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Responses of flower phenology and seed production under cattle grazing impact in sandy grasslands*

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with 6 figures and 3 tables

Abstract. The impact of cattle grazing on selected characteristic and dominant plant species of three sandy grassland communities in northwestern Germany (Spergulo-Corynephoretum typicum, S.-C. cladonietosum and Diantho-Armerietum) is investigated with regard to the loss of above-ground diaspores in the course of a vegetation period. Special attention is given to the importance of the seed bank in the soil as compensation potential. The flower and fruit phenology of the plant species was analyzed by counting. A fence was erected so that data samples outside and within an exclosure could be compared. Extracted soil samples and a germination test give information about the diaspore reservoir in the soil at the beginning of the investigation. The comparison of grazed and ungrazed stands yielded the following results. The Spergulo-Corynephoretum typicum is poor, the S.-C. cladonietosum richer in palatable inflorescences and infructescences (e.g. *Carex arenaria*). In the former only 12–24 % of the inflorescences and infructescences are grazed (*Carex arenaria*, *Corynephorus canescens*), in the latter 45–51 % (*Carex arenaria*). The Spergulo-Corynephoretum can regenerate itself from the diaspore potential to a slight extent if there are gaps, e.g. caused by cattle trampling. The Diantho-Armerietum is quite intensively grazed, entailing a major reduction of flowers and fruits of certain plant species (*Agrostis capillaris*: inflorescences by 71 %, infructescences 72 %, *Dianthus deltoides*: flowers by 61 %, fruits 22 %). In contrast, two species increase flower and fruit numbers (by 36–77 %) in the grazed sites (*Agrostis vinealis*, *Ranunculus bulbosus*). Faeces microsites are important elements for patch dynamic systems in the Diantho-Armerietum. At faeces microsites in the Diantho-Armerietum, which constitute about one-third of the plot areas, many flowers and fruits develop. Flower and fruit development at the faeces microsites and the seed bank in the soil ensure a generative regeneration of the Diantho-Armerietum. Gap dynamics, patch dynamics of faeces microsites and seed bank processes are driving forces for the generative regeneration of the investigated plant communities.

Keywords: Spergulo-Corynephoretum, Diantho-Armerietum, sand vegetation complexes, seed bank, generative regeneration.

1. Introduction

There are numerous investigations dealing with the influence of grazing on vegetation, e.g. on the changes in plant species diversity (HUNTLEY 1991,

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Belsky 1992, Hobbs & Huenneke 1992, Olsvig-Whittaker et al. 1993, Crawley et al. 1997)), in the life-form type spectrum (Milton & Hoffmann 1994, Sternberg et al. 2000), in life strategies (Diaz et al. 1992) and in vegetation structure (Marriott & Carrere 1998, Whicker & Detling 1998).

Some studies have dealt with the immediate reduction in the number of inflorescences and infructescences due to grazing (Milton 1992, 1994, Kerley et al. 1993, Dolek 1994, Wada 1999). Frequently aspects of compensation of the flowers and of the number of inflorescences after grazing and after clipping experiments have been studied (Kotanen & Bergelson 2000, Bridle & Kirkpatrick 2001), as well as correlations of biomass with flower production and reproduction rate (Mulder & Ruess 1998). Several authors, e.g. Jünger & Bergelson (2000), have shown that herbivory of flowering/fruiting plant species may influence plant fitness. However, no information is available concerning the reduction of diaspore numbers due to grazing in combination with the compensation potential of the seed bank of the soil.

The following questions have been investigated in this study:

- Are many diaspores lost due to cattle grazing of flowers and inflorescences, fruits and infructescences, compared to ungrazed reference plots for selected species?

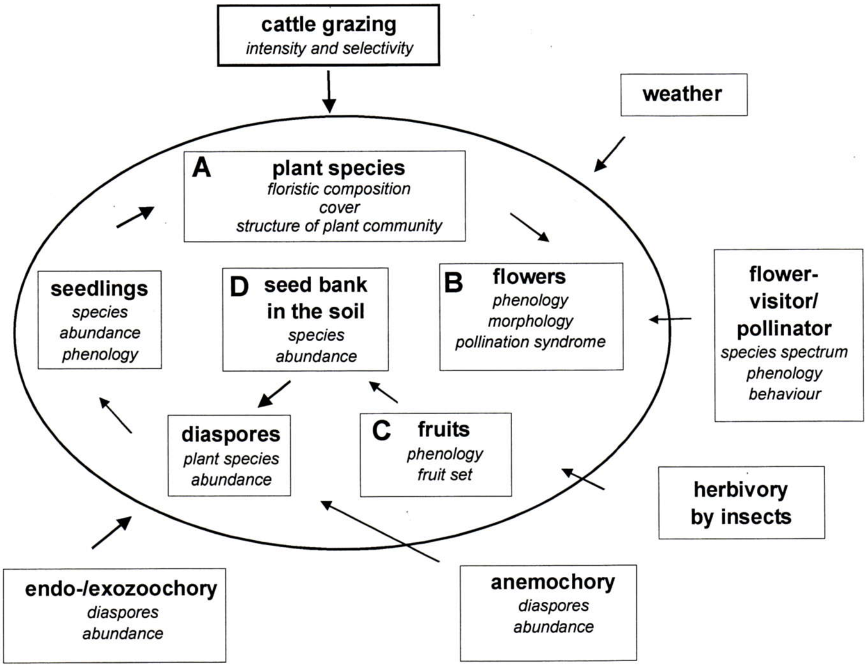


Fig. 1. Model for investigation of the reproduction-ecological relationships within a plant community. The topics A – D are dealt with in this study.

- How great is the importance of the seed bank as regeneration potential ("retention space") for diaspores?

Fig. 1 shows the various influence factors considered in this study:
A. Influence of extensive grazing on specific plant species.
B. Influence of extensive grazing on the number of flowers/inflorescences.
C. Influence of extensive grazing on the number of fruits/infructescences.
D. Number of diaspores available in the seed bank.

2. Study area

Sand vegetation complexes in the river regions of Ems and Hase (northwestern Germany) were used as model ecosystems. The climate is characterized as subatlantic; the mean annual precipitation amounts to about 801 mm, the mean annual temperature to 9.4 °C (monitoring station Lingen). From 1961 to 1990 the mean temperature in January was 1.6 °C, that in July 17.2 °C.

The following plant communities were investigated:

a) Spergulo-Corynephoretum Libbert 1933 with the association character species *Spergula morisonii* and *Teesdalia nudicaulis* and the two subassociations typicum and cladonietosum.
In our investigation area the S.-C. cladonietosum is differentiated by the occurrence of 10 lichen species (see Table 1). Species number and cover (particularly mosses) of S.-C. cladonietosum are higher, and there are fewer vegetation-free sandy sites than in the S.-C. typicum. Both subassociations of the Spergulo-Corynephoretum consist of mainly subatlantically distributed pioneer species on loose sand soils with low calcium carbonate content (Pott 1995).

b) Diantho deltoidis-Armerietum elongatae Pötsch 1962 with the association character species *Dianthus deltoides*. *Armeria elongata*, a second association character species, is very rare in the Ems region; the main distribution area of this species lies east of the river Weser (Jeckel 1984, Haeupler & Schönfelder 1988).
The Diantho-Armerietum is found on alkaline sandy soils, especially in the temporarily flooded areas on the rivers Ems and Hase. The sites are slightly loamy (Pott 1995).

The Spergulo-Corynephoretum was investigated in the nature reserve "Biener Busch" near Lingen and the river Ems (7°15 east, 52°34 north), the Diantho-Armerietum in the area "Hammer Schleife" on the river Hase near Haselünne (7°26 east, 52°39 north). Both communities are integrated in a landscape mosaic characterized by shrub communities (e.g., dominated by *Prunus spinosa*), heathlands (Genisto-Callunetum), hem communities (e.g., Alliario-Chaerophylletum) and grassland (e.g., Lolio-Cynosuretum) that was extensively grazed for a long time by cattle. In the Spergulo-Corynephoretum, the grazing intensity amounts to approximately 0.75 livestock units per ha, in the Diantho-Armerietum, depending on the season, it is 1 to max. 2 livestock units

Table 1. Phytosociological characterization of the investigation areas (May 2000): Spergulo-Corynephoretum typicum (plots: 1a1, 1a2, 1b1, 1b2), S.-C. cladonietosum (plots: 2a1, 2a2), Diantho-Armerietum (plots: 3a1, 3a2, 3b1, 3b2). Ch = Character species, d = differential species.

	1a1	1a2	1b1	1b2	2a1	2a2	3a1	3a2	3b1	3b2
total cover (%)	20	35	35	25	65	90	95	95	95	95
cover of cryptogams (%)	<5	10	15	<5	15	20	40	45	35	35
cover of the field layer (%)	15	25	20	25	50	70	70	70	70	70
size of relevé (m²)	25	25	16	25	21	25	25	25	25	25
species number	33	35	20	13	37	39	25	27	27	30
Ch, d Spergulo-Corynephoretum, Corynephoretalia										
Carex arenaria	2m.1	2m.1	2m.1	2m.1	2m.1	2m.1	.	.	.	2m.2
Corynephorus canescens	2a.3	2b.1	2b.1	2b.1	2a.3	2a.2	.	.	.	.
Aira praecox	2m.1	1.1	2m.1	1.1	2m.1	2m.1	.	.	.	.
Spergula morisonii	1.1	+	1.1	1.1	2m.1	1.1	.	.	.	.
Polytrichum piliferum	1.1	.	1.2	1.1	2m.3	2m.1	.	.	.	.
Teesdalia nudicaulis	.	1.1	1.1	2m.1	2m.1	2m.1	.	.	.	.
Cerastium semidecandrum	2m.1	2m.1	.	+	1.1	+	.	.	.	.
Festuca tenuifolia	2m.3	1.3	.	.	2a.3	3.3	.	.	.	.
Polytrichum juniperinum	1.1	.	.	.	1.1	1.1	.	.	1.1	.
Campylopus introflexus	.	.	1.2	.	2m.3	2a.3	.	.	.	.
Arenaria serpyllifolia	1.1	2m.1	.	.	.	1.1	.	.	.	.
Trifolium campestre	1.1	1.1	.	.	.	.	.	.	.	.
Vicia lathyroides	+	.	.	.	.	+	.	.	.	.
Aira caryophyllea	.	.	.	.	+	1.1	.	.	.	.
Trifolium arvense	.	+	.	.	.	.	.	.	.	.
d Spergulo-Corynephoretum cladonietosum										
Cladonia uncialis	.	+	.	+	+	+	.	.	.	.
Cladonia ciliata	.	.	.	.	1.1	2m.2	.	.	.	.
Cladonia arbuscula	.	.	.	.	1.1	1.1	.	.	.	.
Cladonia portentosa	.	.	.	.	1.1	1.1	.	.	.	.
Cladonia foliacea	.	.	.	.	1.1	+	.	.	.	.
Cladonia pyxidata agg.	.	.	.	.	+	+	.	.	.	.
Cladonia macilenta ssp. floerkeana	.	.	.	.	+	+	.	.	.	.
Cladonia coccifera	.	.	.	.	+	+	.	.	.	.
Cetraria aculeata	.	.	.	.	+	+	.	.	.	.
Cladonia furcata	.	.	.	.	+	+	.	.	.	.
d degradation phase										
Calluna vulgaris	.	.	.	.	2a.3	2a.3	.	.	.	.
Dicranum scoparium	.	.	.	.	2m.3	2m.2	.	.	.	.
Pleurozium schreberi	.	.	.	.	1.1	.	.	.	.	1.2
Ch, d Diantho-Armerietum										
Cerastium arvense	.	.	.	.	+	+	2m.1	1.1	1.1	2m.1
Dianthus deltoides	.	.	.	.	.	.	2a.3	2a.3	2a.3	2m.2
Ranunculus bulbosus	.	.	.	.	.	.	1.1	1.1	1.1	1.1
Galium verum	.	.	.	.	.	.	1.1	1.1	1.1	2m.1
d Diantho-Armerietum: Molinio-Arrhenatheretea species										
Cerastium holosteoides	r	.	.	.	.	+	2m.1	1.1	1.1	1.1
Achillea millefolium	.	.	.	.	.	.	2m.1	2m.3	2a.1	2m.2
Alopecurus pratensis	.	.	.	.	.	.	.	2m.1	2m.1	2a.3
other Koelerio-Corynephoretea species										
Rumex acetosella	2m.1	2m.2	1.1	1.1	2m.1	2m.1	2m.1	2m.1	2m.1	2m.2
Erophila verna	1.1	1.1	.	.	+	+	1.1	1.1	2m.1	2m.1
Sedum acre	2m.2	2m.1	+	.	.	1.1	.	1.2	.	1.2
Herniaria glabra	.	.	.	.	.	.	.	.	+	1.1
Ornithopus perpusillus	1.1	.	.	.	.	.	+	.	.	.
Sedum sexangulare	.	+	.	.	.	.	.	.	.	.
Potentilla argentea	.	r	.	.	.	.	.	.	.	.
Filago minima	.	.	1.1	.	.	.	.	.	.	.
Scleranthus perennis	.	.	.	.	.	.	2m.1	.	.	.
Sedum reflexum	.	.	.	.	.	.	.	.	.	1.3

Table 1. (cont.)

Companions										
Agrostis vinealis	.	2m.1	1.1	2m.1	2a.1	2a.3	2a.3	2b.3	2a.3	2a.1
Ceratodon purpureus	.	2a.2	1.2	1.1	1.1	2m.1	1.1	1.1	1.1	1.2
Hypochoeris radicata	1.1	1.1	r	.	.	+	2m.3	2a.1	+	1.1
Agrostis capillaris	1.1	2m.1	1.1	.	.		2a.1	2m.1	3.3	2b.1
Brachythecium albicans	1.1	2a.1	.	.	1.1	.	3.3	.	2a.2	1.2
Anthoxanthum odoratum	1.1	r	.	.	+	.	1.1	2a.3	.	1.2
Trifolium dubium	1.1	1.1	.	.	.	.	1.1	1.1	1.1	1.1
Leontodon saxatilis	1.1	1.1	.	.	.	.	1.1	+	+	1.1
Poa pratensis	2m.1	1.1	.	.	.	.	2m.1	2a.1	2m.2	2m.1
Rhytidiadelphus squarrosus	1.1	.	.	.	1.1	.	3.3	3.3	3.3	2b.3
Bromus hordeaceus	1.1	.	.	.	.	r	1.1	1.1	2m.1	2a.2
Festuca rubra s.str.	1.1	.	.	.	.	1.1	2a.1	2m.1	2a.3	2m.2
Luzula campestris	1.1	+	.	1.1	1.1	1.1	.	.	.	.
Veronica arvensis	1.1	1.1	.	.	1.1	1.1	.	.	.	2m.1
Sarothamnus scoparius juv.	1.1	1.1	r	.	.	.	.	.	.	.
Taraxacum officinale agg.	+	.	r	.	.	.	r	+	.	.
Plantago lanceolata	.	.	.	.	+	.	1.1	1.1	.	.
Anthoxanthum aristatum	.	.	.	.	.	.	.	2m.3	2m.1	1.2
Linaria vulgaris	.	.	.	.	.	.	.	+	1.1	1.1
Geranium pusillum	1.1	1.1	.	.	.	.	.	.	.	.
Quercus robur (juv.)	.	r	.	.	r	.	.	.	.	.
Stellaria media	.	.	+	.	.	+	.	.	.	.
Geranium molle	.	.	.	.	+	1.1	.	.	.	.
Veronica serpyllifolia	.	.	.	.	.	.	.	.	1.1	1.1

Additional species: Relevé 1a1: *Erodium circutarium* 1.1, *Sagina procumbens* r; relevé 1a2: *Elymus repens* 1.1, *Scleranthus annuus* agg. 1.1, *Arabidopsis thaliana* 1.1, *Scleranthus annuus* agg. 1.1, *Bromus sterilis* 1.1, *Taraxacum laevigatum* r; relevé 1b1: *Conyza canadensis* r, *Viola arvensis* r, *Gnaphalium sylvaticum* r; relevé 1b2: *Senecio inaequidens* +; relevé 3a1: *Euphorbia cyparissias* +; relevé 3a2: *Crepis capillaris* r, *Phleum pratense* 1.1; relevé 3b1: *Aphanes inexspectata* 1.1, *Capsella bursa-pastoris* 1.1.

per ha (grazing period from the beginning of April until the end of October) according to guidelines for conservation management.

Table 1 shows the relevés of the three studied plant communities (method modified from BRAUN-BLANQUET 1964 and extended by the degrees of plant species cover according to BARKMAN et al. 1964; size of the plots: 25 m^2). The sandy dry grasslands in the region were phytosociologically precisely recorded and analyzed using both classical and multivariate methods (OSTENDORP 2001), ensuring the representativeness of the selected sites.

3. Methods

To elucidate the questions indicated above, parts of the grazing area were excluded from grazing in the "Biener Busch" and in the "Hammer Schleife" (Fig. 2). This method has successfully been employed in numerous studies (GRICE & BARCHIA 1995, MEISSNER & FACELLI 1999). The design of the study plots both within and outside these exclosures was precisely determined (Fig. 3). The data sampling starts with setting up a fence for comparing outside and within an exclosure.

Fig. 2. Spergulo-Corynephoretum; in the foreground the area excluded from grazing. The BRAUN-BLANQUET relevé area is marked by the tape.

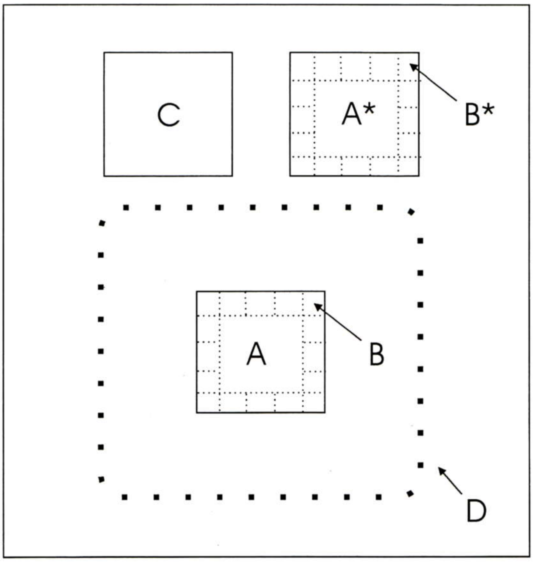


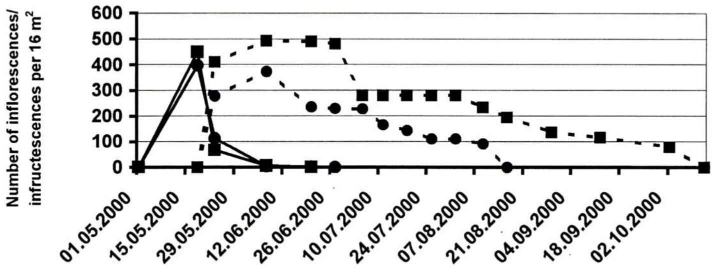
Fig. 3. Example of the arrangement of the study plots for the analyses: A, A* = BRAUN-BLANQUET areas, size 25 m^2 each; B, B* = relevé sites for flower and fruit phenology of 16 m^2 each; C = area for the seed bank studies; D = fence.

The inflorescences and infructescences on an area of 16 m^2 were recorded for the year 2000 from 1 May to 31 August weekly and from 1 September to 12 October at two-week intervals (method after Kratochwil 1984). Only those species were analyzed that characterize the plant community, generally occur in higher phytomass and showed the same degree of cover immediately after the fence was erected, both outside and within the exclosure. The species fulfilling these criteria are listed in Table 2, including the number of units, of flowers per unit and of diaspores per unit. In addition, *Ranunculus bulbosus* and *Teesdalia nudicaulis* were phenologically investigated. A first-order synflorescence is an inflorescence whose main axis branches into single inflorescences, a second-order synflorescence is an inflorescence branching into double or multiple inflorescences (e.g. panicle). Flowers and diaspores of the plant species listed in Table 2 were counted. The largest possible number of diaspores per counting unit was recorded, but also the number of diaspores that failed to develop, due to non-fertilization, unfavourable climatic influences or attacks by parasites.

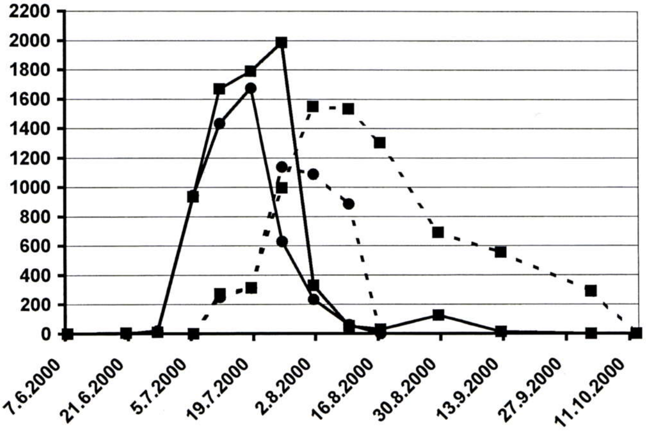
To record the diaspore reservoir in the soil as compensation potential, the germination method was used (Krolupper & Schwabe 1998). The advantages of this technique, compared to extraction methods, have been outlined, e.g., by Thompson et al. (1997). In a 25-m^2 plot 100 soil samples were extracted in a random systematic design. The three communities Spergulo-Corynephoretum typicum (2 plot areas at 100 samples each in spring 2001), S.-C. cladonietosum (2 plot areas at 100 samples in spring 2000; additionally in spring 2001: 1 plot area at 100 samples) and Diantho-Armerietum (2 plot areas at 100 samples in spring 2000) were sampled (topsoil to a depth of 1–6 cm, without litter; subsoil to a depth of 11–16 cm) with the "Eijkelkamp liner sampler" in March and April (see in

Table 2. The number of flowers/inflorescences and fruits/infructescences of the recorded plant species including standard deviation. The counted units, the number of flowers/unit and the number of diaspores/unit are given. n = number of counted individuals; in brackets percentage of loss. * In the case of *Carex arenaria* only ovulate spikelets were considered.

plant species	units counted	number of flowers per unit*	number of diaspores per unit (max.)	number of diaspores per unit (loss included)
Agrostis capillaris	synflorescence second order (panicle)	373 ± 126 (n=16)	373 ± 126 (n=16)	302 ± 128 (19%) (n=16)
Carex arenaria	synflorescence second order (panicle)	4 ± 1* (n=15)	55 ± 19 (n=15)	52 ± 18 (6 %) (n=15)
Corynephorus canescens	synflorescence second order (panicle)	116 ± 43 (n=18)	116 ± 43 (n=18)	114 ± 42 (2%) (n=18)
Dianthus deltoides	single flower	4,3 ± 2,3 (n=13)	64 ± 8 (n=19)	64 ± 8 (n=19)



a) *Carex arenaria* (Spergulo-Corynephoretum typicum)



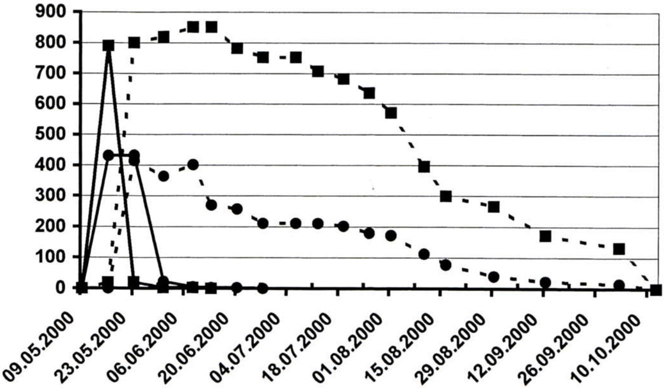
b) *Corynephorus canescens* (Spergulo-Corynephoretum typicum)

Fig. 4. Inflorescence and infructescence phenology of *Carex arenaria* (a) and *Corynephorus canescens* (b) in a Spergulo-Corynephoretum typicum and in a S.-C. cladonietosum (c, d) grazed by cattle, compared to an ungrazed plot (0.75 livestock units/ ha, May–October).

this context also Thompson 1986, Fischer 1987 and Poschlod 1991). Because it was not the intention of this study to analyse the influence of grazing on the seed bank, soil samples were extracted only in grazed sites. All investigation areas were grazed extensively over a long time. Sampling was divided between 2000 and 2001 because of the difficulty in treating 800 samples at once.

Many authors have pointed out that it is better to collect a larger number of smaller samples and to unite them in a composite sample in order to avoid the formation of lumps (Roberts 1981, Thompson 1986, Thompson et al. 1997, Urbanska 1992). The sampled soil surface for each plot and each soil layer measured 0.1698 m^2. On this basis, values for 1 m^2 were calculated.

c) *Carex arenaria* (Spergulo-Corynephoretum cladonietosum)



d) *Corynephorus canescens* (S.-Corynephoretum cladonietosum)

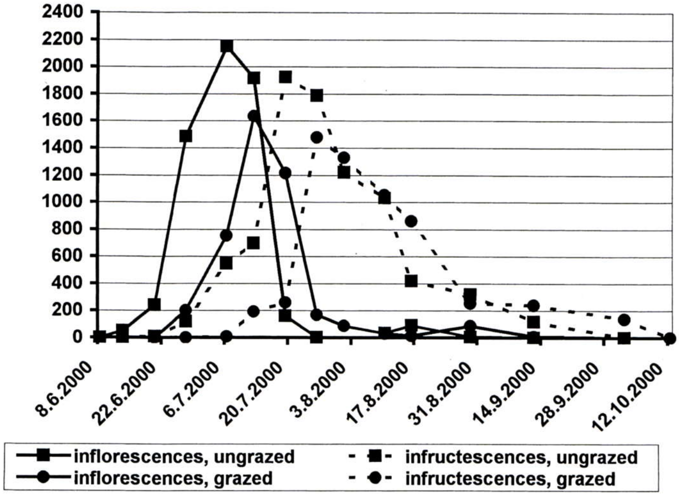


Fig. 4. (cont.)

As suggested above, the samples were united in composite samples per plot area according to their horizons, dried in a greenhouse for 10 weeks and sieved. Then they were streaked onto plastic trays and cultivated in a diaspore house under quasi-field conditions. A roof prevented the germination trays on tables from getting wet, and a gauze tent protected the samples from the penetration of further diaspores.

The material gathered at the beginning of 2000 was cultivated for 20 months and that sampled at the beginning of 2001, for 11 months. The soil was kept wet and turned at certain time intervals. The species were identified according to Csapody (1968) and Muller (1978). For the purposes of this study, we have only checked for germination of the investigated species. An overall analysis of the diaspore banks of the three plant communities will be presented in a separate publication.

The nomenclature of the vascular plants follows Oberdorfer (2001), that of the mosses Frahm & Frey (1992) and that of the lichens Wirth (1995).

4. Results: grazing of flowers/inflorescences and fruits/infructescences, comparison with fruit set, seed bank compensation

4.1. Spergulo-Corynephoretum typicum

In extensively grazed sites, the number of inflorescences of *Carex arenaria* at the peak of flowering was 12 % lower than in ungrazed plots, and the number of infructescences at the peak of fruiting was 24 % lower (Fig. 4a). The number of inflorescences of *Corynephorus canescens* was 16 % lower, the number of infructescences 26 % lower than in ungrazed plots (Fig. 4b).

For *Carex arenaria*, the number of diaspores per m^2 decreased from 1,602 ± 555 to 1,212 ± 420 (= −24 %). The number of diaspores per m^2 of *Corynephorus canescens* decreased from 11,044 ± 4,069 to 8,123 ± 2,993 (= −26 %). An analysis of the seed bank shows that both species are present (Table 3). However, the results are not constant. The diaspore numbers of *Carex arenaria* in the case of plot 1a amount to one-third, in plot 1b two-

Table 3. Number of diaspores of the investigated species (seed bank, 1 m^2, topsoil: 1–6 cm depth, subsoil: 11–16 cm depth) in a Spergulo-Corynephoretum typicum (plots: 1a, 1b), a S.-C. cladonietosum (plots: 2a, 2b) and a Diantho-Armerietum (plots: 3a, 3b); compare Table 1. TS = topsoil, SS = subsoil, COV = cover Table 1. * *Agrostis capillaris* and *A. vinealis* have not been separated.

plot number	**1a**	**1a**	**1a**	**1b**	**1b**	**1b**	**2a**	**2a**	**2a**	**2b**	**2b**	**2b**	**2a**	**2a**	**2a**
year of sampling	**01**	**01**	**01**	**01**	**01**	**01**	**00**	**00**	**00**	**00**	**00**	**00**	**01**	**01**	**01**
stratum	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**
Carex arenaria	0	106	2m	294	0	2m	35	35	2m	218	0	2m	648	47	2m
Corynephorus canescens	53	18	2a	300	18	2a	489	24	2a	583	147	2a	559	29	2m
Teesdalia nudicaulis							77	0	2m	82	6	2m	0	0	2m

plot number	**3a**	**3a**	**3a**	**3b**	**3b**	**3b**	**3a**	**3a**	**3a**
year of sampling	**00**	**00**	**00**	**00**	**00**	**00**	**01**	**01**	**01**
stratum	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**	**TS**	**SS**	**COV**
Dianthus deltoides	913	29	2a	6	0	2m	0	0	2m
Ranunculus bulbosus	18	0	1	0	0	1	0	0	1
Agrostis capillaris	2626*	300	2a	459	47	2b	471	18	2b
Agrostis vinealis	*		2a	94	35	2a	88	0	2a

thirds of the loss by grazing. Losses of diaspores by grazing may be partly compensated in the case of *Carex arenaria*. In plot 1a and in plot 1b lower diaspore numbers of *Corynephorus canescens* have been ascertained. A compensation of diaspore loss by grazing is hardly possible.

It is remarkable that diaspores of *Carex arenaria* are present in plot 1a only in the subsoil, in plot 1b only in the topsoil.

4.2. Spergulo-Corynephoretum cladonietosum

As in the S.-C. typicum, the number of inflorescences and infructescences of *Carex arenaria* and *Corynephorus canescens* is lower in the extensively grazed sites (Figs 4c and 4d). For *Carex arenaria* the values amount to −45 % and −51 % in the two plots, for *Corynephorus canescens* to −24 % and −23 %. For *Carex arenaria*, the number of diaspores per m^2 decreased from 2,766 ± 957 to 1,349 ± 467 (= −51 %). The number of diaspores per m^2 of *Corynephorus canescens* decreased from 13,716 ± 5,053 to 10,545 ± 3,885 (= −23 %). The diaspore production of *Carex arenaria* was much more reduced than in the S.-C. typicum; *Corynephorus canescens* shows a similar value. For one species, *Teesdalia nudicaulis*, the number of flowers and diaspores was actually found to be greater in the grazed area (17 vs 23 infructescences/m^2). *Teesdalia nudicaulis* is a therophyte, which needs gaps to establish itself.

An analysis of the seed bank shows that *Corynephorus canescens*, *Carex arenaria* and *Teesdalia nudicaulis* are present (Table 3). Up to 218 diaspores of *Carex arenaria* were found per m^2, although on a third plot lower values were determined (35/m^2). The same holds true for *Corynephorus canescens*; the values measured here were even much higher (489 to 583/m^2).

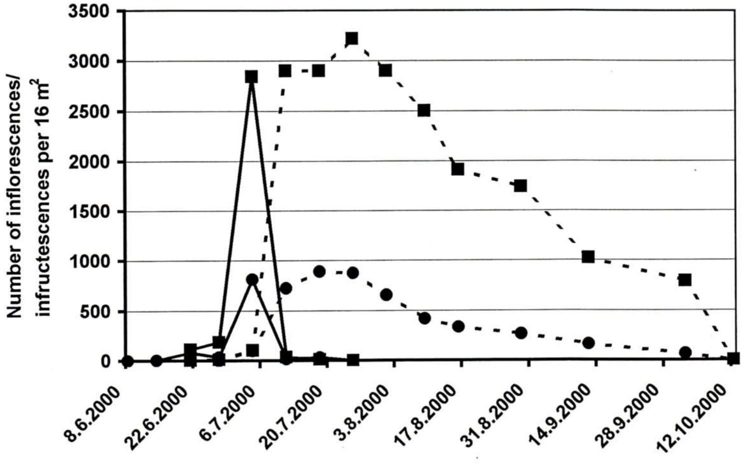
4.3. Diantho-Armerietum

In the Diantho-Armerietum, both species with fewer inflorescences and infructescences in grazed areas (e.g. *Agrostis capillaris*, *Dianthus deltoides*) and species with considerably increased numbers (e.g. *Agrostis vinealis*, *Ranunculus bulbosus*) are present. The number of inflorescences of *Agrostis capillaris* was reduced by 71 %, that of infructescences by 72 % (Fig. 5a). In the ungrazed sites, a maximum number of 60,778 ± 25,760 diaspores was ascertained, while in grazed ones the maximum was only 16,761 ± 7,104.

In the grazed sites the number of flowers of *Dianthus deltoides* is 61 % lower, but that of fruits only 22 % (Fig. 5c). This difference in degree of reduction is remarkable. In the ungrazed sites a maximum of 10,524 ± 1,316 diaspores/m^2 was determined, and in the grazed ones, 8,200 ± 1,025. Grazing thus has much less influence on the diaspore potential of *Dianthus deltoides* than on that of *Agrostis capillaris*.

Two species show much higher flower and fruit numbers in the grazed sites: the number of inflorescences of *Agrostis vinealis* was increased by 44 %, that of infructescences by 36 % (Fig. 5b). For *Ranunculus bulbosus*,

a) *Agrostis capillaris* (Diantho-Armerietum)



b) *Agrostis vinealis* (Diantho-Armerietum)

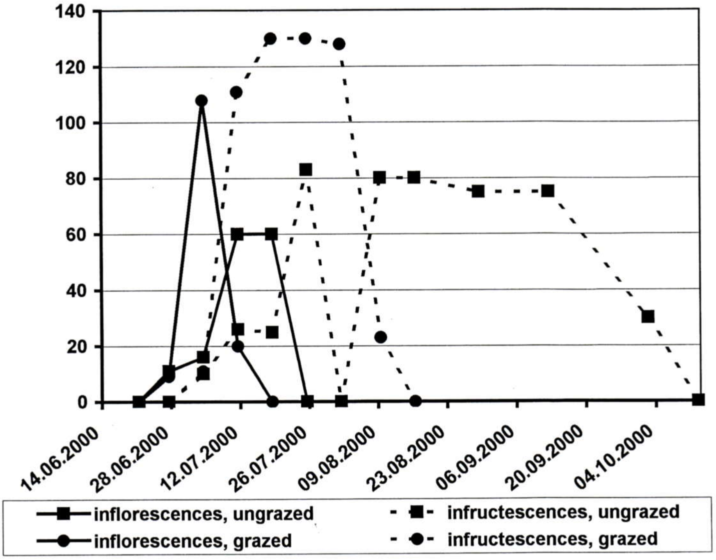
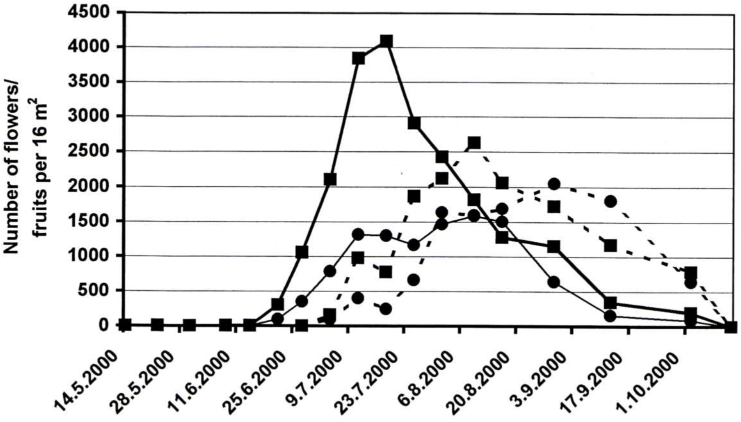


Fig. 5. Inflorescence/flower and infructescence/fruit phenology of *Agrostis capillaris* (a), *Agrostis vinealis* (b), *Dianthus deltoides* (c) and *Ranunculus bulbosus* (d) in a Diantho-Armerietum grazed by cattle, compared to an ungrazed plot (1–2 livestock units/ha, May–October).

c) *Dianthus deltoides* (Diantho-Armerietum)



d) *Ranunculus bulbosus* (Diantho-Armerietum)

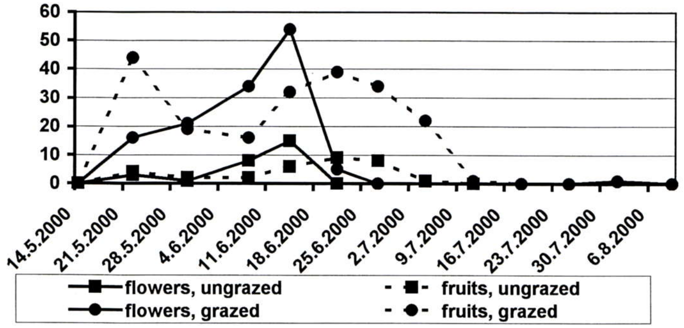


Fig. 5. (cont.)

increases in the number of flowers by 72 % and of fruits by 77 % were found (Fig. 5d).

When sites in the Diantho-Armerietum are more intensively grazed, inflorescences and infructescences are as rule only present at the microsites formerly occupied by cattle faeces.

The analysis of the seed bank in the soil has shown that *Agrostis capillaris*, *Dianthus deltoides*, *Agrostis vinealis* and *Ranunculus bulbosus* (the last in fairly large numbers only in one plot) are present (Table 3). Losses of diaspores by grazing may be partly compensated. The seed bank of *Agrostis capillaris* is larger than the one of *Agrostis vinealis*, although *Agrostis capillaris* is more decimated by grazing than *Agrostis vinealis*.

4.4. Reaction of the selected species in different plant communities

A comparative analysis of the influence of grazing on the numbers of flowers/inflorescences and fruits/infructescences of the investigated species in the respective plant communities has yielded the following results (Fig. 6). When subjected to grazing, *Carex arenaria* and *Corynephorus canescens* show a reaction in the Spergulo-Corynephoretum typicum rather similar to that in the S.-C. cladonietosum. The number of inflorescences and infructescences does decrease, but these differences are very low for *Corynephorus canescens* and more evident for *Carex arenaria* (especially in S.-C. cladonietosum).

In grazed stands of the Diantho-Armerietum some species show reduced numbers of inflorescences/infructescences (*Agrostis capillaris*, *Dian-*

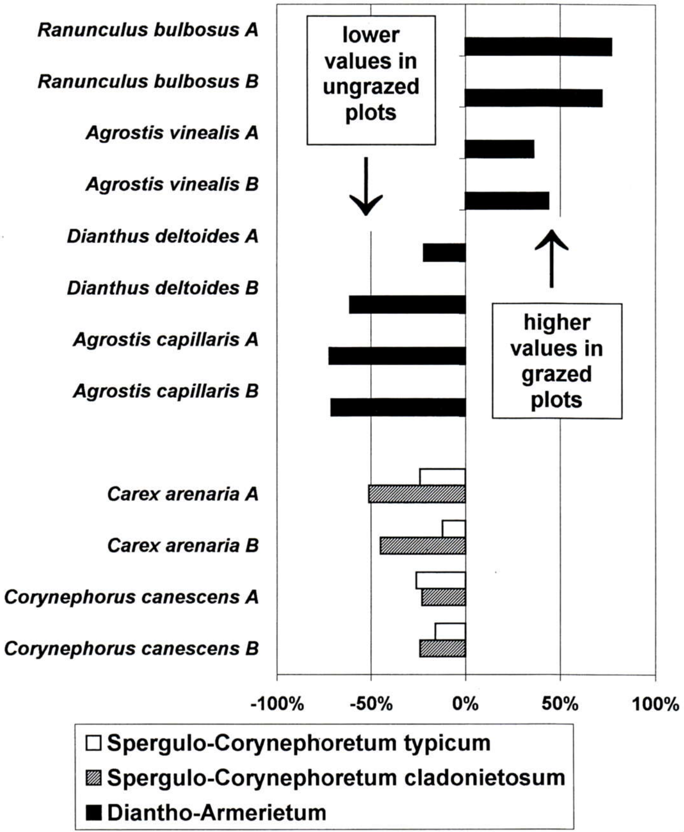


Fig. 6. Percentage differences of infructescences/fruits (A) and inflorescences/flowers (B) in grazed and ungrazed sites in the Spergulo-Corynephoretum typicum, S.-C. cladonietosum and Diantho-Armerietum in the peak period of flowering/fruiting (minus: lower, plus: higher values in grazed sites).

thus deltoides), whereas others become more numerous under grazing (*Agrostis vinealis*, *Ranunculus bulbosus*).

5. Discussion

5.1. Grazing behaviour of the cattle

Numerous plant communities have developed due to selective grazing, which favours unreachable (e.g. rosette plants), "armed" (with stings or thorns), bad-tasting or even toxic plant species. Other plant species, however, are consumed in large quantities and considerably reduced in their biomass (overview in KRATOCHWIL & SCHWABE 2001). Some of the much preferred plant species, especially perennial ones, may compensate the consumed biomass; they show resilience (overcompensation, see e.g. HUHTA et al. 2000a, 2000b). With regard to their response to grazing, plant species can roughly be described as "increaser", "decreaser" or "indifferent" (VESK & WESTOBY 2001).

Cattle are, like sheep, classified as large generalist herbivores (VESK & WESTOBY 2001). Both select the most palatable species from the available food (WESTOBY 1974, OWEN-SMITH & NOVELLIE 1982, WILSON & HARRINGTON 1984). The sheep's diet is more specific and selective than that of the cattle, as they graze plant species with higher protein content, more herbs, water-soluble carbohydrates, lignin, crude protein, phosphorus and gross energy per dry matter unit, and less grass (COOK et al. 1967, BUTTENSCHØN & BUTTENSCHØN 1982a, WILSON & HARRINGTON 1984). But cattle show food preferences as well: they select more grasses than sheep (WILLIAMS et al. 1974) and accordingly take up more cellulose (COOK et al. 1967). Grasses, however, are preferred more by horselike species, whereas cattle frequently also feed on herbs (e.g. leguminous plants).

It is thus to be expected that flowering/fruiting plant species will be decimated to different degrees. Whether a plant species is consumed by these herbivores depends in addition on the available food (VESK & WESTOBY 2001) and finally on the entire plant community and the prevailing site factors.

5.2. Habitat preferences of the grazing cattle and consequences for grazing pressure

The phytobiomass available for grazing cattle in a Spergulo-Corynephoretum typicum is low. However, the sites contribute to the cattle's well-being (greater wind exposure in the upper dune area and thus fewer parasitic insects, high reflection and quicker warming-up of the animals in the morning hours, and other factors). At such sites food is taken only occasionally, in our case *Carex arenaria* (reduction in the number of infructescences by 24 %), although BUTTENSCHØN & BUTTENSCHØN (1982a) stated that *Carex* species tend to be avoided. The fact that the differences are greater in the infructescences can be phenologically explained, since the flowering period only covers 7 weeks, whereas the fruiting period lasts 20 weeks. No clear differences were found for *Corynephorus canescens*, as this species is usually rejected by cattle. Herbivory is very low in this plant community, because the food requirements of the cattle in the area are met in the plant communities of the surroundings (e.g., Lolio-Cynosuretum).

The situation in the S.-C. cladonietosum is similar. Owing to the higher biomass, however, grazing intensity obviously increases; clear differences are ascertained for *Carex arenaria* (reduction by 51 %). *Corynephorus canescens* exhibits values close to those in the S.-C. typicum. The S.-C. cladonietosum is therefore also not an important "food habitat" for cattle.

The Diantho-Armerietum has the highest above-ground plant biomass of the investigated plant communities; accordingly, the cattle are more often found there. The number of infructescences of *Agrostis capillaris* is thus strongly reduced (by 72 %). The smaller differences in the number of inflorescences can be attributed to differences in phenology (flowering period: 5 weeks, fruiting period: 16 weeks). BUTTENSCHØN & BUTTENSCHØN (1982a) had already shown that *Agrostis capillaris* is preferred by cattle.

Clear differences in the number of flowers in grazed and ungrazed plots were found for *Dianthus deltoides*. The results obtained for the number of fruits, in contrast, were not evident; this is probably again due to phenology. Flowers of *Dianthus deltoides* were present on the sample plots for 20 weeks, fruits for 14 weeks only. For *Agrostis capillaris*, *Carex arenaria* and *Corynephorus canescens*, in contrast, shorter flowering and longer fruiting periods were ascertained, therefore the grazing pressure on infructescences is higher than that on inflorescences.

Unlike *Agrostis capillaris*, *Agrostis vinealis* shows no reduction of inflorescences/infructescences in grazed compared with ungrazed sites. Results from other investigation areas (grazing plots near Darmstadt) have revealed that *Agrostis vinealis* is avoided and can thus spread. Taste, surface structures, raw fibre content and other factors may be decisive for the choice of a certain plant species (BUTTENSCHØN & BUTTENSCHØN 1982b). It is a generally known phenomenon that *Ranunculus* species are avoided (BUTTENSCHØN & BUTTENSCHØN 1982a). We can confirm this for flowering and fruiting *Ranunculus bulbosus* individuals.

5.3. Diaspore reduction by grazing

It is plausible that herbivory of flowering/fruiting plant species may influence plant fitness (EHRLEN 1997, JÜNGER & BERGELSON 2000). Accordingly, TODD & HOFFMANN (1999) found a significant reduction in flower and fruit production by many plant species in intensively grazed areas in Namaqualand (South Africa), compared to extensively grazed ones; for one species (*Osteospermum sinuatum*) a reduction of up to 90 % was found.

This loss may later on (partly) be compensated by endozoochory and seed rain. It should be investigated how many flowering/fruiting plant species are grazed at the three different sites and the subsequent loss of diaspores should be determined. This has to our knowledge not yet been done.

The present study shows for these model systems that under extensive grazing of sandy dry grasslands, the reduction of flowers/inflorescences and fruits/infructescences is significant in only a very few cases (diaspores of *Agrostis capillaris* 72 %, of *Carex arenaria* max. 51 %, flowers of *Dianthus deltoides* 61 %), although the plant species are dominant in the respective plant communities and the biomass available to the grazing cattle is low. For *Corynephorus canescens* (inflorescences/infructescences) and *Dianthus deltoides* (fruits) only small differences could be found; for *Agrostis vinealis* and *Ranunculus bulbosus* the number of flowers and fruits was even observed to increase.

Of special importance is the observation that most flowering and fruiting plant individuals occur at microsites, where cattle formerly deposited faeces (see below). Since cattle apparently instinctively avoid such sites for fairly long periods of time to prevent parasitism, vegetation can develop after faeces decomposition has proceeded undisturbed. Within 24 h, a cow or bull produces 10–12 of these faeces sites, covering an area of altogether 1 m^2, which are not grazed for a considerable time (Ellenberg 1996). At such microsites, which make up about one third of the investigated plots, many flowers and fruits develop. In the Diantho-Armerietum the former faeces microsites prevent an excessive grazing of the vegetation, so that the plants can reproduce.

5.4. The seed bank of the studied plant communities

It is generally presumed that inland dunes have a transient or short-term persistent seed bank (see e.g. Sautter 1994, Krolupper & Schwabe 1998, Jentsch & Steinlein 2000). *Corynephorus* caryopses survive for about 2 years and thus have a quite short life-span (Thompson et al. 1997). In the Spergulo-Corynephoretum typicum both *Carex arenaria* and *Corynephorus canescens* build up a short-term persistent seed bank.

The diaspore bank of *Carex arenaria* is on one plot only present in the subsoil; this is probably due to sand shifts. Similar results in sand ecosystems have been obtained by Yamanaka et al. (2000). On a second plot 294 diaspores/m^2 are available for the compensation of the loss by grazing (390 diaspores/m^2; Table 3). The diaspore bank of *Corynephorus canescens* shows very low values on one plot in the S.-C. typicum, while on a second plot 10 % can be compensated (300 diaspores/m^2 in the seed bank: Table 3, 2,921 diaspores/m^2 loss by grazing: Section 4.1).

It can be assumed that in the S.-C. typicum both *Carex arenaria* and *Corynephorus canescens* compensate their diaspore losses in part via the seed bank, *Carex arenaria* to a greater extent than *Corynephorus canescens*. The irregular distribution of the diaspores of the species in the S.-C. typicum, however, makes analysis and prognosis difficult. The seed bank is only activated if the stored diaspores reach the soil surface, owing to trampling by the grazing cattle or to sand shifts caused by the wind in the Spergulo-Corynephoretum.

Similar observations have been made for *Carex arenaria* in the S.-C. cladonietosum. However, the distribution of diaspores of *Corynephorus canescens*, with values between 489/m^2 and 583/m^2 (top layer) in the three investigation areas, was relatively homogeneous.

Krolupper & Schwabe (1998), who investigated a subcontinentally influenced Spergulo-Corynephoretum south of Frankfurt/Germany, ascertained diaspore numbers for *Corynephorus canescens* of about 66 diaspores/m^2. Jentsch (2001) found 860 diaspores of *Corynephorus canescens* per m^2 in the upper soil and 60/m^2 in the subsoil of a S.-C. typicum, as well as 1,100/m^2 and 20/m^2, respectively, in a S.-C. cladonietosum in southern Germany (Erlangen). The higher density of diaspores in the S.-C. cladonietosum in this study corresponds to the findings of Jentsch (l.c.).

In the S.-C. cladonietosum the diaspore bank of *Carex arenaria* shows very low values on one plot, while on a second and a third plot there were between 218 and 648 diaspores/m^2 (Table 3). The loss due to grazing amounts to 1,417 diaspores/m^2 (Section 4.2), 15–45 % of which can be compensated. *Corynephorus canescens* can compensate some of the losses caused by grazing via the seed bank but only 15–17 % (Section 4.2, Table 3). In addition – factors not considered here – diaspores are introduced from the seed rain and by processes of exo- and endozoochory.

In the Diantho-Armerietum the situation is more complex: particularly high losses have been ascertained for *Agrostis capillaris* (max. about 44,000 diaspores; Section 4.3), whereas *Agrostis vinealis* shows an increasing number of diaspores under grazing impact. In the seed bank comparatively few diaspores of *Agrostis capillaris* were present, so that at least for *Agrostis capillaris* only a very small percentage could be compensated. In the case of *Agrostis vinealis* there is no need for compensation by the seed bank in the soil. The results obtained for *Dianthus deltoides* also point to a very irregular diaspore distribution in the soil. Only in one of three plots (seed bank: 913 diaspores/m^2) was 39 % of the loss rate (2,324 fruit/m^2) by grazing regained. *Ranunculus bulbosus*, which is avoided by the grazing cattle, has a small diaspore reservoir in the soil.

Under extensive grazing not only do grazing patterns develop in the vegetation, but also disturbance sites due to trampling ("gaps"), in which new seedlings can establish themselves and thus avoid the strong competitive pressure exerted by other plant species (Bullock et al. 1994). Apart from this "in situ" activation of the seed bank at such disturbance sites, exozoochorous (particularly in the case of grazing by sheep and horses) and endozoochorous processes – not considered here – play a part (Bonn & Poschlod 1998).

5.5. Synopsis and outlook

Our study has shown that the influence of cattle grazing on the inflorescences and infructescences in the three plant communities differs. The

Spergulo-Corynephoretum is subjected to little grazing pressure, as the above-ground phytomass is low and not very attractive to cattle (*Corynephorus*, *Carex*), while the seed bank and surface regeneration potential are high. Edaphic dryness, wind and trampling cause sites devoid of vegetation. These areas are of great importance for the cattle as a place of residence.

The grazing pressure in the Diantho-Armerietum is higher. Some plant species are avoided (*Agrostis vinealis*, *Ranunculus bulbosus*), but others are much appreciated (*Agrostis capillaris*, *Dianthus deltoides*). Even under favourable germination conditions the loss of diaspores could only to a certain extent be compensated from the diaspore bank. Only at the former faeces microsites are there "islands" rich in flowers which might be regeneration places for diaspore production. Faeces deposition causes a different development of the vegetation (flowering and fruiting stages, fertilization effects) and accordingly a different vegetation pattern. The cattle produce a substrate they can temporarily no longer use, so that the surface regeneration potential of the plant species occurring there is retained, and the seed bank can be replenished. The cattle themselves endozoochorically disperse plant species directly and reactivate the seed bank by trampling. The dynamics of the system is based on processes of utilization, transport, retention and reactivation of plant material and diaspores.

On aerial photographs (infrared colour) with a pixel resolution of 7.5 × 7.5 cm a pattern of approximately round microsites is recognizable. It is planned to elucidate this pattern further and to calculate the number of microsites in a model.

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