant and herbivore losses,  $d_P$  and  $d_H$  respectively, will return to the nutrient pool
- Nutrients leach at a constant rate  $l_N$
- Variables and parameters are listed in table 1.

#### 3.2 Water-limited growth

The water-limited growth model is described by the following system of ordinary differential equations (Fig 2B):

$$\frac{dP}{dt} = P * \left( r_{max}^P \frac{W}{W + Kw} - d_P - l_P - r_{max}^H \frac{H}{P + Kp} \right) \quad (4)$$

$$\frac{dH}{dt} = H * \left( r_{max}^H \frac{P}{P + Kp} - d_H - l_H \right) \quad (5)$$

$$\frac{dW}{dt} = w_{in} * \frac{P}{P + Qp} * \frac{Qh}{H + Qh} - r_{max}^P * P * \frac{W}{W + Kw} - W * l_W \quad (6)$$

Variable/Parameter	Symbol	Value	dimension	References
--------------------	--------	-------	-----------	------------

Nutrient	$N$	g nutrient/m <sup>2</sup>	
Plant biomass	$P$	g nutrient/m <sup>2</sup>	
Herbivore biomass	$H$	g nutrient/m <sup>2</sup>	
Water	$W$	g/m <sup>2</sup>	
Nutrient inflow	$n_{in}$	0.6	g/m <sup>2</sup> yr <sup>-1</sup> De Mazancourt et al. (1998)
Nutrient leaching	$l_N$	0.05	g/m <sup>2</sup> yr <sup>-1</sup> De Mazancourt et al. (1998)
Nutrient uptake half saturation rate	$Kn$	5	g nutrient/m <sup>2</sup>
Plant relative growth rate Nutrient-based model	$r_{max}^P$	0.835-0.167 $b$	g/g yr <sup>-1</sup> De Mazancourt et al. (1999) Van der Plas et al. (2013)
Plant relative growth rate Water-based model	$r_{max}^P$	0.835	g/g yr <sup>-1</sup> De Mazancourt et al. (1999)
Plant death rate	$d_P$	0.2269	yr <sup>-1</sup> De Mazancourt et al. (1998)
Plant leaching rate	$l_P$	0.048	yr <sup>-1</sup> De Mazancourt et al. (1998)
Herbivore relative growth rate	$r_{max}^H$	0.5	g/g yr <sup>-1</sup> Van Langevelde et al. (2003)
Herbivore death rate	$d_H$	0.2	yr <sup>-1</sup>
Herbivore leaching rate	$l_H$	0.03	yr <sup>-1</sup>
Water inflow (rain)	$w_{in}$	7-18	dm yr <sup>-1</sup>
Water leaching rate	$l_W$	0.05	yr <sup>-1</sup>
Water uptake half saturation constant	$Kp$	6.67	g nutrient/m <sup>2</sup>
Water uptake half saturation rate	$Kw$	7.5	g/m <sup>2</sup>
Water infiltration half saturation rate with respect to plant	$Qp$	5	g nutrient/m <sup>2</sup>
Inversed water infiltration half saturation rate with respect to herbivores	$Qh$	0.8	g nutrient/m <sup>2</sup>
Vegetation height	$h$	32+48 $b$	cm McNaughton (1984)
Light extinction coefficient	$k$	0.75	J m <sup>-2</sup> yr <sup>-1</sup>
Light uptake half saturation rate	$kh$	0.01	J m <sup>-2</sup> yr <sup>-1</sup>
Light supply	$I_{in}$	1	J m <sup>-2</sup> yr <sup>-1</sup>
Bunchness	$b$	0-1	

Table 1 Variables and parameters of the models.

This system reflects the following assumptions:

- Plant growth is described by a Holling type II function depending on water availability with max per capita growth rate of  $r_{max}^P$  and a half saturation constant  $Kw$
- Herbivore growth is described by a Holling type II function depending on plant density with max per capita growth rate of  $r_{max}^H$  and a half saturation constant  $Kp$
- Plants and herbivores have a per capita loss rate by death  $d_P$ - or  $d_H$ - and leaching  $l_P$  or  $l_H$ , respectively
- Plant loss due to herbivory is equal to the growth of herbivores ( $H * r_{max}^H * \frac{P}{P+Kp}$ )
- Water loss due to plant growth is equal to the plant growth ( $P * r_{max}^P * \frac{W}{W+Kw}$ )
- Water leaches to deeper soil layers at a constant rate  $l_W$

- Water infiltration, water that infiltrates the soil and enters the water pool, is defined by influx ratio  $w_{in}$ , plant density and herbivore density.
- Plant density positively affects water influx following the holling type II function ( $\frac{P}{P+Qp}$ ) (Walker and Langridge 1997), where  $Qp$  is the water half saturation rate with respect to plant biomass.
- Herbivores negatively affect water influx following the holling type II function ( $\frac{Qh}{H+Qh}$ ), where  $Qh$  is the inversed water infiltration rate with respect to herbivores.
- Variables and parameters are listed in table 1.

### 3.3 Competition for light

Bunch grasses are much taller than lawn grasses (McNaughton 1984) and therefore have an advantage in the competition for light. To implement competition for light we modified a model of Huisman and Weissling (1994) for growth in a light gradient. They showed that light limited growth follows the following function:

$$P \text{ growth} = \frac{r_{max}^P}{k} \ln \left( \frac{Kh + I_{in}}{Kh + I_{in} * e^{kW}} \right) \quad (7)$$

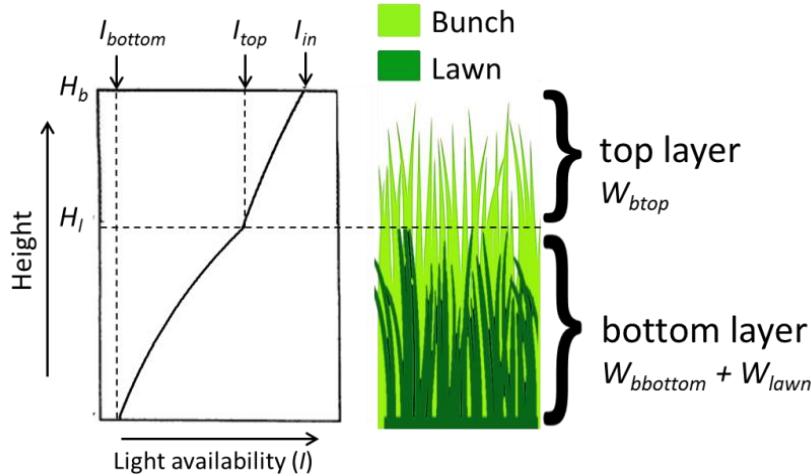
Here,  $k$  is the light extinction coefficient,  $Kh$  is the light intensity required for plant growth at half the maximum rate,  $I_{in}$  is the light supply and  $W$  is the total plant biomass. Note that plant growth is characterized by a Holling type II function. Huisman and Weissling (1994) assumed that biomass is homogeneously distributed. In grasslands however, the plant biomass density in the upper layers is lower than the density of the lower layers of the vegetation. Therefore, we will divide the vegetation in two layers. Whereas the top layer density of the vegetation is equal to the bunch grass density, the bottom layer density of the vegetation is equal to the bunch grass density plus the lawn grass density (Fig. 4).

To implement competition for light in our model we split the vegetation biomass ( $W$ ) into bunch grass biomass in the top layer ( $W_{btop}$ ), bunch grass biomass in the bottom layer ( $W_{bbottom}$ ) and lawn grass biomass ( $W_{lawn}$ ; Fig. 4). Whereas the bunch grass has a monopoly on the light availability in the top layer, in the bottom layer light absorption by bunch and lawn grass is in proportion to their biomass ( $W_{bbottom}$  and  $W_{lawn}$ ). To calculate the proportion of bunch grass biomass in each layer we first calculate the thickness of each layer. The thickness of the vegetation layers depend on the vegetation height ( $h$ ) of the lawn ( $h_l$ ) and bunch ( $h_b$ ) grasses. The bottom layer thickness is equal to the lawn grass vegetation height and top layer thickness is the bunch grass vegetation height minus the lawn grass vegetation height. Accordingly the lawn and bunch biomasses in each layer are given by:

$$W_{lawn} = P_l \quad (8)$$

$$W_{btop} = P_b * \left( 1 - \frac{h_l}{h_b} \right) \quad (9)$$

$$W_{bbottom} = P_b * \frac{h_l}{h_b} \quad (10)$$



**Figure 4.** Schematic view of light absorption.

Light ( $I_{in}$ ) enters the top layer where it will be partly absorbed by bunch grass in the top layer ( $W_{btop}$ ). The remainder ( $I_{top}$ ) enters the bottom layer where light will be partly absorbed by both bunch ( $W_{bbottom}$ ) and lawn ( $W_{lawn}$ ) grasses in proportion to their biomass in this layer.

Here  $P_b$  and  $P_l$  are vegetation biomass of bunch grass and lawn grass respectively. Light absorption in the top ( $I_{top}$ ) and bottom ( $I_{bottom}$ ) layer of the vegetation are given by:

$$I_{top} = \frac{1}{k} * \ln\left(\frac{kh + I_{in}}{kh + I_{in} * e^{-k*W_{btop}}}\right) \quad (11)$$

$$I_{bottom} = \frac{1}{k} * \ln\left(\frac{kh + I_{in} * e^{-k*W_{btop}}}{kh + I_{in} * e^{-k*(P_l + P_b)}}\right) \quad (12)$$

Here,  $I_{in}$  is light that enters the top layer,  $I_{in} * e^{-k*W_{btop}}$  is light that leaves the top layer and enters the bottom layer and  $I_{in} * e^{-k*(P_l + P_b)}$  is the light that leaves the bottom layer.

Light absorption in the bottom layer will be distributed to lawn and bunch grasses in proportion to their biomass in this layer. In the top layer, light was only absorbed by bunch grasses.

Then light absorption of lawn grasses is given by:

$$I_{lawn} = I_{bottom} * \frac{W_{lawn}}{W_{bbottom} + W_{lawn}} \quad (13)$$

Light absorption of bunch grasses is given by:

$$I_{bunch} = I_{top} + I_{bottom} * \frac{W_{bbottom}}{W_{bbottom} + W_{lawn}} \quad (14)$$

The growth of plants in both models is multiplied by the light absorption ( $I$ ). The system of differential equations of the nutrient-limited model including competition for light is:

$$\frac{dP}{dt} = P * \left( r_{max}^P * I * \frac{N}{N + Kn} - d_P - l_P - r_{max}^H \frac{H}{P + Kp} \right) \quad (15)$$

$$\frac{dH}{dt} = H * \left( r_{max}^H \frac{P}{P + Kp} - d_H - l_H \right) \quad (16)$$

$$\frac{dN}{dt} = n_{in} + P * d_P + H * d_H - r_{max}^P * P * I * \frac{N}{N + Kn} - N * l_N \quad (17)$$

The system of differential equations of the water-limited model including competition for light is:

$$\frac{dP}{dt} = P * \left( r_{max}^P * I * \frac{W}{W + Kw} - d_P - l_P - r_{max}^H \frac{H}{P + Kp} \right) \quad (18)$$

$$\frac{dH}{dt} = H * \left( r_{max}^H \frac{P}{P + Kp} - d_H - l_H \right) \quad (19)$$

$$\frac{dW}{dt} = w_{in} * \frac{P}{P + Qp} * \frac{Qh}{H + Qh} - r_{max}^P * P * I * \frac{W}{W + Kw} - W * l_W \quad (20)$$

### ***3.4 Effects of bunchness.***

Since we now have the base-line models, we implemented differences between lawn and bunch grasses. Plants can vary in their bunchness ( $b$ ) which ranges from 0 (lawn grass) to 1 (bunch grass). Bunchness affects three plant characteristics: growth, herbivory and height. This way, plants cannot change one characteristic without changing the two others. For example an investment in anti-herbivore defenses will automatically decrease the growth speed.

#### Growth rate

Under controlled conditions bunch plants grow 20% slower than lawn plants (Van der Plas et al. 2013). According to the nutrient-based hypothesis lawn grasses have a higher productivities (McNaughton 1976, 1979, 1984) however they thought this was due to herbivory rather than a plant intrinsic traits. Out of simplicity we assumed that, in our nutrient-limited model, the growth rate of plants ( $r_{max}^P$ ) linearly depends on bunchness:

$$r_{max(b)}^P = r_{max}^P (1 - 0.2 * b) \quad (21)$$

The water-based hypothesis argues that lawn plants grow faster because they are better adapted to drought due to their higher levels of compatible solutes. We therefore assumed that, in our water-limited model, bunchness affects the water uptake half saturation constant:

$$Kw(b) = Kw(1 + \frac{2}{3}b) \quad (22)$$

#### Herbivory

We assumed that herbivores are specialists, meaning that a plant its palatability only influences its own herbivory pressure and not the herbivory pressure of its neighbors. Bunchness affects herbivory by influencing the plant uptake half saturation constant:

$$Kp(b) = Kp/(1 - \frac{2}{3}b) \quad (23)$$

A higher bunchness will increase the plant uptake half saturation constant and therefore decrease the herbivory pressure.

#### Competition for light

Lawn and bunch plants are 32cm and 80cm, respectively (McNaughton 1984). For simplicity, we assumed vegetation height depends linearly on bunchness:

$$h(b) = 32 + 48b \quad (24)$$

We used invasion analyses for the nutrient-and water-limited model, with and without competition for light. Each model we analyzed with a fixed number of herbivores and a variable number of herbivores. From a biological perspective a fixed number of herbivores means that the number of herbivores is externally controlled, for example in the Serengeti where the large numbers of migrating wildebeest do not depend on the local conditions of one particular grassland they cross.

## 4. Results

### 4.1 Nutrient-limited model

When herbivore biomass is treated as a fixed value we found one repellor, thus depending on the starting conditions a lawn grass or a bunch grass will evolve (Fig.5A). When the fixed number of herbivores is increased the bunchness of the repellor decreases, thus there is an increased probability that evolution will lead to a bunch grass (Fig.5AB). Without herbivores, plants with a lower bunchness have a higher fitness (results not shown). These plants benefit from their high relative growth rate and do not suffer more from herbivory.

When the number of herbivore biomass was variable there was one attractor (see Figure 5c). Thus evolution will lead to a population of plants with one specific bunchness that cannot be invaded by any mutant plant.

Figures 5abc can also be interpreted from an ecological perspective. In case of externally controlled herbivores (Fig. 5ab), lawn patches and bunch patches can be formed depending on the starting conditions. In a heterogeneous ecosystem a variety of initial conditions are available, thus a mosaic pattern of lawn and bunch patches can be formed. Larger numbers of herbivores increase the probability that a bunch patch will be formed. Thus herbivores promote the evolution and patch formation of bunch

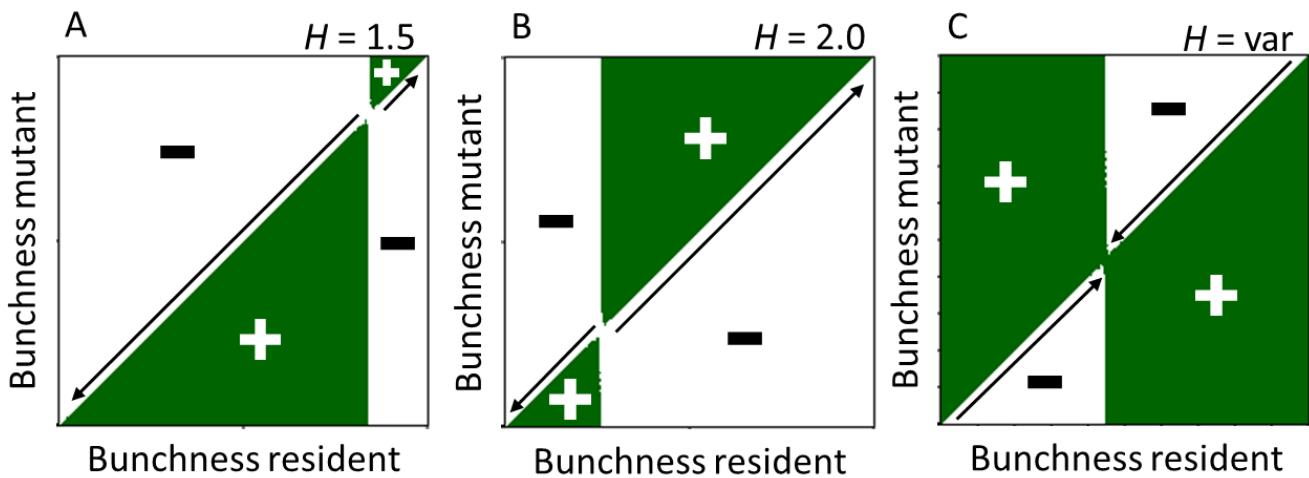


Figure 5. Pairwise invasibility plots of the nutrient-limited model.

For a detailed description on PIPs see figure 3. A,B) PIPs of the nutrient-based model where herbivore numbers are fixed ( $H = 1.5$  in A and  $2.0$  in B). Both plots have one repellor; thus depending on the starting conditions, lawn patches and bunch patches will evolve. A higher herbivore density increases the chance that evolution will lead to a bunch grass, or a bunch patch will be formed (comparing A and B). C) PIP of the nutrient-based model where herbivores are treated as a variable. One attractor was found, indicating that there is one intermediate optimal strategy.

grasses. When herbivores are internally controlled (Fig. 5c) we find a monoculture of plants with one intermediate bunchness. Thus herbivores do not stimulate the co-occurrence of species that differ in bunchness. In both models plant production, which is measure of nutrient cycling speed, increase under moderate levels of herbivory (results not shown).

#### **4.2 Nutrient-limited model, incorporating competition for light**

In the nutrient-limited model where herbivore biomass was fixed and competition for light was included we did not find a biologically relevant equilibrium, an equilibrium where all variable values were positive.

In the nutrient-limited model where competition for light is incorporated and herbivore biomass is variable, we again find one attractor (results not shown). Thus eventually all plants have one intermediate bunchness. When herbivores are internally controlled, herbivores do not stimulate the co-occurrence of species with different bunchnesses, regardless the influence of competition for light. When light availability is implemented in the differential equation (eqn 15 and 17) as a Monod function ( $\frac{I}{I+k_I}$  instead of  $I$ ) the same results are found.

#### **4.3 Water-limited model**

When we consider herbivores as a fixed value in the water-limited model we find one repellor (Fig. 6AB). Thus depending on the initial conditions a lawn or bunch grass will evolve or, from an ecological perspective, a lawn or bunch patch will be formed. When herbivore numbers are low (Fig. 6A) the repellor has a high bunchness. There is a high probability that the starting conditions are left from this repellor and lawn grasses are favored. An increase in herbivore numbers (Fig. 6B) resulted in a repellor with a lower bunchness, indicating a higher probability that initial conditions are right from the repellor and evolution will lead to a bunch grass. Thus, in this model herbivores promoted the evolution of bunch grasses and formation of bunch patches whereas in absence of herbivores lawn grasses are favored.

When herbivore biomass is variable (Fig. 6C) we find one repellor. Thus depending on the initial conditions a lawn or bunch grass will evolve or, from an ecological perspective, a lawn or bunch patch will be formed.

Since the water-based hypothesis states that water availability influences the bunchness of the vegetation we investigated the effect of water influx on invasibility analysis. Figure 6D shows the effect of water influx on the bunchness of the repellor. When the water influx ( $W_{in}$ ) is increased, the repellor has a lower bunchness. Thus water influx increases the probability that a bunch patch will be formed (Fig. 6D).

#### **4.4 Water-limited model incorporating competition for light**

Results show a different pattern after light was incorporated in the water-limited model with fixed herbivore biomass. Low amounts of herbivores almost always lead to evolution of bunch grasses or bunch patch formation since the repellor has a low bunchness (Fig. 7A). When herbivore biomass was increased the bunchness of the repellor increased as well, indicating a higher probability of evolution of lawn grasses or the formation of lawn patches (Fig. 7B). Thus herbivores promote lawn grasses since their indirect effects (induced drought) outweigh their direct effects (herbivory).

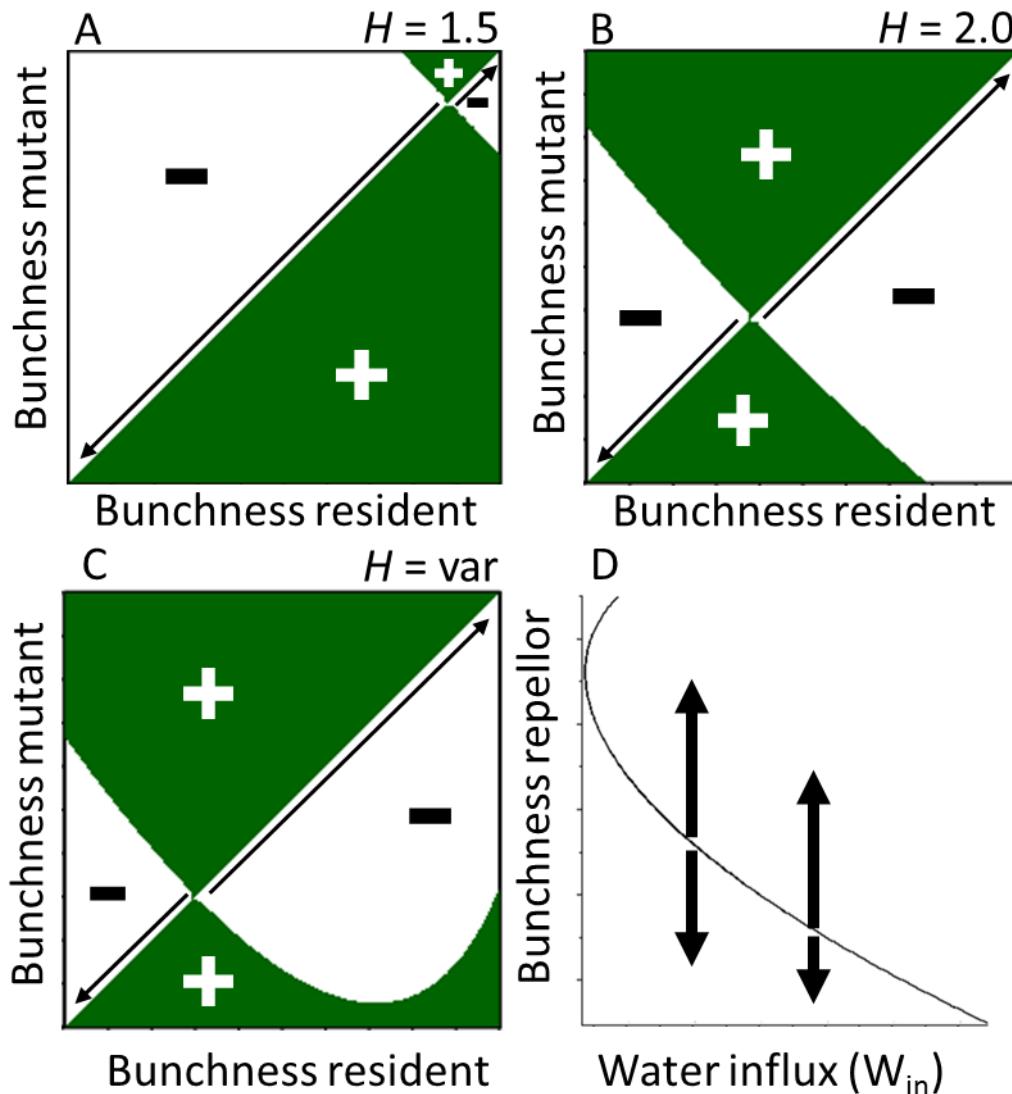


Figure 6. Pairwise invasibility plots (PIPs) for the water-limited model.

For a detailed description on PIPs see figure 3. A,B) PIPs of the water-limited model where herbivore biomass is fixed ( $H=1.5$  and 2 for A and B respectively). In each plot, one repellor was found. An increase in herbivores (comparing A and B) resulted in a repellor on a lower bunchness, which means an increased probability on the evolution of bunch grasses. C) PIP of the water based model where herbivore biomass is variable. One repellor is found. D) Evolutionarily singular strategies across a water influx gradient. The black line shows the bunchness of the repellor for each water influx. When water influx is enhanced the bunchness of the repellor decreases, which means an increased chance evolution will lead to a bunch plant.

When herbivore biomass was variable the same results were found as in the water-limited model without competition for light, one repellor which bunchness decreased when water influx was increased (Fig. 7cd). Thus water influx favored evolution and patch formation of bunch grasses. When light availability is implemented in differential equations (eqn 18 and 20) as a monod function ( $\frac{I}{I+k_I}$  instead of  $I$ ) the same results are found for the model when herbivore biomass is internally controlled. For the model with externally controlled herbivores there only one equilibrium where  $P^*$  equals zero.

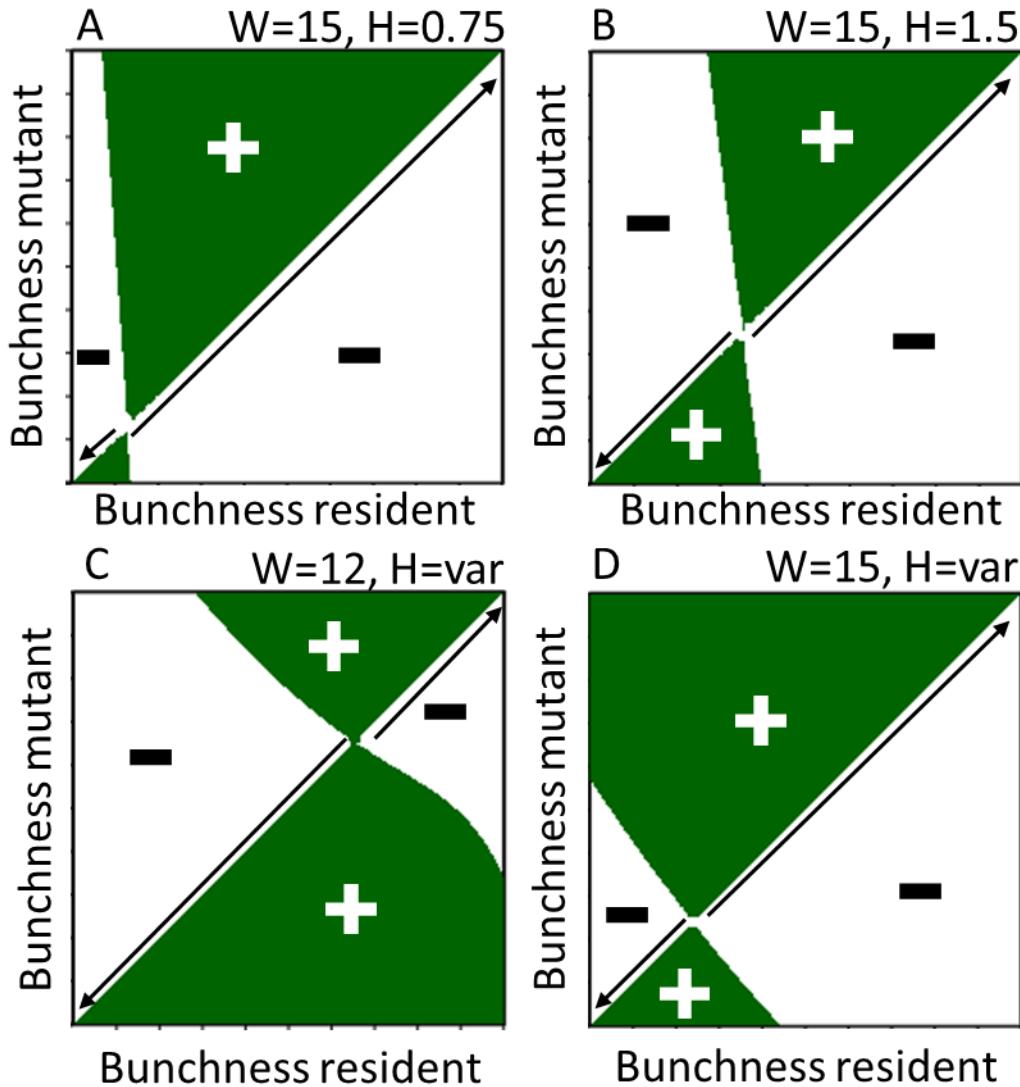


Figure 7. Pairwise invasibility plots of the water-based model including competition for light. For a detailed description on PIPs see figure 3. In all scenarios we found one repellor indicating that both lawn and bunch grasses can evolve or, from an ecological perspective, both lawn and bunch patches can be formed. A,B) When herbivore biomass is fixed, an increase in herbivores stimulate the evolution of lawn grass (A)  $W_{in} = 15, H = 0.75$ ; B)  $W_{in} = 15, H = 1.5$ ). C,D) When herbivore biomass is variable, an increase in water influx will stimulate the evolution of bunch grass ((C)  $W_{in} = 12, H = \text{var}$ ; D)  $W_{in} = 15, H = \text{var}$ ).

## 5. Discussion

Herbivores promote lawn grasses because their indirect positive effects outweigh direct negative effects (McNaughton 1984, Van Coller et al. 2013). Whether the indirect effect of herbivores is increased nutrient cycling, according to the nutrient based hypothesis, or induced drought stress, as stated by the water hypothesis, is unclear. This study modeled both indirect processes to validate each hypothesis. Our nutrient-limited model shows that herbivores only stimulate the evolution of lawn and bunch grasses when herbivores are externally controlled. Thereby herbivores suppress lawn grasses instead of stimulate lawn grasses which contradicts empirical data. Thus indirect positive effects did not

compensate for the direct negative effects of herbivores. Our water-limited model shows that herbivores stimulate the evolution of lawn and bunch grasses, regardless of how herbivore numbers are controlled. After competition for light was implemented in our water-limited model herbivores promote lawn grasses. Thus after implementation of competition for light, our water-limited model supports the water-based hypothesis. We emphasize studying the hypotheses in other, less complicated ecosystems because this might simplify investigating the hypotheses and will provide insights in how environmental conditions may influence the indirect effects proposed by each hypothesis.

### Nutrient based hypothesis

Our nutrient-limited model without competition for light shows that both lawn and bunch grasses evolve only when herbivore numbers are externally controlled. This is remarkable since the nutrient-based hypothesis was inspired on the Serengeti National Park where the great migration of wildebeests (*Connochaetes taurinus*) and zebra (*Equus burchelli*) takes place (McNaughton 1976, 1984, 1985, Ruess and McNaughton 1987). These migrating wildebeests do not depend on the food availability in one particular grassland they cross, thus herbivore numbers were externally controlled. Thus lawn and bunch grasses could evolve following the assumptions of the nutrient-based hypothesis only when herbivores are externally controlled.

According to the nutrient-based hypothesis herbivores promote lawn grasses indirectly by increasing the nutrient cycling speed. Similar to previous studies (McNaughton 1986, De Mazancourt et al. 1998, De Mazancourt and Loreau 2000), our model shows that moderate herbivory indeed increased plant productivity, which reflects an increased nutrient cycling speed. Nonetheless the indirect positive effect did not compensate the direct negative effect of herbivory on lawn plants. In the absence of herbivores lawn grasses are favored and an increase in herbivore biomass suppresses lawn grass formation. The same conclusions were drawn by De Mazancourt and Loreau (2000) who modelled the evolution of lawn plants. In their model plants only differed in their palatability and not in their growth rate. These conclusions do not correspond with empirical data. McNaughton (1984) and Van Coller et al. (2013) used exclosures in their field experiments to test the effect of herbivores on the vegetation. Both studies found that bunch grasses became dominant in plots where herbivores were excluded, indicating that herbivores suppress bunch grasses outside the exclosures. Concluding, the direct negative effect of herbivores on lawn grasses is not compensated by the increased nutrient cycling speed.

When competition for light is added to the nutrient-limited model where herbivores are internally controlled the same conclusions can be drawn. When competition for light is added to the model with externally controlled herbivores there is only one equilibrium for the variables. In this equilibrium the plant biomass is zero.

As suggested by De Mazancourt and Loreau (2000), the indirect effect of herbivory did not compensate for the direct effects probably because of the lack of a spatial component in the models. Dung is deposited homogenously in our model, hence all plants (both lawn and bunch) profit equally from the increased nutrient availability due to herbivory instead of lawn plants only. In addition, herbivores in our model were specialists, whereas in the field both specialists (e.g. impalas) and generalists (rhinos) occur. Specialists eat individual plants, thus one bunch plant in a lawn patch has a huge advantage since it is the

only plant that does not suffer from herbivory and still profits from increased mineralization. Generalists on the other hand eat all or none of the plants in a certain area. The probability of herbivory therefore is influenced by a plant neighbors. A single bunch plant in a lawn patch will therefore suffer equally from herbivory as its lawn plant neighbors. Whereas generalist herbivory reduces successful invasion of bunch plants in lawn patches, it increases the invasion success of lawn plants in bunch patches, as a lawn plant in a bunch patch will not suffer from herbivory. Our nutrient based model did not incorporate spatiality and therefore underestimated indirect positive effects (which promote lawn grasses) and overestimated the direct negative effect of herbivory on lawn grasses.

To improve the model we suggest implementing several cells or patches, where each cell consists of a number of plants. Each individual plant has its own bunchness which alters palatability and relative growth rate. Dung is distributed between cells in proportion to the herbivory at each cell; a cell with many lawn plants will suffer from more herbivory but will also receive more dung than a cell with especially bunch plants. Within each cell dung is distributed homogeneously. This way, dung is distributed according to the nutrient based hypothesis. In case of an herbivore generalist, herbivory does not depend on palatability of one individual plant but on the average palatability all plants within a cell. Each plant in a cell suffers from the same herbivory. This way it is harder for a bunch plant to invade a cell with a low average bunchness (lawn patch) and easier for lawn plant to invade in a cell with a high average bunchness (bunch patch).

### ***Water based hypothesis***

To our knowledge this is the first study that modeled the water based hypothesis. Results of our model correspond with predictions from the water based hypothesis and empirical data, but only after the implementation of competition for light among plants.

Our model without competition for light shows that, depending on the initial conditions, lawn and bunch grasses can evolve. According to our model herbivores suppress lawn grasses which is contradicting to empirical data that show that herbivores stimulate lawn grasses (McNaughton 1985, Van Coller et al. 2013). Water increased bunch patch formation in our model which corresponds to the vegetation patterns in Hluhluwe-imfolozi Park. Hluhluwe-imfolozi Park contains a rainfall gradient ranging from 450 – 850 mm rainfall per year (Van der Plas et al. 2012) Veldhuis et al. (2014) studied the abundance of lawn and bunch patches and found that the abundance of bunch patches positively correlated with rainfall. The same pattern was found in the Serengeti (McNaughton 1985). An increase in water influx in our water-limited model decreased the bunchness of the repellor, indicating an increased probability that a bunch patch is formed.

Implementation of competition for light improved our model. In these models an increase in herbivores enhances the probability of lawn patch formation which is in line with the empirical observations of McNaughton (1985) and Van Coller et al. (2013). The models show that negative direct effects of herbivory are outweighed by indirect positive effects, a drier environment where lawn plants can profit from the competitive advantage in water uptake. Thus only after competition for light was implemented, our water-limited model supports the water-based hypothesis.

### *Application of the model*

The Nutrient-based hypothesis is inspired and especially supported by empirical data of the Serengeti National Park (McNaughton 1976, 1979, 1984, 1985, Ruess and McNaughton 1987). The Nutrient-based hypothesis relies on processes which have a strong influence in this ecosystem. This park contains the great migration of wildebeests and zebra whose numbers do not depend on the food availability in one particular grassland they cross, thus herbivore numbers are externally controlled. This is, according to our nutrient-limiting model, one of the mandatory conditions for the processes of the nutrient based hypothesis. Furthermore, the most important assumption of the nutrient based hypothesis is that herbivores increase nutrient cycling speed. Especially migratory herbivores have a strong positive effect on the productivity of plants (Augustine and McNaughton 2006), which reflects the nutrient cycling speeds as well.

In other ecosystems herbivory did not result in an increase in the nutrient cycling speed. In Hluhluwe-iMfolozi no significant effect of grazers was found on nitrogen mineralization rates (Stock et al. 2010, Coetsee et al. 2011). Hluhluwe-iMfolozi, a relatively small ecosystem, lacks a large herd of migrating herbivores. White rhino and hippopotamus feed in grazing lawns and defecating in middens and rivers respectively (Hempson et al. 2014). They do not increase nutrient cycling speed as assumed by the nutrient based hypothesis (Hempson et al. 2014). Since Hluhluwe-iMfolozi has the highest density of white rhinos in Africa (Stock et al. 2010) we may expect that nutrient based effects are nullified. In an Argentinean grassland bunch patches had even higher mineralization rates than lawn patches (Vaieretti et al. 2013). Thus the strength of the mechanisms described by the nutrient- and water-based hypotheses might differ between ecosystems. Investigating other ecosystems can give new insights in the current two hypotheses and might reveal other mechanisms that can create the mosaic pattern of lawn and bunch patches.

The African savannas are complex ecosystems to investigate the nutrient- and water-based hypotheses because of the very diverse herbivore community (Owen-Smith 2013) and fire events. Herbivore species differ in their effect on the vegetation patterning (Van der Plas et al. unpublished). To simplify their effect, herbivores can be classified in many different ways: based on their diet (grazers vs browers) (Van Langevelde et al. 2003, Holdo et al. 2013), foraging strategy (specialist vs generalist), whether they import or export nutrients (McNaughton 1984, Hempson et al. 2014) or separated in several functional groups (Van der Plas et al. unpublished) etc. There is a trade-off between simplicity (modeling one herbivore species) and reality (dozens of herbivore groups). As argued before, the mosaic vegetation patterns can be found in ecosystems all over the world (Hempson et al. 2014, Howison et al. unpublished), including ecosystems with a lower diversity of herbivores (Owen-Smith 2013). We suggest simplifying the system and simultaneously creating a more realistic model by focusing on less complex ecosystems with less herbivore species or functional groups, for example the North American prairie, where bison, cattle (which are functional equivalents) and deer represent the vast majority of the herbivore biomass (Knapp et al. 1999).

### *Robustness of the model*

We used pairwise invasibility plots to investigate feedback loops of both hypotheses. This enables the analysis from both an evolutionary and an ecological perspective. However, using this method implies

that the equilibria we found for our variables are stable. Nevertheless, unstable equilibria might lead to oscillations of the variables and even a collapse of the system. Therefore the dynamics of the model variables should be further analyzed.

Plant characteristics as relative growth rate (Van der Plas et al. 2013), canopy height (McNaughton 1984) and plant palatability (McNaughton 1984) depend on plant bunchness (Fokkema et al. unpublished). We assumed linear relationships between these characteristics and plant bunchness. Other forms of these relationships can radically change the outcome of the models. Therefore the assumed relationships should be empirically tested.

### Concluding remarks

Currently two hypotheses exist that explain the mosaic vegetation pattern of lawn and bunch grasses. This was the first study that modeled the water based hypothesis. Our models support the water based hypothesis when competition for light is taken into account, but do not support the nutrient based hypothesis.

---

## 6. Bibliography

- Abdelmagid, A. H., G. E. Schuman, and R. H. Hart. 1987. Soil bulk-density and water infiltration as affected by grazing systems. *Journal of Range Management* **40**:307-309.
- Anderson, T. M., B. B. Kumordzi, W. Fokkema, H. V. Fox, and H. Olff. 2013. Distinct physiological responses underlie defoliation tolerance in African lawn and bunch grasses. *International Journal of Plant Sciences* **174**:769-778.
- Augustine, D. J. and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* **9**:1242-1256.
- Bartlett, M. K., C. Scoffoni, and L. Sack. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters* **15**:393-405.
- Coetsee, C., W. D. Stock, and J. M. Craine. 2011. Do grazers alter nitrogen dynamics on grazing lawns in a South African savannah? *African Journal of Ecology* **49**:62-69.
- De Mazancourt, C. and M. Loreau. 2000. Grazing optimization, nutrient cycling, and spatial heterogeneity of plant-herbivore interactions: Should a palatable plant evolve? *Evolution* **54**:81-92.
- De Mazancourt, C., M. Loreau, and L. Abbadie. 1998. Grazing optimization and nutrient cycling: When do herbivores enhance plant production? *Ecology* **79**:2242-2252.
- De Mazancourt, C., M. Loreau, and L. Abbadie. 1999. Grazing optimization and nutrient cycling: Potential impact of large herbivores in a savanna system. *Ecological Applications* **9**:784-797.
- DeAngelis, D. 1992. Dynamics of nutrient cycling and food webs. Springer Netherlands.
- Fokkema, W., B. B. Kumordzi, H. Valls, T. M. Anderson, and H. Olff. unpublished. To which factors are grazing lawn plants mostly adapted? Comparing lawn and bunch grasses in morphological and stoichiometrical traits.
- Geritz, S. A. H., E. Kisdi, G. Meszena, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* **12**:35-57.
- Hasegawa, P. M., R. A. Bressan, J. K. Zhu, and H. J. Bohnert. 2000. Plant cellular and molecular responses to high salinity. *Annual Review of Plant Physiology and Plant Molecular Biology* **51**:463-499.
- Hempson, G. P., S. Archibald, W. J. Bond, R. P. Ellis, C. C. Grant, F. J. Kruger, L. M. Kruger, C. Moxley, N. Owen-Smith, M. J. S. Peel, I. P. J. Smit, and K. J. Vickers. 2014. Ecology of grazing lawns in Africa. *Biological Reviews* **90**:979-994.

- Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2013. Herbivore-vegetation feedbacks can expand the range of savanna persistence: insights from a simple theoretical model. *Oikos* **122**:441-453.
- Howison, R., H. Olff, J. Van de Koppel, and C. Smit. unpublished. Biotically driven vegetation mosaics: the battle between bioturbation and biocompaction.
- Huisman, J. and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments - an elementary model. *Ecology* **75**:507-520.
- Kleynhans, E. J., A. E. Jolles, M. R. E. Bos, and H. Olff. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos* **120**:591-600.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *Bioscience* **49**:39-50.
- McNaughton, S. J. 1976. Serengeti migratory wildebeest - Facilitation of energy-flow by grazing. *Science* **191**:92-94.
- McNaughton, S. J. 1979. Grazing as an optimization process - grass ungulate relationships in the Serengeti. *American Naturalist* **113**:691-703.
- McNaughton, S. J. 1983. Compensatory plant-growth as a response to herbivory. *Oikos* **40**:329-336.
- McNaughton, S. J. 1984. Grazing lawns - animals in herds, plant form, and coevolution. *American Naturalist* **124**:863-886.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem - the Serengeti. *Ecological Monographs* **55**:259-294.
- McNaughton, S. J. 1986. On plants and herbivores. *American Naturalist* **128**:765-770.
- Munns, R. 2002. Comparative physiology of salt and water stress. *Plant Cell and Environment* **25**:239-250.
- Owen-Smith, N. 2013. Contrasts in the large herbivore faunas of the southern continents in the late Pleistocene and the ecological implications for human origins. *Journal of Biogeography* **40**:1215-1224.
- Ruess, R. W. and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos* **49**:101-110.
- Schrama, M., M. P. Berg, and H. Olff. 2012. Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. *Ecology* **93**:2353-2364.
- Schrama, M. J. J., V. Cordlandwehr, E. J. W. Visser, T. M. Elzenga, Y. de Vries, and J. P. Bakker. 2013. Grassland cutting regimes affect soil properties, and consequently vegetation composition and belowground plant traits. *Plant and Soil* **366**:401-413.
- Stock, W. D., W. J. Bond, and C. van de Vijver. 2010. Herbivore and nutrient control of lawn and bunch grass distributions in a southern African savanna. *Plant Ecology* **206**:15-27.
- Vaieretti, M. V., A. M. Cingolani, N. P. Harguindeguy, and M. Cabido. 2013. Effects of differential grazing on decomposition rate and nitrogen availability in a productive mountain grassland. *Plant and Soil* **371**:675-691.
- Van Coller, H., F. Siebert, and S. J. Siebert. 2013. Herbaceous species diversity patterns across various treatments of herbivory and fire along the sodic zone of the Nkuhlu exclosures, Kruger National Park. *Koedoe* **55**.
- Van der Plas, F., T. M. Anderson, and H. Olff. 2012. Trait similarity patterns within grass and grasshopper communities: multitrophic community assembly at work. *Ecology* **93**:836-846.
- Van der Plas, F., R. Howison, N. Mpanza, J. P. G. M. Cromsigt, and H. Olff. unpublished. Herbivore community structure, not total grazing pressure, drives the grassland community structure of an African savanna

- Van der Plas, F., P. Zeinstra, M. Veldhuis, R. Fokkema, E. Tielens, R. Howison, and H. Olff. 2013. Responses of savanna lawn and bunch grasses to water limitation. *Plant Ecology* **214**:1157-1168.
- Van Langevelde, F., C. van de Vijver, L. Kumar, J. van de Koppel, N. de Ridder, J. van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, W. J. Bond, H. H. T. Prins, and M. Rietkerk. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**:337-350.
- Veldhuis, M. P., R. A. Howison, R. W. Fokkema, E. Tielens, and H. Olff. 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant-soil water balance. *Journal of Ecology* **102**:1506-1517.
- Walker, B. H. and J. L. Langridge. 1997. Predicting savanna vegetation structure on the basis of plant available moisture (PAM) and plant available nutrients (PAN): a case study from Australia. *Journal of Biogeography* **24**:813-825.