BIOLOGICAL CONSERVATION 141 (2008) 1687–1694

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon


BIOLOGICAL CONSERVATION

Grazing as a management tool in dune grasslands: Evidence of soil and scale dependence of the effect of large herbivores on plant diversity

Pejman Tahmasebi Kohyani[a,b,*], *Beatrijs Bossuyt*[a], *Dries Bonte*[a], *Maurice Hoffmann*[a,c]

[a]*Terrestrial Ecology Unit, Department of Biology, Ghent University, Ledeganckstraat 35, B-9000 Ghent, Belgium*
[b]*Iranian Ministry of Science, Research and Technology, Tehran, Iran*
[c]*Research Institute for Nature and Forest, Department of Ecosystems, Kliniekstraat 25, B-1070 Brussels, Belgium*

ARTICLE INFO

Article history:
Received 31 August 2007
Received in revised form
7 April 2008
Accepted 12 April 2008
Available online 29 May 2008

Keywords:
Beta diversity
Community structure
Linear mixed model
Local scale
Nutrient availability

ABSTRACT

In nature management, the introduction of large herbivores into human-influenced grasslands is thought to be effective to maintain or enhance plant diversity. In order to test the validity of this assumption, we studied the effect of grazing by large herbivores on plant species richness and community heterogeneity across a soil acidity gradient at different spatial scales in dry coastal dune grasslands in western Belgium and north-western France. The effect of grazing on plant richness varied with scale and soil acidity. Grazing had a predominantly positive effect on plant species richness in all habitats at the small scale (0.25 × 0.25 m). However, at site scale (8 × 8 m) it had only positive effects in grasslands with higher soil pH (6–7.4). Similarly, grazing resulted in a homogenization of grassland vegetation at lower pH, while heterogeneity increased with grazing on soil with higher pH. In general, grazing increased the number of rare species, independent of soil pH. The results confirm that the impact of grazing on plant diversity depends on the scale considered and that the effects further depend on soil acidity which was correlated to biomass production at the given soil pH range in this study. Although grazing seems an appropriate management tool to maintain and even enhance plant biodiversity under many circumstances, it may negatively affect plant species richness, where soil resources limit plant biomass production.

1. Introduction

Grazing by larger herbivores is widely used as a management tool to preserve and enhance plant diversity (Bakker, 1998; Van Diggelen and Marrs, 2003; Hodgson et al., 2005; Dorrough et al., 2006), particularly in productive environments (Pacala and Crawley, 1992; Grime et al., 1988). However, the effect of introducing large herbivores on plant community composition is still highly uncertain (Bakker and Londo, 1998). Available studies indeed yield contrasting results, showing positive to neutral or even negative effects on plant diversity (Mc Intyre et al., 2003; Landsberg et al., 2002; Dorrough et al., 2007). As hypothesized by Milchunas and Lauenroth (1993) and Olff and Ritchie (1998), contrasting effects of herbivores on plant diversity patterns may be due to variations in soil conditions.

Herbivores can directly affect plant species richness through phytomass removal. On productive soils, with a high phytomass production, herbivores may alleviate plant competitive exclusion by tall, dominant plant species (Huisman

---

* *Corresponding author:* Address: Terrestrial Ecology Unit, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium. Tel.: +32 486857954; fax: +32 9 264 88 93.

E-mail address: pejman.tahmasebikohyani@ugent.be (P. Tahmasebi Kohyani).

doi:10.1016/j.biocon.2008.04.010

and Olff, 1998; Kahmen et al., 2002). Small disturbances and a higher light intensity at the soil surface due to a more open canopy, create regeneration opportunities, a higher probability of successful germination and seedling establishment of less competitive species (Jutila and Grace, 2002). Trampling and dung can modify gap and resource availability resulting in changes of local competitive hierarchies. Grazing can also influence spatial heterogeneity in grassland composition by creating gradients in soil disturbance which enables species to coexist through niche differentiation (Olff and Ritchie, 1998; Jutila and Grace, 2002). Alternatively, grazing may negatively affect plant species richness, where soil resources limit the regrowth of plant species (Proulx and Mazumder, 1998).

Additionally, the effect of grazing on community structure and diversity strongly depends of the spatial scale (Olff and Ritchie, 1998; Spiegelberger et al., 2006). At a small scale that corresponds to individuals and their immediate neighbours grazing is predicted to result in an increase of diversity. This may result from both increased local colonization of species from larger scale (enhanced establishment possibilities through gap creation and enhanced dispersal through zoochory) and decreased local extinction by changed local competitive hierarchies and decreasing competitive exclusion by tall graminoid competitive species (Chaneton and Facelli, 1991). However, at the larger scale, a pattern of declining species richness is expected, due to selective grazing of grazing intolerant species. Alternatively, one can expect that at larger scales, plant interactions, which cause local extinctions, are likely to decrease in importance (Dorrough et al., 2007), and will at last lead to an increase in species richness. Whether the latter positive effect on plant richness is outweighed by negative effects of grazing on rare and high palatable, grazing intolerant plant species, remains to be investigated (Grubb, 1977; Olff and Ritchie, 1998).

In the late 1990s, different large herbivore species were introduced in several dune reserves along the Belgian and north-western French coast as a nature conservation tool, aiming at the prevention of succession towards coarse grassland with dominance of tall competitive grass species (largely *Calamagrostis epigejos*), with low plant species diversity (Provoost and Van Landuyt, 2001; Provoost et al., 2004). Soil conditions are a major source of environmental variation determining species composition and productivity of dune grasslands (Tahmasebi Kohyani et al., 2008). In dune soils, nutrient availability is strongly determined by soil acidity, with phosphorus limited growth in acid soils due to the immobilization of phosphorus by aluminium and iron, and a more balanced supply of nitrogen and phosphorus in soils with a higher pH (Kooijman et al., 1998; Kooijman and Smit, 2001). An independent survey by the authors confirmed that there was a significant correlation between aboveground biomass (as a proxy for nutrient availability) and soil pH (Table 1).

While most studies have focused on comparing the effects of grazing on plant diversity between different soil condition or spatial scales, only few have addressed specifically how plant species diversity is affected by their interactive effects (Dorrough et al., 2007). In addition, as Olff and Ritchie (1998) predicted, the loss of plant species richness at larger scales is likely to be attributable to rare species, but whether changes in plant species richness can be related to changes of richness of rare species still remains to be tested. This study assesses the impact of introduced grazing as a conservation tool on different aspects of plant species diversity (community heterogeneity and species richness) from dune grasslands at different scales along a soil acidity gradient. We aimed to address the following questions: (1) is introduction of larger herbivores essential for maintaining or enhancing plant diversity? (2) does the effect of grazing on plant diversity depend on soil acidity, scale or their interaction?

2. Materials and methods

2.1. Data collection

Vegetation data were collected in four coastal dune reserves at the Belgian and north-western French coast (Dunes fossiles de Ghyvelde, Cabour dunes, Westhoek, Ter Yde) and one privately owned and managed grassland (Oostvoorduinen) in the summer of 2006. Depending on plant-compositional or environmental differences or on the extent of the location, two to three areas with grazing management were selected within each location. The investigated grasslands can largely be classified as Plantagini-Festucion (with a minority of Polygalo-Koelerion, Arrhenatherion or Cynosurion grassland; see Table 1 for detailed information on the 12 selected areas). Different large, ungulate herbivores (cattle, different pony breeds and/or sheep) were introduced in all 4 nature reserves in the late 1990s to control further expansion of dominant grasses and woody species (Hoffmann et al., 2005); the animals are free-ranging and mostly remain in the area year-round. Grasslands at the one privately owned location are grazed for a substantially longer period of time and are only grazed in summer. Since the introduction of grazing management, some parts of the areas were excluded from grazing. Before the introduction of grazers, grazed and ungrazed sites within every single area were edaphically and historically largely the same. Within each area, two $8 \times 8\ \mathrm{m}^2$ plots were established randomly in every area, one in the grazed and one in the grazer-excluded site. To minimize differences within the pair of plots other than the presence or absence of grazing, the plots were installed as close as possible to each other, mostly only separated by the grazer excluding fence. Then, these plots were divided into four $4 \times 4\ \mathrm{m}^2$ plots which were further subdivided 4 times up to 1024, $0.25 \times 0.25\ \mathrm{m}^2$ plots. For each subdivision, $A_i - 1/A_i = 4$, where $A_i - 1$ and A_i are the area of the higher and lower scale, respectively. The cover of every vascular plant species was visually recorded within 10 random replicates at each of the 6 spatial scales except for the $4 \times 4\ \mathrm{m}^2$ plot which had only four replicates. Then, 16 soil samples were randomly collected within each $8 \times 8\ \mathrm{m}^2$ plot from the upper 10 cm of the soil, using a 7 cm diameter core. Soil acidity of each sample was measured with a pH meter and the obtained values were averaged per area for grazed and ungrazed sites separately. Species richness at site scale was defined as the number of species in the $8 \times 8\ \mathrm{m}^2$ plots, while local species richness was calculated as the number of species in the smallest plots ($0.25 \times 0.25\ \mathrm{m}^2$). A rarity index which classifies the species into very rare, rare and common

Table 1 – General characteristics of the sampled areas and sites, concerning grazed area, soil pH (means and standard deviations) and introduced grazers

Area name and site number	Latitude	Longitude	Kilometre from coastline	Grazed area (ha)	Grassland area (ha)	Introduced herbivore (1/2)	Grazing regime	Grazed since	Average grazer 1/2	Average AU/ ha grazed area	Average AU/ ha grassland	Phytomass (ungrazed plot) (g/m^2)	Soil pHwater ungrazed	Strongest syntaxonomical affinity
Ghyvelde1	51°03′33″	02°32′44″	3.1	75.0	52.5	HP/-	yr	1996	13/0	0.15	0.22	84	5.0 ± 0.1	Arrhenatherion
Ghyvelde2	51°03′52″	02°33′12″	2.9	75.0	52.5	HP/-	yr	1996	13/0	0.15	0.22	113	5.3 ± 0.6	Plantagini-Festucion
Cabour1	51°03′55″	02°34′34″	3.1	29.8	20.2	SP/-	yr	1997	13/0	0.17	0.26	92	5.7 ± 0.1	Polygalo-Koelerion
Cabour2	51°03′50″	02°34′46″	3.4	29.8	20.2	SP/-	yr	1997	13/0	0.17	0.26	86	6.0 ± 0.6	Plantagini-Festucion
Oostvoorduinen1	51°07′30″	02°41′55″	1.9	3.5	3.5	HC/-	Summer (1.5 month)	>20 yrs	10/0	0.36	0.36	91	6.5 ± 0.7	Plantagini-Festucion
Oostvoorduinen2	51°07′27″	02°42′20″	2.0	1.8	1.8	HC/-	summer (1 month)	>20 yrs	10/0	0.46	0.46	108	6.5 ± 0.7	Koelerio-Corynephoretea
Ter Yde1	51°08′09″	02°41′33″	1.0	16.0	11.0	SP/Sh	yr/winter (September–March)	1998	5/25	0.26	0.37		6.8 ± 0.1	Koelerio-Corynephoretea
Ter Yde2	51°08′05″	02°41′35″	0.9	16.0	11.0	SP/Sh	yr/winter (September–March)	1998	5/25	0.26	0.37		6.9 ± 0.1	Plantagini-Festucion
Ter Yde3	51°07′55″	02°41′40″	0.5	16.0	11.0	SP/Sh	yr/winter (September–March)	1998	5/25	0.26	0.37		7.0 ± 0.1	Plantagini-Festucion
Westhoek-south1	51°04′46″	02°33′10″	1.4	46.6	21.0	SHC/SP	yr	1996	4/16	0.22	0.50	206	7.3 ± 0.2	Koelerio-Corynephoretea
Westhoek-south2	51°04′51″	02°33′53″	1.4	46.6	21.0	SHC/SP	yr	1996	4/16	0.22	0.50	174	7.4 ± 0.2	Koelerio-Corynephoretea
Westhoek-north	51°05′07″	02°33′04″	0.4	52.8	20.3	SHC/KP	yr	1997	4/8	0.19	0.50	152	7.4 ± 0.2	Polygalo-Koelerion

Introduced herbivore (average weight): SHC: Scottish highland cattle (450 kg), HC: Holstein cattle (450 kg); KP: konik pony (350 kg), SP: Shetland pony (180 kg), HP: Haflinger pony (400 kg), Sh: Sheep (75 kg); grazed area: area in which grazers were introduced; grassland area: approximate grassland area within the grazed area (the rest of the grazed area consists of woodland, scrub, blond dune or wet tall forb grassland); grazing regime: yr: year-round grazing, summer: intensive grazing during 1–1.5 months in summer; winter: winter: grazing from September to March; average grazer 1/2: average number of animals of introduced herbivore 1 and 2 during the last 5 yrs; AU/ ha: average number of animal units per ha, assuming year-round grazing (AU is defined here as an animal of 450 kg); phytomass = sum of aboveground dead and live plant material in the ungrazed plots. There is significant correlation between pH and phytomass production at the given soil pH range in the grassland studied ($r = 0.786$; $P = 0.012$).

species (Van Landuyt et al., 2006) was used to assess the response of the diversity of rare species in function of grazing.

2.2. Data analysis

To test whether grazing affected the rate at which species number increased with area, species-area curves were calculated based on the average number of species in the plots in each scale. Species-area curves are commonly used to assess effects of disturbance on plant diversity at different range of scales (Loreau, 2000). These describe the rate at which the species number (S) increases with area (A) (as expressed by z). In the power function, $S = cA^z$, the parameters c and z were estimated through linear regression after log transformation of both variables. Community heterogeneity, a measure of beta diversity, was defined as the dissimilarity in species composition between all $0.25 \times 0.25\ \text{m}^2$ plots in each site. Dissimilarity was calculated with the Euclidean distance as follows:

$$\text{Ed} = \sqrt{\sum_{i=1}^{m} (\text{W}_{\text{ia}} - \text{W}_{\text{ib}})^2}$$

where W_{ia} and W_{ib} are the covers of species i in the sample a and b, and m is the number of species present in at least one of the samples.

An independent t-test was used to determine differences in local species richness between grazed and ungrazed plots for each area separately. Then, in order to test the soil and scale dependence of large herbivores effects on plant diversity, a linear mixed model analysis was used with grazing (categorical), soil acidity (continuous), scale (categorical), and their interactions as fixed factors and species richness as the response variable. Afterwards, two separate mixed models were run to test separately the response of local and site plant richness to grazing, acidity and their interaction. Similarly, the effect of grazing and soil acidity on z values and community heterogeneity was also assessed using mixed models with grazing, soil acidity and their interactions as the fixed factors. In the case of community heterogeneity and species richness at local scale ($0.25 \times 0.25\ \text{m}^2$), site was incorporated as random factor into the model to control for spatial dependence. Because the number of recorded rare and very rare species was zero at local scale in most of the studied grasslands, the response of rare species richness, categorized into three groups, to grazing was only assessed at the site scale. Degrees of freedom were accordingly corrected by Satterthwaite procedure. All the statistical analyses were carried out in SAS 9.1 (SAS Institute 2001; proc mixed).

3. Results

In total, we found 132 plant species, 88 of which (66.66%) occurred in both grazed and ungrazed plots, 42 species (33%) were found only in grazed and 3 (0.023%) only in ungrazed plots. Overall, species richness responded positively to grazing and scale and there was no effect of soil acidity (Tables 2 and 3). However, we found significant interaction terms for both scale and pH with grazing (Table 3), which means that the response of plant species richness to grazing depended both on soil acidity and scale. When we tested local and site scale separately, we found that local species richness ($0.25 \times 0.25\ \text{m}^2$) was significantly positively affected by grazing (Table 4). Grazed plots had an overall higher local species richness than the ungrazed plots within the entire pH range (Tables 2 and 4). In contrast, site species richness ($8 \times 8\ \text{m}^2$) was influenced by grazing and its interaction with soil acidity. Site species richness increased with pH at grazed sites while the opposite pattern was observed in ungrazed situations (Table 4; Fig. 1). This resulted in larger differences in the species richness between grazed and ungrazed sites at higher soil pH compared to sites with a lower pH (Fig. 1).

Contrasting effects of grazing on community heterogeneity were prevalent under different soil conditions: grazing caused a spatial homogenization of the plant community in areas with a low soil pH, but an increased heterogeneity in areas with a higher soil pH (Tables 2 and 4). For example, Cabour 1, Ghyvelde 1 and 2 which occurred on the more acidic soils had a lower dissimilarity in grazed compared to un-

Table 2 – Results of t-test comparing local species richness (0.25 × 025 m plots) and mean value for community heterogeneity defined as the dissimilarity in species composition in grazed and ungrazed plots at each site separately

Area name and site number	Local species richness (0.25 × 0.25 m)		Community heterogeneity	
	Grazed (mean ± SD)	Ungrazed (mean ± SD)	Ungrazed (mean ± SD)	Grazed (mean ± SD)
Ghyvelde1	4.8 ± 0.99	3.2 ± 0.46*	0.31 ± 0.11	0.09 ± 0.07
Ghyvelde 2	9.8 ± 1.9	3.2 ± 1.10***	0.29 ± 0.08	0.15 ± 0.08
Cabour1	12.0 ± 2.2	3.5 ± 1.17***	0.26 ± 0.17	0.20 ± 0.04
Cabour 2	5.3 ± 0.94	3.5 ± 0.70*	0.13 ± 0.19	0.17 ± 0.05
Oostvoorduinen 1	7.9 ± 1.19	5.6 ± 1.12**	0.10 ± 0.05	0.17 ± 0.08
Oostvoorduinen 2	9.8 ± 2.57	1.6 ± 0.75***	0.16 ± 0.19	0.14 ± 0.04
Ter Yde 1	9.5 ± 0.93	4.0 ± 1.00**	0.28 ± 0.10	0.18 ± 0.06
Ter Yde 2	6.5 ± 1.50	4.3 ± 1.50**	0.11 ± 0.07	0.11 ± 0.05
Ter Yde 3	8.3 ± 1.56	4.6 ± 1.50**	0.11 ± 0.07	0.11 ± 0.03
Westhoek-south 1	14.3 ± 1.63	5.9 ± 0.99***	0.19 ± 0.11	0.44 ± 0.22
Westhoek-south 2	10.0 ± 1.69	2.6 ± 0.80***	0.16 ± 0.11	0.22 ± 0.09
Westhoek-north	14.6 ± 3.14	7.4 ± 2.07***	0.16 ± 0.03	0.31 ± 0.08

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Table 3 – F-statistic and value of the mixed model analysis testing the effect of grazing, pH and scale on species richness

Fixed variables	Num. df.	Denum. df.	F	P
Grazing	1	256	37.32	0.000
Scale	1	254	7.95	0.016
Ph	1	115	1.54	0.217
scale*grazing	1	253	47.60	0.000
ph*grazing	1	257	54.71	0.000
ph*scale	1	254	5.19	0.023
ph*scale*grazing	1	253	57.16	0.000

grazed sites (Table 2). In contrast, an increase in dissimilarity with grazing was observed for those areas with a higher pH (Table 2). The z parameter of the species-area relationship followed a similar pattern as community heterogeneity (Table 4; Fig. 2). The richness of very rare species increased with grazing and soil pH and no effect was observed for rare species, while the species richness of common species followed the same pattern as species richness at site level (Table 4).

4. Discussion

Exclusion of large grazers in coastal dunes due to agro-pastoral use abandonment is likely to be the main factor triggering secondary succession towards grass-encroached vegetation (Provoost et al., 2004). It has been hypothesized that fine-scale plant species richness is positively correlated with grazing (Olff and Ritchie, 1998). This is consistent with our results, demonstrating that species richness at a local scale ($0.25 \times 0.25\ m^2$) increased with grazing, independent of soil conditions (Table 2; Fig. 2). At this scale level, the negative effect of biomass removal by grazing on plant individuals is apparently outweighed by positive effects of gap creation or a reduction in competitive pressure (Proulx and Mazumder, 1998). This might also result from the generally low-intensity grazing that is used in the studied areas (Table 1). Although strong plant preferences occur within all areas (Cosyns et al., 2001; Hoffmann et al., 2001, 2005; Lamoot et al., 2005a,b), these caused no local species extinction of preferred species yet. At the site scale, however, an interaction between grazing and soil acidity was observed and the most pronounced positive effect of grazing was observed at sites with a higher pH (Fig. 1). For example, the species richness of Westhoek south1, south2 and north were almost doubled with grazing. Selective grazing on palatable species and a lack of soil resources hampering their regrowth are likely to be responsible for lower species richness in grazed plots at the sites with a lower pH. The results hence confirm that the impact of grazing on plant species richness is soil and scale dependent (Fig. 2).

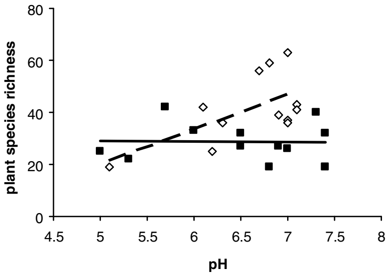

Fig. 1 – Species richness at site scale in function of soil acidity in grazed (dash line: $Y = 10x - 27$; $R^2 = 0.35$; $P = 0.041$) and ungrazed ($y = -0.1181x + 29.433$; $R^2 = 0.0002$; $P < 0.05$) plots.

In addition to overall effects on plant richness, our results showed that soil conditions are most likely to determine the effect of grazing on spatial heterogeneity of vegetation. The results confirmed that grazing induced a spatial homogenization of the plant community composition at lower soil pH, but resulted in an increased spatial heterogeneity at soils with a higher soil pH (Tables 2 and 4). A higher heterogeneity resulted in a higher species richness of grazed plots at site scale (8 × 8 m plot) on soils with a high pH. The obtained interacting effect of grazing with soil acidity on heterogeneity can probably be related to the spatial relationship between grazing and the pre-existing vegetation pattern (see Adler et al., 2001). As confirmed by Cosyns et al. (2001), Hoffmann et al. (2001, 2005) and Lamoot et al. (2005a,b), who all observed preferential plant species and habitat use for foraging of quite different herbivore species (Haflinger, Shetlander and Konik ponies, donkeys Scottish Highland cattle), in most of the coastal dune areas included in this study, continued use of small areas within homogeneous sites caused by a positive feedback between

Table 4 – F-statistics and P-values of the mixed model analysis testing for the effect of grazing and soil pH on the slope of the species-area curve (z), community heterogeneity, species richness at 0.25 × 0.25 and 8 × 8 m site scale

Response variables	Grazing			pH			Grazing*pH		
	Den. df.	F	P	Den. df.	F	P	Den. df.	F	P
Z	17.3	5.98	0.030	10.2	0.21	0.060	19.1	4.48	0.042
Community heterogeneity	33.2	9.60	0.000	46.3	4.98	0.032	33.1	7.71	0.008
Local species richness (0.25 × 0.25 m)	112.0	167.3	0.000	23.2	1.11	0.310	122.0	0.03	0.650
Site species richness (8 × 8 m)	8.3	13.20	0.005	14.5	0.20	0.740	8.33	16.33	0.005
Richness of very rare species	18.5	6.37	0.020	5.6	14.20	0.010	22.0	0.34	0.560
Richness of rare species	15.2	2.56	0.130	17.7	3.08	0.090	15.3	3.50	0.080
Richness of common species	17.1	4.70	0.050	16.3	0.08	0.780	17.2	6.10	0.020

Den. df.: denumerator degree of freedom. Effect of site as a random factor was only significant for community heterogeneity ($Z = 1.82$; $P = 0.034$).

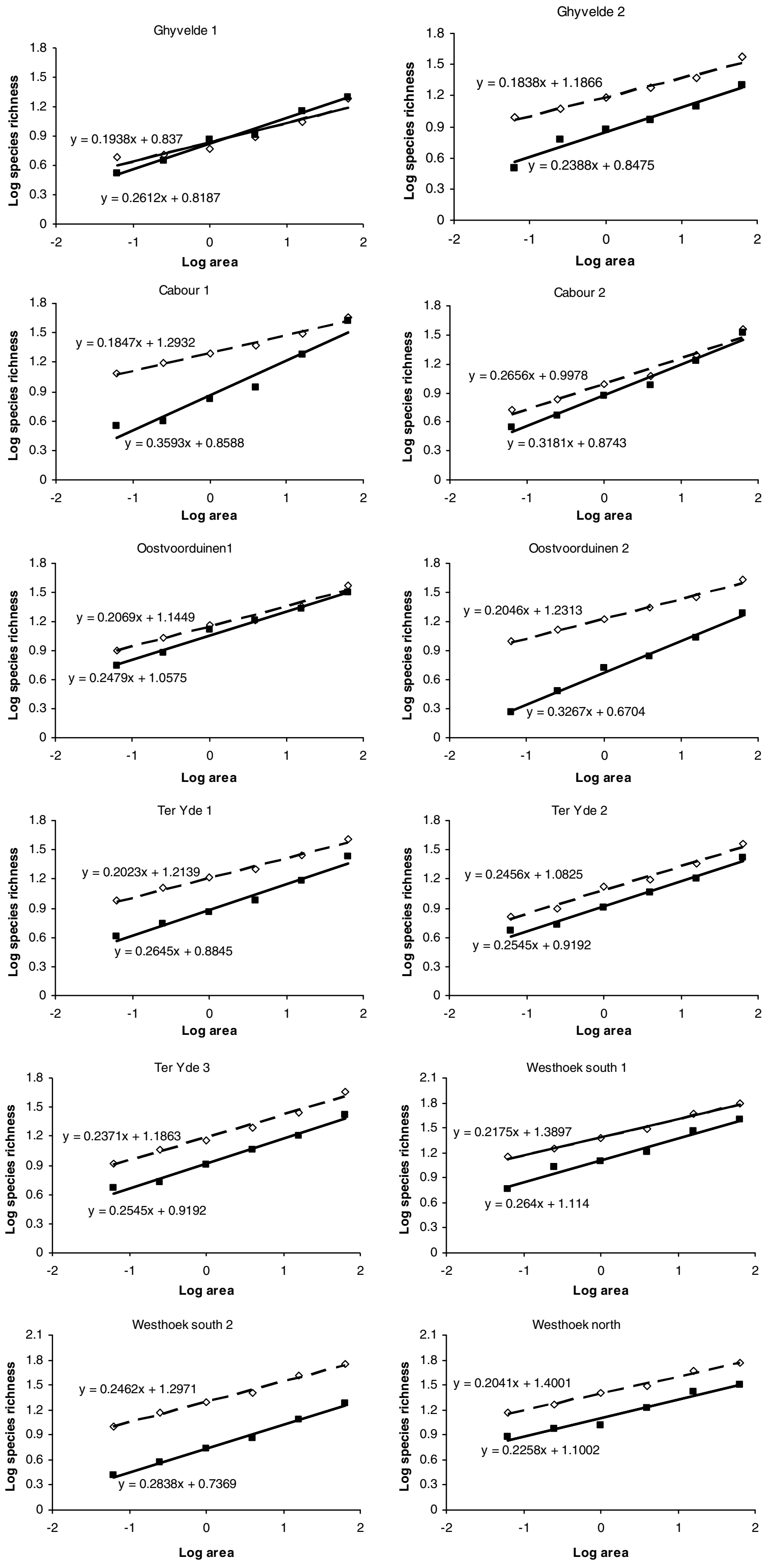

Fig. 2 – Log–log plots of species richness across five spatial scales in grazed (dash lines) and ungrazed (filled lines) plots for 12 studied sites. See Table 1 for description of each site.

grazing and forage quality and quantity, may result in an increased site heterogeneity. Although grazing may increase forage quality over the whole pH range (Mc Naughton et al., 1997), the higher potential for regrowth only supports a continued use by animals at productive sites (Hobbs and Swift, 1988). This may create small differentiated vegetation patches, leading to increased heterogeneity and consequently species richness at larger spatial scales with the highest soil pH.

Although total site plant richness only responded positively to grazing at sites with a higher pH, the number of rare species increased in response to grazing, independent of soil acidity. For example, four of the seven very rare species present (*Carex disticha, Asparagus officinalis, Medicago minima* and *Linum catharcticum*) and four rare species (*Euphrasia stricta, Polygala vulgaris, Sagina nodosa* and *Viola canina*), only occurred in grazed plots. *Rosa pimpinellifolia* and *Koeleria albescens* were present under both treatments but their abundance tended to decrease in grazed situations. This agrees with Hayes and Holl (2003) who found a positive effect of grazing on the richness of forb species, among which some were of conservation concern in Californian coastal grassland plant communities.

The independence of local species richness patterns and soil conditions (in contrast to site species richness), indicates that mechanisms determining species richness are scale specific. Small scale patterns in plant communities are probably mainly influenced by abiotic factors while the interaction between abiotic and biotic factors may explain dynamic patterns at larger scales (Fuhlendorf and Smeins, 1999). The recognition of these scale dependent patterns of the effect of grazing along an acidity gradient is important when delineating appropriate biodiversity conservation strategies in coastal dune grasslands.

Our results suggest that both environmental site conditions and scale needs to be considered when aiming to maintain and enhance botanical diversity by grazing management through the introduction of grazers (Dorrough et al., 2006). The general increase of local species richness, and in particular the richness of rare species, implies that the introduction of large herbivores into natural grasslands may in some cases be essential for the conservation of plant diversity (Bakker et al., 2006). However, negative effects on species diversity in grasslands with lower pH were prevalent at the site scale, suggesting that grazing as a system approach for the management of nutrient-poor vegetation in coastal dune habitats might not be appropriate. In addition, the studied grasslands have a pH range between alkaline and neutral, whether the observed pattern remains the same in grassland with basic soil (pH higher than 8) or more acidic soils ($pH < 4$) and in non-coastal grasslands needs further study. A factor that could not be studied was the possible impact of grazer species on plant diversity. Although a wide spectrum of grazers were included in this study, they could not be exchanged between areas with different soil conditions. However, all detailed and local studies on diet preferences (Ebrahimi, 2007; Hoffmann et al., 2001, 2005; Lamoot et al., 2005a,b) emphasize the strong preference of all herbivores for graminoid species, there are no strong indications that animal species would induce large, herbivore species related differences in plant performance. Further studies are required though to effectively investigate the interactive effect of grazing, grazer species and soil conditions on plant diversity in coastal dune grasslands (Loucougaray et al., 2004; Klimek et al., 2007).

Acknowledgements

Soil analyses were conducted at the Research Institute for Nature and Forest (INBO). DB is a postdoctoral fellow of the Fund for Scientific Research, Flanders. We thank Edward Vercruysse for help with vegetation sampling and plant species identifications. We are grateful to the Agency for Nature and Forest of the Ministry of the Flemish Community and the Conservation du Littoral for their permission to do field research in their nature reserves.

REFERENCES

Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465–479.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Johannes, M.H., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. Ecology Letters 9, 780–788.

Bakker, J.P., 1998. The impact of grazing on plant communities. In: Wallis Devries, M.F., Bakker, J.P., van Wieren, S.E. (Eds.), Grazing and Conservation Management. Kluwer Academic Publisher, Dordrecht, pp. 137–184.

Bakker, J.P., Londo, G., 1998. Grazing for conservation management in historical perspectives. In: Wallis Devries, M.F., Bakker, J.P., van Wieren, S.E. (Eds.), Grazing and Conservation Management. Kluwer Academic Publisher, Dordrecht, pp. 21–54.

Chaneton, E.J., Facelli, J.M., 1991. Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. Vegetatio 93, 143–155.

Cosyns, E., Degezelle, T., Demeulenaere, E., Hoffmann, M., 2001. Feeding ecology of Konik horses and donkeys in Belgian coastal dunes and its implications for nature management. Belgian Journal of Zoology 131 (Suppl. 2), 109–116.

Dorrough, J., Ash, J.E., Bruce, S., McIntyre, S., 2007. From plant neighbourhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. Plant Ecology 191, 186–198.

Dorrough, J., Moxham, C., Turner, V., Sutter, G., 2006. Soil phosphorus and tree cover modify the effects of livestock grazing on plant species richness in Australian grassy woodland. Biological Conservation 130, 394–405.

Ebrahimi, A., 2007. Towards an integrated framework of determining grazing capacity in low-productive, spatially heterogeneous landscapes. Ph.D. Thesis, Ghent University, Ghent, Belgium.

Fuhlendorf, S.D., Smeins, F.E., 1999. Scaling effects of grazing in a semi-arid grassland. Journal of Vegetation Science 10, 731–738.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52, 104–145.

Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative Plant Ecology. Unwin Hyman, London, UK.

Hayes, G.E., Holl, K.D., 2003. Cattle grazing impact on annual forbs and vegetation composition of mesic grassland in California. Conservation Biology 17, 1694–1702.

Hobbs, N.T., Swift, D.M., 1988. Grazing in herds: when are nutritional benefits realized? American Naturalist 131, 760–764.

Hodgson, J.G., Montserrat-Marti, G., Tallowin, J., Thompson, K., Diaz, S., Cabido, M., Grime, J.P., Wilson, P.J., Band, S.R., Bogard, A., Cabido, R., Caceres, D., Castro-Diez, P., Ferrer, C., Maestro-Martinez, M., Perez-Rontome, M.C., Charles, M., Cornelissen, J.H.C., Dabbert, S., Perez-Harguindeguy, N., Krimly, T., Sijtsma, F.J., Strijker, D., Vendramini, F., Guerrero-Campo, J., Hynd, A., Jones, G., Romo-Diez, A., de Torres Espuny, L., Villar-Salvador, P., Zak, M.R., 2005. How much will it cost to save grassland diversity? Biological Conservation 122, 263–273.

Hoffmann, M., Cosyns, E., Deconinck, M., Zwaenepoel, A., 2001. Donkey diet in a Flemish coastal dune area in the first year after introduction. In: Houston, J.A., Edmondson, S.E., Rooney, P.J. (Eds.), Coastal Dune Management, Shared Experience of European Conservation Practice. Liverpool University Press, Liverpool, pp. 95–107.

Hoffmann, M., Cosyns, E., Lamoot, I., 2005. Large herbivores in coastal dune management: do grazers do what they are supposed to do? In: Herrier, J.-L., Mees, J., Salman, A., Seys, J., Van Nieuwenhuyse, H., Dobbelaere, I. (Eds.), Proceedings 'Dunes and Estuaries 2005' – International Conference on Nature Restoration Practices in European Coastal Habitats, Koksijde, Belgium, 19–23 September 2005, pp. 249–268. Oostende, VLIZ Special Publication 19, xiv + 685 pp.

Huisman, J., Olff, H., 1998. Competition and facilitation in multispecies plant-herbivore systems of productive environments. Ecology Letters 1, 25–29.

Jutila, H.M., Grace, J.B., 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. Journal of Ecology 90, 291–302.

Kahmen, S., Poschlod, P., Schreiber, K.F., 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. Biological Conservation 104, 319–328.

Klimek, S., Kemmermann, A.R., Hofmann, M., Isselstein, J., 2007. Plant species richness and composition in managed grasslands: the relative importance of field management and environmental factors. Biological Conservation 134, 559–570.

Kooijman, A.M., Dopheide, J.C.R., Sevink, J., Takken, I., Verstraten, J.M., 1998. Nutrient limitations and their implications on the effects of atmospheric deposition in coastal dunes; lime-poor and lime-rich sites in the Netherlands. Journal of Ecology 86, 511–526.

Kooijman, A.M., Smit, A., 2001. Grazing as a measure to reduce nutrient availability and plant productivity in acid dune grasslands and pine forests in the Netherlands. Ecological Engineering 17, 63–77.

Lamoot, I., Meert, C., Hoffmann, M., 2005a. Habitat use of ponies and cattle foraging together in a coastal dune area. Biological Conservation 122, 523–536.

Lamoot, I., Vandenberghe, C., Bauwens, D., Hoffmann, M., 2005b. Grazing behaviour of free-ranging donkeys and Shetland ponies in different reproductive states. Journal of Ethology 23, 19–27.

Landsberg, J., James, C.D., Maconochie, J., Nicholls, A.O., Stol, J., Tynan, R., 2002. Scale-related effect of grazing on native plant communities in an arid rangeland region of South Australia. Journal of Applied Ecology 39, 427–444.

Loreau, M., 2000. Are communities saturated? On the relationship between alpha, beta and gamma diversity. Ecology Letter 3, 73–76.

Loucougaray, G., Bonis, A., Bouzille', J.-B., 2004. Effects of grazing by horses and/or cattle on the diversity of coastal grasslands in western France. Biological Conservation 116, 59–71.

Mc Intyre, S., Heard, K.M., Martin, T.G., 2003. The relative importance of cattle grazing in subtropical grasslands: does it reduce or enhance plant diversity? Journal of Applied Ecology 40, 445–457.

Mc Naughton, S.J., Banyikwa, F.F., Mc Naughton, M.M., 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278, 1798–2000.

Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63, 327–366.

Olff, H., Ritchie, M., 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13, 261–265.

Pacala, S.W., Crawley, M.J., 1992. Herbivores and plant diversity. American Naturalist 140, 243–260.

Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79, 2581–2592.

Provoost, S., Ampe, C., Bonte, D., Cosyns, E., Hoffmann, M., 2004. Ecology, management and monitoring of dune grassland in Flanders, Belgium. Journal of Coastal Conservation 22, 33–42.

Provoost, S., Van Landuyt, W., 2001. The flora of Flemish coastal dunes (Belgium) in a changing landscape. In: Houston, J.A., Edmondson, S.E., Rooney, P.J. (Eds.), Coastal Dune Management, Shared Experience of European Conservation Practice. Liverpool University Press, Liverpool, UK, pp. 393–401.

Spiegelberger, T., Matthies, D., Muller-Scharer, H., Schaffner, U., 2006. Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps. Ecography 29, 541–548.

Tahmasebi Kohyani, P., Bossuyt, B., Bonte, D., Hoffmann, M., 2008. The importance of grazing and soil acidity for plant community composition and community-wide trait characterization in coastal dune grasslands. Applied Vegetation Science 11, 179–185.

Van Diggelen, R., Marrs, R., 2003. Restoring plant communities. Applied Vegetation Science 6, 105–110.

Van Landuyt, W., Hoste, I., Vanhecke, L., Van den Bremt, P., Vercruysse, W., De Beer, D., 2006. Atlas van de flora van Vlaanderen en het Brussels Gewest. Instituut voor Natuur- en Bosonderzoek, Nationale Plantentuin van België and Flo.Wer.