

# Grazing as a measure against grass encroachment in Dutch dry dune grassland: effects on vegetation and soil

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**Abstract.** A grazing experiment was started in 1984 and 1989 respectively, in two parts of a dune grassland in the nature reserve 'Zwanenwater', North Holland; a third part with similar geology and topography was used as a control area and not grazed. An evaluation of the effects of grazing on vegetation patterns, species composition, vegetation structure and humus form was made with the help of vegetation maps from 1986 and 1992 as well as field surveys.

Dense tall-grass communities dominated by *Ammophila arenaria* increased over the period 1986-1992 in the grazed areas, and especially in the non-grazed area (increase in area to 20 %, 22 % and 50 %, respectively). Open communities decreased in the grazed areas, but are still prevalent, while in the ungrazed area they virtually disappeared, with the result that the present percentage areas are 53 %, 38 % and 17 %.

Field survey data were classified by TWINSPLAN producing four vegetation types. These occur more or less equally in grazed and ungrazed areas, albeit with different percentage areas: (1) open vegetation dominated by *Corynephorus canescens*; (2) open vegetation characterized by *Koeleria macrantha*; (3) heathland dominated by *Empetrum nigrum*; and (4) tall-grass communities dominated by *Ammophila arenaria*. Within a vegetation type, species composition was only marginally affected by grazing regime.

Within the open communities the number of species, vegetation height, vegetation cover and soil organic horizons were not affected by grazing. In the tall-grass communities the number of species was significantly larger and the height of the vegetation significantly lower in the area grazed since 1984. In the heathland community the number of species and cover of the moss layer were significantly higher in the 1984 area and ectorganic and endorganic horizons significantly thicker in the ungrazed area.

It is suggested that these effects are the result of an increased availability of light, but possibly also of a decreased stock of organic matter and nutrients, due to a decreased input of litter and accelerated rates of decomposition.

**Keywords:** Humus profile; Nature management; Organic horizon; Species diversity; Vegetation pattern; Vegetation structure; Zwanenwater.

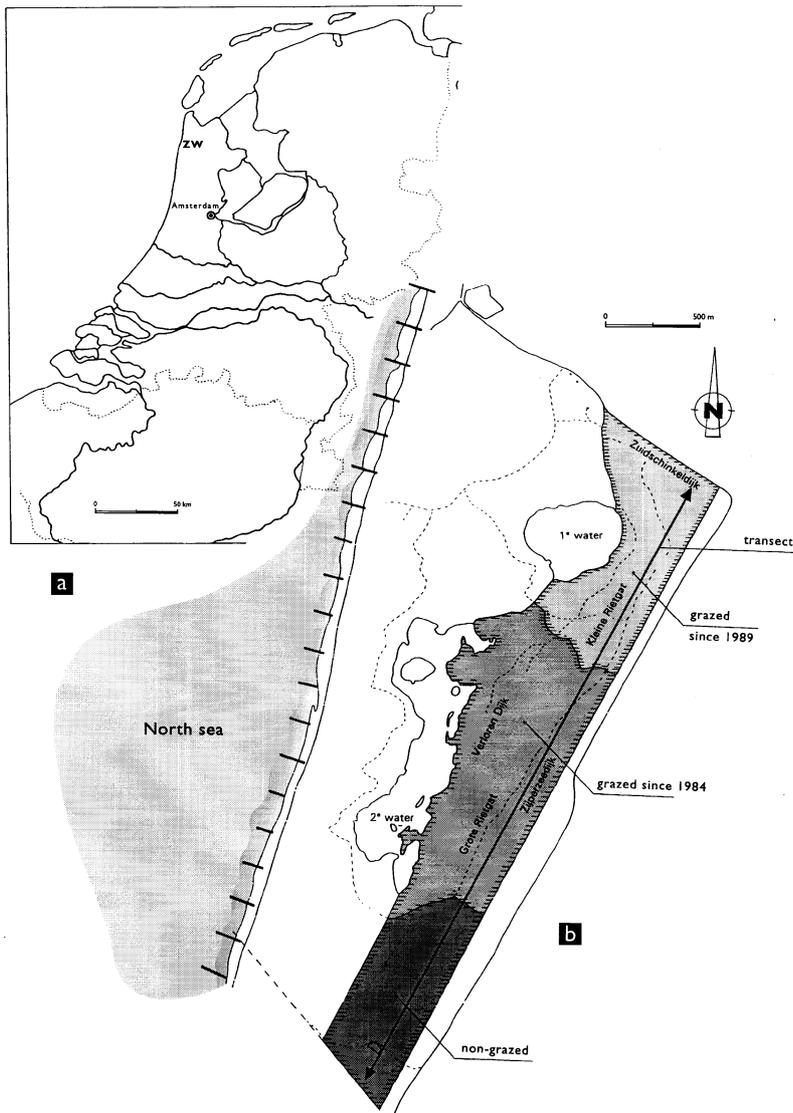
**Nomenclature:** Van der Meijden et al. (1992) for phanerogams; Corley et al. (1981) for mosses; Grolle (1983) for hepatics.

## Introduction

Species-rich, relatively open grasslands in the coastal dunes of the Netherlands have become subjected to 'grass encroachment', i.e., have become dominated by a small number of tall grass species (Vertegaal et al. 1991). These changes in vegetation structure are associated with a loss of species diversity (Kooijman & van der Meulen in press). It is as yet unknown which factor(s) caused this encroachment. It may be atmospheric deposition of nitrogen, as indicated for heathland and limestone grasslands (Aerts 1989; Bobbink 1989) and/or changes in management practices. Whatever the causes, grazing with domestic animals is presently considered one of the management tools to counteract this development and restore original diversity levels. It is used throughout the coastal zone (e.g. van Dijk 1992). In fact this may be seen as a reintroduction of former management, since extensive grazing was common in the dunes until the beginning of this century (e.g. Anon. 1984).

Numerous studies have been carried out on the effects of grazing on vegetation (e.g. Pickworth Farrow 1917; Wyllie Fenton 1940; Gilham 1955; Arnold 1987; Belsky 1992; Hill et al. 1992; Gibson & Brown 1992). Generally, grazing results in a reduction of standing crop and a more open vegetation structure, as well as in changes in the species composition in favour of smaller species, although the precise effects may be site-specific and depend on the type of herbivore, grazing density, etc. (e.g. Grant et al. 1987; Putman et al. 1987).

In this study, we try to assess whether grazing leads to the expected prevalence of open, species-rich dune grassland vegetation; we studied an area which, in contrast to most other areas along the Dutch coast with grazing or grazing experiments, allows for both a comparison over time and a comparison with a control area. Grazing started in two parts of the Zwanenwater area in 1984 and 1989 and vegetation maps of 1986 and 1992 were available to document the situation. In addition to changes in vegetation patterns and species composition, more functional aspects of the effects of grazing on



**Fig. 1.** a. Map of the Zwanenwater area (ZW); b. map of the grazing areas.

vegetation structure and humus characteristics are taken into account. The latter inclusion is important with respect to the cation exchange capacity and nutrient availability and it reflects the actual ecological conditions. More detailed questions are: (1) what are the changes in cover of the occurring vegetation types from 1986 to 1992 in grazed and ungrazed sites and (2) what are the (present) differences in species composition, vegetation structure and soil horizons containing organic matter between grazed and ungrazed sites.

### Study area

*Het Zwanenwater* is a nature reserve located northwest of Amsterdam (Fig. 1). The dunes are poor in lime since they consist of fine sand with an initial lime

content of 0.1 - 0.4 %. The soils of the drier inland parts have been largely decalcified.

The experimental area includes two dune ridges; one originated from a former sand dike (constructed in 1596) which has become broader due to natural sand accumulation, and the other one is a fossil foredune ridge. The dune ridges are located at 1 - 1.5 km distance from the sea and run parallel to the beach. The groundwater table is 2 - 3 m below the soil surface and largely out of reach for plant roots. The wetter parts, in between the two dune ridges, make up 50 % of the area and are not taken into account in this study.

The vegetation consists of short, open grassland communities (belonging to the associations *Violo-Corynephorum* and *Festuco-Galietum maritimi*), heathland communities (*Empetro-Genistetum tinctoriae* and *Polypodio-Empetretum*) and dense grass communities

(*Elymo-Ammophiletum*) (Westhoff & den Held 1969).

The experimental area is divided into three parts of ca. 1 km length and 0.5 km width, with the wetter parts excluded. The southern part is not grazed and served as a control. In the middle part, cattle (Blondes d'Aquitaines) and Iceland ponies were introduced in a small part of the area in 1981 and in the total area in 1984. The northern part has been grazed by cattle since 1989. The different treatments will be called UG (ungrazed), G84 and G89 respectively. The grazing density is relatively low, about one animal per 5 - 6 ha, which is recommended for dune grasslands (Anon. 1984).

## Methods

### *Changes in vegetation patterns*

Two maps of the vegetation structure of the Zwanewater nature reserve were available (ten Haaf 1987, 1993). The maps are based on aerial photographs (1986 map: black-white photos from the 1970s, scale 1 : 18000; 1992 map: false colour photos of 1990, scale 1 : 5000 and were adjusted to the 1986 and 1992 field situation by field checks by the same person. The units on the maps are derived from Barendregt (1980); they include two open communities, two heathland communities (*Calluna vulgaris* and *Empetrum nigrum*) and some tall grass communities. In 1986, only one tall grass community was distinguished (*Calamagrostis epigejos*), while in 1992 this community type was divided into a community dominated by this species and one by *Ammophila arenaria*.

The two vegetation maps were digitized and compared with help of the GIS program GENAMAP. The vegetation maps were constructed without paying attention to the (small) distortion of the photographs, due to their central projection. As a result, the field reference points did not have the same position and hence an overlay of the vegetation maps was not possible. Instead, the surface areas of the map units in each grazing area were calculated for each vegetation map. Changes in the vegetation were based on changes in cover values of each vegetation type. Some map units comprised a mosaic of dominant and subdominant vegetation types with different cover ratios. Based on the 1986 key of the ratios between vegetation types given for each mosaic map unit (ten Haaf 1987), the surface areas of the individual vegetation types could be estimated.

### *Changes in species composition*

To test whether grazing has led to changes in the species composition, the present species composition of the different grazing areas: G84, G89 and UG were compared. In each area, 16 or 17 plots of 2 m × 2 m were

laid out in a stratified random way along a transect across one of the sand ridges (Fig. 1b). When the vegetation changed from one of the types mentioned above into another, a new plot was analyzed in more or less homogeneous vegetation until sufficient replicates of each type were obtained. The vegetation was sampled by estimating the cover values of the individual phanerogam and cryptogam species.

### *Changes in vegetation structure and soil parameters*

In each plot of 2 m × 2 m cover values of the herb and cryptogam layers as well as total cover were estimated. The height of the vegetation was measured in cm. The thickness of the ectorganic (L, F+H and total litter layer) and endorganic (Ah) horizons (Klinka et al. 1981) were measured using a sod of about 10 cm × 10 cm and ca. 15 cm thickness.

### *Multivariate analysis*

The vegetation data were analyzed with the program TWINSpan using standard options (Hill 1979). In addition, the variation in the species composition was analyzed with Correspondence Analysis, as included in the program CANOCO (ter Braak 1987). After extraction of the vegetation axes, the correlation with environmental variables such as grazing area, thickness of the litter layer and Ah horizon, height of the vegetation and cover values of herb and moss layer and total cover was calculated with Canonical Correspondence Analysis.

Differences in cover values of the herb and moss layer and total cover, height of the vegetation and thickness of litter and Ah horizons in relation to vegetation type and grazing regime were tested using two-way analysis of variance; differences between individual mean values were analyzed with least square means tests (Anon. 1985).

## Results

### *Changes in vegetation patterns*

In 1986 (during the first year of, or prior to the introduction of grazing) the vegetation was dominated by species-rich plant communities with a low and open vegetation structure in all three areas (Table 1). Tall-grass communities with species such as *Ammophila arenaria* were (still) almost absent. In all three areas two types of heathland communities were found: a species-rich heathland type with *Calluna vulgaris* and many *Cladonia* spp. and a species-poor type dominated by *Empetrum nigrum*.

In 1992 the situation had changed, especially in the UG area (Table 1). Here, open communities decreased

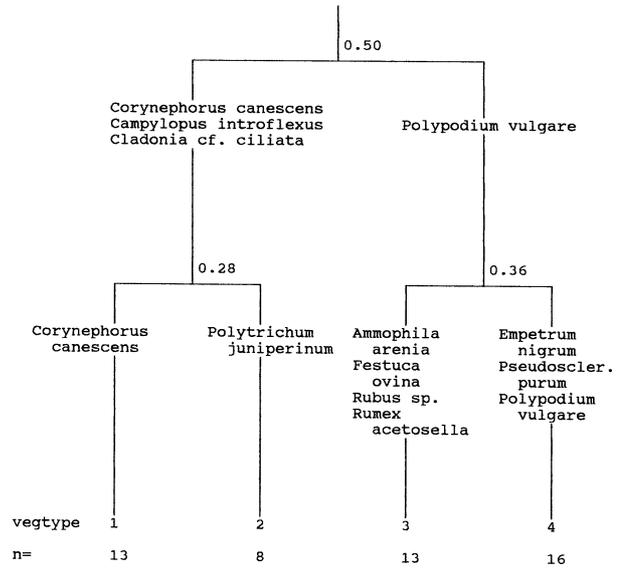
in area from 77 % to 17 %, whereas tall grass communities increased from 3 % to 53 %. In the grazed areas similar, but smaller changes were observed, with a decrease of open communities from 74 % to 53 % in G84 and from 50% to 38% in G89. The open community with *Corynephorus*, which is characteristic of mineral soil, decreased while the open *Koeleria* community increased. Tall-grass communities showed an increase from 1 % to 21 % in G84 and 4 % to 26 % in G89. In all three areas, the species-rich *Calluna vulgaris* heathland decreased, whereas the species-poor *Empetrum nigrum* heathland increased.

### Changes in species composition

Based on TWINSpan-analysis, the 50 vegetation samples were classified into four groups. At the highest level, the samples were separated into a group characterized by *Corynephorus canescens*, *Campylopus introflexus* and *Cladonia cf. ciliata*, i.e. open communities, and a group characterized by *Polypodium vulgare*, a species characteristic of heathland communities (Fig. 2, Table 2).

**Table 1.** Percentage area covered by plant community types in different grazing areas in 1986 and 1992.

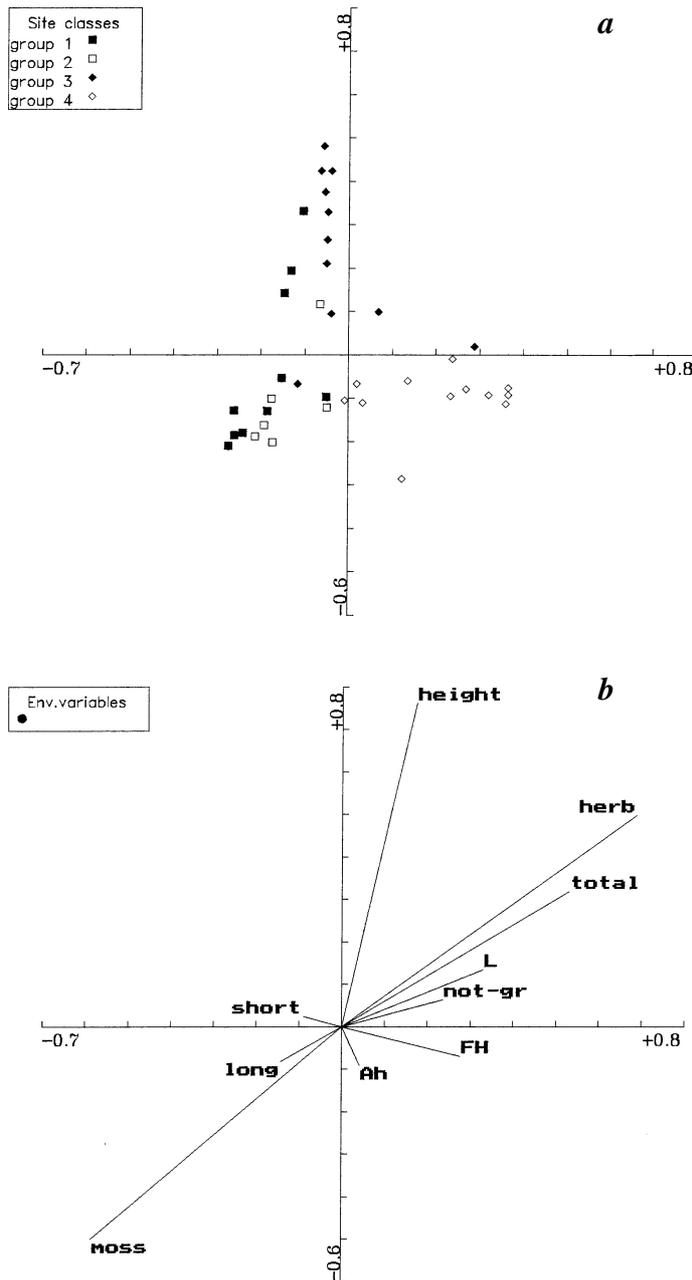
Site / Community	% area	
	1986	1992
<b>Ungrazed communities</b>		
Open <i>Corynephorus canescens</i>	62	9
Open <i>Koeleria macrantha</i>	15	8
Heathland with <i>Calluna vulgaris</i> and <i>Cladonia</i> spp.	9	3
Heathland with <i>Empetrum nigrum</i> (species-poor)	11	28
Dense grassland dominated by <i>Ammophila arenaria</i>	49	
Ibid. dominated by <i>Calamagrostis epigejos</i>	4	
Ibid. dominated by <i>Ammophila/Calamagrostis</i>	3	
<b>Grazed communities (since 1989)</b>		
Open <i>Corynephorus canescens</i>	43	22
Open <i>Koeleria macrantha</i>	7	16
Heathland with <i>Calluna vulgaris</i> and <i>Cladonia</i> spp.	28	8
Heathland with <i>Empetrum nigrum</i> (species-poor)	18	28
Dense grassland dominated by <i>Ammophila arenaria</i>	24	
Ibid. dominated by <i>Calamagrostis epigejos</i>	2	
Ibid. dominated by <i>Ammophila/Calamagrostis</i>	4	
<b>Grazed communities (since 1984)</b>		
Open <i>Corynephorus canescens</i>	40	9
Open <i>Koeleria macrantha</i>	34	44
Heathland with <i>Calluna vulgaris</i> and <i>Cladonia</i> spp.	20	15
Heathland with <i>Empetrum nigrum</i> (species-poor)	18	28
Dense grassland dominated by <i>Ammophila arenaria</i>	17	
Ibid. dominated by <i>Calamagrostis epigejos</i>	4	
Ibid. dominated by <i>Ammophila/Calamagrostis</i>	1	



**Fig. 2.** Twinspan diagram of the Zwanenwater samples. Indicator species and eigenvalues are given.

**Table 2.** Species composition of four vegetation types derived from TWINSpan. Indicator species in bold. I = present in 1 - 20 % of the samples; II = 20 - 40 %; III = 40 - 60 %; IV = 60 - 80 %; V = 80 - 100 %. Frequency values in bold indicate high occurrences in a particular vegetation type. *Ceratodon purpureus* occurs with I in type 1; *Poa pratensis*, *Holcus lanatus* and *Agrostis vinealis* with I in type 3; *Geranium molle* with I in type 3; *Pleurozium schreberi* with III in type 4.

Species/Type	1	2	3	4
<i>Agrostis capillaris</i>	II	IV	I	
<b><i>Polytrichum juniperinum</i></b>		IV	I	I
<i>Cladonia cf. portentosa</i>	IV	IV	II	I
<b><i>Corynephorus canescens</i></b>	V	II		
<i>Leontodon autumnalis</i>	I			
<i>Cladonia cf. furcata</i>	II	I		
<i>C. cf. uncinatis</i>	II	I		
<b><i>Campylopus introflexus</i></b>	V	V	II	II
<i>Coelocaulon aculeatum</i>	III	III		
<i>Cladonia floerkeana</i>	III	I		
<i>C. foliacea</i>	IV	III	I	
<i>Erophila verna</i>	I			I
<b><i>Cladonia cf. ciliata</i></b>	V	IV	I	I
<b><i>Rumex acetosella</i></b>	V	V	III	I
<i>Stellaria media</i>	II	III	I	I
<i>Teesdalia nudicaulis</i>	I	II		I
<i>Cladonia cf. coccifera</i>	IV	IV		
<b><i>Festuca ovina</i></b>	V	V	IV	III
<i>Koeleria macrantha</i>	II	IV	II	I
<i>Luzula campestris</i>	II	III	I	II
<b><i>Carex arenaria</i></b>	V	V	V	V
<i>Dicranum scoparium</i>	III	II	V	III
<b><i>Ammophila arenaria</i></b>	IV		V	II
<b><i>Rubus sp.</i></b>	I		IV	I
<i>Calluna vulgaris</i>	I	III	IV	III
<i>Salix repens</i>			I	I
<i>Lophocolea bidentata</i>			I	I
<i>Calamagrostis epigejos</i>	I	I	I	II
<b><i>Empetrum nigrum</i></b>		II	II	V
<b><i>Polypodium vulgare</i></b>			II	V
<i>Plagiothecium sp.</i>			I	II
<b><i>Pseudoscleropodium purum</i></b>				III
<i>Hypnum cupressiforme</i>	I	II	IV	V
<b><i>Rosa pimpinellifolia</i></b>		III	I	II



**Fig. 3.** Correspondence Analysis of vegetation samples and environmental factors in ‘het Zwanenwater’. **a.** vegetation samples classified according to Twinspan: group 1 = open communities with *Corynephorus canescens*; group 2 = open communities with *Koeleria macrantha*; group 3 = tall-grass communities with *Ammophila arenaria* and group 4 = heathland communities with *Empetrum nigrum*. **b.** environmental factors: height = height of the vegetation; herb = cover of the herb layer; total = total vegetation cover; not-gr = ungrazed; FH = thickness of the FH horizon; Ah = thickness of the Ah horizon; moss = cover of the moss layer; long = grazed since 1984; short = grazed since 1989.

The group with open communities was subdivided into a type characterized by *Corynephorus canescens* (type 1) and a type with *Polytrichum juniperinum* as indicator species and with the frequent occurrence of *Koeleria macrantha* (type 2). The second type with *Polypodium vulgare* as indicator species was divided into a type dominated by *Ammophila arenaria* (type 3) and a type in which *Empetrum nigrum* is a prevalent species (type 4).

The above-mentioned types correspond roughly with the vegetation types described by ten Haaf (1987, 1993),

except for the heathland type dominated by *Calluna vulgaris*. This type is represented in three TWINSpan groups (2, 3 and 4) in which *Calluna vulgaris* is frequent.

Correspondence Analysis further elucidates the division of the TWINSpan types (Fig. 3a). The eigenvalues of axes 1 and 2 are relatively large (0.72 and 0.57 respectively); samples belonging to the open communities 1 and 2, and the heathland and dense grass communities were more or less separated as three clusters. Vegetation structure parameters clearly corresponded

**Table 3.** Vegetation structure parameters in four vegetation types in relation to the grazing regime. Mean values and standard deviations based on  $n = 3 - 6$ . Significant effects ( $p < 0.05$ ) of the grazing regime within a particular vegetation type indicated in bold. Different characters indicate significant differences. Total = total cover (%); Herb = cover of the herb layer (%); Moss = cover of the moss layer (%); Height = height of the vegetation (cm);  $S$  = number of species per sample.

	Regime	Total	Herb	Moss	Height	$S$
Type 1 <i>Corynephorus canescens</i>	Ungrazed	92 ± 10	55 ± 35	45 ± 20	6 ± 4	13 ± 2
	Grazed 1989-	86 ± 14	60 ± 29	29 ± 17	20 ± 34	10 ± 2
	Grazed 1984-	91 ± 7	54 ± 24	44 ± 26	5 ± 3	13 ± 3
Type 2 <i>Koeleria macrantha</i>	Grazed 1989-	96 ± 5	71 ± 23	28 ± 24	6 ± 3	14 ± 1
	Grazed 1984-	98 ± 5	54 ± 19	48 ± 22	5 ± 4	13 ± 3
Type 3 <i>Ammophila arenaria</i>	Ungrazed	100 ± 0	93 ± 10	18 ± 22	<b>52 ± 28<sup>b</sup></b>	<b>7 ± 2<sup>a</sup></b>
	Grazed 1989-	99 ± 3	91 ± 14	9 ± 14	<b>45 ± 35<sup>b</sup></b>	<b>9 ± 2<sup>ab</sup></b>
	Grazed 1984-	100 ± 0	98 ± 3	5 ± 0	<b>13 ± 6<sup>a</sup></b>	<b>11 ± 4<sup>b</sup></b>
Type 4 <i>Empetrum nigrum</i>	Ungrazed	100 ± 0	100 ± 0	<b>2 ± 4<sup>a</sup></b>	24 ± 2	<b>6 ± 3<sup>a</sup></b>
	Grazed 1989-	100 ± 0	96 ± 5	<b>8 ± 3<sup>ab</sup></b>	20 ± 4	<b>10 ± 2<sup>b</sup></b>
	Grazed 1984-	100 ± 0	87 ± 15	<b>29 ± 16<sup>b</sup></b>	14 ± 6	<b>12 ± 1<sup>b</sup></b>

**Table 4.** Thickness of ectorganic and endorganic horizons in four vegetation types in relation to the grazing regime. L = thickness of the L horizon (cm); FH = thickness of the F plus H horizon (cm); Litter = thickness of the ectorganic horizon (L + FH) (cm); Ah = thickness of the Ah (cm). Mean values and standard deviations based on  $n = 3 - 6$ . Significant effects ( $p < 0.05$ ) of the grazing regime within a particular vegetation type are indicated in bold. Different letters indicate significant differences.

		L	FH	Litter	Ah
Type 1 <i>Corynephorus canescens</i>	Ungrazed	0.3 ± 0.6	0.5 ± 0.5	0.8 ± 1.0	3.2 ± 1.6
	Grazed 1989-	0.0 ± 0.0	0.1 ± 0.3	0.1 ± 0.3	2.5 ± 1.0
	Grazed 1984-	0.3 ± 0.4	0.5 ± 0.6	0.8 ± 0.9	2.8 ± 1.6
Type 2 <i>Koeleria macrantha</i>	Grazed 1989-	0.1 ± 0.3	1.1 ± 0.9	1.3 ± 1.0	4.8 ± 1.5
	Grazed 1984-	0.0 ± 0.0	2.3 ± 1.6	2.3 ± 1.6	4.3 ± 0.5
Type 3 <i>Ammophila arenaria</i>	Ungrazed	0.9 ± 1.1	2.4 ± 1.5	3.3 ± 2.5	3.9 ± 1.8
	Grazed 1989-	0.6 ± 0.5	1.6 ± 1.1	2.3 ± 1.3	2.4 ± 0.8
	Grazed 1984-	1.0 ± 0.5	3.0 ± 2.0	4.0 ± 2.3	4.3 ± 3.2
Type 4 <i>Empetrum nigrum</i>	Ungrazed	2.1 ± 0.7 <sup>b</sup>	6.3 ± 2.6 <sup>b</sup>	8.4 ± 2.9 <sup>b</sup>	6.8 ± 3.4 <sup>b</sup>
	Grazed 1989-	1.3 ± 0.5 <sup>a</sup>	4.0 ± 0.9 <sup>a</sup>	5.3 ± 1.3 <sup>a</sup>	3.3 ± 1.5 <sup>a</sup>
	Grazed 1984-	1.3 ± 0.5 <sup>a</sup>	3.8 ± 1.3 <sup>a</sup>	5.2 ± 1.5 <sup>a</sup>	5.7 ± 2.1 <sup>ab</sup>

with the vegetation types (Fig. 3b). Total cover and herb cover increase in the direction opposite to the open communities of types 1 and 2, whereas the presence of a moss cover points to the open communities. The vegetation is taller in the *Ammophila* communities. The thickness of the L and FH horizons increases somewhat in the direction opposite to the open communities. The arrows of the grazing regimes are located around the centre of the diagram; this indicates that the effect of grazing on the species composition within the total data set is of minor importance and overruled by the differences between vegetation types.

#### Changes in vegetation structure and soil characteristics

Differences between vegetation types were significant ( $p < 0.005$ ) for total cover, cover of the herb and moss layer, height of the vegetation, number of species

and thickness of the L, FH, litter and Ah horizons, which is illustrated in Fig. 3. Grazing had significant effects ( $p < 0.05$ ) on the number of species, cover of the moss layer, height of the vegetation and thickness of the FH and the litter horizon. Interactions between vegetation type and grazing regime were not significant, indicating that responses to grazing were similar in all vegetation types.

Within each vegetation type, grazing had no effect on vegetation structure and soil horizons in the open communities (groups 1 and 2), but the heathland and tall-grass communities showed significant differences with regard to grazing (Tables 3, 4). In the communities with *Ammophila* (group 3) vegetation height decreased from 52 cm in UG to 13 cm in G84. The number of species increased accordingly, from 7 to 11. In the *Empetrum* communities (group 4), the cover of the moss layer and the number of species increased with grazing from 2% and six species in UG to 29% and 12 species in G84.

Ectorganic (L, FH and litter) and endorganic (Ah) horizons were all significantly thicker in the ungrazed than in both grazed areas.

## Discussion

Grazing has a positive effect on the persistence of open grassland communities. Although the exact numbers should be treated with some care, especially because of the use of mosaic pattern elements consisting of different vegetation types, the changes are so large that the conclusions remain valid. The cover of tall-grass communities increased and the cover of open communities decreased dramatically in the ungrazed area. At present, the latter consists primarily of *Ammophila* and *Empetrum* communities, whereas open communities are virtually absent. In the grazed areas tall-grass communities have increased as well, although not to the same extent. It is possible that a more intensive grazing regime would have prevented grass encroachment completely. Open communities prevail, but changes have occurred as well. *Corynephorus* communities have decreased in cover, while *Koeleria* communities increased. This may indicate a further succession as the *Koeleria*-type seems characterized by enhanced soil development with greater thickness of the LF, litter and Ah horizons. It may be partly a degeneration type as well, having developed from degenerating heathland communities due to trampling. A direct comparison of transitions from one vegetation type into another is unfortunately not possible.

The changes within vegetation types are less clear with respect to species composition, but the higher number of species and moss/lichen cover and lower height in *Ammophila* and *Empetrum*-communities in G84 suggest that grazing has an effect on the vegetation within a particular vegetation type. Presumably there is a functional relationship between these three parameters. A lower vegetation indicates a lower biomass, due to the removal of plant material by herbivores, and results in a higher availability of daylight at the bottom layer (e.g. Monsi & Saeki 1953). This is beneficial to bryophytes, lichens and other small species with low competitive powers and leads to an increased cover of the moss layer (inclusive lichens) and an increased number of species.

There may be a second reason why the number of species is higher and the open communities are more prevalent in grazed areas. Within the heathland communities, which are known to build up well-developed humus profiles due to their slowly decomposable litter, the thickness of all soil organic horizons was less in the grazed areas. Similar decreases in organic matter in

forest areas as a result of grazing were reported by Pastor et al. (1993). When a rough estimate of the litter volume in an area was made, based on the cover values of each vegetation type in a particular area and the thickness of the L, F and H combined, the volume of ectorganic material in the ungrazed area (ca. 57 m<sup>3</sup>/ha) appears to be approximately twice as much as in the G84 and G89 areas (ca. 24 and 32 m<sup>3</sup>/ha).

The thickness and volume of litter may be poor estimates of the amount of organic matter present in the soil. In the grazed areas, the thinner organic horizons in the heathland communities are possibly more compact only due to trampling, but may also factually contain less organic matter than in the ungrazed area. With lower (above-ground) biomass the input of litter will be lower, but additionally irradiation increases and soil temperatures may rise. Differences in temperature between grass-dominated plots and open vegetation were already 2.2 °C on a sunny day in November (Besse internal report 1992) and are likely to be more in summer. Since temperature -when soil moisture is not limiting decomposition- is one of the factors regulating rates of decomposition (Tinker & Ineson 1990), the result may be increased rates of decomposition and a decrease in soil organic matter. Eventually this may lead to a decrease in the availability of nutrients which limit the primary production. In this case, the open communities consisting of low-demanding and slow-growing species may be in advantage as well.

Thus, it is clear that grazing is a suitable instrument to maintain open dune grassland communities and to some extent prevent grass-encroachment. Whether this is primarily due to an improved light climate at the ground layer, or whether changes in organic matter profile and nutrient availability are important as well, remains to be studied.

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