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Source: *Journal of Vegetation Science*, Vol. 7, No. 3 (Jun., 1996), pp. 445-452
Published by: Opulus Press
Stable URL: http://www.jstor.org/stable/3236288
Accessed: 26/10/2008 23:54

Journal of Vegetation Science 6: 445-452, 1995

Impact of grazing and atmospheric nitrogen deposition on the vegetation of dry coastal dune grasslands

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Abstract. A five-year experimental study was carried out to examine the combined effects of grazing and atmospheric nitrogen deposition on the vegetation of three dry dune grasslands: one short species-rich, one short species-poor, and one predominated by tall graminoids.

Additional fertilization with nitrogen had no significant effect, neither in grazed nor in non-grazed plots. Exclusion of grazing by rabbits resulted in an increase in the frequency of perennial graminoids and a decrease in the frequency of annual graminoids and herbs. Nevertheless, species diversity remained the same in the species-rich grassland. During the experiment, the above-ground biomass increased in all non-grazed plots and the amount of bare soil and mosses decreased.

The vegetation changes occurred mainly within one year after the exclusion of grazing. An exception is the grass-dominated site where the amount of *Calamagrostis epigejos* increased gradually from ca. 20 % in the first two years to about 50 % in the fourth and fifth year.

Grazing by rabbits seems essential to prevent graminoids to become predominant in the dry dunes. If graminoids are dominant, grazing by horses can be an appropriate method to restore the original grassland vegetation. After six months of grazing by horses the grass-dominated site showed a decrease of the frequency of perennial graminoids, from 95 % to 80 %, and an increase of the frequency of perennial herbs, from 2.5 % to between 13 and 20 %.

Keywords: Horse; Management; Meijendel; the Netherlands; Rabbit; Restoration ecology; Species diversity.

Nomenclature: van der Meijden (1990).

Introduction

Recently, semi-natural vegetation in the Netherlands has been under increasing influence of atmospheric deposition of acid and eutrophic components. This has led to a decrease in nature conservation values.

In chalk grasslands and heathlands the influence of atmospheric deposition has been studied to support management programs aiming at restoration of nature values (Heil & Diemont 1983; Roelofs 1986; Bobbink et al. 1988, 1990; Bobbink 1991; Aerts & Heil 1993). So far, such systematic studies have not been initiated in the dunes. The present study was initiated in 1988, in order to understand the relations between atmospheric deposition, grazing and vegetation dynamics. The present paper deals with changes in species composition.

Since the 1970s some tall perennial graminoids, notably *Ammophila arenaria*, *Avenula pubescens*, *Calamagrostis epigejos*, *Elymus athericus* and *Carex arenaria*, have become dominant in many originally short dry dune grasslands of the Netherlands (C.T.M. Vertegaal et al. int. report 1991). As a consequence, these grasslands show now a relatively low species diversity. From the point of view of nature conservation this is considered an unfavourable situation (Westhoff 1985). Nowadays, nature managers try to counteract this development and try to restore the original vegetation composition. This requires understanding of the processes responsible for the predominance of graminoids.

In the past, tall graminoids were usually not dominant because of the low nutrient status of sandy dune soils (Willis & Yemm 1961; Boorman & Fuller 1982). The present dominance of graminoids might be a result of the recent increase of atmospheric nitrogen deposition. From 1930 to 1980 the atmospheric nitrogen deposition ($NH_4^+ + NO_3^-$) on coastal areas in the Netherlands increased from 4 kg $N.ha^{-1}.yr^{-1}$ to 14 kg $N.ha^{-1}.yr^{-1}$ (Stuyfzand 1993). The predominance of graminoids due to high nitrogen loads is also known from heathlands (Heil & Diemont 1983; Roelofs 1986; Bobbink et al. 1990; Aerts & Heil 1993) and chalk grasslands (Bobbink et al. 1988; Bobbink 1991; Willems et al. 1993). Many graminoids have a relative higher growth rate than other plant species and are therefore able to benefit more from increased nitrogen input. This is shown by fertilizing experiments in grasslands (Willis & Yemm 1961; Willis 1963; Van Hecke et al. 1981; Davy & Bishop 1984; Bobbink 1991; Mountford et al. 1993). When grasses are tall, light will not penetrate into the soil and germination of annual species is prevented (Bobbink & Willems 1991; Olff et al. 1993).

It seems that graminoids will not dominate when the vegetation is frequently grazed by animals such as rabbits (Williams et al. 1974; Bhadresa 1977; Zeevalking & Fresco 1977). If the rabbit population decreases, as in the 1950s (due to myxomatosis), graminoids are able to take over (Ranwell 1960; Thomas 1963; Westhoff 1985). The effect of rabbit grazing is also experimentally shown in grazed grasslands where after the exclusion of grazing tall graminoids became dominant (Farrow 1917; Hill et al. 1992). Even after restoration of the rabbit population, graminoids are able to remain dominant for a long time as rabbits do not eat or enter such relatively tall grass swards. Non-grazed vegetation has a relatively low protein content in comparison to grazed vegetation and therefore animals avoid the area (Bakker et al. 1983).

The dominance of graminoids can be counteracted by introducing large herbivores (Williams et al. 1974). If heavy grazing is needed to permit seedling establishment of annual species, it can also prohibit successful completion of the life cycle of these annual species (Farrow 1917; Watt 1962; Silvertown et al. 1992). Recently, horses and cows have been introduced in Dutch nature reserves to reduce the amount of biomass and the vegetation height and thus restore the original species composition.

This paper reports on an experiment in a Dutch coastal dune area where fertilization with nitrogen and exclusion of grazing were combined as a treatment. The purpose was to define the main reason for the dominance of tall graminoids in large parts of comparable dune areas. This dominance may be caused by high atmospheric deposition of nitrogen, or the absence of grazing by rabbits, or a combination of both. In addition, the effects of the introduction of horses and the implications for the management of dune grasslands will be discussed.

Material and Methods

Study sites

The study was carried out in three grassland sites in Meijendel, a coastal dune area north of The Hague, the Netherlands. This area is managed by the Dune Water Company of Zuid-Holland (D.Z.H.).

The first, species-rich site is located at a distance of 0.5 km from the coast. The sandy soil is calcareous, with 2 - 3 % $CaCO_3$, and with a very low organic matter content (2 % in the 10 cm top soil). Phytosociologically, the vegetation can be assigned to the *Festuco-Galietum maritimi* association (Westhoff & den Held 1969). This site has been monitored since the summer of 1989.

The second, species-poor site is situated 2.5 km from the coast. The soil is decalcified down to 50 cm with a pH($CaCl_2$) of 4.2 to 5.4 on similar calcareous dune sand as the first site. The 10 cm thick top soil has an organic matter content of 3 %. The site represents a species-poor variant of the *Violo-Corynephoretum* association (Westhoff & den Held 1969). A certain dominance of graminoids occurred here from the beginning (Table 1). This site has been monitored since the summer of 1988.

The third, grass-dominated site is close to the second site, but the vegetation has become totally predominated by *Carex arenaria*, *Festuca ovina* + *F. rubra* and *Calamagrostis epigejos* (Table 1). This site has been monitored since the summer of 1988.

Table 1. Total number of species and frequency (average for all years) of plant species of the control plots in the three sites (grass-dominated site before the introduction of horses); Rich = species-rich site; Poor = species-poor site; Grass = grass-dominated site.

	Rich	Poor	Grass
Number of species			
Annual herbs	4	3	1
Perennial herbs	9	3	3
Annual graminoids	2	1	1
Perennial graminoids	6	6	6
Annual herbs			
Cerastium semidecandrum	1 - 5	< 1	0
Erodium cicutarium	5 - 10	< 1	0
Senecio sylvaticus	0	0	1 - 5
Teesdalia nudicaulis	0	< 1	0
Veronica arvensis	< 1	0	0
Viola curtisii	1 - 5	0	0
Perennial herbs			
Galium verum	1 - 5	1-5	< 1
Hieracium pilosella	< 1	0	0
Holcus lanatus	0	0	< 1
Leontodon saxatilis	1 - 5	0	0
Lotus corniculatus	1 - 5	0	0
Myosotis arvensis	1 - 5	0	0
Ononis repens	10 - 20	0	0
Rumex acetosella	0	10 - 20	0
Sedum acre	< 1	0	0
Senecio jacobaea	5-10	1-5	< 1
Taraxacum sect. *Erythrosperma*	1 - 5	0	0
Annual graminoids			
Aira praecox	1 - 5	5 - 10	1 - 5
Phleum arenarium	< 1	0	0
Perennial graminoids			
Agrostis stolonifera + *A. capillaris*	0	5 - 10	0
Calamagrostis epigejos	1 - 5	10 - 20	10 - 20
Carex arenaria	5 - 10	5 - 10	> 20
Festuca ovina + *F. rubra*	1 - 5	> 20	10 - 20
Koeleria macrantha	< 1	0	1 - 5
Luzula campestris	10 - 20	10 - 20	1 - 5
Poa pratensis	5 - 10	< 1	< 1

Treatments

At all three sites five homogeneous quadrats of 2 m × 2 m were selected. Each quadrat was divided into four experimental plots of 1 m × 1 m: (1) control; (2) fertilized; (3) excluded from grazing by rabbits and (4) combination of fertilization and exclusion of grazing. The treatments were allocated randomly to the plots (randomized quadrat design).

In the autumn of 1990, horses were introduced in a part of Meijendel to reduce severe grass encroachment and to possibly restore the original species composition. The horses grazed for six months at the grass-dominated site; thereafter the horses were excluded from the quadrats because they demolished the exclosures.

The fertilizer was applied to simulate the effects of high loads of atmospheric nitrogen deposition. It was assumed that addition of nitrogen would speed up grass encroachment and cause the associated loss of characteristic herbs.

From October 1988 until April 1992 the fertilizer applied consisted of pellets of NH_4NO_3 (added in spring and autumn) equal to an extra deposition of 25 kg N/ha/yr. As weekly unsaturated soil water analysis by ceramic cups showed that large amounts leached through the surface soil within a few weeks, a different method of fertilization was applied. Since April 1992 quadrats were fertilized with a 0.0069 M $(NH_4)_2SO_4$ solution once every fortnight, which was equal to an extra nitrogen input of 50 kg N/ha/yr. For osmotic reasons NaCl (sea salt) was added in this solution up to the same NaCl concentration in the rainwater. The non-fertilized plots obtained an equal amount of NaCl solution without $(NH_4)_2SO_4$. The yearly amount of solution given was equivalent to an extra precipitation of 26 mm/yr, which is only 3 % of the average yearly precipitation.

Measurements

Once a year in July, the species composition of the vegetation was recorded in each plot by counting the presence of all separate phanerogams and of the rest (bare soil and mosses) with a point frequency method (Mueller-Dombois & Ellenberg 1974), using 100 cross-points of a grid.

The standing crop biomass (dead+living) was measured each year in July by cutting, drying and weighing three randomly selected subsamples of 20 cm × 20 cm, each at the edge of all plots. The central part of each plot (60 cm × 60 cm) has been left untouched for long-term monitoring.

Statistical analysis

The results were analyzed statistically with the computer package SAS (Anon. 1987). The counts of the plants were standardized to frequencies and will be called frequencies further on.

The effect of grazing and fertilization on the following three frequencies were tested with the SAS-procedure ANOVA with repeated measurements: species groups (annual or perennial herbs and graminoids), individual species, surface without phanerogamic species (bare soil and mosses). The effects on species diversity (see below) and biomass were also tested. A significance leve of 0.05 was chosen. The effects of the treatments were analysed separately for each site. The effects of treatments on the grass-dominated site were analysed twofold: before the introduction of the horses and after six months of grazing by horses.

Species diversity was measured as the Shannon Wiener index:

$$SD = \Sigma p_i \ln p_i \quad (1)$$

where *SD* = species diversity and p_i = the proportion of species $_i$ (on a frequency basis).
The moss species were regarded as one group, and were not included in this calculation.

Results

The species present in the three sites were divided in four groups: annual herbs, perennial herbs, annual graminoids and perennial graminoids (Table 1). The grazed quadrats of the species-rich site contain the largest number of herb species, 13. The numbers of the species-poor and the grass-dominated site were six and four respectively. The number of graminoid species is equal in the sites, i.e. seven or eight. However, in the grazed plots the frequency of perennial graminoids (Table 2) is much higher in the grass-dominated site (92 % prior to grazing by horses) than in the species-poor site (63 %) and the species-rich site (44 %). However, the amounts of perennial graminoid species in the species-rich and grass-dominated systems are the same (Table 1). The species responsible for the dominance of graminoids in grass encroached stages are already present in the species-rich stage.

Effects of fertilization and grazing on species groups

The impact of nitrogen fertilization on the change of species groups and the three other variables was not statistically significant at all sites! Therefore fertilized

Table 2. Average frequency over all years of the species groups in the grazed plots and exclosure plots of the three sites.

Species group	Annual herbs [%]		Perennial herbs [%]		Annual graminoids [%]		Perennial graminoids [%]	
Treatment	G	E	G	E	G	E	G	E
Site								
Species-rich	7.5 **	1.7 **	41.5 *	33.6 *	4.9	2.6	43.8 **	56.0 **
Species-poor	1.2	0.1	24.4 *	12.2 *	10.5	4.3	62.7 **	82.2 **
Grass-dominated[1]	1.1	0.3	2.5	2.5	3.9	3.5	92.4	93.7
Grass-dominated[2]	0.1	0.2	12.8 *	4.1 *	6.9 **	0.4 **	80.0 **	95.3 **

G = grazed plots; [1] = before the introduction of horses;
E = exclosure plots; [2] = after the introduction of horses.

Significance of differences between grazed and exclosure plots: * = $p < 0.05$; ** = $p < 0.01$.

and non-fertilized plots were taken together during the statistical analysis of the effects of grazing.

The effects of the exclusion of grazing by rabbits on the species groups are shown in Table 2. The exclusion resulted in an increase of perennial graminoids in both the species-rich and species-poor sites. No increase was observed in the grass-dominated site, because the frequency of perennial graminoids was high already from the beginning (92 %). The frequency of perennial herbs decreased in both the species-rich and species-poor sites. In the species-rich site the frequency of annual herbs also showed a decrease.

Exclusion of grazing at the species-rich and the species-poor site reduced the amount of bare soil and mosses, while the biomass of the stand increased (Table 3). Moreover, a decrease in species diversity was seen in the species-poor site.

Before the introduction of horses on the grass-dominated site, the amount of bare soil and mosses became lower in the exclosure plots. Six months of grazing by horses resulted in a difference of perennial graminoids between grazed and non-grazed plots (Table 2). In contrast, the frequency of annual graminoids and perennial herbs increased (respectively 0.4% to 7%, and 4% to 13%). The horse-grazed plots showed an increase of the amount of bare soil and mosses, and of the species diversity. In the same time the biomass showed a decrease.

Effects of fertilization and grazing on individual species

Fertilization with nitrogen did not affect individual species. Only *Luzula campestris* decreased in the exclosures of the grass-dominated site. To test the effect of grazing on individual species, fertilized and non-fertilized plots were also taken together.

The significant changes of individual species after the exclusion from grazing are shown in Table 4.

Some species showed a decrease at the species-poor site. No increases were detected. However, in the last paragraph an increase in perennial graminoids was

Table 3. Average percentage of all years of bare soil and mosses, species diversity and biomass of the three sites.

Variable	Bare + mosses [%]		Species diversity (see formula 1)		Biomass [g/m^{-2}]	
Treatment	G	E	G	E	G	E
Site						
Species-rich	43.9 **	8.5 **	1.945	1.983	42 **	264 **
Species-poor	57.1 **	8.1 **	1.635 *	1.356 *	75 **	467 **
Grass-dominated[1]	17.8 **	5.6 **	1.134	1.213	335	536
Grass-dominated[2]	45.2 **	3.7 **	1.664 *	1.465 *	256 **	613 **

G = grazed plot; [1] = before the introduction of horses;
E = exclosure plot; [2] = after the introduction of horses.

Significance of differences between grazed and exclosure plots: * = $p < 0.05$; ** = $p < 0.01$.

shown. This contradiction might be due to an increase of different perennial graminoids in each plot.

In the grass-dominated site no changes due to the exclusion from grazing were found before the introduction of grazing by horses. The whole site is dominated by perennial graminoids.

Species that increased after the exclusion from grazing or decreased after the introduction of grazing by horses are all perennial graminoids. One exception is the increase of *Phleum arenarium* at the species-rich site under non-grazing conditions. This is unexpected as it is a small annual grass and its germination is normally prevented in a vegetation predominated by tall grasses such as *Festuca rubra* + *F. ovina* and *Poa pratensis* (Table 4). Species that showed a decrease after exclusion or an increase after the introduction of grazing by horses, are herbs or small perennial graminoids, such as *Luzula campestris*.

Table 4. Plant species development after excluding grazing or after introduction of horses at the grass-dominated site.

Species-rich site	
Festuca ovina +*F. rubra*	+
Poa pratensis	+
Phleum arenarium	+
Cerastium semidecandrum	- -
Erodium cicutarium	- -
Luzula campestris	-
Myosotis arvensis	- -
Senecio jacobaea	-
Taraxacum sect. *Erythrosperma*	- -
Viola curtisii	- -
Species-poor site	
Rumex acetosella	- -
Senecio jacobaea	-
Grass-dominated site	
Before introduction of horses	no change
After introduction of horses	
Aira praecox	+
Luzula campestris	+
Rumex acetosella	++
Senecio jacobaea	+
Calamagrostis epigejos	- -

\+ = increase ($p < 0.05$);
++ = increase ($p < 0.01$);
\- = decrease ($p < 0.05$);
\- - = decrease ($p < 0.01$).

Vegetation change after the exclusion of grazing

Vegetation change was defined as the difference in frequency between two years of the species that changed in the non-grazed plots relative to the grazed plots (Table 4). The difference remained constant after the first year, the changes measured occurred during the first year. The vegetation change was calculated separately for frequencies which increased or decreased due to grazing.

At the species-rich site the vegetation change of species which benefited from the exclusion of grazing was small, viz. from 11 % to 16 %. The vegetation change of species which decreased after the exclusion of grazing all occurred during the first year.

At the species-poor site all changes occurred during the first year.

At the grass-dominated site the vegetation change for species which increased after grazing by horses was the same for species which increased after the exclusion, i.e. from 3 % to 25 %. *Calamagrostis epigejos* is the only species which increased in the exclosures compared to the control plots. In spite of the introduction of horses the frequency of *Calamagrostis epigejos* remained the same (ca. 20 %) in the grazed plots, therefore it increased from 20 % to ca. 50 % in the exclosures. The exclosures developed from a dominance of several graminoids (Table 1) into a dominance by only one species. The frequency of the species favoured by grazing showed an increase in the grazed plots from 7 % to 30 %, while it remained low in the exclosures (3 %). The increase of these species occurred after the introduction of the horses. The vegetation level of the grazed plots was lowered and this gave the plants an opportunity to grow.

Discussion

This study showed that maintenance of species-rich dry dune grasslands strongly depends on the activity of grazing animals, especially under relatively high atmospheric nitrogen deposition levels. When grazing is excluded, perennial graminoids become dominant within one or two years. These graminoids were already present in the three sites before the treatment (Table 1). As in other grazing experiments (Belsky 1986; Hill et al. 1992) no new plant species invaded the plots.

Under relatively high atmospheric nitrogen deposition levels, fertilization by nitrogen had no effect on the three sites during the 5 yr of this study. This is not consistent with fertilizer experiments in other grasslands (Willis 1963; Van Hecke et al. 1981; Davy & Bishop 1984; Bobbink et al. 1988; Bobbink 1991;

Mountford et al. 1993). Effects of additional nutrient supply were always registered within 5 yr. In our case the amount of nitrogen fertilizer of 50 kg N/ha/yr and background deposition of nitrogen of 10 kg N/ha/yr (ten Harkel et al. 1991) should be sufficient to accelerate changes in species composition if other resources are not limited. Bobbink et al. (1992) gave a critical load of nitrogen for dune grasslands of 20-30 kg N/ha/yr.

Some explanations for these deviating results are given below.

Phosphorus as a limiting factor

Fertilization experiments with different combinations of nutrients (nitrogen, phosphorus, potassium, calcium) showed that the nitrogen content of the soil was the most limiting factor (Milton 1940, 1947; Willis 1963; Boorman & Fuller 1982; Kachi & Hirose 1983; Dougherty et al. 1990; Olff et al. 1993). However, also phosphorus can be an important limiting factor (Milton 1940, 1947; Willis 1963; Boorman & Fuller 1982; Kachi & Hirose 1983; Dougherty et al. 1990). Phosphorus limitation can be an explanation why nitrogen fertilization did not have any effect in this study. At the study sites atmospheric phosphate deposition of 0.3 kg P/ha/yr (ten Harkel et al. 1991) and the water soluble soil phosphate content of ca. 0.3 kg P/ha in the 8 cm surface soil (ten Harkel 1992) are very low. However, in this study we focused on the role of nitrogen in the vegetation development. The availability of phosphorus to the vegetation in the Dutch dunes is currently being studied.

If phosphate would have been the limiting factor in the past, the present dominance of graminoids in parts of the Dutch dunes cannot be explained. Therefore, phosphate can be a limiting factor only at high nitrogen levels. This was also shown by Dougherty et al. (1990).

Changes in ecosystems other than nutrient availability

Research on heathland (Heil & Diemont 1983) showed that a relatively old stand of *Calluna vulgaris* (ca. 15 yr) was not significantly affected by nitrogen application. The closed canopy of *Calluna vulgaris* prevented *Festuca ovina* to take advantage of the nitrogen application. However, when *Calluna vulgaris* died after a heather beetle infestation and the vegetation was opened up, *Festuca ovina* became dominant after repeated application of nitrogen.

Chalk grasslands can sustain high loads of nutrients when the management is appropriate. Mowing and harvesting of vegetation at a site dominated by *Brachypodium pinnatum* was adequate to restore a characteristic species-rich chalk grassland within 5 yr (Bobbink & Willems 1991).

These studies show that when no other changes occur, the vegetation is probably not seriously affected by an increasing availability of nutrients. When grazing is continued, changes will probably be very slow and cannot be measured within 5 yr.

The main conclusion of this study is that with high nitrogen levels a dune grassland does not become grass-dominated as long as the vegetation is grazed, not even when fertilized. When grazing is absent, the relatively high availability of nitrogen gives graminoids the opportunity to become dominant. Effects of a decrease of grazing intensity were reported by Ranwell (1960): an increase in the growth and flowering of graminoids and a decrease of herbs was found after the disappearance of rabbits by myxomatosis in a sand-dune system. Willis & Yemm (1961) and Willis (1963) showed, however, that even without grazing a very nutrient-poor sandy dune system can remain species-rich. However, the system became dominated by grasses after addition of nutrients. Boorman & Fuller (1982) found that the addition of nutrients to grazed dune swards caused a decline of annual species, but, due to the grazing, perennial grasses did not dominate the sward. When grazing animals are present in nutrient-poor systems like chalk grasslands (Bobbink 1991) and heathland (Farrow 1917; Heil & Diemont 1983), no dominance by graminoids occurs. In general, it is seen that moderate grazing increases plant species diversity (Puerto et al. 1990; Gibson & Brown 1991; Belsky 1992).

The introduction of horses at the grass-dominated site showed that the dominance of graminoids can be counteracted by introducing grazing. Light penetrates into the soil surface and provides opportunities for germination of seedlings (Willems 1983; Bobbink & Willems 1991). Herbs increase and species richness may be restored. When atmospheric deposition of nitrogen remains high, grazing will always be necessary to preserve species-rich dune grasslands for the future.

Acknowledgements. We thank the Dune Water Company of Zuid-Holland, notably its Department of Nature and Landscape Management for their substantial financial support and the Department of Implementation of Management for extensive technical facilities to carry out the field experiments. J.H. van Boxel, G.W. Heil and A. Kooijman assisted with the research and gave valuable help during the compilation of this article. We thank P.D. Jungerius and J.M. Verstraten for critical reading of the text. D. Warmerdam is acknowledged for help with the correction of the English text.

References

Anon. 1987. *Statistical Analyzing System Release 6.03.* SAS Institute Inc., Cary, NC.

Aerts, R. & Heil G.W. (eds.) 1993. *Heathlands: patterns and processes in a changing environment.* Kluwer Academic Publishers, Dordrecht.

Bakker, J.P., de Leeuw, J. & van Wieren, S.E. 1983. Micropatterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio* 55: 153-161.

Belsky, A.J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *J. Ecol.* 74: 419-437.

Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3: 187-200.

Bhadresa, R. 1977. Food preference of rabbits *Oryctolagus cuniculus* L. at Holkham sand dunes, Norfolk. *J. Appl. Ecol.* 14: 287-291.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *J. Appl. Ecol.* 28: 28-41.

Bobbink, R. & Willems, J.H. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grassland. *Biol. Conserv.* 56: 1-21.

Bobbink, R., Bik, L. & Willems, J.H. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. *Acta Bot. Neerl.* 37: 231-242.

Bobbink, R., Boxman, D., Fremstedt, E., Heil, G., Houdijk, A. & Roelofs, J. 1992. Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna. In: Grennfelt, P. & Thörnelöf, E. (eds.) *Critical loads for nitrogen*, pp. 111-159. Nordic Council of Ministers, Copenhagen.

Bobbink, R., den Dubbelden, K. & Willems, J.H. 1989. Seasonal dynamics of phytomass and nutrients in chalk grassland. *Oikos* 66: 216-224.

Bobbink, R., Heil, G.W. & Raessen, M.B.A.G. 1990. *Atmospheric deposition and canopy exchange in heathland ecosystems.* Dutch Priority Programme on Acidification, Report 119. Department of Plant Ecology and Evolutionary Biology, University of Utrecht.

Boorman, L.A. & Fuller, R.M. 1982. Effects of added nutrients on dune swards grazed by rabbits. *J. Ecol.* 70: 345-355.

Davy, A.J. & Bishop, G.F. 1984. Response of *Hieracium pilosella* in Breckland grass heath to inorganic nutrients. *J. Ecol.* 72: 319-330.

Dougherty, K.M., Mendelssohn, I.A. & Monteferrante, F.J. 1990. Effect of nitrogen, phosphorus and potassium additions on plant biomass and soil nutrient content of a swale barrier strand community in Louisiana. *Ann. Bot.* 66: 265-271.

Farrow, E.P. 1917. On the ecology of the vegetation of breckland. III. General effects of rabbits on the vegetation. *J. Ecol.* 5: 1-18.

Gibson, C.W.D. & Brown, V.K. 1991. The effects of grazing on local colonisation and extinction during early succesion. *J. Veg. Sci.* 2: 291-300.

Heil, G.W. & Diemont, W.H. 1983. Raised nutrient levels change heathland into grassland. *Vegetatio* 53: 113-120.

Hill, M.O., Evans, D.F. & Bell S.A. 1992. Long-term effects of excluding sheep from hill pastures in North Wales. *J. Ecol.* 80: 1-13.

Kachi, N. & Hirose, T. 1983. Limiting nutrients for plant growth in coastal sand dune soils. *J. Ecol.* 71: 937-944.

Milton, W.E.J. 1940. The effect of manuring, grazing and cutting on the yield, botanical and chemical composition of natural hill pastures. I. Yield and botanical section. *J. Ecol.* 28: 326-356.

Milton, W.E.J. 1947. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. I. Yield and botanical section. *J. Ecol.* 35: 65-95.

Mountford, J.O., Lakhani, K.H. & Kirkham, F.W. 1993. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *J. Appl. Ecol.* 30: 321-332.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York, NY.

Olff, H., Huisman, J. & van Tooren, B.F. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *J. Ecol.* 81: 693-706.

Puerto, A., Rico, M., Matías, M.D. & García, J.A. 1990. Variation in structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. *J. Veg. Sci.* 1: 445-452.

Ranwell, D.S. 1960. Newborough Warren, Anglesey. III. Changes in the vegetation on parts of the dune system after the loss of rabbits by myxomatosis. *J. Ecol.* 48: 385-397.

Roelofs, J.G.M. 1986. The effect of airborne sulphur and nitrogen deposition on aquatic and terrestrial heathland vegetation. *Experientia* 42: 372-377.

Silvertown J., Watt, T.A., Smith, B. & Treweek, J.R. 1992. Complex effects of grazing treatment on an annual in a species-poor grassland community. *J. Veg. Sci.* 3: 35-40.

Stuyfzand, P.J. 1993. *Hydrochemistry and hydrology of the coastal dune area of the Western Netherlands.* Ph.D. Thesis, Free University of Amsterdam.

Thomas, A.S. 1963. Further changes in vegetation since the advent of myxomatosis. *J. Ecol.* 51: 151-183.

ten Harkel, M.J. 1992. Abiotiek-biotiek interacties in de droge duinen van Meijendel. *Meijendel Meded.* (*Den Haag*) 24: 65-89. (In Dutch.)

ten Harkel, M.J., Heil, G.W., van der Hagen, H.G.J.M. & Witter, J.V. 1991. Abiotic-biotic interactions in dry dune ecosystems. *Mitt. Hydrograph. Dienst. Österreich* 65/66: 58-62.

van der Meijden, R. 1990. *Flora van Nederland. 21th ed.* Wolters-Noordhoff, Groningen.

van Hecke, P., Impens, I. & Behaeghe, T.J. 1981. Temporal variation of species composition and species diversity in permanent grassland plots with different fertilizer treatments. *Vegetatio* 47: 221-232.

Watt, A.S. 1962. The effect of excluding rabbits from grassland A (Xerobrometum) in breckland, 1936-60. *J. Ecol.*

50: 181-198.
Westhoff, V 1985. Nature management in coastal areas of Western Europe. *Vegetatio* 62: 523-532.
Westhoff, V. & den Held, A.J. 1969. *Plantengemeenschappen in Nederland.* Thieme, Zutphen.
Willems, J.H. 1983. Species composition and above-ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-180.
Willems, J.H., Peet, R.K. & Bik, L. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *J. Veg. Sci.* 4: 203-212.
Williams, O.B., Wells, T.C.E. & Wells, D.A. 1974. Grazing management of Woodwalton fen: seasonal changes in the diet of cattle and rabbits. *J. Appl. Ecol.* 11: 499-516.
Willis, A.J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* 51: 353-374.
Willis, A.J. & Yemm, E.W. 1961. Braunton Burrows; mineral nutrient status of the dune soils. *J. Ecol.* 49: 377-390.
Zeevalking, H.J. & Fresco, L.F.M. 1977. Rabbit grazing and species diversity in a dune area. *Vegetatio* 35: 193-196.

Received 23 January 1995;
Revision received 23 May 1995;
Accepted 5 September 1995.