CHAPTER 6

Stability and dimensions of grazing-induced vegetation patterns

A.M. Mouissie, R. van Diggelen, M. E. F. Apol and G. W. Heil

Abstract

Patterns of tall stands (‘tussock’) and short stands (‘lawn’) are observed in grazed vegetation throughout the world. Such structural vegetation diversity influences plant and animal diversity. A possible mechanism for the creation and preservation of such patterns is a positive feedback between grazing and plant palatability. The consequences of this feedback mechanism on the stability and dimensions of vegetation patterns are not clear and are difficult to study empirically.

We addressed this issue by analyzing a spatially structured plant-grazer model, based on published empirical relations and the assumption of optimal foraging. Model simulations generated patterns of short and tall stands that were highly constant over time if: 1) productivity was high enough and the grazing area large enough, so that grazers did not shorten the whole vegetation; 2) maximal standing crop was higher than optimal standing crop so that grazers selected previously grazed sites. Even in seasonal habitat, patterns were relatively stable, despite fluctuations in the area of short stands. Heterogeneity of pre-existing vegetation increased heterogeneity of the grazing-induced pattern, but did not affect its stability.

Unlike non spatial plant-herbivore models, our model did not show catastrophic shifts from high to low productivity. Instead the tall stands are a constant maximum plant height and short stands are a variable plant height depending on the time since defoliation. Marginal changes in productivity and stocking rate lead to marginal changes in the area in of short stands. Thanks to the observed stability, we were able to derive scaling relations of the area of short stands with herbivore size (\(\sim M^{0.4}\)) and productivity (\(\sim k^{-0.7}\)). Limitations and implications for the management of heterogeneity in grazed vegetation are discussed.
Introduction

Structural diversity of vegetation implies habitat diversity influencing both plant (Olff and Ritchie 1998) and animal diversity (Grant et al. 1982; Bock et al. 1984; Dennis et al. 1998). Hence for the conservation of biodiversity it is important to gain insight in processes maintaining patterns of vegetation structure (Olff et al. 1999). Although grazing can homogenize fine scaled patterns of plant species, at scales larger than bite size, it often increases structural vegetation heterogeneity (Adler et al. 2001). Patterns of tall stands (‘tussock’) and short stands (‘lawn’) are observed in grazed vegetation throughout the world, including African savanna, grazed by wild ungulates (McNaughton 1984); cattle grazed prairie in North America (Ring et al 1985); sheep and cattle-grazed temperate grasslands in Europe (Bakker et al. 1984; Berg et al. 1997) and sheep-grazed steppe in Tierra del Fuego (Posse et al. 2000).

A possible mechanism for the preservation of short stands is in the diet selection of grazers. Many grazing herbivores prefer short stands irrespective of the availability of tall stands (McNaughton 1984; WallisDeVries and Schippers 1994; Wilmshurst et al. 1995) thus keeping short stands in an immature state with high crude protein content, little structural carbon and high energy content (Van Soest 1982). Theoretical analysis has shown that higher energy content in short stands can outweigh lower biomass intake rate, resulting in higher daily energy gain, than from taller stands (Hobbs 1988; Wilmshurst et al. 2000). However, the consequences of this positive feedback between grazing and forage palatability for the aerial extent and spatial stability of vegetation patterns is not clear and is difficult to study empirically (Adler et al. 2001).

In this paper, we address this issue by analyzing a vegetation-grazer model in a spatially structured environment of feeding station sized cells. Model grazers optimize daily energy gain while being constrained by cropping, digestion and traveling. Vegetation grows according to a modified logistic equation and features a decline in energy content with increasing plant height. All model equations are based on published empirical data. Model simulations provide insight in the consequences of herbivore size, productivity, pre-existing heterogeneity, and seasonality for the stability and aerial extent of grazing-induced vegetation patterns. We discuss the implications for biodiversity in general and the dispersal and establishment of plant species in particular.
Methods

A vegetation-grazer model in a spatially structured environment

The model we present simulates vegetation dynamics and the intake of biomass by a single ruminant grazer, in a spatially structured environment. The model administrates energy intake and expenditure of the ruminant based on published empirical data. Optimal foraging is assumed; i.e. the model ruminant aims to maximize its daily energy gain.

The model is an adaptation of the analytical model of Wilmshurst et al. (2000) that assumes both cropping and digestion constrain metabolizable energy intake in ruminants. The cropping constraint function increases with standing crop due to increasing biomass intake rate. The digestion constraint function decreases with standing crop due to the effect of the maturational decline in forage quality on passage rates in ruminants. Combining both constraints yields an optimal standing crop for most parameter values.

The model of Wilmshurst et al. (2000) is neither spatially explicit nor does it incorporate vegetation dynamics. We made the model spatially explicit by running it on a grid of 200x200 square cells and by incorporating traveling costs ($I_t$, MJ) and time ($t_t$, s). Each cell corresponds to the size of a feeding station ($afs$, m$^2$), being the area an animal can sample without horizontal locomotion (Roguet et al. 1998).

The spatial scale chosen directly affected the time scale of foraging decisions. In the model of Wilmshurst et al. (2000) the optimal patch choice is calculated for a whole day of grazing. However, the time needed to select a feeding station-sized cell, move to it and deplete it, is much shorter. Hence, during a day available stomach space and available grazing time decrease, but not necessarily at a fixed ratio. Therefore we, explicitly modeled fraction available gut space ($f_{SS}$) and grazing time spend during the day ($t_d$). When $f_{SS}$ equals unity and $t_d$ equals zero, our model predicts the same optimal standing crop ($V_{opt}$, kg/m$^2$) as the model of Wilmshurst et al. (2000). This is also the case if $f_{SS}$ equals 0.5 and $t_d$ equals half $t_{max}$. However, if $f_{SS}$ equals 0.5 at the beginning of a grazing day ($t_d=0$) our model predicts a lower $V_{opt}$ and if the stomach is empty ($f_{SS}=0$) when $t_d$ equals 0.5 $t_{max}$, our model predicts a higher $V_{opt}$. (Figure 6. 1).

Vegetation dynamics were added by allowing standing crop ($V_t$, kg/m$^2$) in each cell to increase until a maximum ($k$, kg/m$^2$) and to be depleted when visited by a ruminant. Equations relating to digestion and cropping constraints largely follow the model of Wilmshurst et al. (2000), whereas the equations relating to traveling and vegetation dynamics are from other sources

Feeding station selection

The ruminant selects the cell that maximizes to its daily energy intake. This is the cell with the highest value of the net expected energy intake function ($E(M,V)$, MJ), the minimum of a cropping constraint function ($E_1(M,V_t)$, MJ) and a digestion constraint function ($E_2(M,V)$, MJ) (equation 1).
$E_1$ is calculated as the potential amount of metabolizable energy that can be gained from a cell considering only time constraints on intake rate. The time taken to deplete the cell ($t_c(V_t)$, s) is a function of standing crop ($V_t$, kg/m²) and depends on two herbivore parameters: maximum instantaneous intake rate ($R_{max}$, kg/s) and a half maximum saturation constant ($b$, kg/m²) (equation 7). Time spent in a cell increments total time spent grazing ($t_d$, s) until total daily grazing time ($t_{max}$, s) is reached. Cells are always depleted when selected by the herbivore.

$E_2$ is calculated as the potential amount of metabolizable energy that can be gained from a cell when only digestion (gut fill and passage) constraints are considered. The amount consumed is a function of the size of the feeding station ($a_{SS}$) and its biomass ($V_t$) and increments gut fill (decreases $f_{SS}$) until daily voluntary intake ($DVI(V,M)$, kg) is achieved. $DVI$ is a linear regression function based on feeding trials (Meissner and Paulsmeier 1995) (equation 4). If more cells fulfill the selection criterion of a highest $E$, one cell is chosen at random.

Metabolizable energy contents of the vegetation ($Q(M,V)$, MJ/kg) follows a maturational decline. $Q$ is a function of the fraction neutral detergent fiber ($f_{NDF}(V_t)$) and herbivore size ($M$, kg) (Rittenhouse et al. 1971; Wilmshurst et al. 2000) $Q$ is based on standard combustible energy content of grass (17.1 MJ/kg; (Golley 1961) and accounts for energetic losses in digestion (Van Soest 1982) (equation 6). As $f_{NDF}$ increases with $V_t$ (Wilmshurst et al. 1999) (equation 5), $Q$ is negatively related to $V_t$.

Energy cost of locomotion in 62 mammal and bird species was investigated by (Taylor et al. 1982), who reported an allometric equation in terms of body mass and

![Figure 6.1. Relationship between expected energy intake ($E$, MJ) and standing crop ($V$ kg/m²). Thin lines represent $E_1$ and bold lines represent $E_2$. Continuous lines represent functions for ruminants with empty gut ($f_{SS}$=1) and a full grazing day left ($t_d$=0). The bold dashed line represents the expected energy intake for ruminants with a half full gut ($f_{SS}$=0.5), whereas the thin dashed line represents expected energy intake for a ruminant that has Maximal grazing time is 46800 s, travelling time and costs are assumed zero. The intersections of $E_1$ and $E_2$ predict an optimal standing crop.](image)
velocity of horizontal locomotion \( (v, \text{m/s}) \). Since energy expenditure linearly increases with velocity (Taylor et al. 1982; Parker et al. 1984) velocity can be substituted for distance \((L, \text{m})\) (equation 8).

Traveling time between cells is simply \( L/v \). When grazing, \( v \) averages 0.41 m/s for sheep (Roguet et al. 1998) and 0.88m/s for cattle (WallisDeVries et al. 1999). To calculate \( t_T \) for different herbivores, we assumed quarter power scaling with body mass (Calder 1984) (equation 9).

Length of a feeding station, being the distance an animal can reach without moving its legs, scales to body mass as \( M^{1/3} \) (Calder 1984). Using step size for sheep (Roguet et al. 1998) and cattle (WallisDeVries et al. 1999), we were able to parameterize an allometric relation for feeding station size: \( a_{fs} = 0.0121 M^{2/3} \).

The ruminant state variables \( t_d \) and \( f_{SS} \) are updated each model iteration and reset at the end of the day when either \( f_{SS} \) equals unity or \( t_d \) equals \( t_{max} \). In all simulations \( t_{max} \) is 46800 seconds (13 hours).

If traveling time \( (t_t, \text{s}) \) and costs \( (I_T, \text{MJ}) \) are set to zero and a grid with uniform distribution of \( V_t \) values is offered, the model ruminant selects cells that are exactly the \( V_{opt} \) predicted by the model of Wilmshurst et al (2000).

\[
E = \min[E_1, E_2] 
\]

\[
E_1 = \left[ Q(M,V_t)V_t - I_T \right] \frac{t_{max} - t_d}{t_c(V) + t_T} 
\]

\[
E_2 = \left[ Q(M,V_t)V_t - I_T \right] \frac{DVI(M,V_t)}{V_{afs}} f_{SS} 
\]

\[
DVI(M,V_t) = 2.5 - 2.5f_{NDf}(V_t) + 0.0061M^{0.9} 
\]

\[
f_{NDf}(V_t) = 0.4825 + 0.42V_t 
\]

\[
Q(M,V_t) = 12.38 - 8f_{NDf}(V_t) + 0.00195M 
\]

\[
t_c(V_t) = V_{afs} \frac{b + V}{R_{max}V} 
\]

\[
I_T = 10.7 \cdot 10^{-6}LM^{0.68} 
\]

\[
t_T = 6.25LM^{0.68} 
\]
Vegetation dynamics

A feeding station, when selected by the ruminant is subsequently depleted (equation 10). At the beginning of a new day \((t_d=0)\) vegetation growth is calculated according to a modified logistic growth function after (Fryxell 1991) (equation 11).

\[
\begin{align*}
\text{if } t_d &\neq 0 \quad V_{t+1} = V_t - \text{graze} \\
\text{if } t_d &= 0 \quad V_{t+1} = V_t + r(V_t + s)\left(1 - \frac{V_t + s}{k + s}\right) - \text{graze}
\end{align*}
\]

where \(V_t\) is standing crop at model step \(t\), \(k\) is maximal standing crop \((\text{kg/m}^2)\), \(s\) \((\text{kg/m}^2)\) is the ungrazable residual which is set to \(0.1 \ k\) and \(\text{graze}\) is biomass removed by grazing, being \(V_t\) if a cell is occupied by the ruminant and zero if not.

In summary, each model iteration consists of selecting a cell, subsequent depletion of that cell, update of ruminant state variables \((t_d\ \text{and } f_{SS})\), update of output files, and at the end of a day, the growth of vegetation. The time step per model iteration \((\Delta t)\) varied depending on traveling time and cropping time: \(\Delta t = t_c + t_T\). The model ruminant starts in the centre of the grid. Model-scripts are written in the spatio-dynamic script programming language of PCRaster (PCRaster manual Version 2. 1998).

Model simulations

Simulations were performed with parameter values for sheep and cattle (Table 6.1), starting in initially homogenous short vegetation \((V_t=0.05 \ k)\), initially homogenous tall vegetation \((V_t=k)\) and initially heterogeneous vegetation \((V_t\ \text{in each cell was randomly drawn from a uniform distribution ranging from } 0 - k)\).

To study scaling of the area of short stands with productivity, simulations for cattle and sheep were run with \(k\) values ranging from \(0.1 \ \text{kg/m}^2\) - \(2 \ \text{kg/m}^2\). To study the effect of ruminant size simulations were run with six ruminant species (Table 6.1), both in low productive habitat \((k=0.3 \ \text{kg/m}^2, V_t=0.05 \ k)\) and high productive habitat \((k=0.9 \ \text{kg/m}^2, V_t=0.05 \ k)\). Multiple ruminants of the same species were simulated by simply multiplying the grazing time and stomach size by the number of ruminants.

Seasons were simulated, using a function for \(k\) periodically depending on time, assuming \(k\) in winter to be half the summer value: \(k=k_{max} \ (0.75-0.25 \ \cos (2\pi \ \text{day}/365))\), where \(\text{day}\) is time in days. Simulations in seasonal habitat were run for sheep and cattle starting in homogenous tall vegetation \((V_t=k)\).

Pattern analysis

The diversity index \(H\) \((0 \leq H \leq \ln 2)\) was used to study the heterogeneity of the grazing-induced vegetation patterns. For a pattern of two classes \(H = -(P_h \ln(P_h) + P_l\ln(P_l))\), where \(P_h\) is the proportion of cells with high \(V_t\) and \(P_l\) is the proportion of cells with low \(V_t\), in a matrix of 3x3 cells including the focal cell in the centre. In our
analyses we used the averaged $H$ over the whole grid (40,000 cells). Without further reference, when we mention $H$, this refers to this averaged $H$. If each cell is surrounded by an equal amount of tall and short cells, $H=\ln 2$. If the entire grid is either short or tall, $H=0$. If tall cells are clustered with other tall cells and short cells are clustered with short cells, $H$ is lower than when the same amount of tall and short cells are finely mixed. We refer to low values of $H$ as a clustered pattern and to high values of $H$ as a dispersed pattern.

To evaluate pattern stability, we calculated the similarity ($0 \leq \text{similarity} \leq 1$) between the spatial pattern of short stands at a certain moment ($LPT$) and the pattern at a reference moment ($LP_{ref}$) (equation 12). A similarity of unity indicates that the patterns are identical and zero similarity indicates that the patterns do not share any similarity in the location of short stands.

\[
\text{similarity} = \frac{2A(LP_t \cap LP_{ref})}{A(LP_t) + A(LP_{ref})}
\]  

(12)

In non-seasonal habitat we analyzed the rate at which the pattern can stabilize. $LP_{ref}$ changed over time such that it lagged the present pattern by one day ($LP_{ref} = LP_{t-1\text{day}}$).

In seasonal habitat, we analyzed how similar a pattern remained in the years following its creation. $LP_{ref}$ was fixed as the pattern after 1.5 years (548 days) of simulation ($LP_{ref} = LP_{1.5\text{ yrs}}$). $LP_{ref}$ was chosen such that a fully developed pattern could develop, which was not influenced by initial conditions.

Table 6.1. Parameter values of ruminants used in simulations, $M$, $R_{max}$, $b$. Using these parameter values, optimal standing crop $V_{opt}$ was calculated following the model of Wilmshurst et al (2000).

<table>
<thead>
<tr>
<th>Animal</th>
<th>$M$ (kg)</th>
<th>$R_{max}$ ($10^{-3}$ kg/s)</th>
<th>$b$ (kg/m²)</th>
<th>$V_{opt}$ (kg/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thompson gazelle</td>
<td>20</td>
<td>0.11</td>
<td>0.017</td>
<td>0.0043</td>
</tr>
<tr>
<td>Sheep</td>
<td>42</td>
<td>0.12</td>
<td>0.031</td>
<td>0.015</td>
</tr>
<tr>
<td>Mule deer</td>
<td>42</td>
<td>0.04</td>
<td>0.002</td>
<td>0.049</td>
</tr>
<tr>
<td>Reindeer</td>
<td>70</td>
<td>0.11</td>
<td>0.032</td>
<td>0.040</td>
</tr>
<tr>
<td>Wapiti</td>
<td>170</td>
<td>0.52</td>
<td>0.16</td>
<td>0.055</td>
</tr>
<tr>
<td>Cattle</td>
<td>750</td>
<td>2.16</td>
<td>0.69</td>
<td>0.21</td>
</tr>
</tbody>
</table>

Results

Simulations in non-seasonal habitat

Model ruminants selected most feeding stations close to the optimal standing crop, predicted by the non-spatial model of Wilmshurst (2000). However, when these were not available, or not close enough to outweigh traveling costs, shorter and taller stands were selected. As expected, sheep ($M=42$ kg) selected feeding stations with lower $V_t$, on average, than cattle ($M=750$ kg). Feeding stations, harboring less than 0.05 kg/m$^2$ plant biomass, were exclusively grazed by sheep, whereas feeding stations with higher $V_t$ were almost exclusively grazed by cattle. The only feeding stations where $V_t>0.05$, selected by sheep, harbored maximal standing crop (Figure 6.2).

Despite the observed variation in feeding station selection, the spatial similarity in short stands increased with time. After 150 days the spatial structure of short stands reached fixation in sheep-grazed vegetation, when only one in thousand patches were not short in both the actual vegetation and the vegetation of the previous day (similarity=0.999). In cattle-grazed vegetation this level of similarity was already achieved after 75 days of simulation (Figure 6.3).

Abundance of the pre-existing vegetation influenced grazing-induced patterns, temporarily but not in the long run. Simulations, started with different initial values of $V_t$, all resulted in the same area of short stands and same diversity of the maintained pattern (data not shown). Heterogeneity of the pre-existing vegetation did not affect the area of short stands either, but did affect the diversity of the created pattern. The diversity of the grazing-induced pattern remained higher when cattle started grazing in heterogeneous vegetation than when they started grazing in homogeneous vegetation (Figure 6.4). Higher diversity with equal ratio of short and

![Figure 6.2](image-url)  

**Figure 6.2.** Standing crop ($V$, kg/m$^2$) of feeding stations selected by sheep (open circles) and cattle (filled circles) in time (days). The optimal standing crop ($V_{opt}$) for sheep and cattle are indicated. The initial vegetation was homogenous short ($V=0.015$ kg/m$^2$).
Figure 6.3. Development in time (days), of the similarity in the spatial pattern of short stands between consecutive days. The thin line represents a simulation in sheep-grazed vegetation, whereas the bold line represents a simulations in cattle-grazed vegetation. The initial vegetation was homogenous tall \((V=k=0.3 \text{ kg/m}^2)\).

Figure 6.4. Development in time (days) of the area of short stands (A) and diversity of the spatial pattern of short and tall stands (B). Thin lines represent simulations started in homogenous tall cattle-grazed vegetation \((V_t=k=0.3 \text{ kg/m}^2)\), whereas bold lines represent simulations started in heterogeneous cattle-grazed vegetation \((V_t\) is uniformly distributed from 0 through \(k\)).
tall stands indicates a more dispersed pattern. The observation, that area of short stands became fixed after a certain period of simulation and was independent of the initial vegetation, allows for the possibility to plot the area of short stands against different model parameters.

The more productive the vegetation (higher $k$) the shorter it took to reach optimal standing crop after defoliation. Simulations in sheep and cattle-grazed vegetation, ranging in productivity from $k=0.1$ kg/m$^2$ through $k=2.0$ kg/m$^2$, showed that area of short stands is a negative decelerating function of $k$. As 0.1 kg/m$^2$ is less than the optimal standing crop for cattle (0.21 kg/m$^2$), the simulation in cattle-grazed vegetation did not lead to a stable vegetation pattern and was excluded from the analysis. Area of short stands was larger in cattle-grazed vegetation than in sheep-grazed vegetation, but scaled similarly to $k$ ($\sim k^{-0.7}$). (Figure 6.5).

Higher daily voluntary intake in larger herbivores cause a larger daily grazed area, but more importantly a higher biomass intake per unit area (Figure 6.3). Hence, area of short stands was a positive decelerating function of herbivore size ($\sim M^{0.4}$), scaling independently of $k$ (Figure 6.5).

**Simulations in seasonal habitat**

In seasonal habitat, $k$ was due to periodic change with a maximum of 0.3 kg/m$^2$ in mid summer and a minimum of 0.15 kg/m$^2$ in mid winter. Ruminants grazing in seasonal habitat maintained a smaller area of short stands in summer than in winter (Figures 6.6, 6.7). Optimal $V_t$ of sheep (0.015 kg/m$^2$) was lower than $k$ throughout the year but optimal $V_t$ of cattle (0.205 kg/m$^2$) was not. Consequently, for sheep,

![Figure 6.5](image)

**Figure 6.5.** Scaling of the area of short stands with body mass of ruminants (A) and maximal standing crop ($k$) (B). In chart A, filled squares represent simulations in low productive vegetation ($k=0.3$) and open squares represent simulation in high productive vegetation ($k=0.9$). In chart B, filled points represent simulations of cattle grazing and open points represent simulation of sheep grazing. Lines represent linear regression functions.
Figure 6.6. Snapshots of simulated vegetation patterns in cattle-grazed vegetation (A-C) and sheep-grazed vegetation (D-F) in a spatially structured environment of 200x200 feeding-station-sized cells (5848 m² for sheep and 40000 m² for cattle). Black represents tall stands \( (V_t=k) \) and white represents short stands \( (V_t<k) \). Figure A,D, pattern of the first winter, B,E, first summer and C,F, second winter.

Figure 6.7. Development of area of short stands (m²) in time (days) in sheep-grazed vegetation (thin line) and cattle-grazed vegetation (bold line). Maximal standing crop \( (k) \) is due to seasonal variation (dashed line: right y-axis).
feeding stations visited in summer were also attractive in winter, but for cattle non-visited feeding stations with the highest $V_t$, became most attractive.

*Similarity* in the location of short stands remained higher in sheep-grazed vegetation than in cattle-grazed vegetation. In sheep-grazed vegetation the *similarity* compared with the reference pattern (after 1.5 years of simulation) decreased to 0.65 in the first year and remained above 0.5 in the following nine years. Like area of short stands, the *similarity* also followed a seasonal pattern in sheep-grazed vegetation. In cattle-grazed vegetation, *similarity* quickly decreased to a random level (Figure 6.8).

In summer, part of the area of short stands of the previous winter was left to grow tall, resulting in continuously changing diversity of the pattern (Figure 6.9). In sheep-grazed vegetation the patches that grow tall are located in the inside of the area of short stands rather than at the outside, resulting in a more dispersed pattern in summer than in winter. In the next winter, most of the vegetation that had grown tall was shortened again, but not all (Figure 6.6). Consequently, the diversity of sheep-grazed vegetation increased gradually with time. In cattle-grazed vegetation the diversity of the pattern is higher from the beginning and changes more erratic (Figure 6.9). In more productive vegetation, in which $k$ is not below optimal $V_t$, cattle can maintain patterns that are similarly stable as in sheep-grazed vegetation (data not shown).

**Figure 6.8.** *Similarity* of the spatial pattern of short stands compared to a reference pattern after 1.5 years. The thin line represents a simulation of sheep-grazed vegetation, whereas the bold line represent a simulation of cattle-grazed vegetation. Dashed line indicate similarity of randomly distributed short stands covering the same area as the reference pattern. Maximal standing crop is due to seasonal change.
Discussion

**Grazing-induced vegetation patterns**

Our results show that a positive feedback between grazing and plant palatability can lead to creation and preservation of spatial patterns of short stands and tall stands. A prerequisite is that the grazing area and productivity are sufficiently large, so that grazing does not result in a homogenous short vegetation. Furthermore, maximal standing crop needs be higher than the optimal standing crop of the ruminant. In contrast, models that assume herbivores prefer the highest standing crop patch available, predict homogenization of standing crop across patches (Sutherland 1996; Ungar and Noy-Meir 1988) and can not explain heterogeneity.

Tall stands are not grazed and grow until they reach maximal standing crop. Short stands continuously change, from an ungrazeable residual height, shortly after defoliation, increasing to optimal standing crop, when they are usually visited again. Ruminants need, neither spatial memory, nor long term planning, to maintain part of the vegetation in optimal standing crop, but can achieve this by instantaneous foraging decisions. An important assumption here is that grazing decisions depend on time spent and gut fill. This allows the ruminant to compensate for the encounter of shorter than optimal stands, by the selection of taller than optimal stands in subsequent foraging bouts and vice versa. Simulations with earlier versions of the model in which the state variables, time spent and stomach fill were not included, resulted in stands maintained shorter than optimal (Mouissie, unpublished).

Figure 6.9. Development of the diversity index ($H$) of the pattern of short and tall stands in time (days) in sheep-grazed vegetation (thin line) and cattle-grazed vegetation (bold line). Maximal standing crop ($k$) is due to seasonal change. (dashed line: right y-axis).
spatially explicit model of goose grazing, which does not include these state variables, also suggests that patches are exploited at lower than optimal standing crop (Bos 2002).

The immediate effect of grazing on heterogeneity depends on the spatial pattern of grazing and pre-existing spatial pattern of vegetation (Adler et al. 2001). Our results show that the spatial pattern of grazing interacts with the pre-existing vegetation pattern. Pre-existing heterogeneity in the vegetation enhances heterogeneity of the grazing pattern, which again enhances the heterogeneity of the maintained pattern of short and tall stands. Height of the short stands, area of short stands, and stability of the grazing-induced pattern are neither affected by initial heterogeneity nor by initial abundance. This enabled us to find a fixed relation between area of short stands and the variables: ruminant size, number of ruminants and productivity of the vegetation.

Like Schwinning and Parson (1999), we deviate from the view of dual stability and catastrophic shifts from high to low productivity in grazing systems (Noy-Meir, 1975). Instead, the tall stands are a constant maximal plant height and height of the short stands continuously change, depending on the time since defoliation. Marginal changes in productivity and stocking rate lead to marginal changes in the area of short stands, following a negative decelerating function (short vegetation area $\sim k^{-0.7}$). In the non spatial model of Van der Koppel et al (1996) short and tall stands are only possible over a limited productivity range. An increase in productivity beyond the limit disrupts the dual stability simply because herbivores can no longer consume a sufficient portion of the entire vegetation. Our model does not predict an upper productivity limit, because grazing can be concentrated in a smaller area. Patterns of short and tall stands are observed in grazing systems over a wide range in stocking rate and productivity, (Bakker et al. 1984; McNaughton 1984; Berg et al. 1997; Posse et al. 2000); supporting the predictions of our model.

The observed scaling of the area of short stands with ruminant size ($\sim M^{0.4}$) suggests that small ruminants have a relatively large impact on vegetation, as compared with larger ruminants. Daily voluntary intake is slightly less than proportionate to ruminant size ($\sim M^{0.9}$) (Meissner and Paulsmeier 1995). More important, optimal standing crop increases with ruminant size ($\sim M^{0.86}$) (Wilmshurst et al. 2000) and consequently biomass intake per unit land surface. Longer intervals between grazing of the same feeding station only partly counteract the relative small area of short stands, maintained by large ruminants.

Chartings of vegetation patterns can be strikingly similar for several years, despite seasonal fluctuation in the size of the area of short stands (Bakker et al. 1984; Van den Bos and Bakker 1990; Berg et al. 1997). Although these authors hypothesized that this is the result of an underlying soil pattern, our results show that spatial pattern stability is also possible in an homogenous environment. In simulated seasonal habitat, structural vegetation patterns can remain highly similar for several years. Prerequisite is that maximal standing crop in winter remains higher than the optimal standing crop of the ruminant. Otherwise ruminants select ungrazed patches in
winter, leading to shifting patterns. As optimal standing crop increases with ruminant size (Wilmshurst et al. 2000), in low productive vegetation small ruminants, such as sheep, maintain relatively stable patterns through seasons, while large ruminants, such as cattle, may not.

**limitations and implications**

All equations of the model concerning energy intake and expenditure are based on published empirical studies and our assumption of optimal foraging in terms of daily energy gain is in concordance with foraging theory (Stephens and Krebs 1986). However, our assumption on feeding station depletion after each herbivore visit can be debated. It is quite realistic for cattle that forage by pulling an entire sod with their tongue. It is less realistic for smaller ruminants, such as sheep, that may bite off only a portion of the standing crop. The spatial implicit study of (Schwinning and Parsons 1999) showed that fraction of defoliation should be more that 50% to maintain a pattern of short and tall stands. Therefore our conclusions do not apply to smaller herbivores, such as rodents or insects. Herbivores of the size of impala and smaller do not create lawn-tussock patterns in African savanna (pers. Comm. H. Olff, 2003). Our assumption could be relaxed by the inclusion of a limited bite depth. We chose not to, because different quality and growth rate in plants of the same height but different defoliation fraction complicates vegetation dynamics (Schwinning and Parsons 1999).

Stability of structural vegetation patterns influences ecosystem functions and biodiversity. If stands are maintained short, in the long term soil properties are altered and a shift towards grazing resistant plant species is promoted (McNaughton 1984; Posse et al. 2000). Hence, grazing can indirectly create a soil pattern and a pattern of plant communities. Our formal proof, that grazers can create and maintain relatively stable patterns of short and tall vegetation, demonstrates that the impact of grazers on ecosystems is larger than their direct effect on the biomass of plants.

We simulated single herbivores, but our approach can also be used to study interacting effects of herbivores such as facilitation and competition. Our study provides a formal aid for the management of heterogeneity in grazing systems.

**Acknowledgements**

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grazing-induced vegetation patterns


Box 6.1 Distribution of distances for seeds ingested by fallow deer

A.M. Mouissie and E.F. Apol

Introduction

The ability of deer to disperse seeds over long distances through ingestion and defecation has been suggested by several authors (Pakeman 2001, Myers et al. 2004) but rarely quantified. Recently Vellend et al. (2003) estimated the distribution of distances for *Trillium grandiflorum* seeds dispersed by white-tailed deer. Their estimation corroborates the view that deer are likely vectors of long-distance seed dispersal with 25% of seeds moving beyond 1 km.

However, Vellend et al. (2003) did not base retention time of seeds in the alimentary tract on actual measurement of ingested seeds but on passage of chemically labelled food items. There is high variability in food and seed passage and also of seeds, leaving room for speculations on the accuracy of their predictions. Currently, we have seed retention data available for seeds experimentally fed to fallow deer (Chapter 5), providing an opportunity to improve the estimation of seed dispersal distances.

Vellend et al. (2003) used data from actual observations of deer movements. This is seemingly the most reliable method, but animal movement is very variable depending on landscape structure and behaviour. Hence, it is difficult to assess how representative particular telemetry data are for the displacement of a species in general. In addition, telemetry data of large herbivores taken at time intervals relevant for the retention period of seeds in the alimentary tract are scarce. Such data are not available for fallow deer and obtaining them remains costly and time-consuming.

A modelling approach is a possible alternative to the use of telemetry data. Although the reality of modelled data is not as apparent as empirical data, their general validity is potentially higher, the data collection is faster, more cost-efficient and more detailed.

We combined simulated fallow deer movement data with retention data inside the alimentary tract (Chapter 5) to generate the distribution of distances for seeds ingested and defecated by fallow deer. Movement data are obtained from correlated random walks (Chapter 2) and an optimal foraging model (Chapter 6). Besides estimating the distance distribution of seed dispersal, the objective of this study was to compare these modelling approaches.
Methods

Retention data
Retention of seeds in the alimentary tract of female fallow deer (Chapter 5) was fitted to a cumulative gamma distribution: 

\[ f(t) = \sum_{\alpha, \theta} \frac{\theta^\alpha}{\Gamma(\alpha)} t^{\alpha-1} e^{-\theta t}, \]

where \( t \) is time in hours and \( \alpha \) and \( \theta \) are parameters. The best fit \( (R^2=0.99) \) was obtained for average passage of 25 species \( \alpha=2.9 \) and \( \theta=0.1 \), \( \theta=0.16 \), \( \alpha=6.28 \) for Plantago major; \( \theta=0.3 \), \( \alpha=4.6 \) for Cerastium fontanum (Figure 6.1.1).

Figure 6.1.1. Distribution of retention times in the alimentary tract of fallow deer. The proportion of survived seeds is plotted against time. Squares represent averaged data for 25 plant species, circles represent data for the fastest passing species Cerastium fontanum, and triangles represent data for the slowest passing species Plantago major (Chapter 5). Lines represent best-fitted cumulative gamma distributions: \( \theta=0.1 \), \( \alpha=2.9 \) for average species; \( \theta=0.16 \), \( \alpha=6.28 \) for Plantago major; and \( \theta=0.3 \), \( \alpha=4.6 \) for Cerastium fontanum.

Correlated random walks
Movement of female fallow deer was simulated using the correlated random walk (CRW) approach described in Chapter 2 \((v=25 \text{ m/min, } L=5 \text{m, SDA}=32 \text{ degrees})\). Hours of movement per day were set at a conservative estimate of 13 hours per day: an estimation of the maximal grazing period for ruminants (Wilmshurst et al. 2000). The total period of movement may be longer due to non-foraging behaviour. We assumed all seeds were ingested at the start of the
simulation. After each movement the distance from the source and proportion of seeds excreted was calculated. Seeds excreted at a different moment, but at the same distance from the source, rounded to 100 m intervals, were cumulated. We ran 200 simulations for the dispersal of both the fastest passing species (*Cerastium fontanum*) and the slowest passing species (*Plantago major*) in the feeding experiment. As the simulations ran long enough for almost all seeds (99.9%) to be excreted, it approached the distance distribution for infinite time.

**Optimal foraging simulation**
Seed dispersal simulations were based on a spatially explicit optimal foraging model (Chapter 6). Modelled female fallow deer selected feeding station-sized cells depending on energy contents, time related to cropping, digestion rate, travelling time and travelling costs. Cropping parameter values for fallow deer were obtained from allometric relations of intake rate in related species (Table 6.1.1).

We assumed all seed were ingested at the start of the simulation. Model fallow deer foraged in a map of 1000 x 1000 cells with vegetation biomass ranging from zero to carrying capacity randomly drawn from a uniform distribution. After each move the proportion of seeds defecated was calculated based on the time spend and the fitted gamma distribution for retention times inside the alimentary tract (Figure 6.1.1). Proportion of seeds defecated in the same cell were added. The distribution of distances then followed from summation of the proportion of seeds in cells within 10 m intervals from the departure of the animal (in the centre of the map). Again, we simulated the dispersal of the fastest passing species (*Cerastium fontanum*) and the slowest passing species (*Plantago major*) long enough for almost all seeds (> 99.9%) to be excreted. However, we ran only ten simulations for each species due to the long simulation time required. Still this seemed a representative sample size since increasing the number of simulations from five to ten had little effect on the shape of the distribution.

**Table 6.1.1. Parameter values used in the optimal foraging simulations**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description value</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M$ (kg)</td>
<td>Mass of female fallow deer</td>
<td>45</td>
<td>(McElligott et al. 2001)</td>
</tr>
<tr>
<td>$R_{max}$ (g /s)</td>
<td>Maximum cropping rate</td>
<td>0.15</td>
<td>(Shipley et al. 1994)</td>
</tr>
<tr>
<td>$b$ (kg/m2)</td>
<td>Vegetation density with half maximal cropping rate</td>
<td>0.003</td>
<td>(Shipley et al. 1994)</td>
</tr>
</tbody>
</table>
Results and discussion

The results of the CRW simulations show that endozoochory by fallow deer can render long-distance dispersal. Virtually all seeds that survive ingestion by fallow deer are expected to move at least several hundreds of metres, with 3.3% of *Cerastium fontanum* seeds and 1.0% of *Plantago major* seeds moving < 100m. Of *C. fontanum* seeds 23% are expected to be dispersed beyond 1 km and <0.1% beyond 3 km, while of *P. major* seeds 71% are expected to be dispersed beyond 1 km and 9% beyond 3 km. The modal dispersal distance is 501 m for *C. fontanum* and 850 m for *P. major*. Other species are expected to have intermediate dispersal distances, with a modal dispersal distance for average passing species of 770 m. The distribution of dispersal distances is approximately log-normal ($R^2=0.96$), though the best-fit log-normal distribution slightly overestimated dispersal beyond 3 km and underestimated dispersal distances less than 200 m. Compared to the distribution of distances of seeds dispersed by white-tailed deer (Vellend et al. 2003) the CRW simulations for fallow deer predict a more distant mode, but similar tail of the distribution (Figure 6.1.2). Seeds are dispersed farther in the alimentary tract of fallow deer than on the skin (Chapter 2).

*Figure 6.1.2.* Frequency distribution of distances for seeds excreted by fallow deer moving in correlated random walks. Bars represent means of 200 simulations with slow passing seeds (*Plantago major*) and fast passing seeds (*Cerastium fontanum*). Best-fit log-normal distribution of distances is represented by a dotted line for seeds dispersed by white-tailed deer (Vellend et al. 2003) (Proportion of seeds=$0.1 \exp\{-0.5\ln(Distance/219.80)/1.1\}^2$ ), a thin solid line for *Cerastium fontanum* (Proportion of seeds=$0.11 \exp\{-0.5 \ln(Distance/501)/1.03\}^2$ ) and a bold solid line for *Plantago major* (Proportion of seeds=$0.069 \exp\{-0.5 \ln(Distance/850)/0.96\}^2$ ).
Seed dispersal distances in the optimal foraging simulations are shorter than in the CRW simulations: with a modal dispersal distance of 70 m for *Cerastium fontanum* and 140 for *Plantago major*. The tail of the distributions is about ten times shorter than in the CRW simulations with almost no seeds moving beyond 300 m (Figure 6.1.3). The optimal foraging simulations are strongly influenced by the spatial distribution of resources. Fallow deer foraging in homogenous environment, without variation in vegetation biomass, disperse seeds over shorter distances, whereas fallow deer foraging on more scattered resources disperse seeds farther (data not shown).

Differences between the CRW and optimal foraging simulations are mostly due to differential effective movement periods. In the optimal foraging model a large proportion of the foraging time is spent on cropping rather than moving. While the velocity of horizontal locomotion is principally the same in both models, effectively fallow deer move faster in CRW simulations. In addition not all foraging time is used in the optimal foraging, further reducing the time spent moving. Another issue is that moves are more directed in the CRW simulations. In the optimal foraging model fallow deer do not move back to where they came from, because these cells have been depleted, but for the rest there is no preferential movement direction. Attractive cells are equally likely to be in front or perpendicular to the previous move and this is where the optimal forager is designed to go.

![Figure 6.1.3. Frequency distribution of distances for seeds excreted by fallow deer moving as predicted by the optimal foraging model. Bars represent average proportion of seeds per 10 m intervals in ten simulations with slow passing seeds (*Plantago major*) and fast passing seeds (*Cerastium fontanum*).](image-url)
Conclusion

For seeds ingested by fallow deer that are able to survive chewing and digestion, long-distance dispersal is rule rather than exception. Estimated modal dispersal distances of seeds dispersed by deer is farther than the 99 percentile of seeds dispersed by most other vectors (Nathan & Muller-Landau 2000).

Correlated random walk simulations seem to overestimate dispersal distance distributions while optimal foraging models seem to underestimate dispersal distances. Models, combining aspects of optimal foraging and CRW, could improve the estimation of seed dispersal distances by large herbivores.

References


