The contribution of sheep zoochory to the conservation and restoration of target plant communities in isolated sand ecosystems

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Congress abstracts

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Used abbreviations

Vegetation types :

Ac: Artemisia campestris

AF: Armerio-Festucetum trachyphyllae

AS: Allio-Stipetum capillatae

Kg: Koelerion glaucae

Seed traits:

sm: seed mass

sss: seed surface structure

Germination tests:

TH: Ter Heerdt method

CG: Common garden method

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Chapter 1

General introduction

Background

The species richness of semi-natural grasslands can be reduced by a limitation of seeds (Bakker and Berendse 1999). European grassland ecosystems are assumed to be the result of low-intensity farming (Bignal and McCracken 1996); livestock grazing and migration within the landscape were common in these habitats (Hornberger 1959; Ellenberg 1996; Bruun and Fritzbøger 2002). Such traditional land-use practices are considered to be more important for the dispersal of plant species than the plants' own dispersability (autochory) (Poschlod and Bonn 1998). However, parallel to land-use intensification (Bakker and Berendse 1999), extreme reduction of the numbers of free ranging livestock, especially sheep (Lahrkamp 1928), and increased stable management (Bruun and Fritzbøger 2002), the area of semi-natural grasslands as well as their species richness became dramatically reduced (Poschlod and Bonn 1998). The fragmented European landscape spatially isolates populations of many plant species (Cain et al. 2000). Habitat-typical species often have a low competitive ability, which makes them extra vulnerable to local extinction. Besides, soils of restoration sites mostly lack a long-term persistent seed bank; many species of the European flora only shortly persist in the soil (< 5 years) (Thompson et al. 1997). Long-distance seed dispersal (Box 1.1) could provide a survival opportunity (Brown and Kodric-Brown 1977) for small populations with a high extinction risk (Levin et al. 2003) and increases gene flow (Oostermeijer et al. 1996). Consequently, dispersal and re-colonization processes are crucial for population survival (Opdam 1990) and the regulation of diversity in grassland communities (Foster and Tilman 2003).

Box 1.1 Definitions

Epizoochory: external dispersal of seeds via animal coat (hoofs excluded here).

Endozoochory: internally transported seeds, via gut passage.

Long-distance dispersal: transport of seeds more than 100 m away from individual parent plant (Cain et al. 2000).

Seed: every type of generative diaspore including fruits.

Target species, community: habitat-typical species, community of which preservation is desirable from a conservation point of view (Kratochwil and Schwabe 2001).

Sheep grazing was shown to reverse spontaneous succession in an inland dune area which could positively affect plant species richness (Süss et al. 2004). Moreover, numerous studies have demonstrated grazer-induced internal (endozoochorous) and external (epizoochorous) seed dispersal (Box 1.1) of many plant species via domestic animals, e.g. cattle (e.g. Gardener et al. 1993; Malo and Suárez 1995b; Traba et al. 2003), horses (Janzen 1981; Cosyns et al. 2005a), donkeys (Couvreur et al. 2005), and sheep (e.g. Piggin 1978; Fischer et al. 1996; Eichberg et al. 2007). However, only limited knowledge on long-distance zoochory between isolated areas exists. Additionally, herbivore-induced seed dispersal and post-dispersal recruitment of especially habitat-typical species were hardly studied (although see Eichberg et al. 2005, 2007). Data on seed dispersal by herbivores and the eventual impact on plant species richness are needed for development of habitat management in fragmented landscapes and preservation of target communities (Box 1.1).

Target communities as seed source

Seeds of many plant species can survive the effects of sheep ruminating and gut passage (Welch 1985). Additionally, the wool of sheep was claimed to allow seed attachment of most grassland plant species (Fischer et al. 1996; Couvreur et al. 2004; Mouissie et al. 2005b). Thus, the species composition of the source could be an important determinant for the species composition of sheep zoochorously dispersed seeds. Because of differences in nutritional values, integrated grazing of habitats of different quality probably facilitates seed transport from species of nutrient-rich habitats towards more nutrient-poor sites. Dispersal of strong competitors might seriously threaten the species richness of less productive sites (Mouissie et al. 2005a). Since restoration in our study area (inland sand ecosystems, see *Study area*) aims re-establishment of oligotraphent target communities (Bakker and Berendse 1999), the use of such well-developed communities as source is expected to promote seed dispersal of high proportions of target species.

Seed retention and long-distance dispersal

Digestion of seeds by sheep generally takes 1-3 days and survival after gut passage can be tested (Russi et al. 1992; Cosyns et al. 2005b; Ramos et al. 2006). As a result,

the arrival of seeds in another area via the endozoochorous pathway is mostly predictable. In contrast, potential benefits to seed availability in another habitat via epizoochory are largely unknown. Besides seed and other plant traits influencing the initial attachment probability, it is unknown whether seed retention is negatively affected by sheep movement. Either seeds remain attached to the sheep coat when animals walk from site to site or, alternatively, retention is negatively affected by animal movement and seeds get 'lost'. Considerable numbers of experimentally attached seeds detached within the first few days after attachment; another portion (5 – 50 %, species-dependent) remained present in the sheep coat for weeks (Fischer et al. 1996; Manzano and Malo 2006). These data confirm the possibility of long-distance seed dispersal. Other studies have predicted seed retention and dispersal distances by tests using shake machines (e.g. Carlquist and Pauly 1985; Tackenberg et al. 2006) or mathematical models (Mouissie et al. 2005b). However, dispersal distances of seeds naturally attached to sheep coat were not studied yet. Despite the involvement of stochastic processes in nature, such data probably improve estimations on the contribution of zoochory to dispersal of seeds.

Post-dispersal fate

Eichberg et al. (2005) conducted the first field study on the post-dispersal fate of epizoochorously dispersed seeds. Seeds of *Jurinea cyanoides* were experimentally attached to coats of sheep, which grazed in an early successional Koelerion glaucae stand. The seed shadows of detached achenes were clumped. Such patterns could be initiated by non-random animal movement and possibly result in heterogeneous emergence patterns too. Because of effects on seed predation, competition and recruitment, heterogeneous seed dispersal probably plays an important role in the modification of structure and dynamics of plant populations and communities (Nathan and Muller-Landau 2000). Establishment of *J. cyanoides* took place, albeit only by a few individuals. Seedlings emerged exclusively from seeds which had been incorporated into the soil. Sheep trampling could facilitate soil incorporation (Eichberg et al. 2005), and thereby reduces the risk of seed predation and stimulates seedling emergence (Rotundo and Aguiar 2004). Seed species vary in seed predation risk (Abramsky 1983)

and emergence requirements (light vs. dark germination). Consequently, the impact of sheep trampling on seedling emergence could vary among species.

Post-dispersal fate of dung-embedded seeds was studied before (e.g. Malo and Suárez 1995a; Mouissie et al. 2005a; Cosyns et al. 2006). Only a small proportion of viable seeds in dung emerged under field conditions. Also, not all viable taxa were detected in the field. In productive coastal dune grassland Cosyns et al. (2006) found mostly seedlings from generalist species emerging from horse and cattle dung, although seeds of target species were dung-embedded too. In contrast, despite the high seed availability of competitive species, especially annual herbs with low competitive ability germinated from sheep dung in pioneer stages of inland sand-grassland (Eichberg et al. 2007). These results indicate environmental impact on seedling emergence from out of dung (see *Micro-site availability*).

Micro-site availability

Besides availability of seeds, seedling emergence and species richness are determined by the presence of micro-sites (Eriksson and Ehrlén 1992). Through trampling, scratching and rolling, herbivores can disturb vegetation and/or soil and increase micro-site availability (Zobel et al. 2000). Micro-sites can positively affect species richness through reduced competition (Tilman 1988), litter removal and greater light penetration (Jutila and Grace 2002). Disturbance experiments frequently resulted in increased seedling recruitment and species richness (e.g. Armesto and Pickett 1985; Jutila and Grace 2002; Austrheim and Eriksson 2003). A similar result was found after moss disturbance (*Hypnum cupressiforme*) in one of our target communities, low productive Koelerion glaucae (Eichberg et al. 2007). It is probable that deposition of dung also affects micro-site conditions. Its physical presence can limit the emergence of soil-borne seedlings and existing vegetation, but an increase of fine-scale species richness was also found (Cosyns et al. 2006; Eichberg et al. 2007). On the other hand, dung can locally fertilize the soil (Williams and Haynes 1995), which might stimulate already abundant competitors, like Welch (1985) found. Hence less competitive species might be out-competed, consequently reducing species richness. It was suggested that the

vegetation response to such herbivore activities depends on habitat characteristics, e.g. soil fertility (Olff and Ritchie 1998).

Thesis outline

First of all, seed dispersal via sheep coat between two areas (max. transfer distance 3 km) and within one area (data C. Eichberg) was studied (**Chapter 2**). I tested whether a community-based grazing regime contributes to the dispersal of especially target species. Grazing took place in three well-developed early- and mid-successional target communities: Koelerion glaucae, Armerio-Festucetum trachyphyllae, Allio-Stipetum capillatae (Fig. 1.1). Additionally, I examined the impact of seed surface structure, seed mass, plant seed-releasing height and animal behaviour on seed attachment and seed retention (Fig. 1.1). Finally, the actual arrival of seeds within a "sink" and the impact of animal movement on seed detachment were studied.

The fate of epizoochorously dispersed seeds of a broad spectrum of species was explored by use of an experimental approach under field conditions (**Chapter 3**). Seeds of 14 different species, mostly target species, were attached to the coats of sheep, after which the animals were kept on bare sand fields for 24 hours. I monitored detached seeds and emerging seedlings in time and studied the spatial patterns of animal movement, seed dispersal and seedling emergence (Fig. 1.1). Moreover, the effect of hoof trampling on seedling emergence was tested by use of two habitat-typical species: *Jurinea cyanoides* and *Koeleria glauca* (Fig. 1.1).

The second zoochorous dispersal pathway is via digestion of seeds. Various methods for estimating the viable seed content reveal both qualitative and quantitative differences. In **Chapter 4** seedling emergence via two seedling emergence tests is compared. The first method employs concentrated dung samples under controlled conditions (following Ter Heerdt et al. 1996), whereas the second method uses outdoor exposed, unconcentrated dung samples (common garden conditions) (Fig.1.1).

Chapter 5 deals with the impact of sheep endozoochorous seed dispersal, dung deposition and moss disturbance, and dung removal by dung beetles (*Typhaeus typhoeus* Linnaeus, 1758) on establishment of target species and fine-scale species richness in sandy grasslands. Dung samples from the same target communities as used for epizoochory investigations were collected. Treatments were established in plots with

different productivity. The viable seed content was tested (see also **Chapter 4**) and compared with emergence from samples exposed in the field. The effects of treatments and time on total seedling emergence (from soil and dung) and vegetation were studied (Fig. 1.1).

Impact on seed dispersal, seed shadows and seedling emergence stresses the multi-functional role of herbivore grazing. Studying both seed dispersal and the post-dispersal fate of especially target species will reveal insight into the effective contribution of domestic herbivores to recruitment of those target species (Fig. 1.1). Within this context, a general discussion is presented (**Chapter 6**).
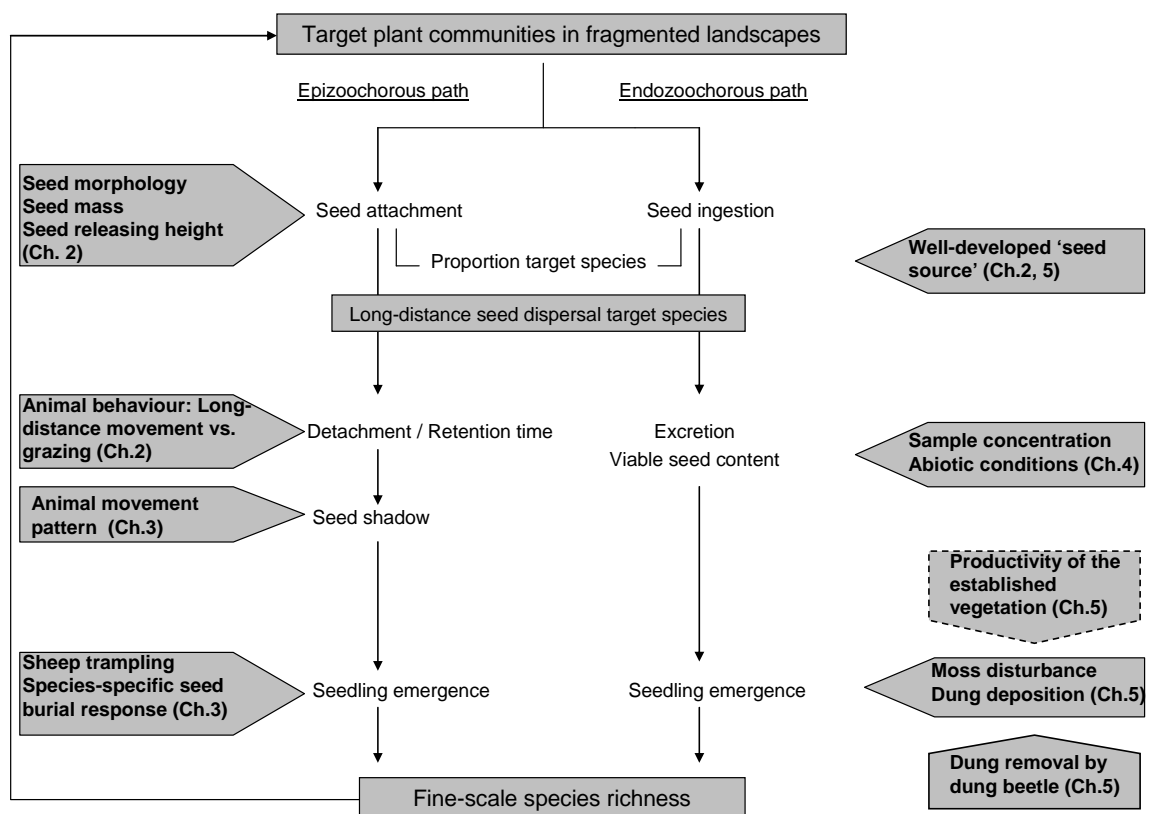
Figure 1.1 Overview of studied topics.

Study area

The study was conducted in three inland sand ecosystems in the Darmstadt region, Germany (Fig. 1.2). These nutrient-poor ecosystems are among the most endangered habitats of Central Europe (Ssymank et al. 1998; Schwabe et al. 2002). Particularly calcareous sand ecosystems have a high diversity of site-specific plant species, adapted to dry and nutrient-poor conditions (Süss 2006); many of them are on the Red List of endangered species (Korneck et al. 1996). The two larger areas within this study, "Griesheimer Düne und Eichwälchen" and "Ehemaliger August-Euler-Flugplatz" are Fauna-Flora-Habitat directive areas. Highly dynamic early successional stages with plant communities belonging to Koelerion glaucae vegetation can be found here. A recent study from the area suggests that well-timed sheep grazing offers a good form of management for mid-successional plant communities (Süss and Schwabe 2007).
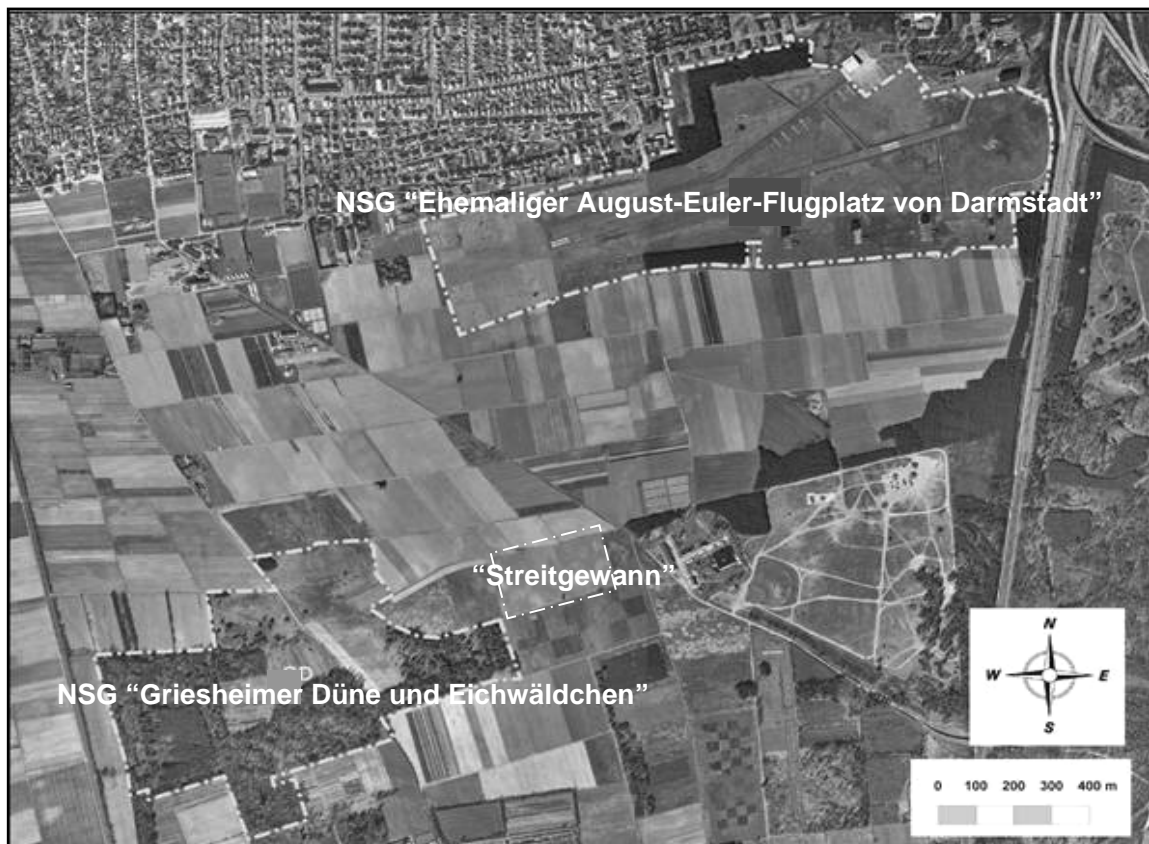
Figure 1.2 Location of study sites.

Testing and development project

This study was conducted in the context of the Testing- and Development project 'Ried und Sand: Biotopverbund und Restitution durch extensive Landbewirtschaftung' (www.riedundsand.de), funded by the Federal Agency for Nature Conservation and the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety (Germany).

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Chapter 2

Do plant-community-based grazing regimes lead to epizoochorous dispersal of high proportions of target species?

Stipa capillata and Agrimonia procera seeds attached to sheep coat.

Abstract

The contribution of large-herbivore epizoochory to the transfer of seeds within and between areas is thought to be significant. But often seeds of ubiquitous species are dispersed, which may enhance ruderalisation processes. In order to study the dispersal of target species by sheep, we employed a community-based grazing approach followed by intra- and inter-area sheep transfers (max. transfer distance 3 km). In case of inter-area transfers, well-developed target communities of an open inland sand ecosystem are used as ''source'', linked to less-developed sand habitats (''sink'') via sheep. Also other factors determining which species become dispersed under field conditions were tested: seed surface structure, seed mass, plant seed-releasing height and animal behaviour. Finally the influence of animal movement on seed detachment and the actual arrival of seeds within a ''sink'' were studied.

Sheep transfers resulted in the dispersal of 56 seed species, dominated by Red List (seven species) and other target species. Quantitatively, most transported seeds belonged to target species, whereas graminoid competitors were highly under-represented. Morphological traits enhance the attachment probability regardless of seed mass. But for seeds without these epizoochory-facilitating traits, mass seems to affect attachment negatively. Plant height affected the number of species present in sheep coats but not the seed quantities, probably certain species in the vegetation produced large numbers of seeds, e.g. low-growing *Medicago minima* with seed surface structures and high-growing species *Verbascum phlomoides* without seed surface structures. Also, although transfer half-times were three times lower than grazing half-times, naturally-attached *Stipa capillata* and *Agrimonia procera* seeds showed no significant detachment rates during transfer, whereas considerable losses were found during grazing. Other 3-km sheep transfers did not result in significant losses of either epizoochorously transported seed or species quantities. Our study shows that community-based grazing can lead to the dispersal of especially target species. Besides that, different habitat fragments can be connected to each other via sheep without significant seed losses along the way.

Introduction

In the cultural European landscape many populations of rare plant species are spatially isolated from each other. Combined with decreasing habitat numbers and population sizes, population isolation has caused a decline in species richness (Oostermeijer et al. 1996; Young et al. 1996). It has been suggested that the loss or decrease of seed dispersal vectors in current landscapes could be an additional factor negatively influencing plant species richness (Poschlod et al. 1998). Especially processes increasing long-distance dispersal (Box 1.1) are necessary in order to maintain plant population dynamics (Cain et al. 2000). For many plant species, animals provide the means for this critical mobile stage in a plant's life history (Stiles 2000). The existence of a ''moving ecological infrastructure'' is often underestimated (Strykstra et al. 1996), although historical data suggest that transhumant shepherding of large animal flocks led to long-distance dispersal of many plant species (Bonn and Poschlod 1998). Marked reductions in livestock numbers, especially sheep (Lahrkamp 1928), and intensified stable or paddock management (Erdmann 1983) took place. Simultaneously, a decrease of target species (Box 1.1), e.g. *Medicago minima* (listed in Germany's Red Data Book, Korneck et al. 1996) was noted (Internet 1). By contrast, this species, known for its well-developed morphological burr structures which enable epizoochorous dispersal, is highly abundant within the inland sand habitats studied here, managed by sheep grazing again since 1999/2000.

   Several field studies have already focused on epizoochorous seed dispersal by large domestic herbivores (e.g. Lodge and Hamilton 1981; Roché et al. 1992; Fischer et al. 1995, Fischer et al.1996; Stender et al. 1997; Dutoit et al. 2003; Couvreur et al. 2004a, b, 2005b; Mouissie et al. 2005b; Manzano and Malo 2006). Fischer et al. (1996) showed that high species and seed numbers can be transported (8511 seeds of 85 species found in 16 coat searches of one sheep), but qualitatively only 33 % of the transported species and 51 % of the detected seeds were target species (Festuco-Brometea, Trifolio-Geranietea, Koelerio-Corynephoretea). Also Mouissie et al. (2005b) found many ubiquitous species to be dispersed epizoochorously via livestock. For endozoochorous seed dispersal it has been shown that free ranging of herbivores in vegetation mosaics consisting of nutrient-poor and -rich vegetation types — e.g., heathlands, oligo- to eutraphent grasslands and woodlands — resulted in the transport

of many seeds from non-target to target areas (Mouissie et al. 2005a). The resulting seed input could lead to establishment of non-target species, which could negatively affect phytodiversity, as found in inland sand ecosystems (Schwabe and Kratochwil 2004; Süss et al. 2004).

There remains a gap in knowledge about seed dispersal of target species in threatened plant communities. No study has evaluated a grazing regime in which well-developed stands of target communities serve as a seed source and less-developed stands of potential target communities serve as sinks, connected to each other via large herbivores. This type of management is expected to positively affect and direct seed dispersal of habitat-specific species. In order to establish conservation measures that enhance long-distance dispersal of especially target species, insight is needed into the factors that determine which seed species are transported epizoochorously. The epizoochorous transport of seeds can be divided into attachment, retention and detachment and each stage depends on several (interacting) factors.

Previous studies have shown that seed attachment is positively correlated with the height at which plants release the seeds (Fischer et al. 1996; Mouissie et al. 2005b). However, the attachment of seeds from low-growing species is possible as well, when sheep lie down or wallow. Only a few studies investigated the distribution of seeds in sheep coats in order to obtain information about attachment mechanisms and the probability for seeds of a plant species to be transported externally (Milton et al. 1990; Fischer et al. 1996; Eichberg 2005; Mouissie et al. 2005b). Especially the belly region has rarely been studied (but see Milton et al. 1990; Eichberg 2005; Mouissie et al. 2005b) and will give additional information on seed attachment of low-growing species. After wallowing a dummy sheep, Fischer et al. (1996) even found seeds of which the primary dispersal period had already finished (transport of the soil-litter seed bank).

Mouissie et al. (2005b) also determined the attachment probability of 18 species by taking into account effects of seed surface structure, seed density in the vegetation, type of animal fur and the surrounding vegetation on seed attachment (using both dummies and real sheep). Seed surface structure was found to influence the attachment to smoother coats like these of cattle significantly, but attachment to sheep wool was less dependent on such structures. All tested seed species without morphological structures were relatively lightweight (≤ 0.7 mg) (Mouissie et al. 2005b). However, attachment of

heavier seeds might depend on seed surface structures. As a result, seed mass and morphology could show interactions and together influence the attachment probability.

The actual seed arrival in a sink area is controlled by a seed's retention time and the moment of detachment. By means of a laboratory study the retention potential of experimentally attached seeds was shown to be strongly correlated with seed surface structure and seed mass (Römermann et al. 2005). So far, potential dispersal distances via sheep were calculated by means of experimentally attached seeds or dummies, varying from several hundred meters up to a few kilometres (Shmida and Ellner 1983; Liddle and Elgar 1984; Fischer et al. 1996; Kiviniemi 1996; Eichberg et al. 2005; Mouissie et al. 2005b). In one study, substantial seed numbers remained attached to sheep of a Spanish transhumant flock over a 400-km distance (Manzano and Malo 2006). Mouissie et al. (2005b) also estimated seed dispersal distances using correlated random-walk simulations, showing that sheep can disperse 1 % of all attached seeds beyond 2.9 km. Retention of naturally (to living animals) attached seeds has not been studied yet and might depend on animal behaviour: it is probable that due to greater vibrations of the coat, seed losses are higher during a 3-km inter-area transfer than during the grazing period on a paddock. As a result, substantial seed numbers might get "lost" when animals walk from one area to another.

In this study the following questions were addressed: (1) Which species and seed quantities are dispersed epizoochorously by sheep in inland sand ecosystems at two spatial scales (intra-area, inter-area)? (2) What is the relation of target versus non-target species of transported seeds in comparison to the grazed vegetation? (3) Does the abundance of epizoochorously transported seed species in comparison to the vegetation differ according to a) seed surface structure and b) seed mass? (4) How are a) species and b) seed quantities distributed over different body parts of a sheep and do plant height and seed surface structure affect the distribution? (5) Is there a significant reduction of seed quantities and species diversity in sheep coats after long-distance (3 km) inter-area sheep transfers? (6a) What are the retention times that naturally attached *Stipa capillata* and *Agrimonia procera* seeds remain within a sheep coat? (6b) Do more seeds detach from the coat during an inter-area sheep transfer compared to a grazing period? (7) Does community-based grazing with subsequent sheep transfers lead to the

dispersal of a high proportion of target species to isolated habitats by sheep epizoochory?

Methods

Study areas

Our investigations were carried out in two nature protection areas of inland sand ecosystems (central-western Germany, northern upper Rhine valley). Sub-continental influences affect the climate (low annual precipitation (650 mm), high mean annual temperatures (9.9 ºC)). On nutrient-poor, mainly base-rich sandy soils both areas bear pioneer and mid-successional stages of inland sand ecosystems with high nature conservation value (Fauna-Flora-Habitat directive, Ssymank et al. 1998). Area 1: The ''Ehemaliger August-Euler-Flugplatz von Darmstadt'' (8°35´E, 49°51´N) is a flat, mostly treeless, 70-ha area with primarily calcareous sandy soils that had been partly acidified in the topsoil. Here three target communities have been investigated: Koelerion glaucae complex (Kg), *Artemisia campestris* community (Ac) and Armerio-Festucetum trachyphyllae (AF). Area 2: The ''Griesheimer Düne und Eichwäldchen'' (8°39´E, 49°53´N) is a 48-ha area with dune relief bearing mainly Allio-Stipetum capillatae (AS) grasslands. The distance between areas 1 and 2 is approximately 3 km. In 1999 (area 1) and in 2000 (area 2), respectively, sheep grazing was newly applied in the study areas for nature conservation purposes. During the grazing periods of each investigation most plant species had fruiting individuals on the paddocks; for species which did not, it was assumed that seeds were available in the litter layer (Eichberg et al. 2006).

Experiment 1 Inter-area sheep transfers

Six inter-area sheep transfers were conducted between areas 1 and 2 (July 2004 and August/September 2005). Every source paddock comprised one target community (Kg, AF, AS) and had a maximum size of 1 ha. Previous to the experiment, a vegetation relevé was made of each paddock. After grazing for three days, an experimental herd of three to four tamed wethers of Rhoen sheep walked from a source to a sink paddock (= actual inter-area sheep transfer) covering a distance of app. 3 km. Walking took place along a field road and sheep - vegetation contact was avoided. Sheep transfers were replicated twofold per vegetation type. Quadrats on the animal's body on five selected

body parts were marked: head (5 cm x 10 cm), chest (4 cm x 12 cm), shoulder (5 cm x 12 cm), back (8 cm x 16 cm), and belly (10 cm x 20 cm). The quadrats were established on both sides of the animal's body except for the chest, at which two quadrats were established next to each other. Per animal, ten quadrats were investigated (972 cm^2 sheep coat). These body parts were selected on the basis of the results from Exp. 2, which showed that these parts contained most seeds.

Experiment 2 Intra-area sheep transfers (data C. Eichberg 2005)

Five intra-area sheep transfers were carried out in area 1 (June-August 2001). The vegetation of the five paddocks (1-4 ha) belonged to three vegetation types (Kg, Ac, AF) with a varying degree of ruderalisation. Vegetation data used in this experiment are based on an established grid-point system (number of grid areas used per paddock ranges from 5 – 9, each grid area = 80 m^2).The paddocks were grazed one after another in the following order: Kg1, AF2, AF1, Ac1-3, AF3-4 (distances between centres of paddocks ca. 50 - 225 m). Three sheep were used, which were integrated into a herd of 90 to 180 sheep. The grazing period per paddock was 3-16 days, depending on the productivity and size of the paddock concerned. Per animal, the coat of quadrats of nine body parts were sampled: head (5 cm x 10 cm), chest (8 cm x 12 cm), shoulder (5 cm x 12 cm), back (8 cm x 16 cm), flank (10 cm x 20 cm), belly (10 cm x 20 cm), foreleg (5 cm x 10 cm), hind leg (5 cm x 20 cm) and tail (5 cm diameter x 40 cm length, tail was investigated completely). All quadrats except chest and tail were established on both body sides, resulting in 16 quadrats (2300 cm²) per animal. Initially, the animals were not used to getting so much attention. Therefore during the first intra-area sheep transfer (Kg 1) we could not sample a few quadrats (Table 2.2).

Seed collection, identification and classification in experiments 1 and 2

Before a grazing period was started, present seeds in the selected coat parts were removed. At the end of a grazing period (Exp. 2) or before and after an inter-area transfer (Exp. 1; per sampling moment one of every two body part quadrats was investigated (side randomly determined)) all intact seeds present in the wool were collected per selected quadrat. Seeds were later on identified, using a reference-seed collection and identification literature (Berggren 1969; Beijerinck 1976; Berggren 1981;

Anderberg 1994; Hanf 1990). In Exp. 2, several times a group of successively grazed paddocks was sampled together (Ac1-3, AF3-4). *Agrostis capillaris/A. vinealis*; *Elymus repens/E. athericus*; *Koeleria macrantha/K. glauca*; *Myosotis stricta/M. ramosissima* were pooled. All seeds were counted individually, except for *Medicago minima* in Exp. 2. In that case the mean number of seeds per fruit was calculated (2.5 ± 1.4; mean ± SD; n = 198) based on the extracted seeds of all fruits found in the coats after grazing paddock AF1.

On the basis of seed surface structure (sss) the seeds were subdivided into four types (slightly modified after Fischer et al. 1996): (a) hooked (hooked appendages), (b) bristly (developed, straight appendages), (c) coarse (wings, ribs, tubercles, hollows, nerves or wrinkles), (d) smooth (smooth or almost smooth surface). To obtain more insight into the species composition of epizoochorously transported seeds, all detected species were classified into the following classes: (i) threatened target species (Red List status in Germany (Korneck et al. 1996)), (ii) non-threatened target species (other species belonging to Koelerio-Corynephoretea or Festuco-Brometea), (iii) graminoid competitors (perennial species of Poaceace or Cyperaceae that establish dominant stands), (iv) other non-target species (species not belonging to a – c).

Experiment 3 Retention times of naturally attached seeds in sheep coats

Half-times of seed retention of two habitat-typical species with elongated appendages (*Stipa capillata, Agrimonia procera*), which had been attached naturally to the sheep coats, were studied with respect to different animal behaviour: 1) long-distance walk, 2) grazing within a paddock. Initially all seeds were removed from the investigated body parts of four sheep. After the animals had grazed an Allio-Stipetum stand for 24 hours, all coat-attached *Stipa* and *Agrimonia* seeds were counted for the first time (t_0). Re-counts were done after 6 (t_1), 24 (t_2) and 75 hours (t_3). Between the first and second count the animals walked a 3-km inter-area transfer, which was followed by a grazing period between the second and the fourth count.

Data analysis

The influence of the body parts on the density of attached seeds was tested with the non-parametric Mann-Whitney U-test. The effects of seed mass and seed surface

structure on seed species abundance in sheep coats and vegetation were tested in a mixed linear model (Littell et al. 2000). Afterwards, per seed mass and per seed surface structure, a Tukey post-hoc test was used to test for differences in abundance. The effects of seed releasing height and seed surface structures on the distribution of species and seed quantities over different sheep body parts were also tested in a mixed linear model. Additionally, a Tukey post-hoc test was used to test for differences in abundance per body part. The efficiency of seed transports via sheep was tested by comparing detected seed and species quantities before and after inter-area sheep transfers, using a One-way ANOVA test. Prior to analysis, data were log-transformed. The non-parametric Friedman test was used to determine whether species specific seed quantities before and after transfers differ. Again, data were previously log-transformed. Per sheep activity (walking, grazing), the naturally attached seed quantities were compared with a One-way ANOVA test. Half-times ($t_{1/2}$) of seed retention during these different activities were calculated per activity by the formula: $t \cdot \ln2/(\ln a - \ln e)$, where 'a' is the number of seeds at the beginning and 'e' is the number of seeds at the end of the experiment, and 't' is the duration of the activity (Kiviniemi 1996). Mixed linear models were produced using SAS 9.1 for Windows; all other tests were conducted with SPSS 11.5 for Windows. The nomenclature for phanerogams follows Wisskirchen and Haeupler (1998).

Results

(1) Seed spectra

In Exp. 1 (Inter-area), a total of 3027 seeds from 48 plant taxa was transported, with an overall mean of 16 ± 2 (mean ± SE) per 100 cm² sheep coat before departure and 14 ± 1 seeds after arrival (mean of 3 - 4 sheep, 5 body parts and 3 communities) (Table 2.1). In Exp. 2 (Intra-area), a total of 6393 seeds from 39 plant taxa were detected (3 sheep, 9 body parts and 3 communities) with 19 ± 2 seeds per 100 cm² sheep coat (mean ± SE) (Table 2.2). Summing up the results of Exp. 1 and 2, seeds from 56 vascular plant taxa were found in sheep coats.

(2) Target versus non-target species

The quality of the species diversity of both grazed vegetation and epizoochorously transported seeds was determined by dividing all species into the categories "Red List species", "other target species", "graminoid competitors" and "other non-target species" (see also *Methods*) (Figs. 2.1a, b). In Exp. 1 (inter-area) transported seed species had an slightly enhanced target (sum of Red List and other target species) vs. non-target (sum of graminoid competitors and other non-target species) ratio, in comparison to species present in the grazed vegetation (Fig. 2.1a). With respect to the grazed vegetation, the ratio of target species to non-target species is roughly 1:1 in all three plant communities. With respect to epizoochorously transported seeds, however, there is an over-representation of target species (only weak in Kg) and an under-representation of graminoid competitors (not in AF).

Figure 2.1 (a) Quality of species diversity of grazed vegetation (V) and epizoochorously dispersed seed species (E) during inter-area transfers. Percentages of seed species in sheep coats and plant species in vegetation (whole paddock) are based on the sum of species detected in sheep coats and two paddocks (replicates) per vegetation type. **(b)** Quantitative ratio of epizoochorously transported seeds before and after inter-area transfers. Percentages of detected seeds are based on the sum of seeds before or after transfer. Both figures divided in categories "Red List species", "other target species", "graminoid competitors" and "other non-target species", after grazing target communities Koelerion glaucae (Kg), Armerio-Festucetum (AF) or Allio-Stipetum (AS).

The vegetation of all grazed paddocks together contained ten Red List species, five of which were detected in sheep coats (Table 2.1 a – c); of 33 other target species present in the grazed vegetation 19 could be detected. The paddocks contained seven

graminoid competitors, of which three were present in the investigated sheep coats (*Agrostis capillaris, Elymus repens, Poa angustifolia*). Finally, 19 out of 47 other non-target species present in the vegetation were found back within the coats. Among the taxa found in the coat two were not be classified.

The transported seed quantities before and after inter-area sheep transfers were organized into the same species groups as above (Fig. 2.1b). Quantitative seed numbers for different species groups are mostly similar before and after sheep transfers of different communities (Fig. 2.1b). Also, target vs. non-target ratios of those communities are roughly similar. However, the distribution over the four categories differs among the three communities. Before and after Kg transfers, seeds from Red List species (mainly *Medicago minima*) were predominantly found in the sheep coats. Relatively few seeds belonged to other target and non-target species, whereas no seeds from graminoid competitors were detected (Table 2.1a). Before and after AF transfers half of the seeds belonged to Red List species (mainly *Medicago minima*) and another 20 % to other target species. One-third of the seeds were non-target species and only a few seeds of graminoid competitors were found in the sheep coats (Table 2.1b). Finally, both before and after Allio-Stipetum transfers high seed numbers of Red List species (mainly *Stipa capillata* and *Medicago minima*) and large seed numbers of other target species (e.g. *Agrimonia procera*) were found, in contrast to the relatively few seeds of non-target species and graminoid competitors (Table 2.1c).

The quality of the species composition as found in sheep coats in Exp. 2 (intra-area) was structured similarly to the compositions in Exp. 1. Again, epizoochorously transported seed species showed a slightly enhanced ratio of target (sum of Red List and other target species) vs. non-target (sum of graminoid competitors and other non-target species) species, in comparison to the vegetation of the grazed mid-successional stands (Ac and AF) (Fig. 2.2a). Epizoochorously transported seeds and Kg vegetation had a comparable target vs. non-target species ratio. Together, the grazed paddocks contained 11 Red List species, six were detected in sheep coats (Table 2.2 a - c); of 32 other target species present in the grazed vegetation 11 could be detected. Four out of six graminoid competitors were present in the investigated sheep coats *(Agrostis capillaris, Calamagrostis epigejos, Elymus repens* and *Poa angustifolia)*. Finally, from 48

other non-target species in the vegetation, 15 were detected within the coats. Three epizoochorously transported taxa could not be categorised.
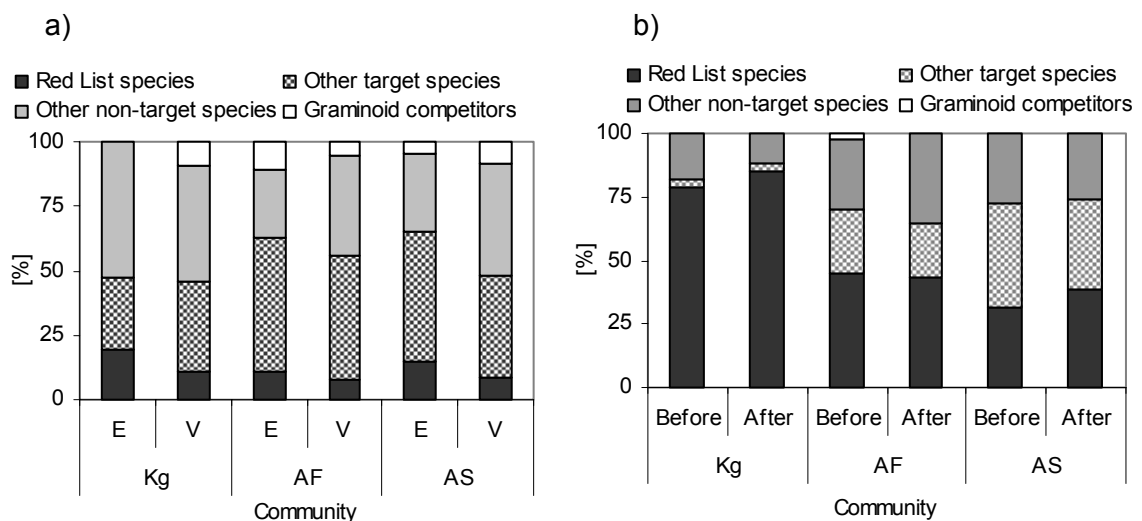
a)

b)
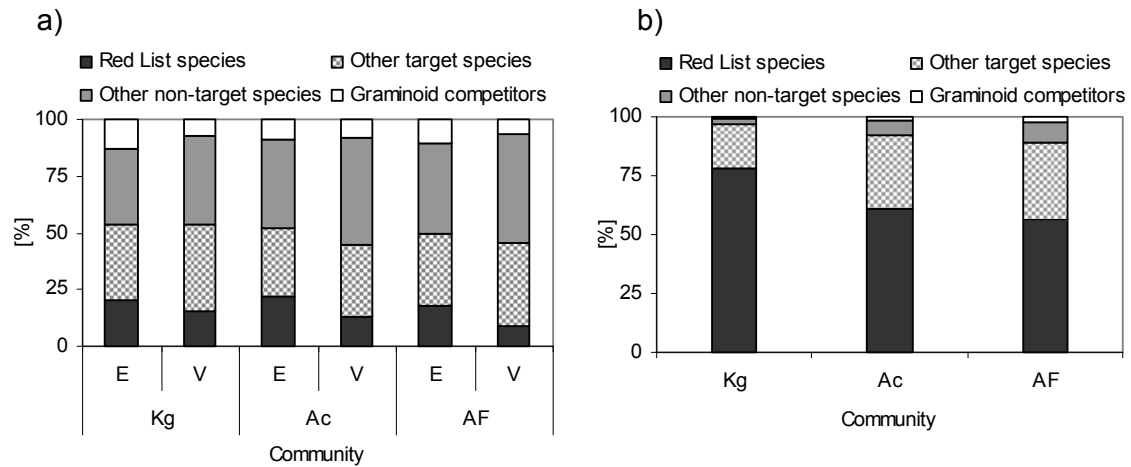
Figure 2.2 (a) Quality of species diversity of grazed vegetation (V) and epizoochorously dispersed seed species (E) during intra-area transfers. **(b)** Quantitative ratio of epizoochorously transported seeds during intra-area transfers. Detected species divided in categories "Red List species", "other target species", "graminoid competitors" and "other non-target species" after grazing target communities Koelerion glaucae (Kg), *Artemisia campestris* (Ac) or Armerio-Festucetum (AF). Per category, species and seed numbers were expressed as percentage of total number of transported species or seeds.

The detected seed quantities before conducting intra-area sheep transfers were organized into the same categories as above. Quantitatively, all intra-area sheep transfers resulted in the transport of large numbers of seeds of Red List species (mainly *Medicago minima*) and other target species (Fig. 2.2b, Table 2.2). Relatively low seed numbers of graminoid competitors and other non-target species were found in the sheep coats.

(3) Influence of seed surface structure and seed mass on seed dispersal

Species from both species pools (Exp. 1: epizoochorously transported species and vegetation) were sorted into 12 groups according to their seed surface structure and seed mass (Fig. 2.3). The detected species numbers were compared per seed surface structure and per seed mass; differences and their direction are shown in Fig. 2.3. Among the coarse seed species medium- ($P < 0.05$) and heavy- ($P < 0.01$) weight species are significantly under-represented in the sheep coat compared to the

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vegetation. In contrast, among the hooked seed species medium-weight species are more frequently abundant in sheep coat, compared to the vegetation ($P < 0.01$). Heavy-weight hooked and medium- and heavy-weight bristly seed species show the same tendency, but differences are not significant. Light-weight, bristly seeds have a tendency to be less abundant in the sheep coat. In each weight class, smooth seed species were found in equal numbers, although heavy-weight species show a trend of being over-represented in vegetation.
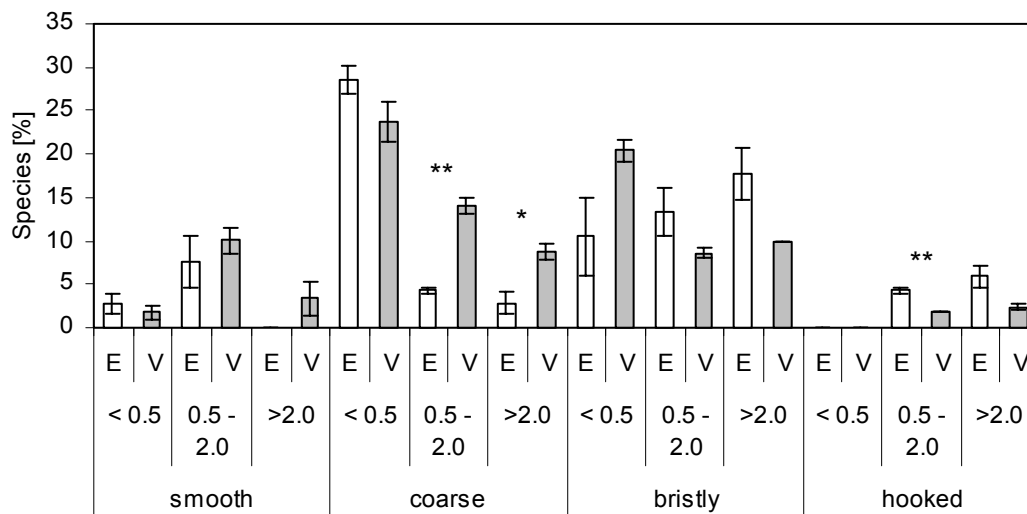
Figure 2.3 Abundance of different seed types in sheep coat (E) and vegetation (V), both $n = 3$. For each seed surface structure, seeds were divided into three groups according to their seed mass (< 0.5, 0.5 – 2.0, > 2.0 mg). Error bars represent standard error of the mean. Comparisons were made per seed surface structure per seed mass. Level of significance; * $P < 0.05$, ** $P < 0.01$.

The effects of seed surface structure and seed mass on the abundance of different seed types (as mentioned above) in sheep coats and their abundance in grazed vegetation were compared (Table 2.3). A highly significant interaction between species pool, seed surface structure and seed mass was found ($P < 0.001$). This means that differences between the relative abundances of these species within the vegetation and sheep coat depend on both type of seed surface structure and seed mass type.

Table 2.3 Results of analysis of variance (Mixed linear model) of species quantities of different seed types in sheep coat and vegetation. Level of significance *** = P < 0.001, N.S. = not significant.

Effect	Num DF	Den DF	F	P	sig.
pool (species pool)	1	48	0.44	0.509	N.S.
sss (seed surface structure)	3	48	49.66	<0.001	***
sm (seed mass)	2	48	10.04	<0.001	***
pool*sss	3	48	2.22	0.098	N.S.
pool*sm	2	48	0.45	0.643	N.S.
sss*sm	6	48	19.09	<0.001	***
pool*sss*sm	6	48	5.92	<0.001	***

(4a) Species density distribution over different body parts

The number of low- (≤ 0.3 m) and high- (> 0.3 m) growing species detected in the investigated sheep body parts are shown in Fig. 2.4. Species with (bristly/hooked) and without (smooth/coarse) seed surface structures were distinguished.
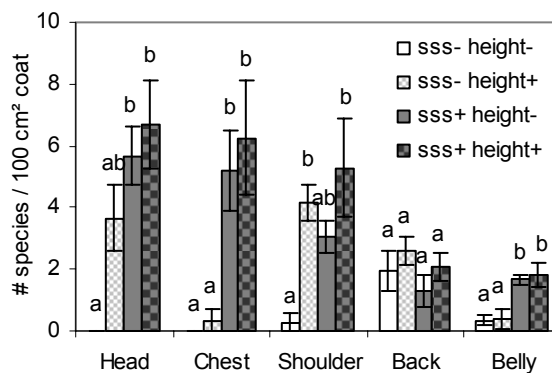
Figure 2.4 Mean number of detected seed species in investigated sheep body parts (per body part *n* = 40). Results represent the mean of three communities and two inter-area transfers per community; error bars indicate standard error of the mean. Low- (low ≤ 0.3 m) and high- (high > 0.3 m) growing species with (sss+ = bristly, hooked) and without (sss- = smooth, coarse) seed surface structures were distinguished from each other. Comparisons were made per body part; letters indicate significant differences (*P* < 0.05).

The shoulder was the only body part which contained significantly more high- than low-growing species without seed surface structures. For plants with well-developed seed surface structures plant height was also relatively unimportant: low- and high-growing species were equally present per investigated body part (Fig. 2.4). The animal's front parts (head, chest, shoulder) overall contained more species than did body parts further away from the front (back, belly). However, low-growing species without seed surface structures were clearly under-represented in all parts, except for the back. Since the four

distinguished categories were equally represented within the vegetation, this was not shown in Fig. 2.4 (One-way ANOVA $F_{3,8}$ = 3.799, P = 0.058).

The effects of seed surface structure, seed-releasing height and body part on the numbers of species detected in sheep coats were tested (Table 2.4). First of all, a significant interaction between seed surface structure and body part was found (P < 0.001), meaning that differences in species numbers between different body parts depend on seed surface structure. Also a strong effect of seed-releasing height was found (P < 0.001). Overall, low-growing plant species were less abundant in the sheep coat, compared to high-growing plant species. This effect was not dependent on seed surface structure, since no significant interaction between seed surface structure and plant height was found.

Table 2.4 Results of analysis of variance (Mixed linear model) of species quantities of different seed types in sheep coat. Level of significance *** = P < 0.001, N.S. = not significant.

Effect	Num DF	Den DF	F	P	sig.
sss (seed surface structure)	1	100	45.68	<0.001	***
height (seed releasing height)	1	100	13.75	<0.001	***
bp (body part)	4	100	7.41	<0.001	***
sss*height	1	100	0.84	0.361	N.S.
sss*bp	4	100	8.53	<0.001	***
height*bp	4	100	2.22	0.072	N.S.
sss*height*bp	4	100	0.72	0.580	N.S.

(4b) Seed density distribution over different body parts

As for species diversity, influence of seed surface structure and seed-releasing height have been analysed for seed densities (Fig. 2.5).
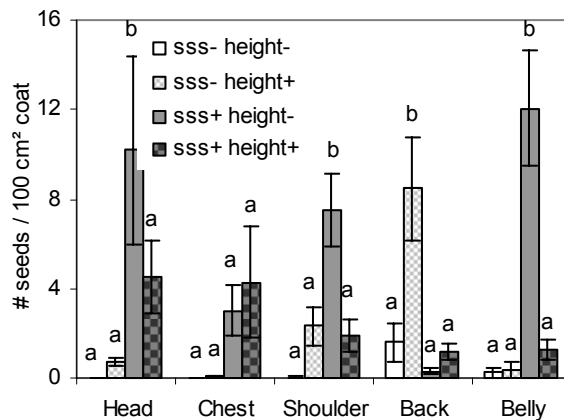
Figure 2.5 Mean number of detected seeds in investigated sheep body parts (per body part n = 40). Results represent the mean of three communities and two inter-area transfers per community; error bars indicate standard error of the mean. Low- (≤ 0.3 m) and high (≥ 0.3 m) growing species with (sss+ =bristly, hooked) and without (sss- = smooth, coarse) seed surface structures were distinguished from each other. Comparisons were made per body part; letters indicate significant differences (P < 0.05).

Seed quantities of low-growing plant types without seed surface structures, as well as those from high-growing species with seed surface structures, were app. equally represented in all body parts. The back contained less seeds of low-growing species with seed surface structures, compared to other body parts. On the other hand, seeds from high-growing species without seed surface structures were over-represented in the back coat. The group of seeds from low-growing species with seed surface structures was dominated by the annual *Medicago minima* and the group of high-growing species without morphological seed adaptations is dominated by the biennial *Verbascum phlomoides*.

As for species number, the effects of seed surface structure, seed-releasing height and body parts on the seed densities detected in sheep coats were tested (Table 2.5). An interaction between seed surface structure and seed-releasing height was found; i.e., depending on the seed surface structure, seed-releasing height did affect the seed numbers found in the sheep coat (Table 2.5). Furthermore, an interaction between seed surface structure and body parts and between seed-releasing height and body parts was found.

Table 2.5 Results of analysis of variance (Mixed linear model) of seed quantities of different seed types in sheep coat. Level of significance ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant.

Effect	Num DF	Den DF	F	P	sig.
sss (seed surface structure)	1	100	23.21	<0.001	***
height (seed releasing height)	1	100	2.14	0.164	N.S.
bp (body part)	4	100	1.04	0.389	N.S.
sss*height	1	100	19.83	<0.001	***
sss*bp	4	100	5.29	0.001	**
height*bp	4	100	8.96	<0.001	***
sss*height*bp	4	100	2.19	0.075	N.S.

(5) Seed and species density in the coats before and after inter-area sheep transfers
Table 2.6 shows the results of comparisons of total seed and species numbers detected in the sheep coat before and after 3-km inter-area sheep transfers. For all three investigated plant communities, none of the body parts showed a significant total seed or species number decrease while the animals were walking a 3-km inter-area transfer (except for the belly, which contained significant more species after the AS transfer).

Table 2.6 Comparison of log-transformed seed and species quantities before and after inter-area ST's (after grazing of the communities Koelerion glaucae (Kg), Allio-Stipetum (AS) and Armerio-Festucetum (AF)). Tests were conducted per body part ($n = 8$; in case of AF, $n = 6$).

		Shoulder		Head		Chest		Belly		Back	
community	Density	$F_{1,14}$	P	$F_{1,14}$	P	$F_{1,14}$	P	$F_{1,14}$	P	$F_{1,14}$	P
Kg	Seeds	0.201	0.660	0.441	0.517	1.511	0.239	0.564	0.465	0.472	0.503
	Species	3.493	0.083	0.402	0.537	3.112	0.100	0.461	0.508	0.146	0.708
AS	Seeds	0.265	0.615	0.840	0.375	1.046	0.324	0.126	0.728	0.011	0.919
	Species	0.065	0.802	0.404	0.535	1.745	0.208	0.617	0.045	0.132	0.722
		$F_{1,10}$	P	$F_{1,10}$	P	$F_{1,10}$	P	$F_{1,10}$	P	$F_{1,10}$	P
Af	Seeds	2.690	0.132	3.332	0.098	0.256	0.624	0.215	0.653	0.059	0.814
	Species	0.463	0.512	4.307	0.650	0.258	0.622	0.142	0.715	1.185	0.302

Per species seed numbers before and after sheep transfers were compared. Out of the 23 species present prior to the KG sheep transfers, only *Bromus tectorum* seeds significantly declined in number within the belly coat ($P = 0.025$). None of the 31 species found before the Armerio-Festucetum sheep transfers started declined significantly in number during the sheep transfers. Finally, after grazing within Allio-Stipetum 22 species were detected in the coats; of these species, *Conyza canadensis* and *Trifolium arvense* seed numbers were significantly reduced from respectively head ($P = 0.025$) and belly ($P = 0.046$) coat regions after the transfers were completed.

(6) *Retention times of naturally attached seeds*

After 24 hours of grazing within an Allio-Stipetum stand, 20.7 ± 3.2 (mean ± SE) seeds of *A. procera* and 6.3 ± 0.9 seeds of *S. capillata* were present (t_0) per 100 cm^2 sheep coat. Seed re-counts were done at t_1, t_2 and t_3 (Fig. 2.6). During the 3-km inter-area sheep transfers seed numbers of both *Agrimonia procera* and *Stipa capillata* did not decline (t_0 vs. t_1: *A. procera*: $F_{1,78} = 0.389$, $P = 0.535$; *S. capillata*: $F_{1,78} = 2.150$, $P = 0.147$). The sheep transfer was followed by a grazing period in which many *A. procera* seeds fell out of the coats, but this decline was not significant (t_1 vs. t_3: $F_{1,78} = 2.423$, $P = 0.124$). The number of *S. capillata* seeds, on the other hand, did decline significantly during the grazing period (t_1 vs. t_3: $F_{1,78} = 19.963$, $P = 0.000$). During the transfer *A. procera*'s $t_{1/2}$ was 33 hours; the grazing period $t_{1/2}$ was 99 hours. For *S. capillata* the transfer $t_{1/2}$ was 14 hours, whereas the grazing period $t_{1/2}$ was 54 hours. Seeds of *S.*

capillata became detached around three times faster during a sheep transfer in comparison to a grazing period.
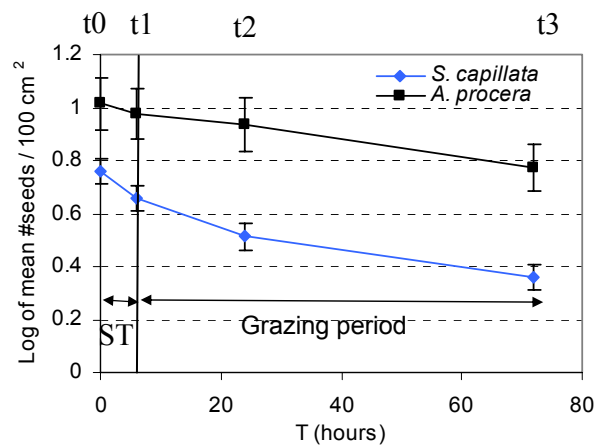
Figure 2.6 Mean *A. procera* and *S. capillata* seed numbers per 100 cm^2 sheep coat (data were log transformed; investigated quadrats *n* = 40). An inter-area sheep transfer (ST) was conducted between t_0 and t_1, followed by a grazing period between t_1 and t_3. Error bars indicate standard error of the mean.

Discussion

The capacity for long-distance dispersal is a key factor in the survival of local plant populations (Soons and Ozinga 2005), especially in fragmented landscapes where it can affect local species composition (Ozinga et al. 2004). The present study gives evidence that the abundance and movement of animals via a highly regulated grazing regime could provide the essential link between plant populations in different habitat fragments (Levey et al. 2005), by epizoochorously dispersing numerous seeds of target species. Several factors determine which seed species and quantities can be transported externally by moving sheep.

Species composition of grazed vegetation

Grazing mostly target communities has led to epizoochorous dispersal of high proportions of target species within and between areas. This is in contrast to indiscriminately grazing of all communities present within a landscape (Fischer et al.1996), which might lead to seed transfer from non-target to target communities (Mouissie et al. 2005a). In our study, the proportion of epizoochorously transported target species was comparable to the species composition of the vegetation of three

communities. Red List species were even slightly over-represented in the sheep coats and quantitatively, most epizoochorously transported seeds belonged to target species, e.g. *Stipa capillata, Medicago minima* and *Agrimonia procera*.

Seed traits

The detection of seeds with and without surface structures might suggest that morphological traits are less relevant in the case of seed transport by sheep, as a result of the wool's curly structure (Mouissie et al. 2005b; Fischer et al. 1996). However, when seed mass is also taken into account, the laboratory-experimental results of Römermann et al. (2005) have shown that seed mass and morphology are both important predictors of the retention potential in sheep wool. As is consistent with these results, in our study seed mass and surface structure were found to affect attachment and interact with each other as well. Seed mass negatively affects the attachment of seeds without pronounced morphological seed features, in contrast to attachment of seeds with morphological adaptations, which is positively affected by seed mass.

Seed-releasing height and sheep behaviour

The presence of more high- than low-growing seed species in sheep coats indicates that the plant's seed-releasing height affects the attachment possibility as well. Nevertheless, the difference is largely controlled by seed surface structures, since low- and high-growing seed species with pronounced structures have equal attachment rates and also occur in equal seed quantities in low- and high-positioned sheep body parts (except for fewer seeds of low-growing species in the back wool). Combined walking/grazing behaviour offers high-growing plants contact with most body parts, whereas low-growing species are almost exclusively touched by the head's wool. Other types of behaviour (e.g. lying down to ruminate or rest) can generate contact between low-growing species and the rest of the sheep's body. Coat contact with low- and high-growing species lacking seed surface structures takes place frequently, but presumably, lack of seed surface structure causes the position of the body part to negatively affect the attachment duration. Consequently, the highest seed quantities were found on the back, from where it is hard for seeds of any morphology to drop out.

Seed distribution over the sheep body

Grazing and walking through vegetation generates more frequent contact between front body parts and vegetation, in comparison to back or belly. As a result, and in line with the results of Fischer et al. (1996), frontal parts of the sheep (head, chest, shoulder) contained higher species numbers compared to body parts further away from the front (back and belly). Although the belly is often in contact with both low- and high-growing vegetation, the fewest seed species were found there. Most probably, this is because the belly faces downwards, so that the seeds more easily drop out of the coat. Additionally, the wool is less dense in the belly region compared to wool of other body parts.

Seed detachment

Seed retention times in here studied sheep coat and Galloway cattle coat (Couvreur et al. 2005a) can both be more than 10 hours, in contrast to limited seed retention time in horse coat (Couvreur et al. 2005a). Different animal movement influences the moment seeds detach from a sheep coat, as shown by lower seed retention when animals intensively move (e.g. walking a 3-km transfer), compared to grazing. However, most *S. capillata* and *A. procera* seeds did not detach during the transfers, whereas seed numbers did severely decline during a 3-day post-transfer grazing period. Moreover, no significant detachment of total seed and species quantities was found during any of the inter-area sheep transfers either. Presumably, the relatively short duration of transfers compared to grazing periods (1-3 hours vs. several days) diminished the seed detachment probability during a transfer. Secondly, seed morphological structures that increase the capacity for adhesive dispersal (e.g. hooks) can be irritating to animals and initiate grooming behaviour (Kiviniemi 1996), accelerating the detachment of seeds. During a sheep transfer the animals do not have the opportunity to groom, whereas sheep are often grooming during a grazing period (pers. observation). As a result, attached seeds show a high persistence during a transfer from one area to another (evidence for seed persistence during long-distance journeys has been found as well by Manzano and Malo 2006), whereas a considerable seed input into the sink area can take place.

Conclusion

The need for dispersing high seed numbers over long distances and the contribution of epizoochory to this process is stressed here. Dispersal promotes genetic homogeneity among populations (Loveless and Hamrick 1984), which could improve the rather reduced genetic diversity of newly established populations, as was shown for *Stipa capillata* (Kilian 2006). High amounts of seed input are required to keep the regenerative potential of semi-natural grasslands at a sufficiently high level, since post-dispersal processes such as seedling emergence and establishment are often limited, e.g. by seed availability (Zobel et al. 2000), granivory or seedling mortality (Eichberg et al. 2005, 2007). In several dry grassland species the population size was indeed regulated by seed limitation (Erikson 1997, 1998). Large herbivores are probably one of the few vectors capable of dispersing those large seed quantities for a high proportion of target plant species over a relatively long distance. This is especially true for sheep, as they tend to be kept in large herds which are relatively easily transferable and possess coats that have a high seed transport capability.

To evaluate the "effective" contribution of epizoochorous dispersal to the restoration and conservation of target communities, post-dispersal processes should also be studied (Nathan 2006). Therefore, the fate of 14 sand-typical species after epizoochorous transport was studied in Chapter 3.

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Table 2.1a Mean seed numbers per 100 cm², before and after Koelerion glaucae inter-area sheep transfers (Exp. 1). Abbreviations: SG: species group (R Red List Status, T Other target, G graminoid competitor, N other non-target). RL: Red List status in Germany/Hessen (Korneck et al.,1996) (2 endangered, 3 vulnerable, * not endangered). SSS: seed surface structure (h hooked, b bristly, c coarse, s smooth (slightly modified after Fischer et al. 1996). SM: seed mass (mg) (Internet 1 and 2). Height (m) (Oberdorfer 2001). M: mean, SE: standard error, before and after 2 inter-area sheep transfers. Seeds were detected in 5 body parts: head, chest (che.), shoulder (sho.), back, belly (bel.). Zero values are indicated with a dot.

Species	SG	RL	SSS	SM (mg)	Height (m)		Before: Head (8)	Che. (8)	Sho. (8)	Back (8)	Bel. (8)	Mean	After: Head (8)	Che. (8)	Sho. (8)	Back (8)	Bel. (8)	Mean
Armeria maritima	R	3/2	b	1.5	0.05-0.5	M	0.3	.	.	.	.	0.1	.	0.3	.	.	.	0.1
ssp. *elongata*						SE	0.3	.	.	.	.		.	0.3	.	.	.	
Berteroa	N	*/*	c	0.7	0.3-0.65	M	.	.	0.2	.	.	0.0	.	.	.	0.2	.	0.0
incana						SE	.	.	0.2	.	.		.	.	.	0.1	.	
Bromus	N	*/*	b	3.5	0.05-0.8	M	.	0.3	.	.	.	0.1	0.3	.	.	.	0.1	0.1
hordeaceus						SE	.	0.3	.	.	.		0.3	.	.	.	0.1	
Bromus	N	*/*	b	7.9	0.3-0.6	M	0.3	.	.	.	.	0.1	0.3	.	.	.	0.1	0.1
sterilis						SE	0.3	.	.	.	.		0.3	.	.	.	0.1	
Bromus	T	*/*	b	3.6	0.1-0.45	M	0.8	2.9	0.6	0.1	1.6	1.2	1.3	1.0	0.2	0.1	0.8	0.7
tectorum						SE	0.4	0.8	0.4	0.1	0.5		0.5	0.4	0.2	0.1	0.4	
Centaurea	T	*/*	b	1.3	0.3-1.2	M	0.3	0.3	0.2	0.1	0.1	0.2	.	.	.	0.1	.	0.0
stoebe						SE	0.3	0.3	0.2	0.1	0.1		.	.	.	0.1	.	
Cynoglossum	N	*/*	h	26.0	0.3-0.8	M	.	0.3	.	.	.	0.1	.	.	.	.	.	0.0
officinale						SE	.	0.3	.	.	.		.	.	.	.	.	
Erodium	T	*/*	b	2.3	0.1-0.6	M	.	.	.	.	0.3	0.1	.	0.3	.	.	0.1	0.1
cicutarium agg.						SE	.	.	.	.	0.1		.	0.3	.	.	0.1	
Festuca	T	*/*	b	0.5	0.2-0.7	M	.	.	.	0.3	.	0.1	.	.	.	.	.	0.0
ovina agg.						SE	.	.	.	0.2	.		.	.	.	.	.	
Festuca sp.	-	-	-	-	-	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
						SE	.	.	.	.	.		.	.	.	0.1	.	
Medicago	R	3/3	h	1.2	0.1-0.3	M	28.0	3.1	9.6	.	12.1	10.6	12.5	5.2	12.7	0.5	7.3	7.6
minima						SE	15.8	1.5	3.9	.	3.9		3.9	5.2	6.7	0.5	1.3	
Papaver	N	*/*	c	0.1	0.3-0.6	M	.	.	.	0.3	.	0.1	.	.	.	0.2	.	0.0
dubium s.l.						SE	.	.	.	0.2	.		.	.	.	0.2	.	
Petrorhagia	T	*/*	c	0.2	0.15-0.45	M	.	.	.	.	.	0.0	.	.	.	.	0.1	0.0
prolifera						SE	.	.	.	.	.		.	.	.	.	0.1	
(cf) *Plantago*	N	*/*	s	1.8	0.1-0.5	M	.	.	.	0.2	.	0.0	.	.	.	.	.	0.0
lanceolata						SE	.	.	.	0.2	.		.	.	.	.	.	
Polygonum	N	*/*	c	2.1	0.05-0.5	M	.	.	0.2	.	.	0.0	.	.	.	.	.	0.0
aviculare agg.						SE	.	.	0.2	.	.		.	.	.	.	.	
Psyllium	N	*/*	s	1.0	0.15-0.3	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
arenarium						SE	.	.	.	.	.		.	.	.	0.1	.	
Rumex	N	*/*	s	0.5	0.3-1.2	M	.	.	.	.	.	0.0	.	.	0.2	.	.	0.0
thyrsiflorus						SE	.	.	.	.	.		.	.	0.2	.	.	
Silene	R	3/2	c	0.4	0.1-0.4	M	.	.	.	0.3	.	0.1	.	.	.	.	.	0.0
conica						SE	.	.	.	0.2	.		.	.	.	.	.	
Silene	R	3/2	c	0.2	0.2-0.6	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
otites						SE	.	.	.	.	.		.	.	.	0.1	.	
Sisymbrium	N	*/*	c	0.2	0.3-0.6	M	0.8	.	2.3	2.1	.	0.0	.	.	0.4	0.6	.	0.2
altissimum						SE	0.4	.	1.0	1.3	.		.	.	0.3	0.5	.	
Vulpia	T	*/*	b	0.5	0.25-0.45	M	.	.	.	0.1	.	0.0	.	.	0.2	.	.	0.2
myuros						SE	.	.	.	0.1	.		.	.	0.2	.	.	
Total seed number							30.3	6.8	13.1	3.4	14.0	13.5	14.3	7.0	14.0	2.1	8.4	9.2
Total species number							6	5	6	8	5	17	4	4	6	10	7	19

Table 2.1b Mean seed numbers per 100 cm², before and after Armerio-Festucetum trachyphyllae inter-area sheep transfers (Exp.1). For abbreviations see Table 2.1a.

Species	SG	RL	SSS	SM (mg)	Height (m)	n	Before transfer Head 6	Che. 6	Sho. 6	Back 6	Bel. 6	Mean	After transfer Head 6	Che. 6	Sho. 6	Back 6	Bel. 6	Mean
Agrostis capillaris/	G	*/*	b	0.1	0.2-0.8	M	.	.	0.3	0.1	.	0.1	.	0.3	.	0.1	0.1	0.2
A. vinealis						SE	.	.	0.3	0.1	.		.	0.3	.	0.1	0.1	
Arabis	T	*/*	c	0.1	0.6-1.2	M	.	.	.	0.5	.	0.1	.	.	.	0.7	0.3	0.2
glabra						SE	.	.	.	0.2	.		.	.	.	0.5	0.3	
Arenaria	T	*/*	c	0.1	0.03-0.3	M	.	.	.	0.4	.	0.1	.	.	.	0.4	.	0.1
serpyllifolia agg.						SE	.	.	.	0.3	.		.	.	.	0.2	.	
Armeria maritima	R	3/2	b	1.5	0.05-0.5	M	0.7	.	.	.	.	0.1	.	.	.	.	0.1	0.0
ssp. *elongata*						SE	0.4	.	.	.	.		.	.	.	.	0.1	
Bromus	N	*/*	b	3.5	0.05-0.8	M	.	.	.	.	.	0.0	.	0.3	.	.	0.2	0.1
hordeaceus						SE	.	.	.	.	.		.	0.3	.	.	0.2	
Bromus	T	*/*	b	3.6	0.1-0.45	M	0.3	0.3	.	0.1	0.2	0.2	.	.	.	.	0.3	0.1
tectorum						SE	0.3	0.3	.	0.1	0.1		.	.	.	.	0.2	
Campanula	T	*/*	c	0.0	0.5-0.8	M	.	.	.	2.1	.	0.4	.	.	.	1.2	0.1	0.3
rapunculus						SE	.	.	.	1.2	.		.	.	.	0.7	0.1	
Centaurea	T	*/*	b	1.3	0.3-1.2	M	.	.	0.3	.	.	0.1	0.3	.	0.3	0.1	0.1	0.2
stoebe						SE	.	.	0.3	.	.		0.3	.	0.3	0.1	0.1	
Cynoglossum	N	*/*	h	26.0	0.3-0.8	M	0.3	.	.	.	0.5	0.2	.	.	0.6	.	0.4	0.2
officinale						SE	0.3	.	.	.	0.3		.	.	0.4	.	0.4	
Echium	T	*/*	c	2.9	0.25-1.0	M	0.3	.	.	.	.	0.1	.	.	0.3	.	.	0.1
vulgare						SE	0.3	.	.	.	.		.	.	0.3	.	.	
Elymus repens/	G/N	*/*	b	3.3	0.3-1.2	M	.	0.3	.	.	.	0.1	.	.	.	.	.	0.0
E. athericus						SE	.	0.3	.	.	.		.	.	.	.	.	
Festuca	T	*/*	b	0.5	0.2-0.7	M	.	.	0.6	0.1	0.1	0.2	.	.	.	0.1	0.1	0.0
ovina agg.						SE	.	.	0.4	0.1	0.1		.	.	.	0.1	0.1	
Festuca	N	*/*	b	1.3	0.3-0.8	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
rubra						SE	.	.	.	.	.		.	.	.	0.1	.	
Koeleria glauca/	T	*/*	b	0.3	0.2-0.6	M	4.0	0.3	1.9	1.0	0.3	1.5	2.7	.	0.3	1.2	0.5	0.9
K. macrantha						SE	0.5	0.3	0.8	0.5	0.2		0.8	.	0.3	0.2	0.3	
Medicago	R	3/3	h	1.2	0.1-0.3	M	2.0	0.3	6.1	0.3	16.8	5.1	0.3	.	2.5	.	20.7	4.7
minima						SE	2.0	0.3	1.7	0.3	3.6		0.3	.	2.5	.	6.3	
Myosotis stricta/	T	*/*	b	0.1	0.03-0.25	M	.	.	.	0.1	.	0.0	.	.	.	.	.	0.0
M. ramosissima						SE	.	.	.	0.1	.		.	.	.	.	.	
Oenothera	N	*/*	c	0.6	0.5-2.0	M	.	.	.	0.1	.	0.0	.	.	.	.	.	0.0
biennis s.l.						SE	.	.	.	0.1	.		.	.	.	.	.	
Papaver	N	*/*	c	0.1	0.3-0.6	M	.	.	.	3.1	.	0.6	.	.	.	3.4	1.3	0.9
dubium s.l.						SE	.	.	.	1.4	.		.	.	.	1.6	1.3	
(cf) *Plantago*	N	*/*	s	1.8	0.1-0.5	M	.	.	.	.	.	0.0	.	.	.	0.3	.	0.1
lanceolata						SE	.	.	.	.	.		.	.	.	0.3	.	
Poa	G	*/*	b	0.3	0.1-0.9	M	0.3	.	0.3	0.3	0.2	0.2	.	.	.	.	.	0.0
angustifolia						SE	0.3	.	0.3	0.3	0.1		.	.	.	.	.	
Potentilla	T	*/*	c	0.1	0.2-0.5	M	.	.	.	0.1	.	0.0	.	.	.	0.1	0.1	0.0
argentea agg.						SE	.	.	.	0.1	.		.	.	.	0.1	0.1	
Rumex	T	*/*	s	0.4	0.1-0.3	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
acetosella s.l.						SE	.	.	.	.	.		.	.	.	0.1	.	
Silene	R	3/2	c	0.4	0.1-0.4	M	.	.	.	.	.	0.0	.	.	.	0.5	.	0.1
conica						SE	.	.	.	.	.		.	.	.	0.3	.	
Sisymbrium	N	*/*	c	0.2	0.3-0.6	M	0.3	0.3	0.3	1.7	.	0.5	.	.	.	1.0	0.5	0.3
altissimum						SE	0.3	0.3	0.3	0.6	.		.	.	.	0.3	0.5	
Trifolium	T	*/*	b	0.4	0.08-0.3	M	.	.	.	.	.	0.0	.	0.3	.	.	.	0.1
arvense						SE	.	.	.	.	.		.	0.3	.	.	.	
Verbascum	N	*/*	c	0.1	0.5-2.0	M	0.3	.	0.3	8.5	.	1.8	0.3	.	0.3	9.5	1.2	2.3
phlomoides						SE	0.3	.	0.3	2.3	.		0.3	.	0.3	3.0	1.2	
Veronica sp.	-	-	-	-	-	M	.	.	.	.	0.1	0.0	.	.	.	.	.	0.0
						SE	.	.	.	.	0.1		.	.	.	.	.	
Vulpia	T	*/*	b	0.5	0.25-0.45	M	0.3	0.7	.	.	.	0.2	.	0.7	0.3	.	0.1	0.2
myuros						SE	0.3	0.4	.	.	.		.	0.4	0.3	.	0.1	
Unidentified	-	-	-	-	-	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
						SE	.	.	.	.	.		.	.	.	0.1	.	
Other	-	-	-	-	-	M	.	.	.	0.1	.	0.0	.	.	.	.	.	0.0
Caryophyllaceae						SE	.	.	.	0.1	.		.	.	.	.	.	
Other	-	-	-	-	-	M	0.3	0.3	.	.	.	0.1	1.0	.	.	0.1	.	0.2
Poaceae						SE	0.3	0.3	.	.	.		1.0	.	.	0.1	.	
Total seed number							9.3	2.8	10.0	18.7	18.1	11.8	4.7	1.7	4.4	19.9	25.9	11.3
Total species number							11	7	8	16	6	24	5	4	7	17	16	25

Table 2.1c Mean seed numbers per 100 cm², before and after Allio-Stipetum capillatae inter-area sheep transfers (Exp. 1). For abbreviations see Table 2.1a.

Species	SG	RL	SSS	SM (mg)	Height (m)		Before transfer Head 8	Che. 8	Sho. 8	Back 8	Belly 8	Mean	After transfer Head 8	Che. 8	Sho. 8	Back 8	Belly 8	Mean
Achillea	N	*/*	c	0.1	0.1-0.5	M	0.3	.	.	.	.	0.1	.	.	.	.	.	0.0
millefolium						SE	0.3	.	.	.	.		.	.	.	.	.	
Agrimonia	T	*/*	h	40.0	05-1.8	M	17.3	11.7	10.2	0.2	1.2	8.1	10.0	11.7	8.3	0.4	1.2	6.3
procera						SE	2.9	3.9	3.1	0.2	0.7		3.1	3.6	3.3	0.4	0.4	
Arabis	T	*/*	c	0.1	0.6-1.2	M	.	.	1.0	0.2	.	0.2	0.3	.	0.4	0.1	.	0.2
glabra						SE	.	.	0.4	0.1	.		0.3	.	0.3	0.1	.	
Arenaria	T	*/*	c	0.1	0.03-0.3	M	.	.	.	.	.	0.0	.	.	.	.	0.1	0.0
serpyllifolia agg.						SE	.	.	.	.	.		.	.	.	.	0.1	
Armeria maritima	R	3/2	b	1.5	0.05-0.5	M	0.8	0.3	.	.	.	0.2	1.3	.	.	.	0.1	0.3
ssp. *elongata*						SE	0.5	0.3	.	.	.		0.5	.	.	.	0.1	
Bromus	N	*/*	b	3.5	0.05-0.8	M	.	.	.	.	.	0.0	0.3	.	0.2	.	0.1	0.1
hordeaceus						SE	.	.	.	.	.		0.3	.	0.2	.	0.1	
Bromus	N	*/*	b	7.9	0.3-0.6	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
sterilis						SE	.	.	.	.	.		.	.	.	0.1	.	
Bromus	T	*/*	b	3.6	0.1-0.45	M	0.3	0.5	.	.	.	0.2	.	.	.	.	0.1	0.0
tectorum						SE	0.3	0.5	.	.	.		.	.	.	.	0.1	
Centaurea	T	*/*	b	1.3	0.3-1.2	M	0.5	0.8	0.2	0.1	0.1	0.3	1.3	0.3	0.2	0.3	0.1	0.4
stoebe						SE	0.3	0.4	0.2	0.1	0.1		1.0	0.3	0.2	0.2	0.1	
Conyza	N	*/*	b	0.0	0.2-1.0	M	3.3	0.3	0.2	.	0.1	0.8	0.3	0.3	0.4	.	0.1	0.2
canadensis						SE	1.4	0.3	0.2	.	0.1		0.3	0.3	0.3	.	0.1	
Cynoglossum	N	*/*	h	26.0	0.3-0.8	M	4.0	8.9	0.4	.	0.4	2.7	2.8	3.9	0.2	.	0.2	1.4
officinale						SE	3.2	6.3	0.3	.	0.3		1.9	2.6	0.2	.	0.1	
Erodium	T	*/*	b	2.3	0.1-0.6	M	.	.	.	.	0.2	0.0	.	.	.	.	.	0.0
cicutarium agg.						SE	.	.	.	.	0.1		.	.	.	.	.	
Medicago	R	3/3	h	1.2	0.1-0.3	M	3.8	1.8	3.5	.	5.6	2.9	7.3	.	8.5	.	5.8	4.3
minima						SE	2.1	1.2	2.6	.	3.0		3.9	.	3.4	.	2.5	
Petrorhagia	T	*/*	c	0.2	0.15-0.45	M	.	.	0.2	.	.	0.0	.	.	.	0.1	.	0.0
prolifera						SE	.	.	0.2	.	.		.	.	.	0.1	.	
Poa	G	*/*	b	0.3	0.1-0.9	M	.	.	.	.	.	0.0	.	0.3	.	.	.	0.1
angustifolia						SE	.	.	.	.	.		.	0.3	.	.	.	
Rumex	T	*/*	s	0.4	0.1-0.3	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
acetosella s.l.						SE	.	.	.	.	.		.	.	.	0.1	.	
Sisymbrium	N	*/*	c	0.2	0.3-0.6	M	0.8	.	1.0	3.1	.	1.0	0.5	.	2.1	2.4	.	1.0
altissimum						SE	0.4	.	0.8	0.7	.		0.3	.	0.9	1.6	.	
Stipa	R	3/2	b	12.0	0.3-1.0	M	6.3	6.0	4.2	2.0	2.0	4.1	5.5	4.4	2.7	1.9	2.6	3.4
capillata						SE	2.7	1.5	1.2	0.7	0.7		2.7	1.3	1.0	0.6	0.6	
Trifolium	T	*/*	b	0.4	0.08-0.3	M	0.8	0.3	.	.	0.3	0.3	0.8	.	.	.	.	0.2
arvense						SE	0.4	0.3	.	.	0.1		0.5	.	.	.	.	
Verbascum	N	*/*	c	0.1	0.5-2.0	M	0.3	.	2.5	6.2	.	1.8	0.3	.	2.5	10.4	.	2.6
phlomoides						SE	0.3	.	1.6	1.6	.		0.3	.	1.6	5.6	.	
Unidentified 1	-	-	-	-	-	M	.	.	.	.	.	0.0	.	.	0.2	.	.	0.0
						SE	.	.	.	.	.		.	.	0.2	.	.	
Unidentified 2	-	-	-	-	-	M	.	.	.	.	.	0.0	.	.	.	0.1	.	0.0
						SE	.	.	.	.	.		.	.	.	0.1	.	
Other Poaceae	-	-	-	-	-	M	0.3	.	.	.	.	0.1	.	.	.	.	.	0.0
						SE	0.3	.	.	.	.		.	.	.	.	.	
Total seed number							38.3	30.5	23.5	11.7	9.8	22.8	30.3	20.8	25.8	15.9	10.2	20.6
Total species number							13	9	10	6	8	16	12	6	11	10	10	20

Table 2.1a Species present in vegetation, but not detected in sheep coat:

Agrostis capillaris / A.vinealis (G, */*, b, 0.1, 0.2-0.8), *Arenaria serpyllifolia* agg. (T, */*, c, 0.1, 0.03-0.3), *Asparagus officinalis (N, */*, s, 18.2, 0.3-1.5),Calamagrostis epigejos* (G, */*, b, 0.1, 0.6-1.5), *Carex hirta* (G, */*, c, 2.4, 0.1-0.8), *Chenopodium album* agg. *(N, */*, s, 1.5, 0.2-1.5), Conyza canadensis* (N, */*, b, 0.0, 0.2-1.0), *Corispermum leptopterum* (N, */*, c, 1.8, 0.1-0.6), *Corynephorus canescens (T,*/3), b, 0.1, 0.15-0.3), Cynodon dactylon* (G, */*, b, 0.3, 0.2-0.4), *Eragrostis minor* (N, */*, c, 0.1, 0.1-0.4), *Euphorbia cyparissias (T, */*, c, 2.5, 0.15-0.3), Helichrysum arenarium* (T, 3/2, b, 0.1, 0.1-0.3), *Herniaria glabra* (T, */*, c, 0.1, 0.05-0.3), *Hypericum perforatum (N, */*, c, 0.1, 0.3-0.6), Koeleria glauca / K. macrantha* (T, */*, b, 0.3, 0.2-0.6), *Medicago falcata* (T, */*, s, 1.5, 0.2-0.5), *Oenothera biennis* s.l. (N, */*, c, 0.6, 0.5-2.0), *Ononis repens* (T, */*, c, 4.8, 0.3-0.6), *Phleum arenarium* (R, 2/2, b, 0.2, 0.05-0.25), *Poa angustifolia* (G, */*, b, 0.3, 0.1-0.9), *Potentilla argentea* agg. (T, */*, c, 0.1, 0.2-0.5), *Salsola kali* ssp. *tragus* (N, */*, c, 2.3, 0.25-0.6), *Saponaria officinale* (N, */*, c, 1.6, 0.3-0.8), *Sedum acre* (T, */*, c, 0.0, 0.03-0.15), *Senecio inaequidens* (N, */*, b, 0.2, 0.3-1.0), *Setaria viridis* (N, */*, c, 0.8, 0.05-0.6), *Stipa capillata* (R, 3/2, b, 12.0, 0.3-1.0), *Trifolium arvense* (T, */*, b, 0.4, 0.08-0.3), *Trifolium campestre* (T, */*, s, 0.5, 0.15-0.3), *Verbascum phlomoides* (N, */*, c, 0.1, 0.5-2.0), *Veronica verna* (T, */*, c, 0.1, 0.03-0.15)
Senecio jacobaea and *Galium sp.* not present in vegetation, 1 seed detected in sheep coat.

Table 2.1b species present in vegetation, but not detected in sheep coat:

Achillea millefolium (N, */*, c, 0.1, 0.2-1.2), *Asperula cynanchica* (T, */*, c, 1.0, 0.05-0.3), *Berteroa incana* (N, */*, c, 0.7, 0.3-0.65), *Carduus nutans* (N, */*, b, 3.3, 0.3-1.0), *Carex hirta* (G, */*, c, 2.4, 0.1-0.8), *Cerastrium arvense* (N, */*, c, 0.3, 0.05-0.3), *Chenopodium album* agg. (N, */*, s, 1.5, 0.2-1.5), *Conyza canescens* (N, */*, b, 0.0, 0.2-1.0), *Crepis capillaris* (N, */*, b, 0.3, 0.15-0.6), *Erodium cicutarium (T, */*, b, 2.3, 0.1-0.6), Eryngium campestre* (T, */*, b, 0.15-0.6), *Euphorbia cyparissias* (T, */*, c, 2.5, 0.15-0.3), *Geranium molle (N, */*, c, 1.1, 0.1-0.3), Helichrysum arenarium* (T, 3/2, b, 0.1, 0.1-0.3), *Hypericum perforatum* (N, */*, c, 0.1, 0.3-0.6), *Medicago falcata* (T, */*, s, 1.5, 0.2-0.5), *Ononis repens* (T, */*, c, 4.8, 0.3-0.6), *Petrorhagia prolifera* (T, */*, c, 0.2, 0.15-0.45), *Psyllium arenarium* (N, */*, s, 1.0, 0.15-0.3), *Polygonum aviculare* agg.(N, */*, c, 2.1, 0.05-0.5), *Rumex thyrsiflorus* (N, */*, s, 0.5, 0.3-1.2), *Trifolium campestre* (T, */*, s, 0.5, 0.15-0.3), *Veronica arvensis* (N, */*, c, 0.1, 0.03-0.25), *Sedum acre* (T, */*, c, 0.0, 0.03-0.15), *Silene latifolia* ssp. *alba* (N, */*, c, 0.8, 0.5-1.0), *Tragopogon dubius* (N, */*, B, 0.3-0.6).
Holcus lanatus is not present in vegetation, 2 seeds detected in sheep coat

Table 2.1c species present in vegetation, but not detected in sheep coat:

Agrostis capillaris/A.vinealis (G, */*, b, 0.1, 0.2-0.8), *Agrostis stolonifera* (G, */*, b, 0.1, 0.1-0.7), *Allium sphaerocephalon (R, 3/2, c, 1.6, 0.3-0.6), Alyssum alyssoides* (T, */*, c, 0.4, 0.07-0.3), *Asparagus officinalis* (N, */*, s, 18.2, 0.3-1.5), *Asperula cynanchica (T, */*, c, 1.0, 0.05-0.3), Berteroa incana* (N, */*, c, 0.7, 0.3-0.65), *Calamagrostis epigejos* (G, */*, b, 0.1, 0.6-1.5), *Carduus nutans (N, */*, b, 3.3, 0.3-1.0), Cerastium semidecandrum* (T, */*, c, 0.0, 0.03-0.2), *Crataegus monogyna* (N, */*, s, 64.9, 10.0), *Crepis capillaris* (N, */*, b, 0.3, 0.15-0.6), *Echium vulgare* (T, */*, c, 2.9, 0.25-1.0), *Elymus repens / E. athericus* (G/N, */*, b, 3.3, 0.3-1.2), *Euphorbia cyparissias* (T, */*, c, 2.5, 0.15-0.3),
Festuca ovina agg. (T, */*, b, 0.5, 0.2-0.7), *Galium album* (N, */*, c, 0.5, 0.25-1.0), *Genista tinctoria* (N, */*, s, 3.9, 0.3-0.6), *Helianthemum nummularium* s.l. (T, */*, s, 1.1, 0.1-0.2), *Helichrysum arenarium* (T, 3/2, b, 0.1, 0.1-0.3), *Hieracium pilosella (T, */*, b, 0.2, 0.05-0.3), Hypochaeris radicata* (N; */*, b, 1.0, 0.15-0.6), *Luzula campestris* (N; */*, c, 0.8, 0.05-0.2), *Oenothera biennis* s.l. *(N, */*, c, 0.6, 0.5-2.0), Ononis repens* (T, */*, c, 4.8, 0.3-0.6), *Phleum phleoides* (T, */*, b, 0.2, 0.3-0.6), *Potentilla argentea* agg. *(T, */*, c, 0.1, 0.2-0.5), Potentilla tabernaemontani* (N, */*, c, 0.6, 0.2-0.5), *Rosa canina* s.l. (N, */*, s, 22.6, 1.0-3.0), *Rubus caesius* (N, */*, c, 3.6, 0.3-0.6), *Rumex thyrsiflorus* (N, */*, s, 0.5, 0.3-1.2), *Salvia pratensis* (T, */*, s, 2.0, 0.3-0.6), *Scabiosa canescens* (T, 3/3, b, 1.1, 0.2-0.5), *Securigera varia* (*/*, s, 3.5, 0.3-0.6), *Sedum acre (T, */*, c, 0.0, 0.03-0.15), Senecio jacobaea* (N, */*, b, 0.4, 0.3-1.0), *Silene latifolia* ssp. *alba* (N, */*, c, 0.8, 0.5-1.0), *Silene otites* (R, 3/2, c, 0.2, 0.2-0.6), *Silene vulgaris* s.l. (N, */*, c, 0.8, 0.15-0.5), *Thymus pulegioides* s.l. (N, */*, s, 0.1, 0.05-0.4), *Trifolium campestre (T, */*, s, 0.5, 0.15-0.3)*
Galium aparine not present in vegetation, 1 seed detected in sheep coat

Table 2.2a Mean seed numbers per 100 cm² sheep coat, before intra-area sheep transfer (Koelerion glaucae, Exp. 2). Abbreviations: SG: Species group (R Red List Status, T Other target, G graminoid competitor, N other non-target). RL: Red List status in Germany/Hessen (Korneck et al.,1996) (2 endangered, 3 vulnerable, * not endangered). SSS: seed surface structure (h hooked, b bristly, c coarse, s smooth (slightly modified after Fischer et al., 1996). SM: seed mass (mg) (Internet 1 and 2). Height (m) (Oberdorfer, 2001). M: mean, SE: Standard error. Seeds were detected in 9 body parts: head (H), chest (C), foreleg (O), shoulder (S), back (B), flank (F), belly (Y), hind leg (I), tail (T). Zero values are indicated with a dot. Data C. Eichberg (2005).

Species	SG	RL	SSS	SM (mg)	Height (m)	Paddock Kg1 Body part # quadr.	H 4	C 2	O 5	S 6	B 6	F 6	Y 5	I 6	T 3	All
Alopecurus pratensis	N	*/*	b	0.8	0.4-1.0	M	.	.	.	.	.	.	0.1	.	.	0.01
						SE	.	.	.	.	.	.	0.1	.	.	
Arenaria serpyllifolia agg.	T	*/*	c	0.1	0.05-0.2	M	3.0	.	.	.	.	.	0.8	.	.	0.42
						SE	3.0	.	.	.	.	.	0.6	.	.	
Armeria maritima ssp. *elongata*	R	3/2	b	1.5	0.15-0.3	M	.	.	.	.	.	.	0.2	.	.	0.02
						SE	.	.	.	.	.	.	0.2	.	.	
Arrhenatherum elatius	N	*/*	b	2.4	0.4-1.5	M		.	.	.	.	.	.	0.1	.	.	0.01
						SE		.	.	.	.	.	.	0.1	.	.	
Bromus hordeaceus	N	*/*	b	3.5	0.2-0.5	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Bromus tectorum	N	*/*	b	3.6	0.1-0.3	M	2.0	.	.	.	.	0.1	0.3	.	0.1	0.27
						SE	1.2	.	.	.	.	0.1	0.1	.	0.1	
Cynoglossum officinale	N	*/*	h	26.0	0.3-0.6	M	.	.	0.7	0.3	.	.	.	.	.	0.10
						SE	.	.	0.7	0.3	.	.	.	.	.	
Elymus repens / E. athericus	G/N	*/*	b	3.3	0.3-1.2	M	.	.	.	.	.	.	0.1	.	.	0.01
						SE	.	.	.	.	.	.	0.1	.	.	
Erodium cicutarium agg.	T	*/*	b	2.3	0.05-0.3	M	.	.	.	.	.	0.2	0.1	0.2	.	0.05
						SE	.	.	.	.	.	0.2	0.1	0.2	.	
Festuca ovina agg.	T	*/*	b	0.5	0.1-0.3	M	2.3	.	.	0.3	0.5	0.6	0.3	0.3	.	0.49
						SE	1.5	.	.	0.3	0.3	0.3	0.2	0.2	.	
Koeleria glauca / K. macrantha	T	*/*	b	0.3	0.2-0.5	M	5.3	.	0.3	0.6	0.3	0.3	0.2	.	0.2	0.79
						SE	2.9	.	0.3	0.6	0.1	0.3	0.2	.	0.1	
Medicago minima	R	3/3	h	1.2	0.1-0.3	M	14.9	4.0	11.8	.	0.3	7.2	52.0	16.5	10.2	12.99
						SE	8.5	4.0	3.4	.	0.3	0.2	3.8	10.3	3.5	
Poa angustifolia	G	*/*	b	0.3	0.1-0.5	M	0.3	0.5	.	.	0.3	.	.	0.2	0.1	0.15
						SE	0.3	0.5	.	.	0.3	.	.	0.2	0.1	
Silene conica	R	3/2	c	0.4	0.05-0.2	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Vulpia myuros	T	*/*	b	0.5	0.1-0.25	M	7.0	1.6	0.7	0.6	0.7	0.8	0.6	0.5	0.1	1.38
						SE	1.7	1.6	0.7	0.6	0.3	0.1	0.3	0.3	0.1	
Further Poaceae	-	-	-	-	-	M	.	.	.	0.3	.	.	0.1	.	.	0.04
						SE	.	.	.	0.3	.	.	0.1	.	.	
Total seed number							34.9	6.0	13.5	1.9	2.3	9.1	54.6	17.7	10.6	16.7
Total species number							7	3	4	4	7	6	11	5	5	15

Table 2.2b Mean seed numbers per 100 cm² sheep coat, before intra-area sheep transfer (*Artemisia campestris* community, Exp. 2). For abbreviations, see Table 2a. Data C. Eichberg (2005).

Species	SG	RL	SSS	SM (mg)	Height (m)	Body part # quadr.	H 6	C 3	O 6	S 6	B 6	F 6	Y 6	I 6	T 3	All
Armeria maritima ssp. *elongata*	R	3/2	b	1.5	0.15-0.3	M	0.3	.	.	.	.	.	0.1	.	.	0.05
						SE	0.3	.	.	.	.	.	0.1	.	.	
Bromus hordeaceus	N	*/*	b	3.5	0.2-0.5	M	0.7	0.3	.	.	0.1	0.4	0.2	0.3	0.2	0.25
						SE	0.3	0.3	.	.	0.1	0.1	0.2	0.3	0.1	
Bromus tectorum	N	*/*	b	3.6	0.1-0.3	M	1.3	.	.	0.3	0.3	0.4	0.6	0.7	.	0.39
						SE	0.3	.	.	0.3	0.3	0.1	0.3	0.4	.	
Calamagrostis epigejos	G	*/*	b	0.1	0.8-1.5	M	.	.	.	.	.	.	0.1	.	.	0.01
						SE	.	.	.	.	.	.	0.1	.	.	
Centaurea stoebe	T	*/*	b	1.3	0.3-1.2	M	3.7	.	.	7.2	7.8	1.8	0.1	1.8	0.1	2.49
						SE	1.5	.	.	0.3	1.1	1.0	0.1	1.8	0.1	
Crepis capillaris	N	*/*	c	0.3	0.15-0.5	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Cynoglossum officinale	N	*/*	h	26.0	0.3-0.6	M	.	.	.	0.3	.	0.2	0.1	0.2	.	0.08
						SE	.	.	.	0.3	.	0.2	0.1	0.2	.	
Festuca ovina agg.	T	*/*	b	0.5	0.1-0.3	M	.	.	0.3	1.4	0.3	0.8	.	.	.	0.31
						SE	.	.	0.3	0.7	0.1	0.4	.	.	.	
Koeleria glauca / K. macrantha	T	*/*	b	0.3	0.2-0.5	M	2.0	.	.	3.6	1.8	0.6	0.2	.	.	0.91
						SE	1.0	.	.	1.4	0.1	0.1	0.1	.	.	
Medicago minima	R	3/3	h	1.2	0.1-0.3	M	6.8	.	8.5	.	0.7	6.6	42.5	8.9	11.9	9.52
						SE	5.5	.	2.2	.	0.7	0.9	4.0	3.8	3.2	
Myosotis stricta / M. rammosissima	T	*/*	h	0.1	0.05-0.2	M	0.7	.	.	.	.	0.1	.	.	.	0.08
						SE	0.7	.	.	.	.	0.1	.	.	.	
Oenothera biennis s.l.	N	*/*	c	0.6	0.5-1.0	M	.	.	.	0.3	0.8	.	.	.	.	0.12
						SE	.	.	.	0.3	0.2	.	.	.	.	
Papaver dubium s.l.	N	*/*	c	0.1	0.3-0.6	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Phleum arenarium	R	2/2	b	0.2	0.05-0.20	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Poa angustifolia	G	*/*	b	0.3	0.1-0.5	M	0.3	.	1.0	0.3	0.5	0.3	.	.	0.1	0.27
						SE	0.3	.	0.6	0.3	0.5	0.1	.	.	0.1	
Potentilla argentea agg.	T	*/*	c	0.1	0.1-0.3	M	.	.	.	0.3	.	.	.	.	.	0.03
						SE	.	.	.	0.3	.	.	.	.	.	
Psyllium arenarium	N	*/*	s	1.0	0.15-0.4	M	.	.	.	.	.	.	0.3	.	.	0.04
						SE	.	.	.	.	.	.	0.2	.	.	
Silene conica	R	3/2	c	0.4	0.05-0.2	M	.	.	.	.	.	.	.	.	0.1	0.01
						SE	.	.	.	.	.	.	.	.	0.1	
Silene otites	R	3/2	c	0.2	0.2-0.5	M	.	.	.	0.3	1.2	0.2	.	.	.	0.18
						SE	.	.	.	0.3	0.6	0.2	.	.	.	
Taraxacum sect. *Ruderalia*	N	*/*	c	0.7	0.05-0.4	M	.	.	.	.	.	0.1	.	.	.	0.01
						SE	.	.	.	.	.	0.1	.	.	.	
Trifolium arvense	T	*/*	b	0.4	0.05-0.2	M	0.3	.	.	.	.	.	0.1	.	.	0.05
						SE	0.3	.	.	.	.	.	0.1	.	.	
Verbascum phlomoides	N	*/*	c	0.1	0.5-2.0	M	.	.	.	0.3	0.3	.	.	.	.	0.06
						SE	.	.	.	0.3	0.1	.	.	.	.	
Vulpia myuros	T	*/*	b	0.5	0.1-0.25	M	2.0	3.1	.	0.3	0.5	0.8	1.5	1.3	0.2	1.09
						SE	1.5	2.1	.	0.3	0.3	0.2	0.3	0.4	0.1	
Further Poaceae	-	-	-	-	-	M	0.3	.	.	.	.	.	.	.	.	0.04
						SE	0.3	.	.	.	.	.	.	.	.	
Further unidentified	-	-	-	-	-	M	0.3	.	.	.	.	.	.	.	.	0.04
						SE	0.3	.	.	.	.	.	.	.	.	
Total seed number							18.8	3.5	9.8	14.4	14.6	12.1	45.7	13.2	12.5	16.06
Total species number							10	2	3	11	14	12	11	6	6	23

Table 2.2c Mean seed numbers per 100 cm² sheep coat, before intra-area sheep transfer (*Armerio-Festucetum trachyphyllae* community, Exp. 2). For abbreviations, see Table 2a. Data C. Eichberg (2005).

Species	SG	RL	SSS	SM (mg)	Height (m)	Paddock AF1 Body part # quadr.	H 6	C 3	O 6	S 6	B 6	F 6	Y 6	I 6	T 3	All
Agrostis cap. / *A. vinealis*	G/N	*/*	b	0.1	0.2-0.6	M	0.3	0.3	.	.	.	.	0.3	.	.	0.11
						SE	0.3	0.3	.	.	.	.	0.3	.	.	
Arenaria serpyllifolia agg.	T	*/*	c	0.1	0.05-0.2	M	.	.	.	.	.	0.1	0.1	.	.	0.02
						SE	.	.	.	.	.	0.1	0.1	.	.	
Armeria maritima ssp. *elongata*	R	3/2	b	1.5	0.15-0.3	M	0.3	.	.	.	.	.	.	.	.	0.04
						SE	0.3	.	.	.	.	.	.	.	.	
Bromus hordeaceus	N	*/*	b	3.5	0.2-0.5	M	1.7	0.3	0.3	.	0.1	0.3	0.5	0.3	0.6	0.46
						SE	1.7	0.3	0.3	.	0.1	.	0.4	0.3	0.1	
Bromus tectorum	N	*/*	b	3.6	0.1-0.3	M	1.0	0.3	.	0.3	0.3	0.7	0.7	0.3	0.2	0.41
						SE	0.6	0.3	.	0.3	0.3	0.4	0.3	0.2	0.1	
Calamagrostis epigejos	G	*/*	b	0.1	0.8-1.5	M	.	.	0.3	.	.	.	.	.	.	0.04
						SE	.	.	0.3	.	.	.	.	.	.	
Carex praecox	R	3/3	b	0.4	0.1-0.3	M	.	0.3	.	.	.	.	.	.	.	0.04
						SE	.	0.3	.	.	.	.	.	.	.	
Cerastium cf. *holosteoides*	N	*/*	c	0.1	0.1-0.4	M	.	.	.	.	.	0.1	.	.	.	0.01
						SE	.	.	.	.	.	0.1	.	.	.	
Cynoglossum officinale	N	*/*	h	26.0	0.3-0.6	M	.	2.8	1.0	0.6	.	0.2	0.1	0.5	0.2	0.58
						SE	.	2.8	0.6	0.3	.	0.1	0.1	0.5	0.1	
Erodium cicutarium agg.	T	*/*	b	2.3	0.05-0.3	M	.	.	.	.	.	.	0.1	.	.	0.01
						SE	.	.	.	.	.	.	0.1	.	.	
Festuca ovina agg.	T	*/*	b	0.5	0.1-0.3	M	7.3	4.2	0.7	3.1	3.1	1.6	1.0	0.5	0.4	2.43
						SE	3.3	2.1	0.7	1.2	0.8	0.5	0.1	0.3	0.3	
Koeleria glauca / *K. macrantha*	T	*/*	b	0.3	0.2-0.5	M	5.3	0.3	0.3	4.2	5.3	1.6	2.1	1.2	0.3	2.29
						SE	2.6	0.3	0.3	0.5	0.9	0.6	0.5	0.2	0.1	
Medicago minima	R	3/3	h	1.2	0.1-0.3	M	0.8	1.8	2.5	1.4	0.7	3.6	25.8	4.2	5.3	5.12
						SE	0.8	0.9	1.5	0.7	0.7	0.8	5.8	1.1	0.6	
Oenothera biennis s.l.	N	*/*	c	0.6	0.5-1.0	M	.	.	.	.	0.5	0.1	.	.	.	0.07
						SE	.	.	.	.	0.5	0.1	.	.	.	
Poa angustifolia	G	*/*	b	0.3	0.1-0.5	M	1.7	0.7	.	0.3	0.7	0.3	0.1	0.2	0.1	0.43
						SE	0.9	0.7	.	0.3	0.3	0.1	0.1	0.2	0.1	
Rumex acetosella s.l.	T	*/*	s	0.4	0.05-0.15	M	.	.	.	0.3	.	0.1	.	.	.	0.04
						SE	.	.	.	0.3	.	0.1	.	.	.	
Silene conica	R	3/2	c	0.4	0.05-0.2	M	.	.	.	.	0.3	.	.	.	.	0.03
						SE	.	.	.	.	0.3	.	.	.	.	
Silene latiffolia ssp. *alba*	N	*/*	c	0.8	0.4-0.9	M	.	.	.	.	0.3	.	.	.	.	0.03
						SE	.	.	.	.	0.3	.	.	.	.	
Silene otites	R	3/2	c	0.2	0.2-0.5	M	.	.	.	0.6	0.5	0.3	.	0.2	.	0.17
						SE	.	.	.	0.6	0.3	.	.	0.2	.	
Verbascum phlomoides	N	*/*	c	0.1	0.5-2.0	M	0.3	.	.	.	0.5	.	.	.	.	0.09
						SE	0.3	.	.	.	0.1	.	.	.	.	
Vulpia myuros	T	*/*	b	0.5	0.1-0.25	M	2.7	3.8	.	0.8	0.5	0.5	1.2	1.5	1.0	1.33
						SE	1.8	0.9	.	0.5	0.1	0.3	0.3	0.3	0.3	
Unidentified 1	-	-	-	-	-	M	.	0.3	.	.	.	.	.	.	.	0.04
						SE	.	0.3	.	.	.	.	.	.	.	
Unidentified 2	-	-	-	-	-	M	.	.	.	.	.	.	0.2	.	.	0.02
						SE	.	.	.	.	.	.	0.2	.	.	
Further Dicotyledoneae	-	-	-	-	-	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Further Poaceae	-	-	-	-	-	M	0.3	0.3	0.7	.	0.3	.	0.2	.	.	0.20
						SE	0.3	0.3	0.3	.	0.3	.	0.2	.	.	
Further Unidentified	-	-	-	-	-	M	.	.	.	.	0.1	.	0.1	.	.	0.02
						SE	.	.	.	.	0.1	.	0.1	.	.	
Total seed number							21.8	15.7	5.9	11.4	13.3	9.2	32.3	8.9	7.9	14.0
Total species number							10	11	6	9	12	12	12	9	8	23

Table 2.2c continued

Species	SG	RL	SSS	SM (mg)	Height (m)	Paddock Body part # quadr.	AF2 H 6	C 3	O 6	S 6	B 6	F 6	Y 6	I 6	T 3	All
Agrostis cap. /	G/N	*/*	b	0.1	0.2-0.6	M	.	-	1.0	.	.	.	.	.	.	0.11
A. vinealis						SE	.	.	1.0	.	.	.	.	.	.	
Arenaria	T	*/*	c	0.1	0.05-0.2	M	.	.	.	.	.	0.4	.	.	.	0.05
serpyllifolia agg.						SE	.	.	.	.	.	0.4	.	.	.	
Arrhenatherum	N	*/*	b	2.4	0.4-1.5	M	0.3	.	.	.	.	0.1	.	.	0.1	0.05
elatius						SE	0.3	.	.	.	.	0.1	.	.	0.1	
Bromus	N	*/*	b	3.5	0.2-0.5	M	.	.	.	0.8	0.1	.	.	.	.	0.11
hordeaceus						SE	.	.	.	0.5	0.1	.	.	.	.	
Bromus	N	*/*	b	3.6	0.1-0.3	M	0.3	.	.	.	.	0.1		.	.	0.05
tectorum						SE	0.3	.	.	.	.	0.1		.	.	
Cerastium	N	*/*	c	0.1	0.1-0.4	M	.	.	.	.	.	0.1	.	.	.	0.01
cf. *holosteoides*						SE	.	.	.	.	.	0.1	.	.	.	
Erodium	T	*/*	b	2.3	0.05-0.3	M	.	.	.	.	.	0.1	.	0.2	.	0.03
cicutarium agg.						SE	.	.	.	.	.	0.1	.	0.2	.	
Festuca	T	*/*	b	0.5	0.1-0.3	M	2.7	1.4	1.0	2.2	1.0	1.1	0.1	0.7	0.6	1.20
ovina agg.						SE	0.7	1.4	0.6	1.2	0.3	0.6	0.1	0.2	0.3	
Koeleria glauca /	T	*/*	b	0.3	0.2-0.5	M	4.7	0.3	0.3	3.3	1.8	0.4	0.2	0.2	0.1	1.26
K. macrantha						SE	0.9	0.3	0.3	0.5	0.3	0.1	0.1	0.2	0.1	
Medicago	R	3/3	h	1.2	0.1-0.3	M	0.8	.	1.7	.	0.3	1.5	24.5	7.2	2.3	4.26
minima						SE	0.8	.	0.8	.	0.3	0.9	9.6	1.8	0.5	
Phleum	T	*/*	b	0.2	0.2-0.5	M	.	36.1	.	.	.	.	.	.	.	4.01
*phleoides**						SE	.	36.1	.	.	.	.	.	.	.	
Poa	G	*/*	b	0.3	0.1-0.5	M	2.7	.	.	0.8	0.7	.	0.3	0.2	.	0.52
angustifolia						SE	2.2	.	.	0.5	0.3	.	0.2	0.2	.	
Potentilla	T	*/*	c	0.1	0.1-0.3	M	.	.	.	.	.	0.1	.	.	.	0.01
argentea agg.						SE	.	.	.	.	.	0.1	.	.	.	
Silene	R	3/2	c	0.4	0.05-0.2	M	.	.	.	.	.	.	0.1	.	.	0.01
conica						SE	.	.	.	.	.	.	0.1	.	.	
Vulpia	T	*/*	b	0.5	0.1-0.25	M	1.7	0.3	.	0.6	0.9	0.5	0.1	0.2	0.2	0.49
myuros						SE	0.3	0.3	.	0.6	0.6	0.3	0.1	0.2	0.1	
Further	-	-	-	-	-	M	1.0	.	.	0.3	.	0.1	0.1	.	.	0.16
Poaceae						SE	0.6	.	.	0.3	.	0.1	0.1	.	.	
Total seed number							14.2	38.2	4.0	8.1	5.3	4.1	25.3	8.5	3.2	12.3
Total species number							7	4	4	5	9	7	6	6	5	15

Table 2.2c continued

Species	SG	RL	SSS	SM (mg)	Height (m)	Paddock AF3-4 Body part # quadr.	H 6	C 3	O 6	S 6	B 6	F 6	Y 6	I 6	T 3	All
Agrostis cap. / A. vinealis	G/N	*/*	b	0.1	0.2-0.6	M	.	.	.	.	.	0.1	.	.	.	0.01
						SE	.					0.1	.	.	.	
Armeria maritima ssp. *elongata*	R	3/2	b	1.5	0.15-0.3	M	0.3	.	.	.	.	0.2	.	.	.	0.06
						SE	0.3	.	.	.	.	0.1	.	.	.	
Arrhenatherum elatius	N	*/*	b	2.4	0.4-1.5	M	.	.	.	.	.	0.1	0.1	.	.	0.02
						SE	.	.	.	.	.	0.1	0.1	.	.	
Berteroa incana	N	*/*	c	0.7	0.2-0.4	M	.	.	.	.	0.3	.	.	.	.	0.03
						SE	.	.	.	.	0.1	.	.	.	.	
Bromus hordeaceus	N	*/*	b	3.5	0.2-0.5	M	1.0	0.3	0.3	0.6	0.4	0.2	0.8	0.7	0.3	0.51
						SE	1.0	0.3	0.3	0.3	0.2	0.2	0.1	0.3	0.3	
Bromus tectorum	N	*/*	b	3.6	0.1-0.3	M	1.0	.	.	0.3	0.3	0.3	1.3	0.5	0.1	0.41
						SE	1.0	.	.	0.3	0.1	0.1	0.4	0.3	0.1	
Calamagrostis epigejos	G	*/*	b	0.1	0.8-1.5	M	.	.	.	.	.	.	.	.	.	.
						SE	.	.	.	.	.	.	.	.	.	
Centaurea stoebe	T	*/*	b	1.3	0.3-1.2	M	18.7	0.3	4.3	59.7	84.6	8.9	0.3	0.5	0.6	19.77
						SE	8.7	0.3	3.4	19.5	16.0	3.4	0.3	0.3	0.2	
Cerastium cf. *holosteoides*	N	*/*	c	0.1	0.1-0.4	M	.	.	.	.	.	0.1	.	.	.	0.01
						SE	.	.	.	.	.	0.1	.	.	.	
Cynoglossum officinale	N	*/*	h	26.0	0.3-0.6	M	0.3	.	.	.	.	.	0.1	.	0.2	0.06
						SE	0.3	.	.	.	.	.	0.1	.	0.2	
Erodium cicutarium agg.	T	*/*	b	2.3	0.05-0.3	M	.	.	.	.	.	.	.	0.2	.	0.02
						SE	.	.	.	.	.	.	.	0.2	.	
Festuca ovina agg.	T	*/*	b	0.5	0.1-0.3	M	1.7	.	.	0.6	0.1	0.1	0.3	0.3	0.4	0.38
						SE	0.3	.	.	0.6	0.1	0.1	0.3	0.3	0.1	
Koeleria glauca / K. macrantha	T	*/*	b	0.3	0.2-0.5	M	2.0	.	.	1.4	1.3	0.3	0.1	0.7	.	0.63
						SE	0.6	.	.	0.6	0.3	0.1	0.1	0.4	.	
Medicago minima	R	3/3	h	1.2	0.1-0.3	M	4.2	5.3	11.8	2.1	0.3	6.1	40.5	9.3	14.2	10.43
						SE	0.8	4.0	3.4	1.2	0.3	1.5	3.0	2.6	1.7	
Oenothera biennis s.l.	N	*/*	c	0.6	0.5-1.0	M	.	.	.	3.1	10.0	0.8	.	.	.	1.55
						SE	.	.	.	1.9	4.4	0.5	.	.	.	
Papaver dubium s.l.	N	*/*	c	0.1	0.3-0.6	M	.	.	.	.	0.4	.	.	.	.	0.04
						SE	.	.	.	.	0.4	.	.	.	.	
cf. *Plantago lanceolata*	N	*/*	s	1.8	0.1-0.4	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Poa angustifolia	G	*/*	b	0.3	0.1-0.5	M	.	.	1.0	0.8	0.4	0.1	0.3	0.2	.	0.30
						SE	.	.	0.6	0.8	0.2	0.1	0.1	0.2	.	
Potentilla argentea agg.	T	*/*	c	0.1	0.1-0.3	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Silene latifolia ssp. *alba*	N	*/*	c	0.8	0.4-0.9	M	.	.	.	.	0.1	0.2	.	.	.	0.03
						SE	.	.	.	.	0.1	0.1	.	.	.	
Silene otites	R	3/2	c	0.2	0.2-0.5	M	.	.	.	0.3	0.5	0.1	.	.	.	0.10
						SE	.	.	.	0.3	0.3	0.1	.	.	.	
Verbascum phlomoides	N	*/*	c	0.1	0.5-2.0	M	.	.	.	1.1	3.6	0.8	.	.	.	0.62
						SE	.	.	.	0.6	1.4	0.7	.	.	.	
Vulpia myuros	T	*/*	b	0.5	0.1-0.25	M	1.0	1.0	.	0.3	.	0.4	0.2	0.8	0.1	0.43
						SE	1.0	0.6	.	0.3	.	0.4	0.1	0.2	0.1	
Unidentified 3 (Asteraceae)	-	-	-	-	-	M	.	.	.	.	0.1	.	.	.	.	0.01
						SE	.	.	.	.	0.1	.	.	.	.	
Further Dicotyledoneae	-	-	-	-	-	M	.	.	.	.	.	0.1	.	.	.	0.01
						SE	.	.	.	.	.	0.1	.	.	.	
Further Poaceae	-	-	-	-	-	M	.	.	0.3	0.3	.	.	0.1	.	0.1	0.08
						SE	.	.	.	0.3	0.3	.	0.1	.	0.1	
Total seed number							30.2	7.0	17.8	70.4	102.8	18.7	43.9	13.1	15.8	35.5
Total species number							9	4	4	11	16	16	10	9	7	23

Chapter 3

The fate of epizoochorously dispersed seeds:
Emergence and spatial patterns

Experimentally to sheep coat attached seeds (top); Emergence of Medicago minima seedling after epizoochorous dispersal (below).

Abstract

Sheep epizoochory has often been proposed as an important dispersal vector, and as such should help to overcome the dispersal limitation of plant species in fragmented landscapes and restoration sites. However, the post-dispersal fate of such seeds has been largely ignored. The present study took into account both dispersal and post-dispersal processes involving 14 model species (mainly target species of inland sand ecosystems). In a field experiment sheep with seeds experimentally attached to their coats (evidence of epizoochorous dispersal found for most species) were present at three open sand plots for 24 h. Seed detachment, seed shadow and trampling intensity were measured immediately, whereas seedling emergence and survival were recorded over an 8-month period. In addition, the effect of sheep trampling on seedling emergence and survival of two model species, *Jurinea cyanoides* (EU Fauna-Flora-Habitat directive species) and *Koeleria glauca*, were studied.

A high proportion of seeds had detached from the sheep coats and even threatened species became well established, e.g. *Alyssum montanum* ssp*. gmelinii*, *Silene conica* and *Stipa capillata*. Using Spatial Analysis by Distance Indices (SADIE), it was shown that patterns of trampling, seed shadow, and seedling emergence were non-randomly distributed over the plots. Between most of those patterns spatial associations existed. Overall, sheep abundance was positively correlated with detected seed numbers and seedling emergence rates. However, on species level, a variable impact of trampling on seedling emergence and survival was found; it enhanced seedling emergence of large-seeded *J. cyanoides*, whereas no difference between the treatments was found in case of *K. glauca.* In conclusion, in the presence of, e.g. a sheep flock, which predominantly moves between target areas from which dispersal of even threatened species takes place, the establishment of target species in restoration sites can be enhanced through a high seed input and the creation of safe sites.

Introduction

Restored ecosystems could have lower site-specific plant species richness than their unaltered counterparts, as shown, e.g., in calcareous grassland communities (Graham and Hutchings 1988). When abandoned agricultural fields are in the process of being restored to their former species-rich grassland communities, there are several restraints

concerning the recruitment of (target) plant species that need to be taken in consideration.

Successful restoration requires seeds to be made available (Bakker and van Diggelen 2006) through dispersal in time (soil seed bank) and/or space (seed dispersal). Dispersal in time was found to be mostly insufficient (Bekker et al. 1997; Stroh et al. 2002); grassland species often have a transient or short-lived soil seed bank in which the seeds survive less than one or five year(s), respectively (Thompson et al. 1997). Dispersal in space is severely reduced as well, e.g. due to fragmentation of former large ecosystems (Poschlod et al. 1996). To overcome the dispersal limitation of plant species of semi-natural habitat communities, area management by use of large domestic herbivores could be applied. Several studies showed that transhumance could result in the long-distance epizoochorous dispersal of considerable quantities of seeds belonging to a broad spectrum of species of different habitats (e.g. Fischer et al. 1996; Mouissie et al. 2005; Manzano and Malo 2006) without significant seed losses (Chapter 2; Wessels et al. 2008). In our study area high proportions of target species seeds are dispersed if sheep grazing and flock movement takes place within and between target areas (most frequently transported species: Red List species *Medicago minima* and *Stipa capillata* (Chapter 2; Wessels et al. 2008). Large quantitative variation among plant species was shown; factors such as seed mass, seed morphology and the plant's seed-releasing height affect the attachment to and detachment from an animal's coat (e.g. Fischer et al. 1996; Mouissie et al. 2005; Wessels et al. 2008), although Will et al. (2007) found no influence of seed mass on experimentally measured attachment potential.

The fate of epizoochorously dispersed seeds was not investigated in the above-mentioned studies, though it must be known in order to evaluate the real contribution of herbivores to the recruitment of target species. To our knowledge, so far only one study has investigated the germination success of epizoochorously dispersed seeds (Eichberg et al. 2005, one plant species).

At locations where animals spend a disproportional amount of time, seed detachment probably takes place more frequently. Inter-specific detachment differences could also cause different seed shadows. As in the case of wind-induced seed shadows (Willson 1993), epizoochorously dispersed seeds without clear dispersal structures should have

more clumped spatial patterns, whereas seeds with dispersal structures have longer retention times and as a result could have more scattered patterns. However, Eichberg et al. (2005) found that the seed shadow of experimentally attached, pappus-bearing achenes of *Jurinea cyanoides* was largely clumped as well (< 5 m from attachment location). Such a non-random spatial distribution of dispersed seeds could result in heterogeneous emergence patterns and presumably modifies structure and dynamics of plant populations and communities through its consequences with respect to seed predation, competition and recruitment (Nathan and Muller-Landau 2000).

Besides their contribution to dispersal and the resulting seed shadow, sheep can also alter seed fate by trampling (Rotundo and Aguiar 2004). In the absence of trampling vectors, small and/or round seeds can be incorporated into the soil more easily than large and/or irregularly shaped seeds (Thompson et al. 1994; Bekker et al. 1998). However, sheep trampling can incorporate large seeds into the soil and buried seeds can escape from predation by above-ground granivores (Eichberg et al. 2005). On the other hand, many species show higher germination rates when light is available, though large seeds may require less light for germination than smaller ones (Baskin and Baskin 1998).

A further difference in recruitment of species could be caused by site characteristics, acting as "environmental sieves" (Harper 1977). It has been proposed that a high residual soil fertility brought about by the long-term use of fertilisers impedes the establishment of species-rich grassland communities on abandoned agricultural land (e.g. Bakker and Berendse 1999); in dry grasslands the relation between low soil-extractable phosphorus and potassium and high plant diversity was shown by Süss et al. (2004).

Generally, large-seeded species have a higher chance of survival in early seedling establishment compared to small-seeded species (n = 112), especially under hazards (Westoby et al. 2002), although no relation between seed mass and seedling emergence was found (Moles and Westoby 2004). Therefore, large-seeded ruderal species are expected to become established at high rates. But since the soil nutrient content in the present study was lowered by adding a top layer of nutrient-poor sand, stress-tolerating species probably establish as well.

In order to gain more information on the contribution of domestic herbivores to plant recruitment, epizoochorous dispersal and post-dispersal processes of 14 mainly target species (open inland sand ecosystems) were studied (Table 3.1). Natural epizoochorous dispersal was shown for most of those species (Chapter 2; Wessels et al. 2008).

Table 3.1 Overview of study species. Traits and abbreviations: Epi., epizoochory, seed species detected in animal coat: *, detected by Wessels et al. (2008); -, no data as yet. Life form: T, therophyte; B, bi-annual; H, hemicryptophyte. Succes. stage, successional stage: p, pioneer; m, mid-successional. Func. type, functional type (Internet 1): r, ruderal; s, stress-tolerators; cs, competitors/stress-tolerators; sr, stress-tolerators/ruderals; csr, competitors/stress-tolerators/ruderals (Frank and Klotz 1988). RL, Red List status in Germany/Hessen (Korneck *et al.*, 1996): 2, endangered; 3, vulnerable; *, not endangered. SSS, seed surface structure: h, hooked; b, bristly; c, coarse; s, smooth. N, Nitrogen value (Ellenberg 1996). R, Reaction value (Ellenberg 1996). SM, seed mass (mg): structure mass, p = painted. Germination test: light preference is tested by establishing seeds (%, seeds n = 80) on top of (0 cm) or inserted in the soil (-2 cm). Bold values indicate better performance.

Species	Epi.	Life form	Succ. stage	Func. type	RL	SSS	N	R	SM	Germination test [%]	
										0 cm	2 cm
Dispersal and recruitment											
Alyssum montanum ssp. *gmelinii*	-	H	p,m	csr	2/2	c	1	7	0.6	**60.0**	1.3
Armeria maritima ssp. *elongata*	*	H	m	csr	3/2	b	2	6	1.5	**58.8**	2.5
Centaurea stoebe	*	B	m	csr	*/*	b	3	8	1.3	70.0	63.8
Cynoglossum officinale	*	B	m	cs	*/*	h	7	7	29.6 (p)	5.0	**62.5**
Jasione montana	-	H	p	csr	*/*	s	2	3	0	**36.3**	0.0
Koeleria glauca	*	H	p	cs	*/*	b	1	8	0.3	48.8	40.0
Medicago minima	*	T	p	sr	3/3	h	2	8	10.3 (p)	20.0	15.0
Myosotis stricta	*	T	p	sr	*/*	b	2	6	0.1	11.3	3.8
Phleum arenarium	*	T	p	sr	2/2	b	3	7	0.2	**56.3**	2.5
Scabiosa canescens	-	H	m	csr	3/3	b	3	8	1.1	**42.5**	6.3
Silene conica	*	T	p	sr	3/2	c	2	5	0.4	**61.3**	13.8
Silene otites	*	T	p,m	s	3/2	c	2	7	0.2	41.3	35.0
Stipa capillata	*	H	m	cs	3/2	h	2	8	12.7 (p)	11.3	12.5
Tragus racemosus	-	T	p	r	*/2	h	7	x	1.9	**26.3**	0.0
Trampling impact											
Jurinea cyanoides	-	H	m	csr	2/2	b	2	7	7.6	45.0	30.0
Koeleria glauca	*	H	p	cs	*/*	b	1	8	0.3	48.8	40.0

The following questions were addressed: (1) How many seeds detach from sheep coat and become incorporated in the soil? (2) What are the germination and establishment rates of different plant species after epizoochorous seed dispersal? (3) How are seed shadows spatially distributed after detachment from the sheep coat? How stable are these patterns in time? (4) Could a relation between spatial patterns of sheep visitation, seed shadows and seedling emergence be detected? (5) Does sheep trampling affect seedling emergence and survival?

Methods

Study area

The study was conducted on a former agricultural field, 'Streitgewann' (ca. 5.5 ha, northern upper Rhine valley, Central Germany, 8°35′E, 49°51′N). Sheep graze the area yearly (500-700 animals). As a 'stepping stone' this area reconnects two nutrient-poor inland sand ecosystems ''Ehemaliger August-Euler-Flugplatz von Darmstadt'' and 'Griesheimer Düne und Eichwäldchen', both nature protection areas under the Fauna-Flora-Habitat directive of the EU.

At 'Streitgewann' three 81 m^2 plots (each plot contains a nine by nine grid of 81 sub-plots, each 1 m^2) were created from deep sand (app. 70 cm thick, extensively seed-free), which became available after construction work (≥ 1 m depth). The plots were fenced completely against sheep. From every plot soil samples were taken (*n* = 5, October 2006) to analyse the pH and nutrient content (N_{total}, PO_4^{3-}). Each sample consisted of a mixture of three sub-samples. Prior to analysis samples were sieved. Mean plant available phosphorus = 9.6 mg/g (measured by use of Calcium-Acetate-Lactate soil extract; PO_4^{3-} target area = 8.0 – 20.0 mg/g). PH = 7.7 (measured with 0.01 mol l^{-1} $CaCl_2$ suspension; pH target area = 7.3). After samples were dried (70 °C/24 h) the mean total nitrogen was measured (N analyzer Carlo Erba), N_{total} = 0.01 mg (N_{total} target area = 0.25 – 1.69 mg/g). These values guarantee nutrient-poor conditions.

Seedling emergence capacity

For all study species (Table 3.1) a germination experiment was conducted to test for light or dark germination (growth chamber, 4 - 7 weeks). Seeds were placed in trays on the sand surface (0 cm depth, full light availability) or were inserted in the soil (2 cm depth, complete darkness). Per treatment two trays with 40 seeds each were exposed to a day/night temperature regime of 25/18 ºC (later reduced to 20/6 ºC to improve germination conditions) and light regime of 16 h light/8 h darkness. Due to low germination rates, germination tests for *Cynoglossum officinale, Alyssum montanum* ssp*. gmelinii* and *Medicago minima* were repeated after the seeds had been stored for 24 hours at -12 ºC; in addition, *C. officinale* seeds were scarified by making a small cut in the robust seed skin.

Experimental design

In October 2005, on each of the three plots two sheep of the local flock were abundant (24 h). One sheep served as seed vector, whereas the other was present to increase the trampling effect as well as to accompany the other animal. Seeds from 14 species (Table 3.1) were experimentally attached to the coat of three body parts on both sides of the animal (shoulder, back and flank). Per body part, per species 100 seeds were applied (600 seeds per species per sheep). Seed structures most probably involved in epizoochorous transport were used. Seeds with clear seed surface structures were attached by pressing them gently to the coat. Seeds without such structures were sprinkled into the coat from a 10 cm height, while opening the coat slightly by hand. As a result, seeds landed within the coat at a depth of approx. 1 cm. The animals walked around for at least 10 min./hour. Commercial pellet food and late-summer cut grass (non-sand grassland) were provided.

Experiment 1 Dispersal patterns

Dispersal processes were studied by use of three large-seeded species: *C. officinale, M. minima* (burrs) and *Stipa capillata* (including awn). Before attaching them to the sheep coats, seeds were marked with fluorescent tree marker dye (Mark-it, Landmark) as already used by Couvreur et al. (2005). After 24 h, still-attached seeds were re-collected. Detached seeds were detected on the soil surface and marked with small sticks. After 2 months they were checked for secondary dispersal.

Before starting the experiment the germination capacity of painted and unpainted seeds was compared (paired t-test). The germination test (three replicates per treatment, n = 33) showed no effect of paint on germination of *C. officinale* and *M. minima* (P = 0.773, P = 0.440 respectively), whereas rates of painted *S. capillata* seeds were slightly lower (P = 0.014).

Experiment 2 Post-dispersal processes

To study the post-dispersal fate of seeds, emerging seedlings of all study species were mapped and followed in time (4 periodic relevés, Oct. 2005 – Jul. 2006). The development stage (seedling emergence, establishment: survival ≥ 2 months, flowering,

fruiting or dying off) was recorded per individual. Additionally, the seed production of two species was calculated.

Experiment 3 Trampling effects

A trampling experiment with two model plant species *J. cyanoides* and *Koeleria glauca* (Table 3.1) was conducted. These Red List species (Korneck et al. 1996) are target species of the Fauna-Flora-Habitat type 'xeric sand calcareous grassland (Koelerion glaucae)'. The perennial herb *J. cyanoides* forms relatively large pappus-bearing achenes (mean achene length (without pappus) = 0.6 ± 0.05 cm (mean ± SD, *n* = 100); longest pappus bristle = 1.1 ± 0.1 cm (Eichberg et al. 2005)). The perennial grass *K. glauca* has much smaller caryopses with dispersal units 3.5 mm in length (Internet 1).

Per species, five quadrats (25 cm x 25 cm) were established inside (trampling treatment) and outside (control) the fences. Per quadrat, 100 *K. glauca* seeds or 25 *J. cyanoides* seeds were sown on top of the soil surface. Seeds were soil-fixated by lightly spraying tap water. The trampling treatment lasted for 24 hours. Seedling relevés were made once per month (Oct. 2005 – Apr. 2006).

Data analysis

Spatial patterns of trampled soil, seed shadow and seedlings were analysed by use of SADIE (Spatial Analysis by Distance Indices) (Perry 1998). The system measures potential overall aggregation through *D* ('distance to regularity') which is the minimum total distance individuals should move to achieve an equal sample number *m* in each sub-plot. A larger *D* indicates a more spatially aggregated arrangement of counts. After a number of randomizations, E_a ('simulated mean distance to regularity') can be calculated. The index of aggregation can now be defined as $I_a = D / E_a$. Generally, a sample is aggregated if $I_a > 1$, randomized if $I_a = 1$, or regular if $I_a < 1$. The test statistic P_a is the probability that the observed counts are arranged randomly among the given sample units. A two-tailed test at the 5% level was used with $P_a > 0.975$ indicating a regular dispersion, $P_a < 0.025$ indicating aggregation and $0.025 < P_a < 0.975$ indicating randomness (Perry 1998).

Additionally, the index of clustering *v* is given. The use of so called 'red-blue' plots can quantify the degree to which the count for each sub-unit contributes towards the

overall degree of clustering, either as part of a patch or a gap (Perry et al. 1999). Each sub-plot with count greater than the overall mean is assigned a patch cluster index v_i, which by convention is positive. Sub-plots with a count less than the overall mean are assigned a gap cluster index, v_j, by convention negative. The index v_i measures the degree to which a unit contributes to clustering as a member of a group of units that together form a patch, whereas v_j does the same measurement, this time to test a unit's contribution as a member of a group of units that form a gap. Large values of v_i ($> \sim 1.5$) indicate patchiness, large negative values of v_j ($< \sim -1.5$) reflect membership of a gap and values close to unity indicate a random placement of that unit in relation to others nearby. When plotted on a map of the sample units, the values of the indices v_i and v_j show the location and extent of clusters in the data (Perry et al. 1999).

Finally, SADIE can test for spatial association χ between two data sets, by comparing both clustering indices of each sampling unit (Perry and Dixon 2002). Spatial association might also be used to measure stability of a certain pattern in time. The significance of χ is determined through randomizations, with reassigned values of the cluster indices amongst the sample units (Winder et al. 2001). In case a value is not completely independent of its neighbours, SADIE can take into account this 'spatial autocorrelation' through the method of Dutilleul (1993). Positive association values ($\chi >$ 0.5) indicate similarity in location of two datasets' patches and/or gaps, whereas negative values ($\chi <$ 0.5) point out dissociation (Perry and Dixon 2002). Again, a two-tailed test at the 5% level was used with $P_a > 0.975$ for significant dissociation and $P_a <$ 0.025 for significant association.

The germination rates of painted and unpainted seeds and the effect of light availability on germination were compared by use of paired t-tests (see above *Methods Exp. 1*). Prior to analysis, data were log-transformed, after which homogeneity of variance was assumed. Detachment and seed burial rates of the three painted seed species were compared with a One-way ANOVA.

Linear regressions between number of emerged seedlings and seed mass, nitrogen and reaction indicator values were calculated. Spearman rank correlations between a) the number of detected seeds and the amount of trampled soil, b) seed numbers and seedling numbers and c) trampled soil and seedling numbers were conducted. The species-specific effect of sheep trampling on seedling emergence was tested in a mixed

linear model (Littell et al. 2000). Per replicate, the number of newly emerged seedlings, the total number of individuals and the number of seedlings which died off were used as response variables for emergence and performance.

To calculate the mean seed production of *A. gmelinii* and *S. conica,* per plant (resp. *n* = 21, *n* = 23) the seed number per capsule was multiplied with the number of capsules per plant.

Spatial patterns were analysed with SADIEShell v. 1.22 and Surfer 8.02 was used to create red blue plots. Mixed linear models were produced using SAS 9.1, whereas all other tests were conducted with SPSS 11.5.

Results

Seedling emergence test

Clear germination differences among species and light conditions were found (Table 3.1). Only seeds of *C. officinale* germinated better in darkness (inserted in the soil), whereas seven other species showed a higher emergence in light (Table 3.1). Seeds of *C. stoebe, C. officinale, S. conica* and *A. gmelinii* emerged most frequently.

Seed detachment and burial

At the end of the experiment (after 24 h) many seeds had detached from the sheep coats (studied for *C. officinale, M. minima* and *S. capillata*) and many of them became completely buried in the soil (Table 3.2). Significantly more *C. officinale* seeds fell out of the sheep coats compared to *M. minima* (lowest detachment rate). Nevertheless, most *M. minima* seeds became buried completely, especially in comparison to *S. capillata* (Table 3.2).

Table 3.2 Numbers of sheep-coat-detached and soil-buried seeds (mean ± SE) (sheep *n* = 3). Among the species, rates are compared to each other (One-way ANOVA). Significant differences ($P < 0.05$) are indicated with different letters.

Seed species	detachment [%]	burial [%]
C. officinale	78.8 ± 10.7 a	67.1 ± 7.4 ab
M. minima	43.6 ± 7.5 b	72.7 ± 7.1 a
S. capillata	46.3 ± 4.4 ab	42.3 ± 3.2 b

Germination and establishment rates

Most high-performing species (*C. officinale, A. gmelinii, S. conica, M. stricta, P. arenarium*) survived longer than 2 months, and in the case of annuals, reached flowering stage (Table 3.3). All small-seeded (seed weight < 0.4 mg) pioneers (*S. conica, M. stricta, P. arenarium*) were abundant in relatively high numbers. The only stress tolerator in this experiment, *S. otites* (Table 3.1), had an extremely low survival rate: only one seedling managed to survive longer than 2 months.

Table 3.3 Individual numbers (mean ± SE) per species (*n* = 3). Individuals younger and older than 2 months, flowering, fruiting, died off with or without having fruited were distinguished. Species are arranged from high to low performance.

Species	< 2 months	> 2 months	flowering	fruiting	Died off (-fruits)	(+fruits)	Total
C. officinale	45 ± 8	138 ± 37	.	.	8 ± 2	.	192 ± 41
A. gmelinii	4 ± 4	52 ± 18	10 ± 8	62 ± 32	17 ± 2	.	145 ± 8
S. conica	.	3 ± 1	120 ± 12	.	11 ± 5	1 ± 1	136 ± 14
M. stricta	1 ± 1	3 ± 3	73 ± 8	6 ± 3	24 ± 8	10 ± 6	116 ± 8
P. arenarium	4 ± 2	2 ± 0	105 ± 8	1 ± 1	2 ± 1	.	114 ± 9
C. stoebe	27 ± 3	42 ± 6	.	.	18 ± 9	.	88 ± 9
M. minima	47 ± 16	3 ± 1	3 ± 1	.	23 ± 11	.	76 ± 10
A. elongata	6 ± 1	31 ± 13	.	.	21 ± 7	.	58 ± 19
K. glauca	27 ± 9	2 ± 1	.	.	7 ± 3	.	36 ± 8
S. otites	1 ± 1	1 ± 1	.	.	23 ± 6	.	26 ± 5
S. capillata	20 ± 6	1 ± 1	.	.	1 ± 0	.	22 ± 7
S. canescens	.	.	.	.	10 ± 4	.	11 ± 4
T. racemosus	9 ± 4	.	.	.	.	.	9 ± 4
J. montana	.	.	.	.	1 ± 1	.	1 ± 1

In addition to variation in detachment (Table 3.2) large variation in recruitment was found among the three largest-seeded species; of all the dispersed seeds of *C. officinale, M. minima* and *S. capillata,* 41 %, 30 % and 8 % respectively emerged. No significant regression between total number of seedlings and seed mass (SM) (r^2 = 0.18, *P* = 0.131), soil nitrogen status (N) (r^2 = 0.02, *P* = 0.597) or soil reaction (R) (r^2 = 0.00, *P* = 0.954) was found (Table 3.1).

Seed production

In July 2005, high individual numbers of *A. gmelinii* (*n* = 372) and *S. conica* (*n* = 374) produced large seed numbers per plant (mean ± SE, *A. gmelinii:* 1556 ± 193, *S. conica:* 5335 ± 848). Within 8 months the number of seeds had increased 300-fold for *A. gmelinii* and 1100-fold for *S. conica*.

Spatial patterns

Spatial patterns *C. officinale*, *M. minima* and *S. capillata* are presented in Fig. 3.1 (plot 1, other two fields have aggregated patterns as well, therefore not shown). All patterns (sheep trampling, seed dispersal (primary: Oct. 2005, secondary: Dec. 2005)) showed significant overall aggregations, with distinguishable patches and gaps (Table 3.4, Fig. 3.1).
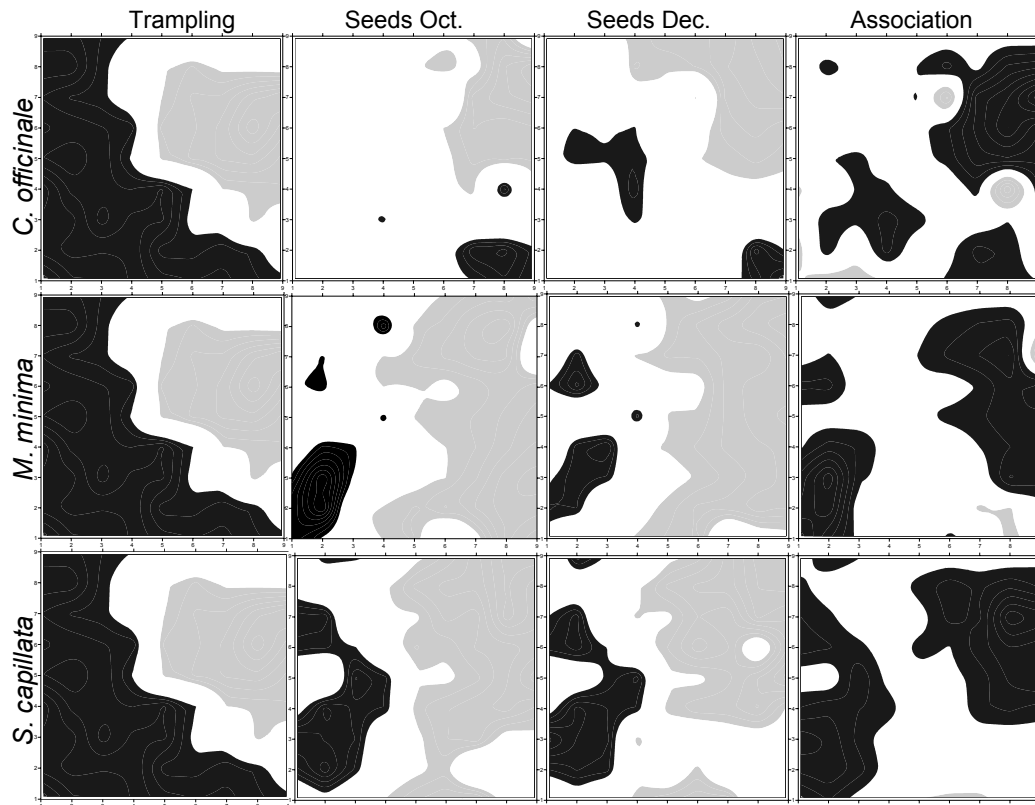
Figure 3.1 Red blue plots of sheep trampling ('Trampling'), sheep dispersed seeds ('Seeds Oct.'), sheep dispersed seeds, 2 months later ('Seeds Dec') and association between sheep trampling and dispersed seeds (Oct. 2005) ('Association') at plot 1. Only significant values are mapped, clustering indices $v_i > 1.5$ (patch, black), $v_j < -1.5$ (gap, grey) and association measure $\chi > 0.5$ (positive, black), $\chi < - 0.5$ (negative, grey).

Significant positive associations between trampling and seed patterns were found at plots 1 and 2, although the mean spatial association in most cases was < 0.5. No association between trampling and either one of the seed patterns was found at plot 3 (Table 3.5). Seed patterns themselves showed large spatial stability in time; original

existing patterns hardly changed over a 2-month period (Table 3.5, Fig. 3.1); the lowest

stability was found for *M. minima* at plot 3.

Table 3.4 Spatial patterns of sheep trampling and epizoochorously dispersed seeds. Sampling plots n = 81. Index of regularity, I_a, shows aggregation if I_a > 1; Level of significance, P_a < 0.025. Mean clustering indices v_i > ~ 1.5 (patch) and v_j < ~ -1.5 (gap). Level of significance; P_i, P_j < 0.025.

T	Pattern	Plot	Overall		Patches		Gaps	
			I_a	P_a	v_i	P_i	v_j	P_j
Oct. 2005	trampling	1	2.428	< 0.0002	2.417	0.0000	-2.344	0.0000
		2	2.467	< 0.0002	2.356	0.0000	-2.382	0.0000
		3	2.736	< 0.0002	2.622	0.0000	-2.597	0.0000
Oct. 2005	*C. officinale*	1	1.454	0.0137	1.262	0.0573	-1.437	0.0116
		2	1.830	0.0002	1.918	0.0000	-1.767	0.0005
		3	1.623	0.0012	1.838	0.0003	-1.604	0.0020
	M. minima	1	1.873	< 0.0002	2.102	0.0000	-1.877	0.0000
		2	1.842	0.0003	1.554	0.0032	-1.837	0.0000
		3	1.561	0.0050	1.481	0.0072	-1.515	0.0055
	S. capillata	1	2.211	< 0.0002	2.123	0.0000	-2.125	0.0000
		2	1.459	0.0124	1.384	0.0161	-1.366	0.0278
		3	1.891	< 0.0002	1.675	0.0005	-1.826	0.0000
Dec. 2005	*C. officinale*	1	1.587	0.0027	1.419	0.0134	-1.587	0.0039
		2	2.035	< 0.0002	1.986	0.0000	-1.935	0.0000
		3	1.801	0.0003	1.851	0.0002	-1.791	0.0005
	M. minima	1	1.943	< 0.0002	1.901	0.0000	-1.949	0.0000
		2	2.078	< 0.0002	2.179	0.0000	-2.080	0.0000
		3	1.505	0.0060	1.489	0.0077	-1.492	0.0094
	S. capillata	1	2.179	< 0.0002	1.537	0.0000	-2.195	0.0000
		2	1.981	< 0.0002	2.055	0.0000	-1.849	0.0002
		3	2.030	< 0.0002	1.843	0.0000	-1.826	0.0002

The number of dispersed seeds and the amount of trampled soil were positively

correlated with each other for all three study species within plots 1 and 2 and *S.

capillata*, plot 3 (Table 3.6). In plots 1 and 2 trampling was correlated with the dispersal

rate. However, in plot 3 also relatively many seeds were detected in hardly trampled

sub-plots. Consequently, no correlations for *C. officinale* or *M. minima* were found

(Table 3.6).

Corresponding to patterns of trampling and seed dispersal, heterogeneous seedling

emergence patterns for almost all species were detected. Seedling patterns of all study

species showed significant spatial aggregations (except for *A. elongata*: plot 2; *M.

stricta*: 1; *S. capillata*: 2, 3; see Appendix 3.1). Moreover, all patterns show clearly

distinguishable patches and gaps, containing relatively high and low seedling numbers,

respectively.

Table 3.5 Spatial association χ between cluster indices of dispersed seeds and trampled soil ('Trampling'), between dispersed seeds directly after the experiment and 2 months later ('Time', Oct., Dec. 2005), and between dispersed seeds and emerged seedlings ('Seedlings'). Cluster indices $n = 81$. Association measure $\chi > 0.5$ (positive), $\chi < -0.5$ (negative). Level of significance; $P < 0.025$ (association), $P > 0.975$ (dissociation).

Seed species	Plot	Trampling		Time		Seedlings	
		X	P	X	P	X	P
C. offficinale	1	0.4770	< 0.0001	0.7135	< 0.0001	0.6359	< 0.0001
	2	0.4688	< 0.0001	0.7326	< 0.0001	0.5774	< 0.0001
	3	0.1843	0.0619	0.8084	< 0.0001	0.4795	< 0.0001
M. minima	1	0.5262	< 0.0001	0.8094	< 0.0001	0.5546	< 0.0001
	2	0.4037	< 0.0001	0.6533	< 0.0001	0.6175	< 0.0001
	3	-0.0435	0.6496	0.5382	< 0.0001	0.4962	< 0.0001
S. capillata	1	0.6213	< 0.0001	0.9442	< 0.0001	0.6429	< 0.0001
	2	0.4662	0.0002	0.7769	< 0.0001	0.5007	0.0513
	3	0.1589	0.0970	0.7703	< 0.0001	-0.2054	0.6746

Table 3.6 Spearman rank correlations (r_s) between dispersed seeds (Oct. 2005) and trampled soil. Per plot, $n = 81$. Level of significance: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, N.S. = not significant.

Seed species	Plot	Correlation	
		r_s	P
C. offficinale	1	0.292	**
	2	0.323	**
	3	0.165	N.S.
M. minima	1	0.345	**
	2	0.236	*
	3	0.083	N.S.
S. capillata	1	0.614	***
	2	0.410	***
	3	0.397	***

In total, 41 seedling emergence patterns could be distinguished (no emergence *J. montana*: plot 2; Appendix 3.1). Patterns of all frequently recorded species (high and medium emergence) had significant overall aggregations (except for *M. stricta*: plot 1). Species with low emergence rates showed mostly no aggregation (*J. montana*, *S. canescens*, *S. otites*, *S. capillata*, *T. racemosus*). Emergence patterns of all study species were compared with trampling patterns. Most patterns of species with relatively high or medium abundance had significant positive associations with trampling patterns or exhibited a trend in that direction. However, several species showed associations at only one or two plots, whereas such similarity could not be detected in a third plot. Seedling patterns with associations had positive correlations between seedling numbers and trampling intensity as well. Hardly emerged species consequently showed no as- or

dissociation with trampling patterns (except *T. racemosus*: plot 2; *S. capillata*: 1) and in most cases trampling intensity and seedling emergence did not correlate either (Appendix 3.1).

Comparisons of seed and seedling patterns show significant positive associations for all three tested species (except *S. capillata*: plots 2, 3) (Table 3.7). Furthermore, significant positive correlations between seed and seedling numbers were found (except *S. capillata*: plot 3) (Table 3.7).

Table 3.7 Spatial association (χ) and Spearman rank correlations (r_s) between seeds and seedlings. Per plot, n = 81. Association measure χ > 0.5 (positive), χ < - 0.5 (negative). Level of significance; P < 0.025. Correlation level of significance: *P < 0.05, ***P < 0.001.

Species	Plot	Association		Correlation	
		χ	P	r_s	P
C. officinale	1	0.6359	< 0.0001	0.484	***
	2	0.5774	< 0.0001	0.548	***
	3	0.4795	< 0.0001	0.535	***
M. minima	1	0.5546	< 0.0001	0.405	***
	2	0.6175	< 0.0001	0.471	***
	3	0.4962	< 0.0001	0.475	***
S. capillata	1	0.6429	< 0.0001	0.457	***
	2	0.5007	0.0513	0.380	***
	3	-0.2054	0.6746	0.243	*

Trampling effects on seedling emergence and survival

Dependent on time, in trampled quadrats a significantly higher total number of *J. cyanoides* seedlings was found compared to non-trampled quadrats (time*treatment $F_{1,7}$ = 12.57, P < 0.000) (Table 3.8, Fig. 3.2a). A trend towards a higher total *K. glauca* seedling number in non-trampled quadrats in time was found, but the difference was not significant (time*treatment, $F_{1,7}$ = 1.93, P = 0.079) (Table 3.8, Fig 3.2b). Significantly more new seedlings of *J. cyanoides* emerged within the trampled quadrats in time (time*treatment, $F_{1,7}$ = 3.74, P < 0.001) (Table 3.8, Fig. 3.2c), in contrast to *K. glauca* seedlings which emerged significantly more in time within the non-trampled quadrats (time*treatment, $F_{1,7}$ = 3.74, P < 0.001) (Table 3.8, Fig. 3.2d).
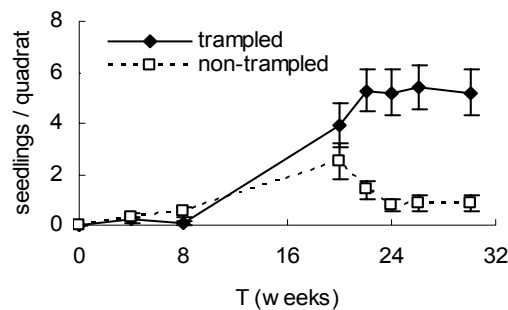
a) *J. cyanoides*   b) *K. glauca*
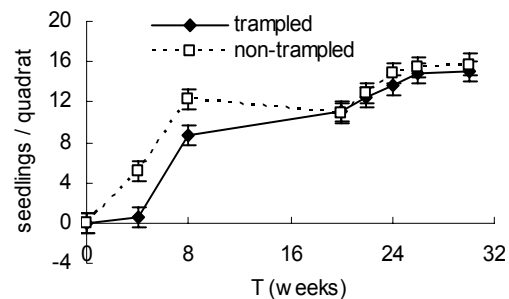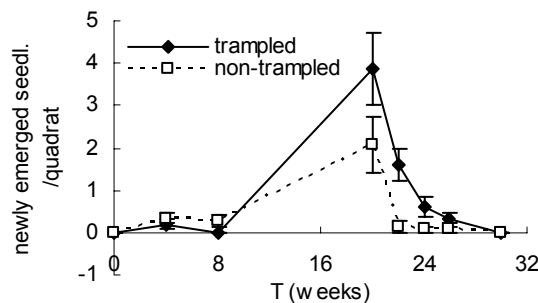
c) *J. cyanoides*   d) *K. glauca*
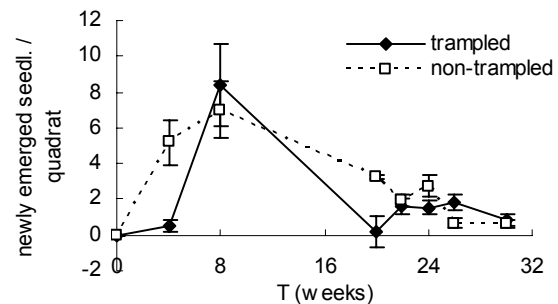
Figure 3.2 Total number of *J. cyanoides* (a) and *K. glauca* (b) seedlings and number of newly emerged *J. cyanoides* (c) and *K. glauca* (d) seedlings in trampled and non-trampled quadrats in time. Per species, per treatment quadrat *n* = 15. Error bars indicate standard error.

Table 3.8 Treatment effects on seedling numbers (total present, newly emerged and died off) of *J. cyanoides* and *K. glauca* in time (mixed linear model). Per species, per treatment quadrat *n* = 15. Level of significance; ** = *P* < 0.01, *** = *P* < 0.001, N.S. = not significant.

Seedlings	Species	Effect	Num DF	Den DF	F	P
all	*J. cyanoides*	treatment	1	25.7	11.04	**
		time	7	61.8	15.31	***
		time*treatment	7	61.8	12.57	***
	K. glauca	treatment	1	31.6	0.33	N.S.
		time	7	64.8	33.72	***
		time*treatment	7	64.8	1.93	N.S.
newly emerged	*J. cyanoides*	treatment	1	27.6	8.92	**
		time	7	117	23.83	***
		time*treatment	7	117	3.74	***
	K. glauca	treatment	1	28	0.01	N.S.
		time	7	118	16.74	***
		time*treatment	7	118	3.74	***
died off	*J. cyanoides*	treatment	1	80.2	0.24	N.S.
		time	7	146	9.21	***
		time*treatment	7	146	3.86	***
	K. glauca	treatment	1	83.6	0.33	N.S.
		time	7	133	5.36	***
		time*treatment	7	133	1.15	N.S.

Finally, dependent on time, mortality of *J. cyanoides* seedlings was significantly higher in non-trampled compared to trampled quadrats (time*treatment $F_{1,7}$ = 3.86, *P* < 0.001), whereas equal numbers of *K. glauca* seedlings died off (Table 3.8).

Discussion

Knowledge about seed movements and fates is essential for ecosystem restoration and conservation efforts (Chambers and MacMahon 1994). The present study has investigated the 'effective' contribution of epizoochorous dispersal to the recruitment of mainly target species in open inland sand ecosystems.

Germination, establishment and seed production

Although individuals of almost all study species emerged and established after sheep-epizoochorous dispersal, large differences in individual numbers were found. Many factors may have controlled their performance. The dispersal phase led to initial differences among species. In line with other studies (Couvreur et al. 2004; Tackenberg et al. 2006), the degree of detachment varied among species. The overall negative effect of seed mass on retention time (Tackenberg et al. 2006) could explain the higher detachment rate of *C. officinale* in comparison to *S. capillata* and *M. minima.* The over-representation of medium- and heavy-weight (respectively, 0.5 - 2.0 mg and > 2.0 mg) seed species with well-developed appendages (bristles, hooks) in sheep coat in comparison to the visited vegetation indicates low detachment rates. In contrast, equally or under-represented seeds without clear appendages in sheep coat suggest higher detachment rates of those seed species (Chapter 2; Wessels et al. 2008). Since other species used here are all lighter in weight (compared to *C. officinale, M. minima* and *S. capillata*) and/or have no morphological dispersal structures, they presumably reached comparable detachment rates (> 50%). *J. montana* could be an exception: its extremely light-weight seeds (< 0.01 mg) are highly adhesive to any surface, which probably limited the number of detached seeds. This probably also explains the absence of *Jasione* in later stages of recruitment.

Seed burial rates seem to have differed less among species. Sheep trampling did cause high numbers of large-seeded *C. officinale* and *M. minima* (both around 70%) to be buried, whereas in the absence of trampling vectors, large and/or irregularly shaped

seeds incorporate less easily into the soil profile compared to small and/or round seeds (Thompson et al. 1994; Bekker et al. 1998). As a result, smaller seeds probably were incorporated into the soil at least equally well. Fewer *S. capillata* seeds were buried completely (< 50 %); in many cases its exceptionally long awn was at least partly visible.

The high germination rate of *C. officinale* in the field was probably stimulated by sheep trampling; *C. officinale* is almost exclusively able to germinate in a buried condition (germination test). Comparably large-seeded competitive perennials with a wide ecological amplitude, high seed viability and high germination rates established most successfully from a sowing experiment (Pywell et al. 2002). Furthermore, a higher recruitment was found with increased seed size in undisturbed sward (Jakobsson and Eriksson 2000). Although large-seeded species generally have a higher survival advantage over small-seeded species (Moles and Westoby 2004), in this study high germination and establishment rates were found as well for small-seeded *S. conica, A. gmelinii* and *P. arenarium* (all included in top-5 highest emergence, Table 3.3). Although their seed input is unknown, it suggests that recruitment was not driven by seed size. Moreover, germination tests demonstrated higher seedling emergence rates when seeds were established on top of the soil surface, compared to their buried counterparts. For buried seeds reduced light is apparently compensated in the field by other factors, e.g. higher moisture content. Additionally, the absence of seedling-adult plant competition may have resulted in the seedling emergence of small-seeded stress tolerators/ruderals e.g. *A. gmelinii* and *S. conica* as well.

On the other hand, the reduction of light due to trampling may have severely limited the germination and/or recruitment of several other species (germination: *J. montana* and *T. racemosus* light exclusively, *S. canescens* seven-fold better with light). Light limitation apparently could not be compensated by higher soil moisture content in the field. Additionally, some poorly performing species, e.g. *S. otites* and *S. canescens,* are characteristic for more consolidated conditions of mid-successional stages. Dormancy mechanisms can prevent germination under conditions unsuitable for establishment (Fenner 1985), but species able to build up persistent seed banks could emerge later on. Although most species successfully established, considerably lower recruitment rates were recorded compared to initial seed input, as predicted by Edwards et al. (2000). This emphasizes the need of dispersing high seed numbers.

After one season, emerged individuals of *S. conica* and *A. gmelinii* produced high seed numbers. Weed species *Viola arvensis* and *Papaver rhoeas* had increased seed numbers with lowering of crop density (Wilson et al. 1996); possibly, the relatively low overall plant density — i.e. low competition at the plots — promoted seed production by our study species.

Spatial patterns

Highly trampled patches and rarely sheep-visited gaps indicated an unequal division of sheep abundance in space. Generally, and regardless of plot size, patterns are formed as a response of foraging behaviour to spatial patterns of resources (Gross et al. 1995) and use of resting places. Immediately after the experiment, dispersed seeds of *C. officinale, S. capillata*, *M. minima* were present in clumped groups as well. Associations and correlations suggest clear relations between trampling patterns and seed shadows. Eichberg et al. (2005) found clumped seed shadows even in five-fold larger paddocks of established grasslands. Comparable heterogeneity among seed densities is also found in soil seed banks (Thompson 1987).

Depending on soil microtopography (Thompson and Grime 1979) and seed size and shape (Reichman 1981), original sheep-induced seed shadows can change in time, for instance due to wind, rain and animals (e.g. seed beetles, ants) (Bastida and Talavera 2002). Nevertheless, the above-mentioned processes seem to have had little effect on *C. officinale* and *S. capillata*, since seed patterns showed high spatial stability and the total number of seeds of both species hardly changed. Large seed size and/or appendages could have limited secondary transport (Reichman 1981). The lower spatial stability of *M. minima* was probably caused by a reduction of burrs in time, especially from sub-plots with higher seed densities. Seed predation by granivores varies among plant species (Reader and Beisner 1991) and the nitrogen-rich seeds of Leguminoses are presumably preferred over other seed species.

Seedling emergence, the third investigated pattern type, showed all frequently emerged study species to be non-randomly distributed (except *M. stricta,* plot 1; see Appendix 3.1). Similarities among trampling, seed dispersal and seedling emergence suggest that heterogeneous sheep abundance results in comparable heterogeneous seed input and seedling emergence patterns and in most cases, a higher intensity of

trampling positively affects seed input and seedling emergence. Seed burial prevented seeds from detection after the experiment. Moreover, seedlings might have died off before being detected.

Trampling effects

As was observed for *Bromus pictus* seeds in Patagonian steppe (Rotundo and Aguiar 2004), seedling emergence of *J. cyanoides* was positively affected by seed burial. This experimentally confirms the results of Eichberg et al. (2005). Additionally, a higher seedling mortality rate was found for *J. cyanoides* in the non-trampled plots. However, under optimal conditions (germination test) some more unburied *J. cyanoides* seeds emerged (not significant). It is likely that granivory and drought limit germination of unburied seeds in the field. By contrast, unburied seeds of *K. glauca* showed a tendency towards higher seedling emergence than buried seeds under optimal and field conditions. Possibly, smaller seeds are less easily encountered by granivores (Getty and Pulliam 1993) and more strongly affected by reduced light availability than larger seeds.

In conclusion, it was shown that the presence of herbivores can contribute significantly to the recruitment of certain target species. Since a few species failed to emerge or survive, dispersal should not be studied independently from establishment (Poschlod et al. 2006). In order to optimize restoration efforts, both seed dispersal and abiotic conditions should be taken into account.

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Appendix 3.1. Analysis of spatial patterns of emerged seedlings of different study species. Per plot, n = 81. Index of regularity, I_a, aggregation if $I_a > 1$; Level of significance, $P_a < 0.025$. Mean clustering indices $v\_i > \sim 1.5$ (patch) and $v\_j < \sim -1.5$ (gap). Level of significance; P_i, $P_j < 0.025$. Spatial association (X) between seedling emergence and trampling patterns; $\chi > 0.5$ (positive), $\chi < -0.5$ (negative). Level of significance; $P < 0.025$ (association), $P > 0.975$ (dissociation). Spearman rank correlations (r_s) between seedling emergence numbers and amount of trampled soil. Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant.

Species	Plot	Overall		Patches		Gaps		Association		Correlation	
		I_a	P_a	v_i	P_i	v_j	P_j	X	P	r_s	P
A. gmelinii	1	1.634	0.0022	1.397	0.0189	-1.596	0.0032	0.4761	0.0001	0.402	***
	2	1.750	0.0005	1.691	0.0005	-1.685	0.0010	0.4807	0.0001	0.331	**
	3	2.031	0.0002	1.862	0.0002	-2.039	0.0000	0.5171	0.0001	0.232	*
A. elongata	1	1.397	0.0179	1.286	0.0513	-1.412	0.0282	0.5815	0.0001	0.453	***
	2	1.377	0.0256	1.198	0.1179	-1.405	0.0231	0.3036	0.0129	0.037	N.S.
	3	1.636	0.0017	1.649	0.0017	-1.514	0.0064	0.2553	0.0157	0.387	***
C. stoebe	1	1.591	0.0028	1.601	0.0020	-1.547	0.0039	0.5831	0.0001	0.449	***
	2	1.777	0.0026	1.697	0.0000	-1.806	0.0000	0.5380	0.0001	0.381	***
	3	1.908	0.0002	1.780	0.0000	-1.935	0.0000	0.3983	0.0002	0.309	**
C. officinale	1	1.853	0.0026	1.535	0.0077	-1.700	0.0026	0.5705	0.0001	0.564	***
	2	2.214	0.0026	2.086	0.0000	-2.102	0.0000	0.4420	0.0009	0.412	***
	3	2.239	0.0026	2.016	0.0000	-2.171	0.0000	0.6630	0.0001	0.514	***
J. montana	1	0.749	0.9795	0.993	0.4308	-0.726	0.9795	0.2396	0.0369	0.091	N.S.
	2	-	-	-	-	-	-	-	-	-	-
	3	0.863	0.7641	0.969	0.5077	-0.856	0.7615	0.2546	0.0176	0.029	N.S.
K. glauca	1	1.408	0.0179	1.451	0.0128	-1.411	0.0077	0.5081	0.0002	0.318	**
	2	1.315	0.0205	1.440	0.0128	-1.320	0.0487	0.2450	0.0195	0.134	N.S.
	3	1.457	0.0154	1.487	0.0026	-1.464	0.0051	0.5135	0.0001	0.438	***
M. minima	1	1.846	0.0026	1.738	0.0000	-1.842	0.0000	0.6359	0.0001	0.436	***
	2	2.114	0.0026	1.671	0.0000	-2.120	0.0000	0.4068	0.0003	0.273	*
	3	1.996	0.0026	1.803	0.0000	-1.959	0.0000	0.5666	0.0001	0.375	***
M. stricta	1	1.238	0.0913	1.129	0.1763	-1.218	0.1049	0.4229	0.0006	0.379	***
	2	1.490	0.0096	1.603	0.0017	-1.383	0.0186	-0.2757	0.9741	0.364	***
	3	1.628	0.0025	1.675	0.0013	-1.619	0.0030	0.3274	0.0018	0.410	***
P. arenarium	1	2.348	0.0026	1.904	0.0000	-2.347	0.0000	0.5794	0.0001	0.438	***
	2	2.005	0.0026	1.732	0.0000	-1.929	0.0000	0.4782	0.0001	0.295	**
	3	1.776	0.0026	1.677	0.0000	-1.743	0.0000	0.6237	0.0001	0.390	***
S. canescens	1	1.297	0.0590	1.276	0.0692	-1.294	0.0590	0.3335	0.0064	0.163	N.S.
	2	1.182	0.1385	0.914	0.7256	-1.225	0.1179	-0.1963	0.9135	0.013	N.S.
	3	1.682	0.0026	1.565	0.0026	-1.689	0.0000	0.4104	0.0001	0.312	**
S. conica	1	1.689	0.0007	1.476	0.0070	-1.623	0.0020	0.5665	0.0001	0.541	***
	2	1.734	0.0003	1.838	0.0000	-1.606	0.0020	0.4969	0.0001	0.444	***
	3	2.153	0.0002	1.875	0.0002	-2.128	0.0000	0.4157	0.0001	0.328	**
S. otites	1	1.083	0.2564	1.113	0.1667	-1.090	0.2333	0.3099	0.0047	0.180	N.S.
	2	1.962	0.0026	1.872	0.0000	-1.966	0.0000	-0.0621	0.6666	-0.023	N.S.
	3	1.233	0.0769	1.193	0.1385	-1.239	0.1154	0.2341	0.0237	0.208	N.S.
S. capillata	1	1.887	0.0026	1.864	0.0000	-1.877	0.0000	0.5893	0.0001	0.395	***
	2	1.344	0.0385	1.132	0.1821	-1.344	0.0308	0.4436	0.0001	0.169	N.S.
	3	1.395	0.0179	1.283	0.0487	-1.399	0.0154	0.2269	0.0277	0.210	N.S.
T. racemosus	1	1.048	0.3077	1.143	0.1897	-1.041	0.3487	-0.0664	0.6857	-0.015	N.S.
	2	1.297	0.0615	1.355	0.0359	-1.287	0.0744	0.5948	0.0001	0.199	N.S.
	3	1.143	0.1735	1.124	0.1919	-1.137	0.1825	0.3249	0.0045	0.270	*
all seedlings	1	1.734	0.0005	1.710	0.0005	-1.575	0.0032	0.5894	0.0001	0.611	***
	2	2.15	0.0002	2.009	0.0000	-1.860	0.0002	0.4994	0.0001	0.484	***
	3	2.235	0.0002	2.075	0.0000	-2.0320	0.0000	0.4775	0.0001	0.530	***

Chapter 4

Testing the potential seed availability in dung samples: comparison of two seedling emergence methods

Seedling emergence from dung samples in climate room.

Abstract

To optimize the estimation of species composition and viable seed content of herbivore dung and to make different approaches comparable, two seedling emergence methods are evaluated. The Ter Heerdt method (TH) employs concentrated samples, which potentially increases and accelerates seedling emergence, as shown for soil samples (95 % of all seedlings emerged within 6 weeks). Samples are kept under controlled conditions (glasshouse or climate room). Secondly, a common garden method (CG) was applied by use of unconcentrated samples. Seasonal changes could fulfill the germination requirements of a broad species spectrum (experiment duration approx. 15 months). The methods were tested by use of sheep dung samples, collected during a 6-day grazing period in threatened dry grassland (Allio-Stipetum capillatae).

Both methods proved largely similar in species composition (QS = 0.81) and viable seed content (QS = 0.69). More species (e.g. monocotyls) and a higher seedling emergence of hard-seeded species (Fabaceae and Cistaceae) were found by use of the CG method. Besides a higher emergence of some small-seeded winter annuals, few other species emerged exclusively by use of the TH method. Nevertheless, all species detected by a single method were found in low individual numbers (≤ 4).

Depending on research interest and availability of space and time, the most appropriate method can be chosen. If the main focus is on the species composition, unconcentrated dung samples can be studied by use of CG. In case the overall viable seed content is more important and/or a shorter time period is available, TH serves as a suitable alternative.

Introduction

Herbivory by large grazers leads to endozoochorous dispersal of many plant species (Ridley 1930). Selective grazing, induced by palatability (Olff and Ritchie 1998; Pakeman et al. 2002), availability (White and Trudell 1980; Pakeman et al. 2002) and animal density (Kausrud et al. 2006), might cause unequal consumption and, as a result, disproportional dispersal of certain species over others. Moreover, endozoochory itself is somewhat selective (Malo and Suárez 1995); not all seed species survive the effects of ingestion and gut passage (Welch 1985). Generally, small seeds (e.g. Malo and Suárez 1995; Mouissie et al. 2005b) and/or hard-coated seeds (Cocks 1988) have a higher

recovery chance than larger or soft-coated seeds. However, germinable seeds of large non-dormant *Triticum aestivum* (5 x 3 mm) have been detected as well, in red deer and cattle dung (Malo and Suárez 1995). Thomson et al. (1990) also found that higher seed numbers affected survival probability, though other studies did not show comparable results (Jones and Simão Neto 1987).

To obtain more insight into the above-mentioned mechanisms, parameters like species composition and viable seed content of faecal material need to be known. Techniques like those originally developed to analyze soil seed banks are now being used to test the seed content of dung substrate for a broad range of large herbivores (e.g. white-tailed deer, Myers et al. (2004); horse, Cosyns and Hoffmann (2005); cattle, pony and sheep, Mouissie et al. (2005a), sheep, Eichberg et al. (2007)). One often used method is the extraction technique, in which seeds are physically extracted from the sample by a combination of sieving, flotation, or air-flow separation, followed by manual selection (Ball and Millner 1989). Since many unviable seeds are detected as well (Brown 1992), this technique was excluded here. A frequently applied alternative is the seedling emergence method (Roberts 1981), in which the seed content is evaluated on the basis of the number of seedlings that develop. In contrast to extraction, only the germinable fraction of seeds in dung can be detected (Brown 1992). However, if viable seeds fail to emerge, i.e. remain dormant, or die before detection, germination tests may likewise be inaccurate (Malo 2000). Several variants of the seedling emergence method have been designed, possibly differing in their ability to detect viable seeds (Malo 2000).

One variant was introduced by Ter Heerdt et al. (1996). In this method the samples are concentrated, which could cause greater gas exchange and diminished water potential of the soil (Fenner 1985). This could increase the appearance of seedlings, as found by Bossuyt et al. (2000) and consequently requires shorter usage of glasshouse or climate room space.

However, Traba et al. (1998) demonstrated that concentration of samples could result in a significantly lower seedling appearance, especially in the case of species with smaller seeds. Nevertheless, from concentrated and unconcentrated samples an equal number of species emerged. Secondly, temperature and light regulation, as applied in a glasshouse or climate room, could negatively affect the germination results, whereas fluctuations of abiotic parameters might fulfill specific germination requirements of

different (dormant) species (Poiani and Johnson 1988; Baskin and Baskin 1989). A seedling emergence experiment that is conducted outdoors does undergo these abiotic fluctuations as a result of daily and seasonal changing conditions.

Methological comparisons could illustrate the relative correctness of different procedures for estimating the survival of seeds after ingestion and additionally indicate the potential contribution of endozoochory to seed dispersal. The objective of this study was to compare two methods and to find an accurate way to assess the viable seed content of herbivore dung. The methods compared were (i) the Ter Heerdt method (concentration and fixed 'optimal' abiotic conditions (TH)) and (ii) an outdoor seedling emergence method using unconcentrated samples exposed to seasonal changes (here termed a Common Garden experiment (CG)).

Materials and methods

Dung collection

Dung samples were taken from four tamed male Rhoen sheep, which grazed for six days (Oct. 2004) in a species-rich mid-successional Allio-Stipetum capillatae stand (part of European Union Fauna-Flora-Habitat directive area 'Griesheimer Düne und Eichwäldchen', Northern upper Rhine valley Central Germany, 8°39´E, 49°53´N). During the grazing period dung were collected, by means of faecal collecting bags (Brenner et al. 2004). The material was air-dried at room temperature (e.g. Malo and Suárez 1995; Constible et al. 2005; Eichberg et al. 2006). Dung dries up under field conditions as well; therefore this treatment simulates the natural conditions of the seeds (Malo and Suárez 1995). Besides, drying was needed to define weight of dung as reference quantity, allowed a synchronous start of the experiment with samples from different sampling days and minimized fungal and bacterial growth until further processing. Per day, per sheep sub-samples of 50 g dry weight (24 in total) were taken and crushed by hand.

Method 1 Ter Heerdt

The following steps were undertaken to prepare samples before the actual germination period was started. The samples were concentrated by washing them through a fine sieve (0.212 mm) by use of running water (10 min. per sample); as a result, fine organic material was partly removed. Aluminium trays (15 cm x 25 cm) were filled with 2 cm of

steam-sterilized potting soil and 4 mm sand (to distinguish between sample and potting soil); each concentrated sample was divided into two sub-samples and poured into a 2- to 3-mm-thick layer, on top of the two other layers (Ter Heerdt et al. 1996). In total, 48 sub-samples were established in a climate room with a day/night temperature of 25/18 °C and 16 h light availability per day. Water was provided daily up to field capacity.

After 2 months, when no new seedlings emerged, the samples were dried for a week and stirred (Ter Heerdt et al. 1996). Seedling emergence was recorded throughout another 3 months. In order to reduce the abundance of flies, nematodes (Steinernema feltiae (Sf), Schneckenprofi) were added to the samples. Results of each two sub-samples were pooled.

Method 2 Common garden experiment
A 10- to 15-mm sample layer was directly established on a 2-cm layer of steam-sterilized sandy soil (from the study area) in aluminium trays (15 cm x 25 cm). Small logs in the tray bottom, covered with fine gauze, improved rain water drainage and prevented seeds from being washed out. Trays were placed within an outdoor ground construction, developed for germination tests. The construction's upper side is covered with fine-meshed gauze, preventing the entry of seeds and insects. To control for air-borne seed input seven soil-only trays were similarly positioned. Temperature and light were not regulated; consequently, samples were affected by daily and seasonal fluctuations (Mean T_{mean} = 12.8 °C, 109 days T < 0.0 °C, 123 days T > 25.0 °C (Internet 1)). To prevent samples from drying out, water was provided frequently. Bryophyte growth and crust formation were reduced by stirring the dung material regularly. To limit the abundance of flies, Sf nematodes were added twice. The experiment was conducted throughout a 15-month period.

Seedlings were identified by use of determination literature (Csapody 1968; Muller 1978; Hanf 1999), counted and removed regularly. The nomenclature follows Wisskirchen and Haeupler (1998). Unidentified individuals were transplanted into bigger pots, until determination was possible.

Data analysis

To determine the degree of similarity of both seedling emergence methods, Sørenson's Quotient of Similarity = (Sørenson 1948) was calculated according to the following formula:

$$QS = \frac{2C}{A+B} * 100$$

In this equation, *C* is the sum of shared abundances and *A, B* are the sums of abundances in individual sample units. The Sørenson Quotient was originally applied to presence-absence data, but works equally well with quantitative data (McCune and Mefford 1999). A value of 1.0 indicates identical results, while a value of 0.0 shows both datasets have no elements in common.

Also, a species-specific comparison was made. For each species which emerged via both methods, the number of seedlings was log-transformed and data were compared by use of a paired t-test.

Results

With time, seedling emergence of both methods clearly decreased in number. The experiments were stopped after a period in which only sporadically new seedlings were recorded (TH 5 months, CG 15 months, Fig. 4.1). In total, 4804 seedlings of 30 taxa (TH) and 4068 seedlings of 34 taxa (CG) could be distinguished (Table 4.1). From the control trays (CG) three *Cardamine hirsuta* seedlings emerged (regarded as contamination). A more or less similar number of taxa with emergence rate > 5 seedlings was found via both methods (TH 17 taxa, CG 19 taxa; resp. 99.3 % and 99 % of all detected seedlings).

After 6 weeks, via TH 82 % of all seedlings and 97 % of all species that were found during the course of the experiment had emerged. CG showed three seedling emergence peaks: directly after the experiment had started (June) and one year later in spring and autumn. Via CG 82 % of all species could be detected after 7 weeks, whereas one year later (46 weeks) another 18 % was found (Fig.4.2). Seedling

emergence rates were highest during the first three months (68 %); seedlings emerged more gradually compared to TH (Fig. 4.1).
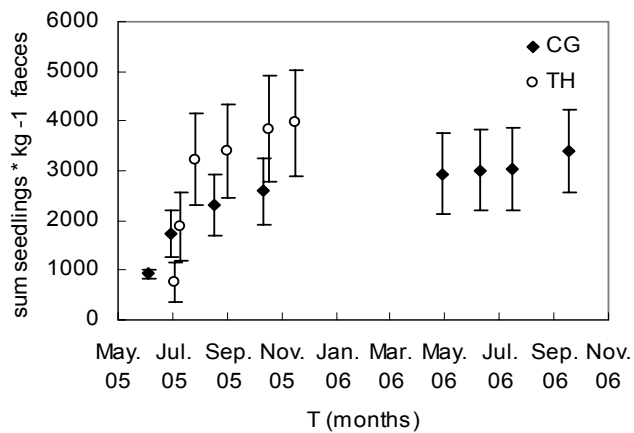
Figure 4.1 Time span of seedling emergence (number of seedlings kg^{-1} sheep dung), via Ter Heerdt (TH, 5 months) and common garden (CG, 15 months). For both methods, sheep n = 4. Error bars indicate standard error.
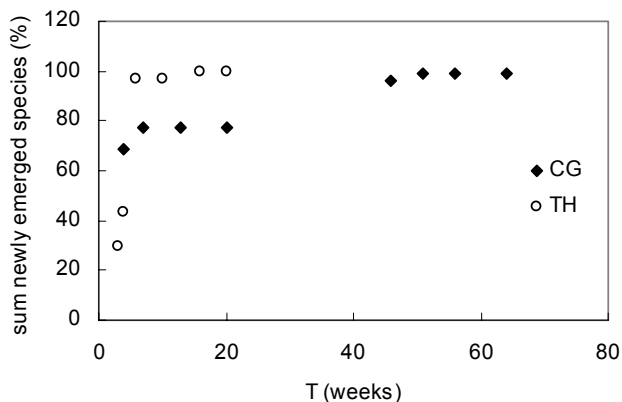
Figure 4.2 Time span in which species newly emerged via Ter Heerdt (TH, 5 months) and common garden (CG, 15 months). Per point, sum of all newly emerged species (%) over all samples is shown.

The results obtained with the two methods show large similarities: among their five most commonly occurring species, four identical species were detected, although the emergence rank order in terms of most frequently found plants was in part different between the two methods (*Arenaria serpyllifolia* (TH, CG: 1, 4); *Verbascum phlomoides* (2, 1); *Helianthemum nummularium* (3, 3); *Trifolium arvense* (5, 2)). Additionally, *Potentilla argentea* (TH, 4) and *T. campestre* (CG, 5) emerged frequently, but did not reach high emergence numbers under the respective other treatment (Table 4.1).

Seedlings of these most frequently detected species accounted for 84 and 86 % (TH, CG) of all emerged seedlings, respectively.

Table 4.1 Species list and number of emerged seedlings found with each method (mean ± S.E.). The two methods had 25 species in common. The mean number of emerged seedlings per method was calculated over 4 sheep, per sheep sample $n = 6$ (total per sheep 300 g dung) was investigated. Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant.

Species	Family	TH (mean ± S.E.) nrs	TH (mean ± S.E.) %	CG (mean ± S.E.) nrs	CG (mean ± S.E.) %	TH ≠ CG t-value	P
Better or only germinated via TH:							
Arabis glabra	Brassicaceae	12.3 ± 2.1	1.1 ± 0.21	2.8 ± 1.2	0.24 ± 0.06	3.87	*
Arenaria serpyllifolia agg.	Caryophyllaceae	420 ± 95.6	36.6 ± 6.6	120 ± 26.3	14.2 ± 5.2	5.68	*
Cerastium semidecandrum	Caryophyllaceae	1.0 ± 0.4	0.08 ± 0.04	.	.	2.72	0.072~
Potentilla argentea agg.	Rosaceae	77.3 ± 23.9	6.3 ± 1.5	42.5 ± 8.5	4.4 ± 0.75	2.59	0.081~
Urtica dioica	Urticaceae	26.3 ± 13.5	2.5 ± 1.6	13.5 ± 7.0	1.5 ± 0.90	2.99	0.058~
Veronica arvensis	Scrophulariaceae	42.5 ± 10.1	3.8 ± 0.89	3.0 ± 0.9	0.30 ± 0.08	26.71	***
Better or only germinated via CG:							
Carex hirta	Cyperaceae	.	.	1.0 ± 0.4	0.10 ± 0.05	2.72	0.072~
Helianthemum nummularium	Cistaceae	86.3 ± 26.0	6.9 ± 0.78	156 ± 41.3	15 ± 1.6	13.19	***
Medicago minima	Fabaceae	0.3 ± 0.3	0.04 ± 0.04	2.3 ± 0.9	0.31 ± 0.18	7.65	**
Trifolium arvense	Fabaceae	76.8 ± 17.6	6.7 ± 1.3	157 ± 34.2	16.8 ± 4.0	6.38	**
Trifolium campestre	Fabaceae	21.5 ± 6.8	1.8 ± 0.47	93.3 ± 26.6	9.6 ± 2.6	22.32	***
No sig. difference:							
Achillea millefolium	Asteraceae	3.8 ± 1.1	0.30 ± 0.06	1.5 ± 0.3	0.17 ± 0.04	2.06	N.S.
Agrostis capillaris	Poaceae	2.3 ± 0.9	0.18 ± 0.05	1.0 ± 0.6	0.14 ± 0.08	1.08	N.S.
Agrostis viridis	Poaceae	0.8 ± 0.3	0.08 ± 0.03	0.8 ± 0.3	0.07 ± 0.04	0.32	N.S.
Asperula cynanchica	Rubiaceae	0.3 ± 0.3	0.04 ± 0.04	.	.	1.00	N.S.
Berteroa incana	Brassicaceae	0.3 ± 0.3	0.04 ± 0.04	.	.	1.00	N.S.
Calamintha acinos	Lamiaceae	.	.	0.3 ± 0.3	0.01 ± 0.01	1.00	N.S.
Carex praecox	Cyperaceae	.	.	0.5 ± 0.5	0.03 ± 0.03	1.00	N.S.
Chenopodium album agg.	Chenopodiaceae	17.3 ± 8.3	1.8 ± 1.2	10.5 ± 3.8	1.3 ± 0.72	0.48	N.S.
Convolvulus arvense	Convolvulaceae	.	.	0.5 ± 0.3	0.06 ± 0.04	1.73	N.S.
Conyza canadensis	Asteraceae	22.0 ± 7.9	1.7 ± 0.44	19.0 ± 2.0	2.2 ± 0.47	0.13	N.S.
Diplotaxis tenuifolia	Brassicaceae	0.3 ± 0.3	0.01 ± 0.01	0.3 ± 0.3	0.03 ± 0.03	0.00	N.S.
Geranium molle	Geraniaceae	0.5 ± 0.5	0.07 ± 0.07	.	.	1.00	N.S.
Hypericum perforatum	Hypericaceae	1.3 ± 0.3	0.11 ± 0.01	1.8 ± 0.8	0.20 ± 0.11	0.25	N.S.
Koeleria macrantha	Poaceae	.	.	0.3 ± 0.3	0.04 ± 0.04	1.00	N.S.
Luzula campestre	Juncaceae	0.5 ± 0.5	0.04 ± 0.04	0.3 ± 0.3	0.03 ± 0.03	1.00	N.S.
Medicago falcata	Fabaceae	0.5 ± 0.5	0.07 ± 0.07	1.5 ± 0.6	0.19 ± 0.11	2.17	N.S.
Petrorhagia prolifera	Caryophyllaceae	0.8 ± 0.3	0.09 ± 0.07	0.5 ± 0.3	0.08 ± 0.08	1.00	N.S.
Poa angustifolia	Poaceae	4.3 ± 1.0	0.43 ± 0.15	3.5 ± 0.3	0.40 ± 0.09	0.49	N.S.
Rubus caesius	Rosaceae	.	.	0.3 ± 0.3	0.03 ± 0.03	1.00	N.S.
Rumex acetosella s.l.	Polygonaceae	15.8 ± 6.0	1.2 ± 0.39	6.0 ± 1.7	0.68 ± 0.23	1.85	N.S.
Sedum acre	Crassulaceae	0.3 ± 0.3	0.01 ± 0.01	1.5 ± 0.9	0.21 ± 0.15	1.51	N.S.
Setaria viridis	Poaceae	.	.	0.3 ± 0.3	0.03 ± 0.03	1.00	N.S.
Silene conica	Caryophyllaceae	.	.	0.3 ± 0.3	0.01 ± 0.01	1.00	N.S.
Sisymbrium altissimum	Brassicaceae	.	.	0.5 ± 0.3	0.06 ± 0.04	1.73	N.S.
Stellaria media	Caryophyllaceae	3.8 ± 2.2	0.26 ± 0.10	0.5 ± 0.5	0.06 ± 0.06	1.76	N.S.
Thymus pulegioides s.l.	Lamiaceae	4.3 ± 0.9	0.40 ± 0.12	5.3 ± 2.9	0.76 ± 0.53	0.11	N.S.
Verbascum phlomoides	Scrophulariaceae	368 ± 195	27.0 ± 10.9	354 ± 185	29.1 ± 12.0	-0.48	N.S.
Vicia lathyroides	Fabaceae	0.8 ± 0.5	0.05 ± 0.03	.	.	1.65	N.S.
Agrostis sp.	Poaceae	.	.	0.3 ± 0.3	0.04 ± 0.04		
unidentified		1.0 ± 0.6	0.08 ± 0.05	10.8 ± 4.9	0.95 ± 0.33		
Caryophyllaceae		.	.	0.3 ± 0.3	0.04 ± 0.04		
Fabaceae		.	.	0.5 ± 0.3	0.07 ± 0.04		
Poaceae		.	.	2.3 ± 0.9	0.23 ± 0.11		
total nr.of seedlings		4804		4068			
total nr.of taxa		30		34			

The two methods had 25 species and 3082 seedlings (minimum seedling number of each species present in both methods) in common. Both species composition (QS = 0.81) and seedling density (QS = 0.69) showed a large degree of similarity. Additionally, no significant difference in seedling emergence rate was found (data log-transformed, paired t-test, P = 0.54). A Pearson correlation shows a significant positive association between the seedling densities of both methods per species (r = 0.80, P < 0.001) (Fig. 4.3).
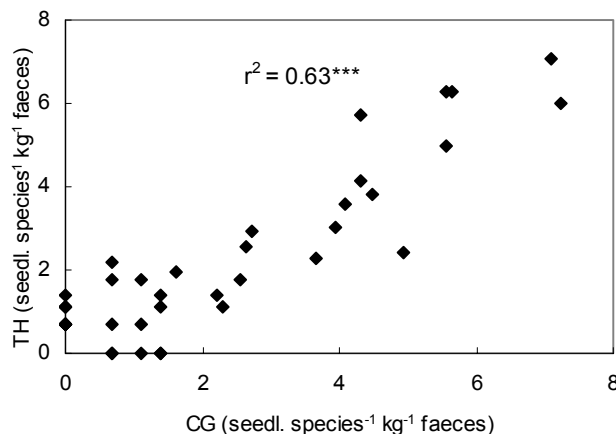
Figure 4.3 Coefficient of determination (r^2) between both emergence methods, shown per number of seedlings species^{-1} kg^{-1} dung. Species n = 40. Level of significance; *** = P < 0.001.

In total, five herbal 'single-method species' (= species found to emerge by only one method) were recorded in TH (*Asperula cynanchica, Berteroa incana, Cerastium semidecandrum, Geranium molle, Vicia lathyroides*), whereas four herbs (*Convolvulus arvense, Calamintha acinos, Sisymbrium altissimum, Silene conica*), one hemi-shrub (*Rubus caesius*) and four graminoids (*Carex hirta, C. praecox, Setaria viridis, Koeleria macrantha*) emerged only in CG (Table 4.1). Dissimilarity between the two methods on the level of species composition was shown by the relative number of monocotyl species (CG 23.5 % vs. TH 13.3 %). This difference was not found for mono- and dicotyl seedling numbers; both methods resulted in equal relative numbers (mono CG: 0.7 %, TH: 0.6 %; dico CG: 99.3%, TH: 99.4 %).

The higher total seedling content of TH was predominantly caused by a three-fold higher *Arenaria serpyllifolia* emergence rate (P = 0.01) (Table 4.1). Also significantly more *Veronica arvensis* (P < 0.001) emergents were recorded. Despite no significant

difference, *Potentilla argentea* (*P* = 0.08) and *Urtica dioica* (*P* = 0.06) were detected more frequently as well. However, three other species, *Helianthemum nummularium* (*P* < 0.001), *Trifolium arvense* (*P* = 0.01) and *T. campestre* (*P* < 0.001) occurred at significant lower rates.

Discussion

Although no overall significant differences were found between the two methods, seedlings emerged more gradually in time from CG (experimental duration TH and CG: 5 and 15 months). The two dominant differences in the experimental setups (concentration treatment and abiotic conditions), probably both contributed to this more gradual emergence. The thicker sample layers of CG samples reduced the number of seeds close enough to the sample surface to germinate. Regular mixing re-located many more deeply positioned seeds to the sample surface and enabled them to emerge as well (Ter Heerdt et al. 1996). Nevertheless, as is comparable to Roberts (1981), in the second year a relatively small proportion of seeds germinated from CG (Fig. 4.1). Besides, due to climatic variation the species-specific germination requirements were only periodically fulfilled in CG samples.

Seedling density

As mentioned above, the detected viable seed contents were generally similar, although slightly more seedlings (not significant) emerged from TH. Both Ter Heerdt et al. (1996) and Bossuyt et al. (2000) found a significantly higher seedling emergence rate in concentrated soil seed bank samples from marsh and forest ecosystems, respectively. On the species level, however, we recorded some significant differences. First of all, several small-seeded winter annuals (*A. serpyllifolia*, *Arabis glabra, V. arvensis*) showed higher germination rates via TH. Bossuyt et al. (2000) measured higher germination rates of small-seeded species (<1 mg) as well. By contrast, Traba et al. (1998) found that concentrating soil samples from a Mediterranean dehesa led to reduced seedling emergence of smaller-seeded species. Since our samples were concentrated by use of an even larger-meshed sieve (0.212 mm compared to Traba's 0.1 mm), it seems that small seeds were not reduced in number by the concentration procedure. All three species are soil seed bank species in open inland sand ecosystems (Eichberg et al.

2006) with relatively broad ecological amplitude, which are expected to survive the seasonal changes of CG. However, high daytime temperatures (max.T_{max} = 35.8 °C) might have caused some dehydration even though CG samples were watered frequently. Pemadasa and Lovell (1975) found evidence, for five dune annuals, that even a short period of dehydration (12 h) could cause a one week delay in germination. Additionally, seed burial was shown to have a significant inhibitory effect on germination (Pemadasa and Lovell 1975) of primarily small-seeded species (Froud-Williams et al. 1984), e.g. *A. serpyllifolia* (Pons 1991).

On the other hand, significantly more individuals of several hard-seeded species (*T. arvense, T. campestre*, *H. nummularium)* emerged from CG samples. Both families of Fabaceae and Cistaceae show dormancy (Thanos et al. 1992; Thompson and Booth 1993), which could be broken by strong (seasonal) temperature fluctuations (Pritchard et al. 1988; Thanos et al. 1992). For these species the more extreme abiotic fluctuations of CG probably acted as a signal to induce water uptake and germinate (Van Assche et al. 2003). Although *H. nummularium* did not show a germination difference after heat treatment during Thanos' investigations, seeds may have been stimulated by the larger temperature differences during the CG experiment (min. T_{min} = - 12.9 °C, max.T_{max} =35.8 °C).

Species composition
The species composition found with both methods shows a high similarity as well (QS = 0.81). All 'single method species' (species detected by only one method) emerged in very low densities (most species were represented by one individual). Taking sub-samples (one for each method) out of an original sample might have resulted in seed abundance within a single sub-sample whereas other samples are lacking this species; especially for species which are represented by only one or a few seeds in the original samples, this could have taken place relatively easily.

However, some more monocotyl species were found in CG. Next to possible seed absence in TH samples, the stronger abiotic fluctuations working on CG samples could have stimulated emergence of those species. Schütz (2000) found dormancy of many Carices to be broken by low-temperature stratification. Moreover, the probability of germination was significantly higher after cold-wet stratification, in light and after

fluctuating temperatures. The potential emergence of *Setaria viridis* is affected by duration of after-ripening and secondary (summer) dormancy, both regulated by seasonally and diurnally varying soil oxygen, water and temperature signals (Dekker 2003). Finally, Dixon (2000) detected the highest germination rates of *Koeleria macrantha* after the highest levels of pre-heating and -chilling. Seasonal changes in CG may have periodically fulfilled the species-specific germination requirements, whereas this was not the case in TH.

Overall, despite some differences it seems that both methods, in comparison to each other, provide a reliable estimate of species composition and germinable seed numbers of sheep dung, in our model ecosystem. Depending on the main research interest (species composition and/or viable seed content) and/or the availability of space and time, the most appropriate method can be selected.

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Chapter 5

Impact of endozoochorous seed dispersal, dung deposition, moss disturbance and dung beetle activity on recruitment of plant species in open sand-grasslands

Experimental sheep dung deposition with three dung beetle holes.

Abstract

Various types of herbivore activity, such as endozoochorous seed dispersal, dung deposition, disturbance of the moss layer (*Hypnum cupressiforme*), and dung removal by the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758) probably affect the fine-scale phytodiversity of inland sand-grasslands. An input of seeds (mostly target species) and alteration of micro-site conditions could promote establishment of target species and increase species richness. Alternatively, seed dispersal of more competitive species, e.g. graminoids, may enhance ruderalisation, which could seriously threaten habitat-specific species of nutrient-poor ecosystems. A multi-factorial experiment was conducted in stands with different productivity levels (from relatively low to higher values). After well-developed source target communities — Koelerion glaucae (Kg), Armerio-Festucetum trachyphyllae (AF), Allio-Stipetum capillatae (AS) — had been grazed by sheep, their dung was collected and analysed, and its effects tested together with the other treatments established in sink areas.

In total, viable seeds of 59 taxa could be detected from Kg, AF and AS dung; 23 taxa were able to emerge under field conditions. Although relatively few dung-borne seedlings were found, many (threatened) target species were represented. Far more herbs than grasses emerged, both from germination tests and in the field. The target species *Helianthemum nummularium*, which was absent in the sink area, became successfully established from dung. In the most productive plots a few dung-borne individuals of competitive graminoid species were detected.

On the seedling level several treatment effects could be distinguished. Moss disturbance stimulated emergence from especially herbs out of dung and soil, which increased fine-scale species richness in mid-productive AF plots. Seedling emergence in the most productive AF plots seemed less affected. Dung deposition suppressed the total seedling emergence. Dung beetle activity could reverse this effect: after complete removal of exposed dung samples and some topsoil disturbance in low-productive Kg plots, especially disturbance species *Oenothera biennis* and *Polygonum aviculare* emerged. In the case of low-productive Kg and mid-productive AF plots, dung deposition positively affected fine-scale species richness of emerging seedlings.

On the level of the total vegetation, mid-productive AF plots were positively affected by moss disturbance; the presence of herbal species was especially stimulated. Dung

deposition reduced their abundance. Graminoid competitors were mostly affected in time; treatments hardly altered their presence. However, both treatments increased the total species richness. By contrast, in the most productive AF plots both treatments initially suppressed phytodiversity and plant density. Dung deposition at first reduced competing species such as *Carex hirta* and *Cynodon dactylon.* But subsequently those same competitors benefited, presumably owing to reduced competition and nutrients leaching out of the dung.

Results suggest that the effects of different herbivore activities on fine-scale species richness at least partly depend on productivity of existing vegetation. Non-ruderalised early successional stands can profit from these herbivore-initiated processes, whereas more productive stands might need more intensive herbivore activity in order to reduce the abundance of (graminoid) competitors, create micro-sites and eventually increase species richness.

Introduction

An increase of fine-scale species richness and the establishment of target species benefit conservation and restoration sites (Mouissie et al. 2005a). Herbivores, e.g. sheep, can contribute to those processes by increasing the availability of seeds (Eichberg et al. 2007) and micro-sites (Bullock et al. 1994; Bakker and Olff 2003), two determinants of recruitment (Klinkhamer and de Jong 1989; Eriksson and Ehrlén 1992).

Grassland species often persist only briefly in the soil seed bank (Thompson et al. 1997). Sowing experiments, on the other hand, documented the successful establishment of numerous species (e.g. Kiviniemi and Eriksson 1999; Zobel et al. 2000; Jacobsson and Eriksson 2000), which could lead to an increased species richness as has been found, e.g., in oak savannah grassland (Tilman 1997; Foster and Tilman 2003). Herbivores can (endozoochorously) disperse seeds of many plant species (e.g. Ridley 1930; Welch 1985; Pakeman et al. 2002; Mouissie et al. 2005b). The species composition of these endozoochorously dispersed seeds is one of several factors determining the effect of herbivores on vegetation species richness. Grazing of well-developed grassland target communities optimizes epizoochorous transport of target species (Chapter 2; Wessels et al. 2008), whereas Cosyns and Hoffmann (2005) showed a positive correlation between plant species abundance in a grazing area and

dung seed content. In line with those results it is expected that the use of a target community as source positively affects the species composition of endozoochorously dispersed seeds, potentially stimulating recruitment of favourable species.

Species-specific survival after passage through a herbivore's digestive tract 'filters' the composition of viable seeds and reduces the original number of species. Generally, smaller-seeded species have a better survival chance than larger-seeded species (e.g. Pakeman 2001; Cosyns & Hoffmann 2005; Couvreur et al. 2005). Additionally, dormancy of some hard-coated seeds, e.g. seeds of Fabaceae and Cistaceae, may be broken after digestion (Russi et al. 1992b; Ramos et al. 2006; Chapter 4, Wessels and Schwabe 2008). Those species are probably represented by relatively high seed numbers, whereas species with larger seeds and/or no hard seed coat can be under-represented among dung-transported seeds.

Nevertheless, only actual emergence from dung-embedded seeds can effectively act on vegetation species richness. The species composition of dung-borne seedlings differed greatly among studies (e.g. Welch 1985; Malo and Suárez 1995; Mouissie et al. 2005a; Cosyns et al. 2005, 2006; Eichberg et al. 2007). Next to the species composition of endozoochorously transported seeds, micro-site conditions could determine their colonization ability, as is known for soil-embedded seeds. Generally, higher productivity facilitates the abundance of competitors, and suppresses colonization of "fugitive" species, whereas less productive sites could show an opposite response (Kondoh 2001). Within a not ruderalised early successional Koelerion glaucae stand with low cover of vascular plant species, limited light competition and high temperature fluctuations target species of meso- to oligotrophic habitats have emerged from sheep dung, despite the presence of large amounts of viable seeds of graminoid competitors and other non-target species in the dung seed bank (Eichberg et al. 2007). In contrast, within species-poor perennial grass-dominated dune grassland (compared to the above-mentioned Kg conditions, probably higher cover of vascular plant species, greater light competition, and smaller temperature fluctuations near the soil) only common grassland species, mostly graminoids, emerged from cattle and horse dung. Viable seeds of rare species were abundant but did not emerge (Cosyns et al. 2006). Consequently, colonization from dung and local productivity might interactively affect species richness.

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The physical presence of dung is also likely to affect micro-site conditions. It can reduce the availability of space for seedlings to emerge from the soil; fewer seedlings were detected in plots with pellets, compared to control plots (Eichberg et al. 2007). Additionally, dung deposition could reduce established vegetation. Yet such suppression might enable other species to establish, which could increase (local) species richness, as found in ruderalised dune grassland (Cosyns et al. 2006) and early successional Koelerion glaucae (first year; Eichberg et al. 2007).

Dung deposition can also affect micro-site conditions by locally fertilizing the soil (e.g. Williams and Haynes 1995). Increased nutrient availability probably stimulated emergence of *Cerastium semidecandrum* and *Festuca ovina* in an alvar limestone grassland (Dai 2000), whereas deposition of goose pellets on salt-marsh vegetation significantly increased the standing crop (Bazely and Jefferies 1985). Adding nutrients to nutrient-poor rabbit-grazed dune swards favoured a few unpalatable perennials, but most annuals declined in frequency (Boorman and Fuller 1982). Nutrient enrichment via dung deposition in sandy grassland could advantage competitive species, at the same time suppressing less competitive (annual) species.

Potential effects of sheep-dung deposition could be reduced by foraging activity of the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758). To provision the larvae with food, adult beetles transport dung pellets into brood chambers which are located relatively deep beneath the soil surface (> 40 cm) (Brussaard 1983). It is unknown whether seeds survive this process (Brussaard pers. comment). In any case, it can be assumed that, at least temporarily, dung-embedded seeds are excluded from the system. On the other hand, digging out tunnels results in the transport of soil substrate to the surface (Brussaard and Visser 1987), which might activate the soil seed bank.

Besides dung deposition, herbivore presence can affect micro-sites by another pathway. Different types of behaviour, e.g. scratching and trampling, can create gaps in vegetation cover (Bakker and van Diggelen 2006), enabling "fugitive" species to persist because of reduced competition (Tilman 1988). Disturbance of moss probably increases the amount of radiation, water, and seeds reaching the soil surface (Keizer et al. 1985). Experimental removal of *Hypnum cupressiforme* var. *lacunosum*, a dominant pleurocarpous moss species in our study area which was observed to form thick layers in more consolidated stands, led to increased seedling emergence in pioneer vegetation

of Koelerion glaucae (Eichberg et al. 2007). Gaps could also affect post-dispersal processes of endozoochorously transported seeds, as shown by Cosyns et al. (2006), who found a higher probability of successful establishment of dung-embedded seeds in sod-cut plots than in controls. Disturbance, in this case of the moss layer, is expected to stimulate seedling emergence from both the soil and dung seed banks and possibly also promotes local species richness.

The aim of this study was to get more insight into the contribution of herbivores (via dung deposition and moss disturbance) and dung beetles (via dung removal and soil disturbance) to recruitment of target species and their effect on small-scale species richness of target communities within open inland sand ecosystems.

Methods

Study area

The experiments were conducted in two open inland sand areas of high conservation value (Fauna-Flora-Habitat directive, Ssymank et al. 1998) located in the northern Upper Rhine valley, central Germany. The region is affected by sub-continental influences with low annual precipitation (650 mm) and high mean annual temperatures (9.9 ºC). Area 1, the Nature Protection Area 'Ehemaliger August-Euler-Flugplatz von Darmstadt' (8°35´E, 49°51´N), is a flat, almost treeless, 70-ha area with primarily calcareous sandy soils. Besides well-developed stands of Koelerion glaucae (Kg) and Armerio-Festucetum trachyphyllae (AF), some ruderalised parts dominated by graminoid competitors (e.g. *Cynodon dactylon*, *Carex hirta*) are present. Area 2, the Nature Protection Area 'Griesheimer Düne und Eichwäldchen' (8°39´E, 49°53´N) consists of a 48-ha sand dune area with well-developed stands of mainly Allio-Stipetum capillatae (AS). Sheep grazing was newly applied in both areas for nature conservation purposes since 1999/2000. The dung beetle *Typhaeus typhoeus* is present in both areas (larger population in Area 1); most of its above-ground activities take place from autumn until early spring.

Dung collection

In each target community (Kg, July 2004; AF, Aug. 2005; AS, Oct. 2004) a well-developed stand was grazed for four to seven days (dependent on available phytomass)

by three or four tamed male Rhon sheep. During the grazing period dung was collected by means of faecal collecting bags (Kg and AS) (Brenner et al. 2004) or collected by hand (AF). In the case of AF, possible seed contamination (due to vegetation contact) was limited by washing the fresh samples with running water. All samples were air-dried in a dark and ventilated room.

Field experiments

	Exp. 1a	Exp. 1b	Exp. 1c
Community dung collected	Koelerion glaucae	Allio-Stipetum	Armerio-Festucetum
Treatments	D - D+	D+ M+ B+- D+ M+ B- D+ M- B+ D+ M- B- D- M+ B+ D- M- B+	D+ M+ B+- D+ M+ B- D+ M- B+ D+ M- B- D- M+ B+ D- M- B+
Relative productivity exp. site	low	medium	high
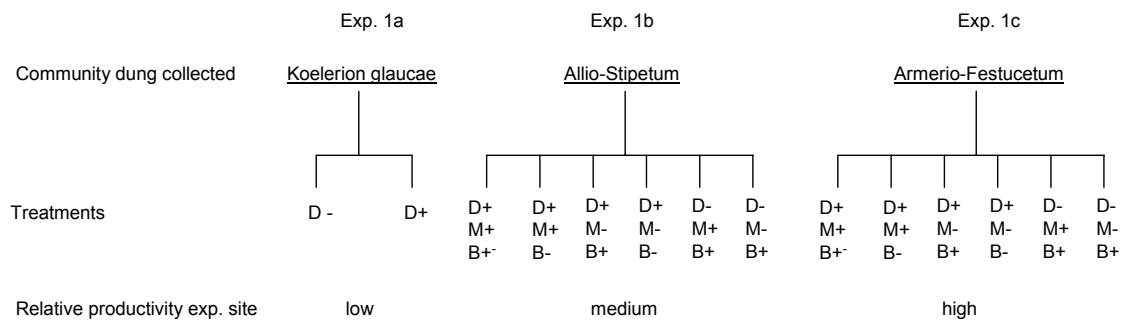
Figure 5.1 Overview of Exp. 1a, b and c, specific treatments (with, without dung (D+, D-); with, without moss (M+, M-); with, without dung beetles (B+, B-)) and relative productivity per experimental site (Peak standing crop phytmass of higher plants was used to define productivity, data S. Bergmann (2004)).

Experiment 1a Koelerion glaucae dung

The emergence of dung-borne seedlings and the impact of dung deposition on total seedling emergence (dung- and soil-borne) were investigated by use of a one-factorial experiment (Fig. 5.1). Investigated factor here was sheep dung (with, without (D^+, D^-)). In Area 2 four sub-areas with relatively unproductive early successional stands were selected. Per sub-area 14 blocks, each containing one sample and one control plot (20 x 20 cm) were established (Oct. 2004). All plots had a relatively low cover of higher plants (< 30 %) and large parts of the soil were covered by mosses (*Hypnum cupressiforme*). After collecting dung (see d*ung collection*), dung pellets were aggregated and homogenised (two grazing periods, three grazing days (2, 3, 4), 200 g dung sheep^{-1} day part $^{-1}$; see *dung collection*). In total, 56 120 g sub-samples were taken. The position of each treatment within a block was randomly determined. After installing the samples the soil was covered (almost) completely with pellets. Pellets were prevented from moving, by fixing them to the soil with 5-mm garden gauze; control plots received the same

cover. Existing vegetation was able to grow through the gauze. Rabbits were excluded from the plots by small exclosures (chicken mesh manchettes). One seedling relevé (Dec. 2004) was made before dung beetles (*Typhaeus typhoeus*) removed sample material from most plots. Afterwards, one final vegetation relevé (April 2005) was made.

Fertilizer effect

To test dung nutrient availability to plants during a short exposure period (dung present 3 weeks – 5 months), vitality measures were conducted by means of the annual herb *Arenaria serpyllifolia*. From each plot (sample/control with more than 5 individuals) all above-ground biomass per individual was sampled (5 – 10 individuals, depending on availability). Per individual the number of flower heads was counted and maximum growth height was measured. After drying (70 °C/24 h) and grinding, the mean N content per plot was analysed (Carlo Erba).

Experiment 1b Allio-Stipetum dung

A multi-factorial design with six different treatments was used to study the impact of a) moss disturbance and dung beetles on the emergence of dung-borne seedlings from AS dung, and b) dung deposition, moss disturbance and dung beetle activity on overall (dung- and soil-borne) seedling emergence and vegetation (Fig. 5.1). Because of intensive impact of dung beetles during Exp. 1a and unexpected activity of *T. typhoeus* within Area 1, the factor '*Dung beetle*' was added. Within a moderately ruderalised Koelerion glaucae/Armerio-Festucetum stand four sub-areas were selected, each of them containing 24 plots (20 cm x 20 cm). In most plots graminoid competitive species were present (e.g. *Carex hirta, Cynodon dactylon*, *Poa angustifolia*) and large parts of the soil were moss-covered (*Hypnum cupressiforme,* cover ≥ 75%). The vegetation was more productive than the vegetation of Exp. 1a.

A mixture of AS dung material was made (200 g dry weight sheep^{-1} day part $^{-1}$, grazing days 2, 3, 4, 5, 6, 7; see also *dung collection*). Dung distribution over sample plots and gauze cover as in Exp. 1a. Additionally, in half of the plots the moss layer was removed by use of a hand rake. Secondly, half of the samples were protected from dung beetle activity by placing small-meshed exclosures (mesh size = 6 mm) over the plots. Also to prevent dung beetles from entering the plots by digging, solid plastic boards

were additionally established below-ground (app. 10 cm deep). Exclosures were only present during the main dung beetle activity period (app. November – March). Finally, all plots were fenced against rabbits by establishing small exclosures (chicken mesh manchettes). Grazing was simulated by clipping all plots once (summer 2006). A summary of the six different treatments is given in Table 5.1.

Table 5.1 Overview of treatments in Exp. 1b (Allio-Stipetum dung), their abbreviations and the number of plots per sub-area per treatment. The factor '*Dung beetle*' was added after starting the experiment due to unexpected activity of *T. typhoeus* within Area 1. As a result, several treatments have a slightly different *n*.

Dung	Moss	Dungbeetle	Abbreviation	*n* plots in sub-area			
				1	2	3	4
+	+	+	D+M+B+	3	3	5	3
+	+	-	D+M+B-	4	4	2	4
+	-	+	D+M-B+	4	4	3	4
+	-	-	D+M-B-	3	3	4	3
-	+	+	D-M+B+	7	7	7	7
-	-	+	D-M-B+	7	7	7	7

In addition to the three vegetation and seedling relevés which were made (June, December 2005, June 2006), the establishment of dung-borne *Helianthemum nummularium* individuals was followed in time for an additional year (total period May 2005 - June 2007).

Experiment 1c Armerio-Festucetum trachyphyllae dung

The design of this experiment was as described for Exp. 1b. (Fig. 5.1). Compared to the first two experiments, it was conducted in the most productive vegetation, a ruderalised Armerio-Festucetum stand (Area 1). Four sub-areas were selected, and each sub-area contained 24 20 cm x 20 cm plots (16 samples and 8 controls). Graminoid competing species (e.g. *Cynodon dactylon*, *Poa angustifolia, Festuca rubra*) and extensive moss cover (*Hypnum cupressiforme,* ≥ 75%). were found within each plot. In total, 64 120-g sub-samples were taken from one aggregated and homogenised dung mixture (1100 g dry weight day $^{-1}$, grazing days 3, 4, 6, 7, 8, 9, 10; see *dung collection*). Similar treatments from Exp. 1b (AS) were applied (Table 5.2). Per sub-area, different treatments were randomly distributed over the plots. Two relevés (May, Oct. 2006) regarding seedling emergence and complete vegetation were made.

Table 5.2 Different treatments Armerio-Festucetum, their abbreviations and the number of plots sub-area^{-1} per treatment.

Dung	Moss	Dungbeetle	Abbreviation	n plots
+	+	+	D+M+B+	4
+	+	-	D+M+B-	4
+	-	+	D+M-B+	4
+	-	-	D+M-B-	4
-	+	+	D-M+B+	4
-	-	+	D-M-B+	4

Experiment 2 Feeding of seeds

To test for seed viability and seedling emergence after gut passage, seed feeding experiments were conducted. Target species *Jasione montana* and *Linum perenne* are currently absent in the vegetation of Area 1, although soil conditions (pH) in the western part of Area 1 would be suitable. *Jasione* seeds are small sized (length 0.6 mm, width 0.3 mm) compared to larger seeded *Linum* (length 3.6 mm, width 1.9 mm) (Internet 1). During the grazing period within a Koelerion glaucae stand (Exp. 1a) each of the four animals was fed 1000 *Linum perenne* seeds and while grazing an Armerio-Festucetum stand (Exp. 1c) three sheep were fed 3500 *Jasione montana* seeds per animal.

From established dung plots in the field or from the germination test not a single seedling from either species was detected. Therefore, it will not be mentioned in the results.

Germination tests

The viable seed content of the three dung types was studied via two germination tests. The seed content of Kg and AS (1400 g and 1200 g dung, respectively) was tested by use of an outdoor method, conducted in the common garden. Samples were crushed and a 10-15 mm layer was directly established on a 2-cm steam-sterilized sandy soil layer (from study area) in aluminium trays (15 cm x 25 cm). Small holes, covered with fine gauze in the tray bottom, improved rainwater drainage and prevented seeds from being washed out. Trays were placed within an outdoor ground construction with a cover consisting of fine-meshed gauze, which obstructs the entry of seeds and insects. As an airborne seed input control, seven soil-only trays were placed. Temperature and light were not regulated; consequently, samples were affected by daily and seasonal

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fluctuations. To prevent samples from drying out, water was provided frequently. Moss growth and crust formation were reduced by stirring the dung material regularly. To limit flies, nematodes were added twice. The experiment was conducted throughout a 21-month (Kg) and 19-month (AS) period.

AS and AF samples (1050 g and 1200 g dung, respectively) were tested by use of the Ter Heerdt method (Ter Heerdt et al. 1996). Additionally, seedling emergence from AS dung was tested by the common garden method as well to allow methodological comparison (Chapter 4; Wessels and Schwabe 2008). Since Ter Heerdt provided a relatively fast alternative to the common garden method, AF was tested exclusively by TH. Samples were concentrated by washing them through a fine sieve (0.2 mm) with running water (10 min. per sample). Trays (15 cm x 25 cm) were filled with 2 cm steam-sterilized potting soil and 4 mm sand (to distinguish between sample and potting soil); each concentrated sample was divided into two sub-samples and poured into a 2- to 3-mm-thick layer on top of the two other layers. In total, 48 sub-samples were established in a climate room with temperature regulation (day (16 h)/night (8 h): 25/18 °C). Water was provided daily. Fly abundance was reduced by use of nematodes. After two months no new seedlings emerged and samples were dried for a week and stirred (Ter Heerdt et al. 1996). Three months later seedling emergence was reduced so dramatically that the procedure was stopped.

All seedlings were identified by use of determination literature (Csapody 1968; Muller 1978; Hanf 1999), counted and removed regularly. Unidentified individuals were transplanted into bigger pots, until determination was possible. The nomenclature follows Wisskirchen and Haeupler (1998).

Data analysis

The impact of dung pellets ('Dung', Exp.1a, b and c), disturbance of the moss layer ('Moss', Exp. 1b and c) and dung beetle activity ('Dung beetle', Exp. 1b and c) in time ('Time') on seedling emergence (total and species-specific) and species richness was tested by mixed linear models, which allowed us to include fixed (above-mentioned) and random factors ('Sub-area' and 'Plot') (Littell et al. 2000). Dung-borne seedlings were first analysed separately, by use of the model described above. Afterwards, the effect of dung deposition and moss disturbance on the total seedling emergence (soil- and dung-

borne seedlings) and total vegetation (sum of dung- and soil-borne plant individuals) was tested by one model. The impact of dung beetle activity was tested separately; only plots with dung were included in this analysis. Since AF plots were not visited by dung beetles and the temporary presence of dung beetle exclosures did not significantly affect the number of plant species or individuals per plot (t-test), the factor 'Dung beetle' was excluded from further analysis within the AF experiment. Mixed linear models were performed by use of SAS 9.1.

Plant species composition of different treatments and its potential change in time was analysed by means of detrended correspondence analysis (PC-ord 4.25). Raw data were log (x+1) transformed to prevent strong influence of dominant species. Analyses were conducted with down weighting and rescaling, the number of segments was 26. In Exp. 1a, the density per species per plot was used, whereas in Exp. 1b and 1c a mean density per species was calculated per treatment.

Results

Experiment 1a Koelerion glaucae dung

Viable seed content

Viable seeds of (at least) 40 taxa emerged from the Kg sheep dung (results of field and germination test together), so 67 % of the species pool of the grazed source paddocks could be dispersed endozoochorously (total 60 species). In the field removal of dung by dung beetles limited the time available for dung-embedded seeds to emerge (samples were removed completely within 3 weeks – 5 months) from 49 dung plots (7 others were disturbed and excluded from analysis). At least 10 dung-borne species were detected (seven target species), from which 220 seedlings emerged. Most of them belonged to the non-target species *Psyllium arenarium* (highest seedling number via the germination test as well), but also several individuals of the Red List species *Medicago minima* and *Phleum arenarium* were able to emerge from out of sheep pellets (Table 5.3). The germination test showed a potential of 924 germinable seeds kg^{-1} dung, whereas under field conditions 43.7 seedlings kg^{-1} dung emerged (4.7 % of the potential).

Table 5.3 Number of dung-borne seedlings emerged from germination test (CG, common garden) and in the field. Dung was collected after grazing Koelerion glaucae community. Results are shown per 1000 g of dung. Abbreviations: SG, species group; R, Red List species; T, other target species; N, non-target species; G, graminoid competitor. Species which were present in the source paddocks, but did not emerge from germination test or field, are: *Armeria maritima* ssp. *elongata* (R, Plumbaginaceae), *Asparagus officinalis* (N, Lilaceae), *Berteroa incana* (N, Brassicaceae), *Bromus tectorum* (T, Poaceae), *Calamagrostis epigejos* (G, Poaceae), *Corispermum leptoterum* (N, Chenopodiaceae), *Cynodon dactylon* (G, Poaceae), *Echium vulgare* (T, Boraginaceae), *Erodium cicutarium* (T, Geraniaceae), *Euphorbia cyparissias* (T, Euphorbiaceae), *Helichrysum arenarium* (T, Asteraceae), *Hypericum perforatum* (N, Hypericaceae), *Koeleria glauca* (R, Poaceae), *Petrorhagia prolifera* (T, Caryophyllaceae), *Potentilla tabenaemontani* (N, Rosaceae), *Salsola kali* ssp. *tragus* (N, Chenopodiaceae), *Senecio inaequidens* (N, Asteraceae), *Silene otites* (R, Caryophyllaceae), *Sisymbrium altissimum* (N, Brassicaceae), *Stipa capillata* (R, Poaceae).

Species	Source	SG	Family	Emergence	
Emerged both via CG and field:				CG	Field
Arenaria serpyllifolia	x	T	Caryophyllaceae	19.3	1.59
Medicago minima	x	R	Fabaceae	39.3	1.19
Myosotis stricta		T	Boraginaceae	0.71	0.20
Phleum arenarium	x	R	Poaceae	82.1	0.20
Polygonum aviculare agg.	x	N	Polygonaceae	27.1	0.40
Psyllium arenarium	x	N	Plantaginaceae	237	32.1
Sedum acre	x	T	Crassulaceae	45.0	0.20
Thymus pulegioides		N	Lamiaceae	0.71	0.20
Trifolium arvense	x	T	Fabaceae	35.0	0.20
Veronica arvensis		N	Scrophulariaceae	11.4	1.19
Poaceae			Poaceae	15.0	2.78
Unidentified				27.9	3.37
Emerged only via CG:					
Agrostis capillaris	x	N	Poaceae	0.71	.
Amaranthus sp.		N	Amaranhaceae	5.00	.
Bromus hordeaceus	x	N	Poaceae	0.71	.
Carex hirta	x	G	Cyperaceae	9.29	.
Cerastium semidecandrum		T	Caryophyllaceae	0.71	.
Chenopodium album	x	N	Chenopodiaceae	36.4	.
Conyza canadensis	x	N	Asteraceae	1.43	.
Corynephorus canescens	x	R	Poaceae	0.71	.
Diplotaxis tenuifolia		N	Brassicaceae	40.0	.
Eragrostis minor	x	N	Poaceae	0.71	.
Erophila verna		T	Caryophyllaceae	2.14	.
Geranium molle		N	Geraniaceae	1.43	.
Herniaria glabra	x	T	Caryophyllaceae	1.43	.
Luzula campestris		N	Juncaceae	0.71	.
Medicago falcata	x	T	Fabaceae	42.9	.
Oenothera biennis	x	N	Onagraceae	37.1	.
Ononis repens	x	T	Fabaceae	0.71	.
Plantago lanceolata	x	N	Plantaginaceae	0.71	.
Poa angustifolia	x	G	Poaceae	11.4	.
Potentilla argentea	x	T	Rosaceae	57.9	.
Rumex acetosella s.l.		T	Polygonaceae	4.29	.
Saponaria officinalis	x	N	Caryophyllaceae	2.14	.
Saxifraga tridactylites		T	Dipsacaceae	5.71	.
Setaria viridis	x	N	Poaceae	7.86	.
Silene conica	x	R	Caryophyllaceae	0.71	.
Stellaria media		N	Caryophyllaceae	2.14	.
Trifolium campestre	x	T	Fabaceae	67.9	.
Verbascum phlomoides	x	N	Scrophulariaceae	64.3	.
Veronica verna	x	T	Scrophulariaceae	1.43	.
Vulpia myuros	x	T	Poaceae	14.3	.
Asteraceae			Asteraceae	2.86	.
Fabaceae				12.1	.
# seedlings 1000 g dung				924	43.7
# taxa total				40	10
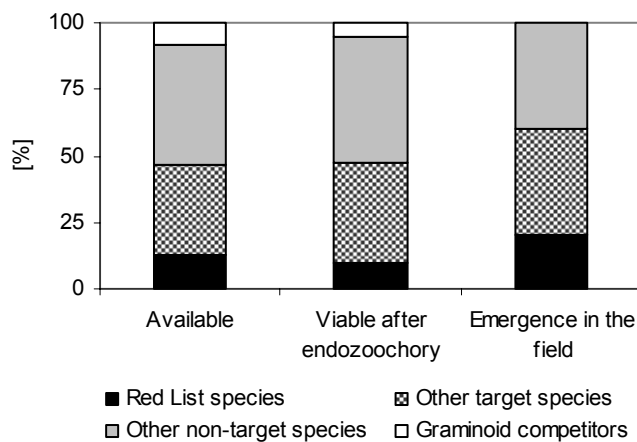
Figure 5.2 Species composition quality of (i) grazed Koelerion glaucae vegetation ('Available'), (ii) viable seeds after gut passage ('Viable after endozoochory') and (iii) dung-borne seedlings under field conditions ('Emergence in the field').

The grazed vegetation and detected endozoochorous seeds showed a relatively similar species quality: half of the species are classified as Red List and other target species. In relation to the total number of dung-borne species, in the field slightly more Red List species have emerged (Fig. 5.2). No dung-borne graminoid competitors emerged in the field, although viable seeds of two species were detected by use of the germination test (source paddocks contained four gram. competitor species) (germination test, Table 5.3).

Effects of dung on seedling emergence in the field
The effect of dung deposition on total seedling emergence was time-dependent ($F_{1,144}$ = 7.03, P = 0.009) (Table 5.4). Two months after samples were installed, sheep pellets clearly inhibited the total seedling emergence. Only half of the mean number of control seedlings emerged on the sample plots and the number of dung-borne seedlings compared to the number of soil-borne seedlings was extremely low (Fig. 5.3). In spring, after dung beetles had removed the pellets, several more seedlings were detected in sample plots, e.g. many seedlings of *Oenothera biennis* emerged from dung beetle-disturbed soil. Species richness was positively affected by dung deposition ($F_{1,144}$ = 16.38, P < 0.001) (Table 5.4).

Koelerion glaucae

Dung removed

Dung seed content   Treatment   Emergence field winter

	D-	Soil 82
110		
		Soil 46
	D+	Dung 4.5

Soil 7.9

Soil 12
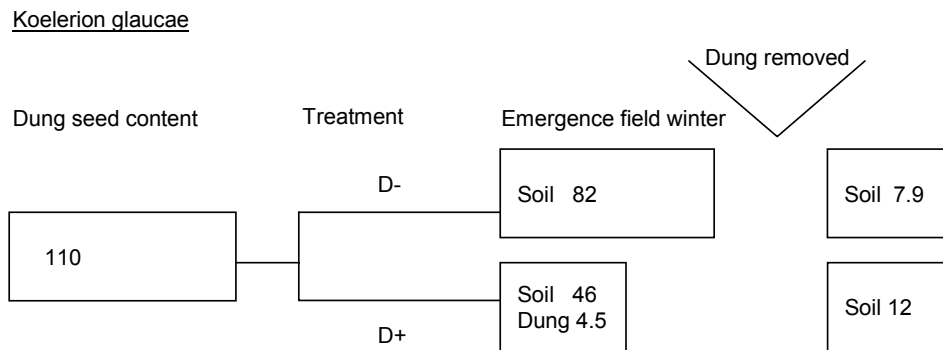
Figure 5.3 Flow diagram of mean number of viable seeds detected per 120 g Koelerion glaucae dung ('Dung seed content') and mean number of soil- and dung-borne seedlings (emerged in 400 cm^2) in different treatments (with, without dung (D+, D-)). Dung was collected after sheep had grazed Koelerion glaucae vegetation. Between winter and spring relevés, dung samples were removed by dung beetles.

On species level, several species showed significantly different emergence rates in sample and control plots (Table 5.4). Depending on time, significantly more *P. arenarium*, *O. biennis*, *P. aviculare* and undetermined Poaceae seedlings emerged from dung plots (*P. arenarium*: $F_{1,144}$ = 27.94, *P* < 0.001; *O. biennis*: $F_{1,144}$= 3.91, *P* = 0.050; *P. aviculare* $F_{1,144}$ = 12.31, *P* < 0.001; Poaceae: $F_{1,144}$= 5.28, *P* = 0.024), whereas significantly more *C. canadensis* and *S. tridactylites* emerged from controls (*C. canadensis*: $F_{1,144}$ = 5.20, *P* = 0.024; *S. tridactylites*: $F_{1,144}$ = 6.19, *P* = 0.014). Finally, in autumn more *H. arenarium* seedlings emerged from sample plots, whereas in spring more *H. arenarium* seedlings were detected from controls ($F_{1,144}$= 4.62, *P* = 0.033) (Table 5.4).

Table 5.4 Effect of time ('Time') and Koelerion glaucae dung deposition ('Dung') on number of seedlings plot^{-1}, number of species plot^{-1} and number of seedlings species^{-1} plot^{-1} (results of mixed linear models). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant. Species with an abundance ≤ 0.04 % of the total number of seedlings didn't show any effects: *Centaurea stoebe, Hypericum perforatum, Avena pubescens, Cerastium semidecandrum, Convolvulus arvense, Festuca ovina* agg.*, Festuca rubra, Potentilla argentea* agg.*, Trifolium campestre, Veronica praecox, Asperula cynanchica, Cynoglossum officinale, Elymus repens, Medicago falcata, Petrorhagia prolifera, Phleum arenarium, Rumex thyrsiflorus*.

Effect	Abundance (% ind.)	Time	Dung	T*D
sum individuals		***	*	**
sum species		***	***	N.S.
Arenaria serpyllifolia agg.	18.5	***	N.S.	N.S.
Conyza canadensis	14.7	**	**	*
Saxifraga tridactylites	12.2	***	**	*
Veronica arvensis	11.6	***	N.S.	N.S.
Alyssum alyssoides	6.4	***	N.S.	N.S.
Cerastium arvense	5.8	***	N.S.	N.S.
Oenothera biennis agg.	4.8	*	*	*
Psyllium arenarium	4.6	***	***	***
unknown	3.3	***	N.S.	N.S.
Erophila verna	1.9	*	N.S.	N.S.
Asteraceae	1.9	***	N.S.	N.S.
Holosteum umbellatum	1.7	N.S.	N.S.	N.S.
Poaceae	1.4	N.S.	**	*
Arabidopsis thaliana	1.2	*	N.S.	N.S.
Veronica verna	1.1	**	N.S.	N.S.
Helianthemum nummularium s.l.	1	N.S.	N.S.	N.S.
Myosotis ramosissima / M. stricta	1.0	*	N.S.	N.S.
Silene conica	0.9	**	N.S.	N.S.
Sedum acre	0.6	**	N.S.	N.S.
Sisymbrium altissimum	0.6	*	N.S.	N.S.
Silene otites	0.4	N.S.	N.S.	N.S.
Stipa capillata	0.4	**	N.S.	N.S.
Erodium cicutarium	0.3	***	N.S.	N.S.
Medicago minima	0.3	**	N.S.	N.S.
Ononis repens s.l.	0.3	*	N.S.	N.S.
Verbascum phlomoides	0.3	N.S.	N.S.	N.S.
Vicia lathyroides	0.3	***	N.S.	N.S.
Calamintha acinos	0.2	*	N.S.	N.S.
Euphorbia cyparissias	0.2	N.S.	N.S.	N.S.
Helichrysum arenarium	0.2	N.S.	N.S.	*
Achillea millefolium agg.	0.1	N.S.	N.S.	N.S.
Carex hirta	0.1	N.S.	N.S.	N.S.
Chenopodium album agg.	0.1	N.S.	N.S.	N.S.
Crepis sp.	0.1	N.S.	N.S.	N.S.
Galium album	0.1	N.S.	N.S.	N.S.
Geranium molle	0.1	*	N.S.	N.S.
Malva alcea	0.1	N.S.	N.S.	N.S.
Papaver rhoeas / P. dubium s.l.	0.1	N.S.	N.S.	N.S.
Poa angustifolia	0.1	N.S.	N.S.	N.S.
Polygonum aviculare	0.1	***	***	***
Rumex acetosella s.l.	0.1	N.S.	N.S.	N.S.
Salsala kali ssp. *tragus*	0.1	N.S.	N.S.	N.S.
Senecio vernalis	0.1	N.S.	N.S.	N.S.
Setaria viridis	0.1	N.S.	N.S.	N.S.
Stellaria media	0.1	N.S.	N.S.	N.S.
Thymus pulegoides	0.1	N.S.	N.S.	N.S.
Trifolium arvense	0.1	N.S.	N.S.	N.S.

The species composition and development of the plots in time were analysed by use of detrended correspondence analysis (DCA) (Fig. 5.4a). The species composition of plots showed a clear temporal development along the first axis. Autumn plots with and without dung were all situated on the far left side of the first axis. The species composition of those plots is dominated by autumn germinators, which had a negative correlation with the first axis, e.g. *S. tridactylites* (- 0.483), *A. alyssoides* (- 0.432) and *A. serpyllifolia* (- 0.581). Spring plots were situated on the right side of the graph, and showed a more scattered distribution. Spring germinators were also positioned on the right side of the graph, and had a positive correlation with the first axis, e.g. *S. capillata* (r = 0.618). In spring, after the dung samples had been removed completely by dung beetle activity, plots of both treatments showed some differences: *O. biennis* and *P. aviculare* almost exclusively germinated from plots which previously contained dung (r = 0.417; r = 0.241, respectively). *P. arenarium,* located in the centre of the figure, germinated both in autumn and spring from dung plots (Fig. 5.4b).
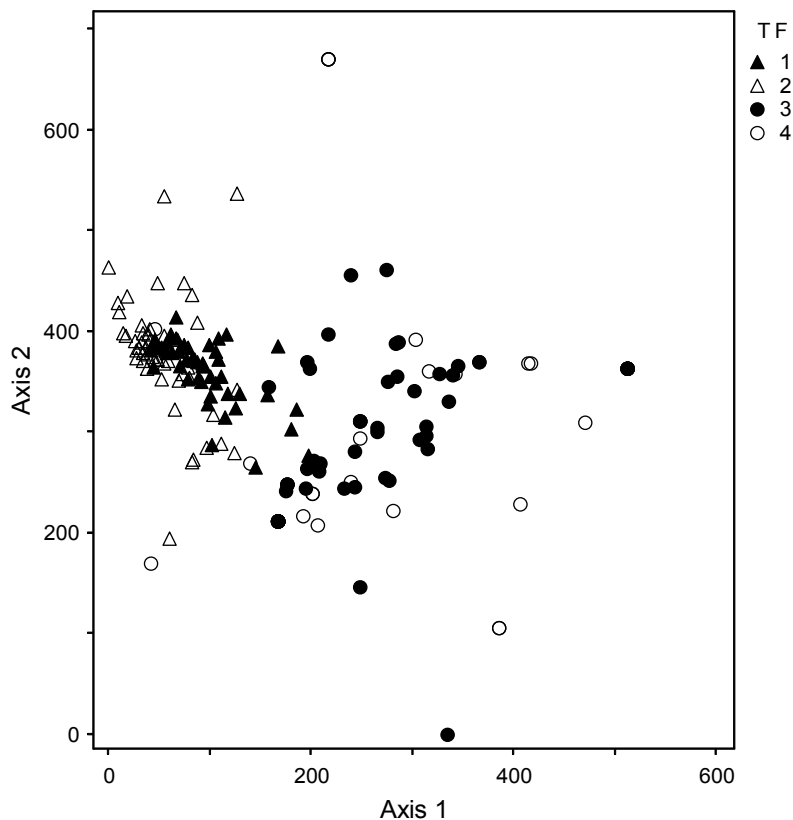
Figure 5.4a DCA of the investigated plots for two seasons (autumn 2004 and spring 2005). Eigenvalues and length of gradient: First axis, 0.71, 5.1 SD; Second axis: 0.41, 6.7 SD. The legend numbers indicate the following: 1 = sample, autumn 2004; 2 = control, autumn 2004; 3 = sample, spring 2005; 4 = control, spring 2005.

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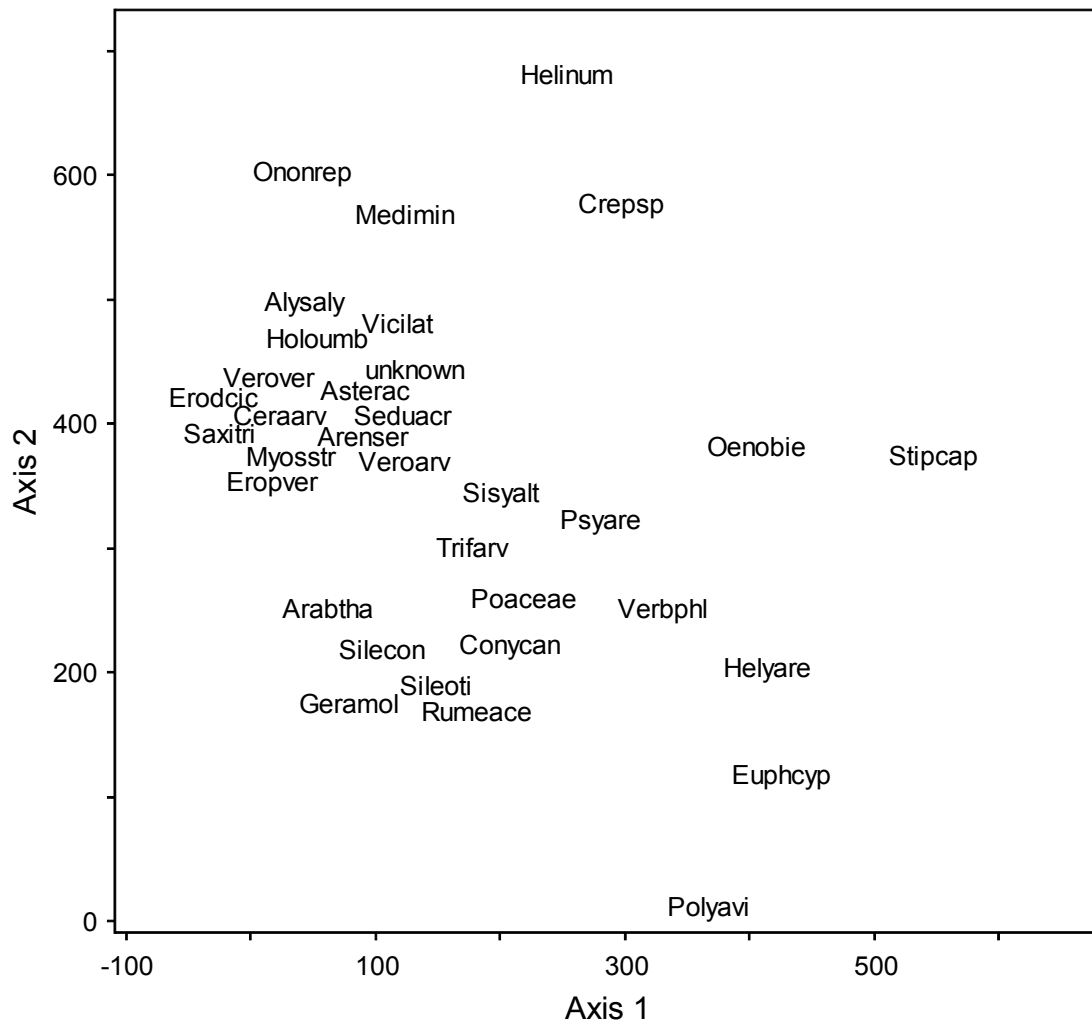
Figure 5.4b Seedling species: Alysaly *Alyssum alyssoides,* Arabtha *Arabidopsis thaliana,* Arenser *Arenaria serpyllifolia* agg.*,* Asterac Asteraceae, Ceraarv *Cerastium arvense*, Conycan *Conyza canadensis*, Crepsp *Crepis* sp., Erodcic *Erodium cicutarium*, Eropver *Erophila verna* s.l., Euphcyp *Euphorbia cyparissias*, Geramol *Geranium molle*, Helinum *Helianthemum nummularium* s.l., Helyare *Helichrysum arenarium,* Holoumb *Holosteum umbellatum*, Medimin *Medicago minima*, Myosstr *Myosotis stricta/M. ramosissima*, Oenobie *Oenothera biennis* agg., Ononrep *Ononis repens* s.l., Poaceae, Polyavi *Polygonum aviculare* agg., Psylare *Psyllium arenarium*, Rumeace *Rumex acetosella* s.l., Saxitri *Saxifraga tridactylites*, Seduacr *Sedum acre*, Silecon *Silene conica*, Sileoti *Silene otites,* Sisyalt *Sisymbrium altissimum*, Stipcap *Stipa capillata*, Trifarv *Trifolium arvense*, unknown, Verbphl *Verbascum phlomoides*, Veroarv *Veronica arvensis,* Verover *Veronica verna*, Vicilat *Vicia lathyroides.*

Plant vitality response after dung deposition

Arenaria serpyllifolia individuals from sample plots had significantly more flowers and were longer than control individuals (flowers: $F_{1,347}$ = 11.38, *P* < 0.001; length: $F_{1,347}$ =

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42.71, *P* < 0.001; Fig. 5.5, Table 5.5). Other vitality parameters, C and N content and the number of *A. serpyllifolia* individuals per plot did not show a difference (Fig. 5.5, Table 5.5).
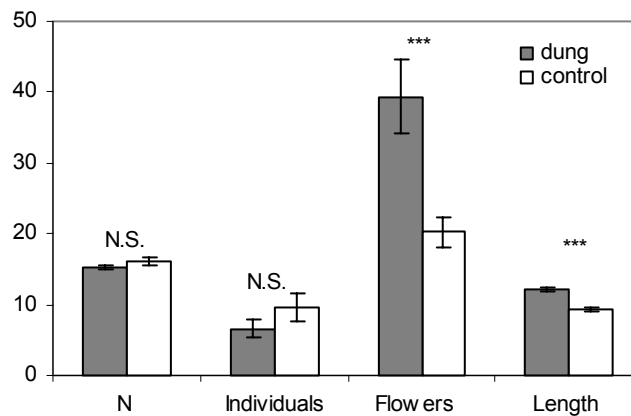
Figure 5.5 Vitality measures of A. serpyllifolia in Koelerion glaucae dung plots and controls. Measured parameters: 'N' plant N content (mg/g) (*n* = 40, 38); 'Individuals' number of A. serpyllifolia individuals per plot (*n* = 56, 56); 'Flowers' number of flowers per individual (n = 205, 190); 'Length' length per individual (*n* = 205, 190). Error bars indicate standard error of the mean. Level of significance; *** = *P* < 0.001, N.S. = not significant.

Table 5.5 Effect of dung on vitality of *A. serpyllifolia* (results of mixed linear model) measured by use of parameters (a) plant N content, 'N' (%) (sample, control plots *n* = 40, 38); (b) number of *A. serpyllifolia* individuals per plot, 'Individuals' (*n* = 56, 56); (c) number of flowers per individual, 'Flowers' (*n* = 205, 190); (d) length per individual, 'Length' (*n* = 205, 190). Level of significance; *** = *P* < 0.001, N.S. = not significant.

Parameter	Num DF	Den DF	F	*P*
N	1	26	3.41	NS
Individuals	1	55	2.52	NS
Flowers	1	347	11.38	***
Length	1	347	42.71	***

E*xperiment 1b Allio-Stipetum dung*

Viable seed content

From AS dung viable seeds of 41 species could be detected (under field conditions and germination tests; 52 % of total species number). Since two different germination tests (Ter Heerdt and a common garden method, see Methods) were used, results were combined by summing up the highest emergence value per species (for comparison of both methods see Chapter 4, Wessels and Schwabe 2008). A potential of 4897 viable seeds per 1000 g AS dung was found. In the field 246 seedlings of 15 taxa were detected (6720 g dung, 0.7 % of the potential); most emerged seedlings belonged to target species (96 %), e.g. *Helianthemum nummularium* (76 %). All species detected in

the field also emerged via both seedling emergence tests, except for *C. dactylon* and

Myosotis stricta/M. ramosissima, both exclusively found in the field (Table 5.6).

Table 5.6 Total number of dung-borne seedlings as emerged from two types of germination tests (TH, Ter Heerdt method and CG, common garden) and in the field. Dung collected after grazing an Allio-Stipetum capillatae community. Results are shown per 1000 g of dung. The following species were present in the source paddocks, but did not emerge in CG or field: *Agrimonia procera* (T, Asteraceae), *Agrostis stolonifera* (G, Poaceae), *Allium sphaerocephalon* (R, Liliaceae), *Alyssum alyssoides* (T, Brassicaceae), *Armeria maritima* ssp. *elongata* (R, Plumbaginaceae), *Asparagus officinalis* (N, Lilaceae), *Bromus hordeaceus* (N, Poaceae), *Bromus tectorum* (T, Poaceae), *Calamagrostis epigejos* (G, Poaceae), *Carduus nutans* (N, Asteraceae), *Centaurea stoebe* (T, Asteraceae), *Crataegus monogyna* (N, Rosaceae), *Crepis capillaris* (N, Asteraceae), *Cynoglossum officinale* (N, Boraginaceae), *Echium vulgare* (T, Boraginaceae), *Elymus repens* (G, Poaceae), *Erodium cicutarium* (T,Geraniaceae), *Euphorbia cyparissias* (T, Euphorbiaceae), *Festuca ovina* agg. (T, Poaceae), *Galium album* (N, Rubiaceae), *Genista tinctoria* (N, Fabaceae), *Helichrysum arenarium* (R, Asteraceae), *Hieracium pilosella* (T, Asteraceae), *Hypochaeris radicata* (N, Asteraceae), *Oenothera biennis* s.l. (N, Onagraceae), *Ononis repens* (T, Fabaceae), *Phleum phleoides* (T, Poaceae) *Potentilla tabenaemontani* (N, Rosaceae), *Rosa canica* s.l. (N, Rosaceae), *Rumex thyrsiflorus* (N, Polygonaceae), *Salvia pratensis* (T, Lamiaceae), *Scabiosa canescens* (R, Dipsacaceae), *Securigera varia* (N, Fabaceae), *Senecio jacobaea* (N, Asteraceae), *Silene latifolia* ssp. *alba* (N, Caryophyllaceae), *Silene otites* (R, Caryophyllaceae), *Silene vulgaris* s.l. (N, Caryophyllaceae), *Stipa capillata* (R, Poaceae).

Species	Source	SG	Family	Emergence		
				TH	CG	field
Emerged both via TH / CG and field:						
Achillea millefolium	x	N	Asteraceae	11.7	5.00	0.15
Arenaria serpyllifolia agg.	x	T	Caryophyllaceae	1398	401	0.74
Carex hirta		G	Cyperaceae	.	3.33	0.15
Geranium molle		N	Geraniaceae	1.67	.	0.15
Helianthemum nummularium s.l.	x	T	Cistaceae	283	520	27.8
Medicago falcata		T	Fabaceae	1.67	5.00	0.15
Medicago minima	x	R	Fabaceae	0.83	7.50	0.60
Potentilla argentea agg.	x	T	Rosaceae	255	142	0.45
Sedum acre	x	T	Crassulaceae	0.83	5.00	0.30
Trifolium arvense	x	T	Fabaceae	255	525	0.45
Trifolium campestre	x	T	Fabaceae	74.2	311	2.08
Veronica arvensis		N	Scrophulariaceae	138	10.00	0.60
Vicia lathyroides		R	Fabaceae	2.50	.	0.74
Fabaceae			Fabaceae	.	1.67	0.30
Poaceae			Poaceae	.	7.50	0.15
unidentified				2.50	38.3	0.74
Emerged only via TH / CG:						
Agrostis capillaris	x	G	Poaceae	7.50	3.33	.
Agrostis sp.			Poaceae	.	0.83	.
Agrostis vinealis	x	G	Poaceae	2.50	2.50	.
Arabis glabra		T	Brassicaceae	38.3	9.17	.
Asperula cynanchica	x	T	Rubiaceae	0.83	.	.
Berteroa incana	x	N	Brassicaceae	0.83	.	.
Calamintha acinos		T	Lamiaceae	.	0.83	.
Carex praecox		R	Cyperaceae	.	1.67	.
Cerastium semidecandrum	x	T	Caryophyllaceae	3.33	.	.
Chenopodium album agg.		N	Chenopodiaceae	57.5	35.0	.
Convolvulus arvense		N	Convolvulaceae	.	1.67	.
Conyza canescens	x	N	Asteraceae	73.3	63.3	.
Diplotaxis tenuifolia		N	Brassicaceae	0.83	0.83	.
Hypericum perforatum	x	N	Hypericaceae	4.17	5.83	.
Koeleria macrantha		T	Poaceae	.	0.83	.
Luzula campestris	x	N	Juncaceae	1.67	0.83	.
Petrorhagia prolifera	x	T	Caryophyllaceae	3.33	1.67	.
Poa angustifolia	x	G	Poaceae	12.50	11.7	.
Rubus caesius	x	N	Rosaceae	.	0.83	.
Rumex acetosella s.l.	x	T	Polygonaceae	50.8	20.0	.
Setaria viridis		N	Poaceae	.	0.83	.
Silene conica		R	Caryophyllaceae	.	0.83	.
Sisymbrium altissimum	x	N	Brassicaceae	.	1.67	.
Stellaria media		N	Caryophyllaceae	9.17	1.67	.
Thymus pulegioides s.l.	x	N	Lamiaceae	14.2	17.5	.
Urtica dioica		N	Urticaceae	86.7	45.0	.
Verbascum phlomoides	x	N	Scrophulariaceae	1211	1179	.
Caryophyllaceae			Caryophyllaceae	.	0.83	.
Emerged only in the field:						
Cynodon dactylon	x	G	Poaceae	.	.	0.30
Myosotis ramosissima / stricta		T	Boraginaceae	.	.	0.15
# seedlings 1000 g dung				4003	3390	36.0
# taxa total				30	34	15

A similar species quality of viable seeds after gut passage (germination test) and species detected in the grazed Allio-Stipetum stand was shown (roughly 50 % target vs. 50 % non-target species, Fig. 5.6). However, relatively more target species emerged directly out of dung under field conditions (67 %) compared to the number of non-target species (Fig. 5.6).
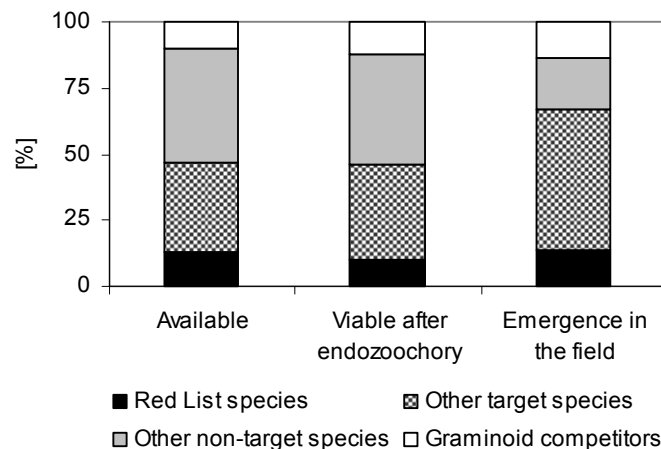

Figure 5.6 Species composition quality of (i) grazed Allio-Stipetum capillatae vegetation ('Available'), (ii) viable seeds after gut passage ('Viable after endozoochory') and (iii) dung-borne seedlings under field conditions ('Emergence in the field').

Treatment effects

The effects of the different treatments were tested at the levels of dung-borne seedlings, all (dung- and soil-borne) seedlings and complete vegetation.

Dung-borne seedlings A significant negative effect of moss on total number of seedlings and species was found (seedlings: $F_{1,95}$ = 12.45, P < 0.001; species: $F_{1,95}$ = 20.06, P < 0.001;Table 5.7). As a result, more seedlings and species emerged from dung in experimentally disturbed plots (moss layer removed) than in undisturbed plots, e.g. *H. nummularium* ($F_{1,95}$ = 11.88, P < 0.001) and *T. campestre* ($F_{1,95}$ = 8.42, P = 0.005). Depending on the elapsed time, a group of Fabaceae seedlings seem to have been affected by dung beetle activity or the presence of dung beetle exclosures ($F_{2,95}$ = 3.37, P = 0.039).

Table 5.7 Effect of time, moss, dung beetles and interactions between those factors on number of dung-borne seedlings plot^{-1}, number of dung-borne species plot^{-1} and number of dung-borne seedlings species^{-1} plot^{-1} (Allio-Stipetum dung; results of mixed linear models). Level of significance; * = P < 0.05 ** = P < 0.01, *** = P < 0.001, N.S. = not significant. Species with an abundance < 1.2 % of the total number of seedlings didn't show any effects: *Cynodon dactylon, Sedum acre, Achillea millefolium, Carex hirta, Chenopodium album* agg., *Geranium molle, Medicago falcata (incl. x varia), Myosotis stricta / M. ramosissima*, Poaceae.

	Abundance (% ind.)	Time	Moss	Dungbeetle	T*M	T*B	M*B	T*M*B
sum seedlings		***	***	N.S.	N.S.	N.S.	N.S.	N.S.
sum species		***	***	N.S.	N.S.	N.S.	N.S.	N.S.
Helianthemum nummularium	76.0	***	***	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium campestre	5.7	N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.
Arenaria serpyllifolia agg.	2.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium arvense	2.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
unknown	2.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vicia lathyroides	2.0	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Medicago minima	1.6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Veronica arvensis	1.6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Potentilla argentea agg.	1.2	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Fabaceae	1.2	*	N.S.	N.S.	N.S.	*	N.S.	N.S.

Of the perennial species which emerged in the field (*A. millefolium*, *C. hirta*, *C. dactylon*, *H. nummularium*, *S. acre*, *P. argentea*) only 18 individuals of *H. nummularium* survived longer than one year (Table 5.8).

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Table 5.8 Emergence and survival of dung-borne seedlings, shown per treatment: M^-B^+, moss layer removed and dung beetles could enter; M^-B^-, moss layer removed and dung beetles excluded from entering; M^+B^+, intact moss layer and dung beetles could enter; M^+B^-, intact moss layer and dung beetles excluded from entering (Allio-Stipetum dung).

Treatment	Species	Total emerged	< 3 months	3 - 6 months	7 - 12 months	> 1 year
M^-B^+	*Arenaria serpyllifolia*	3	1	1	1	.
	Chenopodium album	1	.	1	.	.
	Fabaceae	1	.	1	.	.
	Helianthemum nummularium	70	15	18	33	4
	Medicago minima	3	2	1	.	.
	Myosotis ram./stricta	1	1	.	.	.
	Trifolium arvense	3	.	2	1	.
	Trifolium campestre	6	1	4	1	.
	Veronica arvensis	1	.	1	.	.
	Vicia lathyroides	3	1	2	.	.
	Sum	92	21	31	36	4
M^-B^-	*Arenaria serpyllifolia*	1	1	.	.	.
	Cynodon dactylon	1	1	.	.	.
	Helianthemum nummularium	54	12	16	15	11
	Medicago falcata	1	.	.	1	.
	Medicago minima	1	.	.	1	.
	Potentilla argentea	1	.	1	.	.
	Sedum acre	2	2	.	.	.
	Trifolium arvense	2	.	1	1	.
	Trifolium campestre	5	3	2	.	.
	unknown	1	.	1	.	.
	Veronica arvensis	1	1	.	.	.
	Sum	70	20	21	18	11
M^+B^+	*Arenaria serpyllifolia*	1	.	1	.	.
	Carex hirta	1	.	.	1	.
	Fabaceae	2	.	2	.	.
	Helianthemum nummularium	27	6	11	9	1
	Potentilla argentea	1	.	.	1	.
	Trifolium campestre	1	.	1	.	.
	Veronica arvensis	2	.	2	.	.
	Sum	35	6	17	11	1
M^+B^-	*Achillea millefolium*	1	1	.	.	.
	Cynodon dactylon	1	.	.	1	.
	Geranium molle	1	.	1	.	.
	Helianthemum nummularium	36	11	8	15	2
	Poaceae	1	.	.	1	.
	Potentilla argentea	1	.	1	.	.
	Trifolium campestre	2	2	.	.	.
	unknown	4	.	4	.	.
	Vicia lathyroides	2	.	1	1	.
	Sum	49	14	15	18	2

Total seedling emergence Depending on time, moss significantly inhibited the total number of seedlings (T*M: $F_{2, 214} = 6.27$, $P = 0.002$) and species richness per plot ($F_{1, 214} = 14.06$, $P < 0.001$; Table 5.9). There was also a significant time-dependent effect of

dung on total seedling emergence (T*D: $F_{2,\ 214}$ = 4.90, *P* = 0.008). In spring 2005, plots with dung on average contained some more seedlings, due to the presence of more soil-borne seedlings compared to control plots and the additional emergence of several seedlings from dung (Fig. 5.7). In autumn 2005, however, dung deposition inhibited emergence from the soil. This lower rate was not compensated by the number dung-borne seedlings. Consequently, dung plots had a lower overall seedling emergence. Finally, in spring 2006 dung deposition in moss-disturbed plots slightly facilitated seedling emergence again. Overall, plots with dung contained significantly more species ($F_{1,\ 214}$ = 5.12, *P* = 0.025).

Among species different responses were found. Depending on time, the seedling numbers of *S. acre*, *P. lanceolata*, *O. biennis* and *T. arvense* increased in plots where moss was disturbed (*S. acre*, $F_{2,\ 214}$ = 3.90, *P* = 0.022; *P. lanceolata*, $F_{2,\ 214}$ = 3.18, *P* = 0.045; *O. biennis*, $F_{2,\ 214}$ = 3.48, *P* = 0.033*; T. arvense*, $F_{2,\ 214}$ = 4.36, *P* = 0.011) and *E. athericus* was more frequently detected in plots with an intact moss layer ($F_{2,\ 214}$ = 3.15, *P* = 0.045, nevertheless only a few seedlings were present). A time-dependent inhibiting effect of dung was also found for *M. falcata*, *R. acetosella*, *C. semidecandrum*, *A. serpyllifolia* and *M. stricta* (*M. falcata*: $F_{2,\ 214}$ = 4.33, *P* = 0.014; *R. acetosella*: $F_{2,\ 214}$ = 3.34, *P* = 0.037; *C. semidecandrum*: $F_{2,\ 214}$ = 4.95, *P* = 0.008; *A. serpyllifolia* $F_{2,\ 214}$ = 4.02, *P* = 0.019; *M. stricta* $F_{2,\ 214}$ = 3.11, *P* = 0.047), whereas more seedlings of *T. campestre*, *H. nummularium*, *T. repens* and Fabaceae were found (*T. campestre*: $F_{2,\ 214}$ = 4.47, *P* = 0.013; *H. nummularium*: $F_{2,\ 214}$ = 16.47, *P* < 0.001; *T. repens*: $F_{2,\ 214}$ = 3.08, *P* = 0.048; Fabaceae: $F_{2,\ 214}$ = 5.04, *P* = 0.007). *H. nummularium* was also positively affected by the absence of moss ($F_{1,\ 214}$ = 12.87, *P* < 0.001). The number of seedlings of *S. tridactylites* and *C. canadensis* were, depending on time, negatively affected by both moss and dung (*S. tridactylites:* $F_{2,\ 214}$ = 4.87, *P* = 0.009; *C. canadensis*: $F_{2,\ 214}$ = 4.57, *P* = 0.011). Finally, the emergence rates of almost all species changed in time (Table 5.9).

Table 5.9 Effects of Allio-Stipetum dung deposition ('Dung') and disturbance of moss layer ('Moss') on seedling number, seedling species richness and number of seedlings per species in time ('Time') (results from mixed linear models). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant. Species with abundance ≤ 0.03 % of the total seedling number didn't show any effects: *Silene otites, Asparagus officinalis*, Poaceae and Asteraceae.

	Abundance (% ind)	Time	Dung	Moss	T*D	T*M	D*M	T*D*M
sum seedlings		***	N.S.	**	**	**	N.S.	N.S.
sum species		***	*	***	N.S.	N.S.	N.S.	N.S.
Veronica arvensis	31.9	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Arenaria serpyllifolia agg.	9.9	***	*	N.S.	*	N.S.	N.S.	N.S.
Cerastium semidecandrum	7.2	***	*	N.S.	**	N.S.	N.S.	N.S.
Medicago falcata (incl. x varia)	6.3	***	N.S.	N.S.	*	N.S.	N.S.	N.S.
Saxifraga tridactylites	6.1	***	*	**	**	***	*	**
Vicia lathyroides	5.7	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Helianthemum nummularium	5.1	***	***	***	***	N.S.	***	N.S.
Geranium molle	3.3	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Poa angustifolia	3.1	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Medicago minima	2.8	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Sedum acre	1.9	*	N.S.	*	N.S.	*	N.S.	N.S.
Trifolium campestre	1.9	***	N.S.	N.S.	*	N.S.	N.S.	N.S.
Erodium cicutarium	1.8	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Myosotis stricta / M. ramosissima	1.8	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Rumex acetosella s.l.	1.8	**	N.S.	N.S.	*	N.S.	N.S.	N.S.
Myosotis stricta	1.3	***	N.S.	N.S.	*	N.S.	N.S.	N.S.
Centaurea stoebe	0.9	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Conyza canadensis	0.7	***	N.S.	**	N.S.	N.S.	N.S.	*
Achillea millefolium	0.6	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
unknown	0.6	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Oenothera biennis s.l.	0.4	***	N.S.	*	N.S.	*	N.S.	N.S.
Plantago lanceolata	0.4	N.S.	N.S.	N.S.	N.S.	*	N.S.	N.S.
Veronica verna	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium arvense	0.3	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Chenopodium album agg.	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Euphorbia cyparissias	0.3	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Helichrysum arenarium	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Koeleria macrantha	0.3	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Potentilla argentea agg.	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Salsola kali ssp. *tragus*	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium arvense	0.3	***	*	**	N.S.	*	N.S.	N.S.
Carex hirta	0.2	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Erophila verna	0.2	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Fabaceae	0.2	**	*	N.S.	**	N.S.	N.S.	N.S.
Hypericum perforatum	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Agrostis sp.	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Arabidopsis thaliana	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Artemisia campestris	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Elymus athericus	0.1	*	N.S.	N.S.	N.S.	*	N.S.	N.S.
Festuca rubra	0.1	N.S.	Dung	Moss	N.S.	N.S.	N.S.	N.S.
Ononis repens	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Psyllium arenarium	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Silene conica	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium repens	0.1	*	N.S.	N.S.	*	N.S.	N.S.	N.S.
Verbascum phlomoides	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vulpia myuros	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Allio-Stipetum

Dung seed content	Treatment	Spring 05	Autumn 05	Spring 06
	D+M+B+	Soil 1.2 Dung 0.15	Soil 17 Dung 1.4	Soil 0.38 Dung 0.62
	D+M+B-	Soil 0.67 Dung 0.20	Soil 20 Dung 2.0	Soil 1.7 Dung 0.73
	D+M-B+	Soil 1.0 Dung 1.2	Soil 20 Dung 4.3	Soil 2.7 Dung 1.8
588	D+M-B-	Soil 0.69 Dung 1.4	Soil 36 Dung 2.4	Soil 0.56 Dung 1.8
	D-M+B+	Soil 0.54	Soil 27	Soil 1.0
	D-M-B+	Soil 0.57	Soil 45	Soil 1.9

Figure 5.7 Flow diagram of viable seeds, mean number detected per 120 g Allio-Stipetum dung ('Dung seed content') and mean number of soil- and dung-borne seedlings per treatment per season (emerged in 400 cm^2). Dung was collected after sheep grazed Allio-Stipetum vegetation. Treatment abbreviations: D+/-, with/without dung; M+/-, with/without moss; B+/-, with/without dung beetle.

The total number of seedlings, species richness or species-specific seedling numbers were not affected by potential dung beetle visitation and/or dung beetle exclosures except for *Oenothera biennis*, from which in the first period more seedlings were detected in dung beetle-protected exclosures ($F_{2, 63}$ = 4.88, *P* = 0.011, see Appendix 5.1).

On level of **the complete vegetation** (dung- and soil-borne seedlings and adult plants), in periods 2 and 3 moss disturbance increased ($F_{2, 209}$ = 13.55, *P* < 0.001) and dung pellets reduced the number of individual plants ($F_{2, 209}$ = 4.26, *P* = 0.015). Also in periods 2 and 3 moss disturbance significantly promoted the species richness ($F_{2, 209}$ = 8.52, *P* <

0.001), whereas the presence of dung seemed to do the same ($F_{1,209}$ = 3.37, *P* = 0.068) (Table 5.10).

On the species level, the total number of individuals of *F. rubra, R. acetosella, T. campestre,* Fabaceae and especially *H. nummularium* were significantly higher in the presence of dung (Table 5.10). This effect is time-dependent, as more individuals were found in a later stage (*F. rubra*: $F_{2,209}$ = 3.70, *P* = 0.026; *R. acetosella*: $F_{2,209}$ = 3.05, *P* = 0.050; *T. campestre:* $F_{2,209}$ = 3.54, *P* = 0.031; Fabaceae: $F_{2,209}$ = 4.76, *P* = 0.009 , *H. nummularium*: $F_{2,209}$ = 25.91, *P* < 0.001). Additionally, and depending on the presence of dung, significantly more *H. nummularium* individuals were found when bryophytes had been removed ($F_{1,209}$ = 14.66, *P* < 0.001).

On several other species, *C. hirta*, *C. semidecandrum, M. stricta/M. ramosissima*, the deposition of dung had a time-dependent, inhibiting effect (*C. hirta*: $F_{2,209}$ = 4.05, *P* = 0.019; *C. semidecandrum*: $F_{2,209}$ = 4.07, *P* = 0.019; *M. stricta/M. ramosissima:* $F_{2,209}$ = 3.20, *P* = 0.043). Moreover, in a later stage of the experiment the abundance of *C. semidecandrum* individuals was positively affected by moss disturbance ($F_{2,209}$ = 4.34, *P* = 0.014). The number of *S. tridactylites* individuals was, depending on time, negatively affected by both dung and an intact moss layer ($F_{2,209}$ = 5.32, *P* = 0.006) and also more *C. canadensis* individuals were found in plots without dung and moss ($F_{1,209}$ = 5.92, *P* = 0.016).

In particular six and twelve months after moss disturbance, increased individual numbers of *A. serpyllifolia, V. arvensis, T. arvense* and *S. acre* were found (*A. serpyllifolia*: $F_{2,209}$ = 6.93, *P* = 0.001; *V. arvensis*: $F_{2,209}$ = 5.33, *P* = 0.006; *T. arvense*: $F_{1,209}$ = 5.92, *P* = 0.016; 0.010*S. acre*: $F_{2,209}$ = 4.72, *P* = 0.010). Furthermore, the number of *S. acre* individuals was also dependent on the presence of dung ($F_{1,209}$ = 5.30, *P* = 0.022). Without dung, fewer individuals were present in moss-covered plots than in disturbed plots, whereas in the presence of dung, moss-covered plots contained more *S. acre* individuals than disturbed plots.

Table 5.10 Effects of Allio-Stipetum dung deposition ('Dung') and disturbance of the moss layer ('Moss') on total individual and species numbers and individual numbers per species in time ('Time') (results of mixed linear models). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant. Species with abundance ≤ 0.03 % of the total individual number didn't show any significant effects: *Agrostis* sp., Arabidopsis *thaliana, Bromus tectorum, Silene otites, Phleum arenarium, Psyllium arenarium, Silene conica, Vicia* sp., *Rumex thyrsiflorus, Sisymbrium altissimum, Verbascum phlomoides, Carduus nutans, Armeria maritima* ssp. *elongata, Asparagus officinalis*, *Echium vulgare, Senecio vernalis*, Poaceae and Asteraceae.

	Abundance (% ind.)	Time	Dung	Moss	T*D	T*M	D*M	T*D*M
sum individuals		***	N.S.	N.S.	*	***	N.S.	N.S.
sum species		***	~	*	N.S.	***	N.S.	N.S.
Poa angustifolia	19.3	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Veronica arvensis	16.1	***	N.S.	N.S.	N.S.	**	N.S.	N.S.
Elymus athericus	8.5	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Arenaria serpyllifolia agg.	5.7	**	N.S.	N.S.	N.S.	**	N.S.	N.S.
Carex hirta	5.7	***	N.S.	N.S.	*	N.S.	N.S.	N.S.
Medicago falcata (incl. x varia)	5.0	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cynodon dactylon	4.7	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Koeleria macrantha	3.8	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium semidecandrum	3.4	***	N.S.	N.S.	*	*	N.S.	N.S.
Medicago minima	3.1	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vicia lathyroides	2.7	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Saxifragha tridactylites	2.2	**	~	*	**	***	N.S.	**
Festuca rubra	1.8	N.S.	N.S.	N.S.	*	N.S.	N.S.	N.S.
Geranium molle	1.7	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Myosotis stricta / M. ramosissima	1.7	***	**	N.S.	*	N.S.	N.S.	N.S.
Helianthemum nummularium	1.5	***	***	***	***	N.S.	***	N.S.
Rumex acetosella s.l.	1.3	**	N.S.	N.S.	*	N.S.	N.S.	N.S.
Plantago lanceolata	1.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Sedum acre	1.2	**	N.S.	N.S.	N.S.	**	*	N.S.
Achilea millefolium	0.9	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Festuca ovina agg.	0.8	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Erodium cicularium agg.	0.8	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium campestre	0.8	***	*	N.S.	*	N.S.	N.S.	N.S.
Centaurea stoebe	0.7	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Calamagrostis epigejos	0.6	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Ononis repens	0.6	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Euphorbia cyparissias	0.6	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Potentilla argentea agg.	0.5	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Veronica verna	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium arvense	0.3	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Conyza canadensis	0.3	**	N.S.	***	N.S.	N.S.	*	N.S.
Acinos arvensis	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vulpia myuros	0.2	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Chenopodium album	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Artemisia campestris	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Oenothera biennis s.l.	0.2	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
unknown	0.2	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Hypericum perforatum	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vicia angustifolia	0.2	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium arvense	0.1	**	N.S.	*	N.S.	N.S.	N.S.	N.S.
Erophila verna	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Salsola kali	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Helichrysum arenarium	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Koeleria glauca	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium repens	0.1	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Fabaceae	0.04	**	*	N.S.	**	N.S.	N.S.	N.S.
Veronica praecox	0.04	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

Additionally, relatively many species did change in time, regardless of treatment. Of the most abundant species, *P. angustifolia, C. dactylon* and *K. macrantha* increased especially from the first spring to autumn (*P. angustifolia,* $F_{1,209}$ = 12.37, *P* < 0.001; *C. dactylon,* $F_{1,209}$ = 24.29, *P* < 0.001; *K. macrantha,* $F_{1,209}$ = 4.31, *P* = 0.015). In contrast, the abundance of *E. athericus* and *M. falcata* decreased in time (*E. athericus,* $F_{1,209}$ = 9.44, *P* < 0.001; *M. falcata,* $F_{1,209}$ = 17.52, *P* < 0.001).

Neither total number of individuals, species richness or, except for *E. athericus*, species-specific individual numbers of the complete vegetation was affected by potential dung beetle visitation and/or dung beetle exclosures (*E. athericus*: $F_{2,103}$ = 5.28, *P* = 0.007; also see Appendix 5.2).

The temporal development of the species composition associated with different treatments was analysed by detrended correspondence analysis (DCA) (Fig. 5.8a). Although eigenvalues were relatively small, the analysis suggests that different temporal changes took place among the various treatments. The number of annuals probably decreases along the first axis, indicated by many annual species with negative correlations positioned on the left side of the figure (*V. lathyroides*, *r* = - 0.713 and *V. arvensis*, *r* = - 0.823) (Fig. 5.8b). Especially plots with moss disturbance showed large changes between the first spring and following autumn along this first axis, whereas plots with an intact moss layer (also those with dung deposition) changed less. Afterwards, from autumn to spring plots undergoing all treatments developed in the direction of the first spring again.

The second axis might indicate ruderalisation. Most treatments remained more or less in the same development state from the first spring to the following autumn, which fits with increase and decrease of several graminoids in time (see results above). During winter, ruderalisation was moderately reduced, as indicated by slightly lower values of the second axis in the last spring.
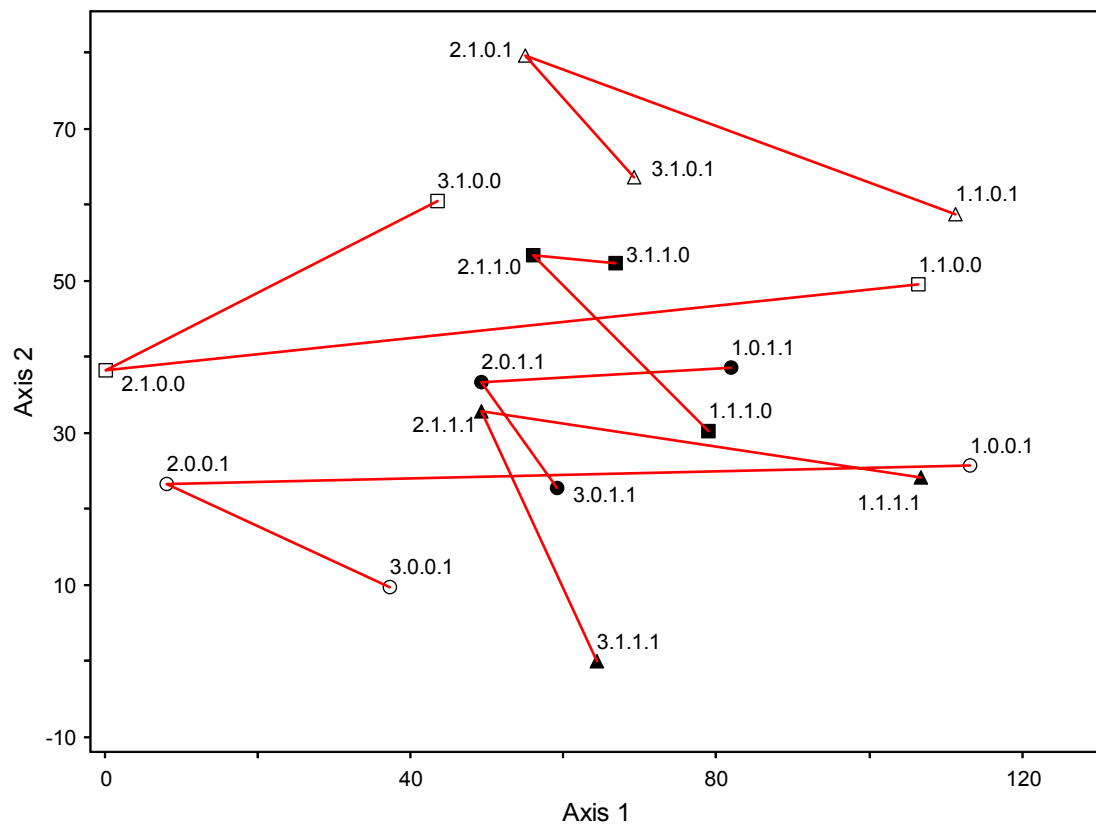
Figure 5.8a DCA of species composition of different treatments in time (used data: mean density per species). Eigenvalues and lengths of gradients: First axis, 0.11, 1.13; second axis, 0.04, 0.80; third axis (not shown), 0.02, 0.67. First number in treatment names indicates date of relevé: 1, spring 2005; 2, autumn 2005; 3, spring 2006. Second number dung deposition: 1, with; 0, without dung. Third number moss layer: 1, intact; 0, disturbed. Fourth number dung beetle activity: 1, with; 0, without.
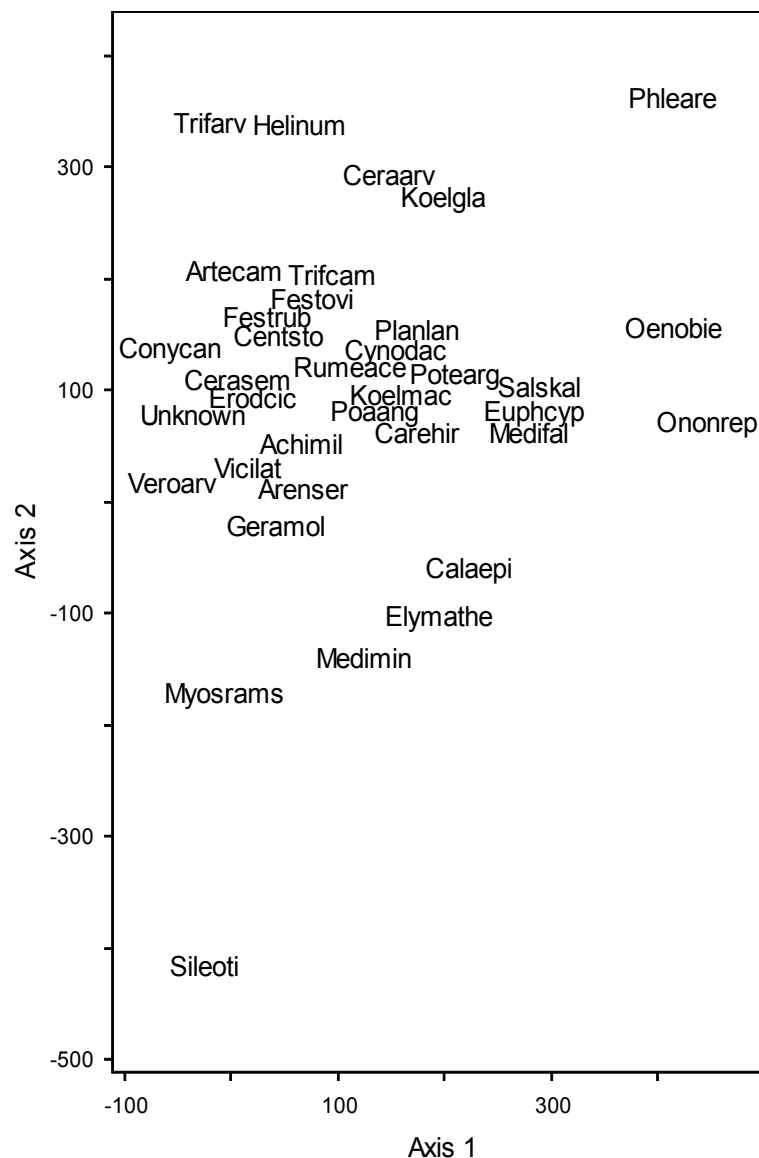
Figure 5.8b Species: Achimil *Achillea millefolium,* Arenser *Arenaria serpyllifolia*, Artecam *Artemisia campestris,* Calaepi *Calamagrostis epigejos*, Carehir *Carex hirta*, Centsto *Centaurea stoebe,* Ceraarv *Cerastium arvense*, Cerasem *Cerastium semidecandrium,* Conycan *Conyza canadensis,*Cynodac *Cynodon dactylon,* Elymath *Elymus athericus,* Erodcic *Erodium cicutarium,* Euphcyp *Euphorbia cyparissias,* Festovi *Festuca ovina* agg., Festrub *Festuca rubra,* Geramol *Geraniummolle,* Helinum *Helianthemum nummularium* s.l., Koelgla *Koeleria glauca,* Koelmac *Koeleria macrantha,* Medimin *Medicago minima*, Medifal *Medicago falcata,* Myosrams *Myosotis ramosissima / M. stricta,* Oenobie *Oenothera biennis* s.l., Ononrep *Ononis repens,* Phleare *Phleum arenarium,* Planlan *Plantago lanceolata,* Poaang *Poa angustifolia,* Potearg *Potentilla argentea* agg.*,* Rumeace *Rumex acetosella* s.l., Salskal *Salsola kali* ssp. *tragus,* Sileoti *Silene otites,* Trifarv *Trifolium arvense,* Trifcam *Trifolium campestre,* unknown, Veroarv *Veronica arvensis*, Vicilat Vicia lathyroides.

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Experiment 1c Armerio-Festucetum dung

Viable seed content

Via the germination test (Ter Heerdt method) 5052 seedlings of 29 taxa emerged (57 %
of total species number). Most seedlings belonged to *Verbascum phlomoides*, *P.
argentea* and *Rumex acetosella* (76 % of all seedlings, Table 5.11). In the field, a total of
596 dung-borne seedlings of at least 18 taxa were detected. Seedlings of *T. campestre,
P. argentea* and *V. arvensis* emerged in high numbers (81 %, Table 5.11).

The seed species which were viable after gut passage and the ones which emerged
under field conditions showed a relatively similar species quality in comparison to the
grazed Armerio-Festucetum paddocks (50 % target species, Fig. 5.9). Nevertheless,
several frequently occurring species, e.g. *Armeria maritima* ssp. *elongata* did not
emerge from the dung samples. Quantitatively, target species seedlings were over-
represented (73 %).
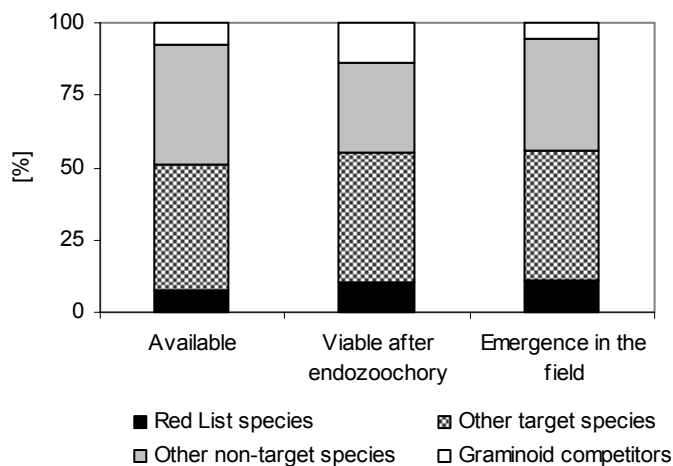
Figure 5.9 Species composition quality of (i) grazed Armerio-Festucetum vegetation ('Available'),
(ii) viable seeds after gut passage ('Viable after endozoochory') and (iii) dung-borne seedlings
under field conditions ('Emergence in the field').

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Table 5.11 Total number of dung-borne seedlings (dung collected after grazing Armerio-Festucetum trachyphyllae community), as emerged from a germination test (TH, Ter Heerdt method) and in the field. Results are shown per 1000 g of dung. Species which were present in the source paddocks, but did not emerge in germination test or field, are: *Armeria maritima* ssp. *elongata* (R, Plumbaginaceae), *Asperula cynanchica* (T, Rubiaceae), *Berteroa incana* (N, Brassicaceae), *Bromus hordeaceus* (N, Poaceae), *Bromus tectorum* (T, Poaceae), *Carduus nutans* (N, Asteraceae), *Centaurea stoebe* (T, Asteraceae), *Conyza canadensis* (N, Asteraceae), *Cynoglossum officinale* (N, Boraginaceae), *Echium vulgare* (T, Boraginaceae), *Erodium cicutarium* (T, Geraniaceae), *Eryngium campestre* (T, Apiaceae), *Euphorbia cyparissias* (T, Euphorbiaceae), *Festuca rubra* (N, Poaceae), *Helichrysum arenarium* (T, Asteraceae), *Hypericum perforatum* (N, Hypericaceae), *Medicago falcata* (T, Fabaceae), *Plantago lanceolata* (N, Plantaginaceae), *Rumex thyrsiflorus* (N, Polygonaceae), *Silene latifolia* ssp. *alba* (N, Caryophyllaceae), *Sisymbrium altissimum* (N, Brassicaceae), *Tragopogon dubius* (N, Asteraceae).

Species	Source	SG	Family	Emergence	
				TH	field
Emerged both via TH and field:					
Arenaria serpyllifolia agg.	x	T	Caryophyllaceae	415	0.78
Cerastium semidecandrum	x	T	Caryophyllaceae	2.86	0.39
Geranium molle	x	N	Geraniaceae	4.76	1.30
Medicago minima	x	R	Fabaceae	0.95	0.52
Petrorhagia prolifera	x	T	Caryophyllaceae	0.95	0.26
Poa angustifolia	x	G	Poaceae	14.3	1.82
Potentilla argentea agg.	x	T	Rosaceae	1575	13.4
Rumex acetosella s.l.	x	T	Polygonaceae	508	2.08
Trifolium campestre	x	T	Fabaceae	144	37.5
Verbascum phlomoides	x	N	Scrophulariaceae	1590	3.78
Veronica arvensis	x	N	Scrophulariaceae	454	12.0
Vicia lathyroides	x	R	Fabaceae	0.95	0.52
Unidentified				3.81	0.65
Emerged only via TH:					
Achillea millefolium	x	N	Asteraceae	0.95	.
Agrostis capillaris	x	G	Poaceae	10.5	.
Agrostis vinealis	x	G	Poaceae	4.76	.
Carex hirta	x	G	Cyperaceae	0.95	.
Festuca ovina	x	T	Poaceae	2.86	.
Oenothera biennis s.l.	x	N	Onagraceae	18.1	.
Sedum acre	x	T	Crassulaceae	4.76	.
Silene conica	x	R	Caryophyllaceae	1.90	.
Trifolium arvense	x	T	Fabaceae	32.4	.
Veronica verna	x	T	Scrophulariaceae	15.2	.
Vulpia myuros	x	T	Poaceae	3.81	.
Emerged only in the field:					
Chenopodium album agg.	x	N	Chenopodiaceae	.	1.04
Crepis (cf) *capillaris*	x	N	Asteraceae	.	0.13
Myosotis stricta / M. ramosissima	x	T	Boraginaceae	.	0.52
Ononis repens	x	T	Fabaceae	.	0.13
Psyllium arenarium	x	N	Plantaginaceae	.	0.13
Polygonum aviculare	x	N	Polygonaceae	.	0.13
Fabaceae				.	0.39
Poaceae				.	0.65
# seedlings 1000 g dung				4811	77.5
# species total				23	18

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Treatment effects

Dung-borne seedlings Within the ruderalised AF stands, seedling emergence (species richness and sum individuals) from out of dung on disturbed and undisturbed plots was fairly similar (Table 5.12). Most species were not affected by moss disturbance either, except for a group of undetermined Fabaceae seedlings; after the experiment had started more Fabaceae seedlings were found in disturbed plots ($F_{1,62}$ = 3.21, *P* = 0.078) (Table 5.13). In contrast, *V. lathyroides* did show a trend of being negatively affected by the disturbance treatment (*V. lathyroides*, T*M: $F_{1,62}$ = 2.82, *P* = 0.098). *V. lathyroides* and also *P. prolifera* exclusively emerged in plots with intact moss layer, but only a few individuals were found. Several other species showed significant changes in time (Table 5.13).

Table 5.12 Number of dung-borne seedlings and species per treatment (M⁻, moss layer disturbed; M⁺, intact moss layer) in Armerio-Festucetum dung plots.

Species	M+	M -
Arenaria serpyllifolia s.l.	3	3
Cerastium semidecandrum	3	0
Chenopodium album agg.	2	4
Crepis sp.	1	0
Geranium molle	3	7
Medicago minima	3	1
Myosotis ramosissima / M. stricta	3	1
Petrorhagia prolifera	2	0
Poa angustifolia	12	2
Polygonum aviculare agg.	0	1
Potentilla argentea agg.	39	64
Psyllium arenarium	0	1
Rumex acetosella s.l.	5	11
Trifolium campestre	154	134
Verbascum phlomoides	13	16
Veronica arvensis	46	46
Vicia lathyroides	4	0
Fabaceae	0	3
Poaceae	2	2
unknown	4	1
sum individuals	299	297
sum species	17	16

Table 5.13 Effect of time ('Time') and moss layer ('Moss') on seedling emergence from out of Armerio-Festucetum dung (results mixed linear model). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, ~ ≤ 0.078, N.S. = not significant.

	Abundance (% ind.)	Time	Moss	T*M
sum individuals		***	N.S.	N.S.
sum species		***	N.S.	N.S.
Trifolium campestre	48.3	***	N.S.	N.S.
Potentilla argentea agg.	17.3	***	N.S.	N.S.
Veronica arvensis	15.4	***	N.S.	N.S.
Verbascum phlomoides	4.9	***	N.S.	N.S.
Rumex acetosella s.l.	2.7	**	N.S.	N.S.
Poa angustifolia	2.3	N.S.	N.S.	N.S.
Geranium molle agg.	1.7	N.S.	N.S.	N.S.
Arenaria serpyllifolia s.l.	1.0	*	N.S.	N.S.
Chenopodium album	1.0	*	N.S.	N.S.
unknown	0.8	N.S.	N.S.	N.S.
Medicago minima	0.7	N.S.	N.S.	N.S.
Myosotis stricta / M. rammosissima	0.7	N.S.	N.S.	N.S.
Vicia lathyroides	0.7	~	~	~
Poaceae	0.7	N.S.	N.S.	N.S.
Cerastium semidecandrum	0.5	N.S.	N.S.	N.S.
Fabaceae	0.5	~	~	~
Petrorhagia prolifera	0.3	N.S.	N.S.	N.S.
Crepis sp.	0.2	N.S.	N.S.	N.S.
Polygonum aviculare agg.	0.2	N.S.	N.S.	N.S.
Psyllium arenarium	0.2	N.S.	N.S.	N.S.

Complete seedling emergence Dung did positively affect the total seedling emergence in intact moss plots (Fig. 5.10) although no significant effect was found (D*M: $F_{1,89}$ = 3.26, P = 0.074) (Table 5.14). Seedling emergence in moss-removed plots was not affected by dung deposition. The total number of species was positively affected by moss removal ($F_{1,89}$ = 4.28, P = 0.042).

On species level (Table 5.14), especially in the second period a higher number of *T. campestre* and *P. argentea* seedlings were found in dung plots (*T. campestre*: $F_{1,89}$ = 30.51, P < 0.001; *P. argentea*: $F_{1,89}$ = 8.86, P = 0.004), whereas emergence of *M. minima*, *C. semidecandrum, E. cyparissias* and *E. cicutarium* was significantly lower (*M. minima:* $F_{1,89}$ = 13.74, P < 0.001; *C. semidecandrum*: $F_{1,89}$ = 6.13, P = 0.015; *E. cyparissias:* $F_{1,89}$ = 4.98, P = 0.028; *E. cicutarium*: $F_{1,89}$ = 9.73, P = 0.002). Also *V. lathyroides* showed, depending on time, a higher emergence in plots without dung ($F_{1,89}$ = 5.78, P = 0.018) and in moss plots ($F_{1,89}$ = 4.87, P = 0.030). An interaction between the effects of moss and dung was found for *M. falcata*. In moss-disturbed plots dung deposition inhibited the emergence of *M. falcata,* whereas undisturbed plots showed no

difference with and without dung ($F_{1,89}$ = 6.77, *P* = 0.010). In presence of an intact moss layer more *G. molle* seedlings were found ($F_{1,89}$ = 3.97, *P* = 0.049), whereas disturbance stimulated the emergence of *Crepis sp.* ($F_{1,89}$ = 11.27, *P* = 0.001). Finally, especially in the second period, *A. serpyllifolia* and *C. arvense* showed a higher emergence in plots without moss and dung (*A. serpyllifolia:* $F_{1,89}$ = 9.03, *P* = 0.003; *C. arvense*, $F_{1,89}$ = 4.58, *P* = 0.035).

Armerio-Festucetum

Dung seed content	Treatment	Spring 06	
	D+M+	Soil 0.59 Dung 0.38	Soil 10 Dung 9.0
	D+M-	Soil 0.25 Dung 0.75	Soil 10 Dung 8.5
577	D-M+	Soil 0.25	Soil 12
	D-M-	Soil 1.25	Soil 22
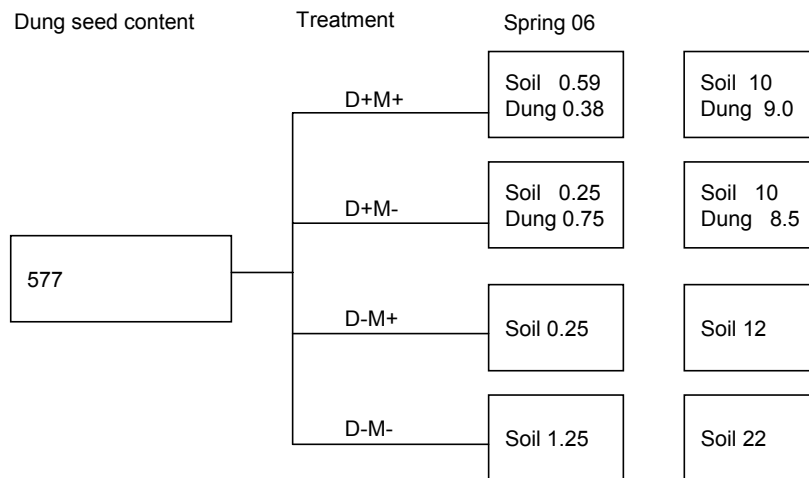
Figure 5.10 Flow diagram of mean number of viable seeds detected per 120 g of Armerio-Festucetum dung ('Dung seed content') and mean number of soil- and dung-borne seedlings per treatment per season (emerged in 400 cm²). Dung was collected after sheep grazed Armerio-Festucetum vegetation. Treatment abbreviations: D+/-, with/without dung; M+/-, with/without moss.

Table 5.14 Effects of Armerio-Festucetum dung deposition ('Dung') and disturbance of moss layer ('Moss') on seedling number (soil- and dung-borne), species richness and number of seedlings per species in time ('Time') (results from mixed linear models). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant. Species with abundance ≤ 0.2 % of the total number of seedlings didn't show any effects: *Polygonum aviculare* agg., *Petrorhagia prolifera, Sedum acre, Festuca rubra, F. brevipila, Trifolium arvense, Psyllium arenarium, Ononis repens, Myosotis ramosissima, Koeleria macrantha, Centaurea stoebe, Armeria maritima* ssp. *elongata*, Poaceae and Asteraceae.

	Abundance (% ind.)	Time	Moss	Dung	T*M	T*D	M*D	T*M*D
sum individuals		***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
sum species		***	*	N.S.	N.S.	N.S.	N.S.	N.S.
Veronica arvensis	19.7	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium campestre	17.9	***	N.S.	***	N.S.	***	N.S.	N.S.
Vicia lathyroides	11.8	***	*	*	*	*	N.S.	N.S.
Arenaria serpyllifolia s.l.	10.1	***	**	**	**	**	**	**
Poa angustifolia	7.2	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Potentilla argentea agg.	6.9	**	N.S.	**	N.S.	**	N.S.	N.S.
Geranium molle agg.	3.9	**	*	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium arvense	2.9	**	*	N.S.	*	N.S.	*	*
Medicago minima	2.6	***	N.S.	***	N.S.	***	N.S.	N.S.
Cynodon dactylon	2.5	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Verbascum phlomoides	2.4	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium semidecandrum	1.7	***	N.S.	N.S.	*	*	N.S.	N.S.
Medicago falcata (incl. x varia)	1.5	***	**	*	N.S.	N.S.	*	N.S.
Elymus athericus	1.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Crepis sp.	1.3	N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.
Rumex acetosella s.l.	1.2	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Euphorbia cyparissias	0.6	N.S.	N.S.	*	N.S.	N.S.	N.S.	N.S.
Myosotis stricta / M. rammosissima	0.9	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vicia angustifolia	0.5	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Berteroa incana	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
unknown	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Chenopodium album	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Erodium cicutarium	0.3	N.S.	N.S.	**	N.S.	N.S.	N.S.	N.S.

Complete vegetation Initially (spring), both or combined treatments inhibited the number of individuals, control plots showed the highest abundance. Six months later, an opposite response was found: both combined treatments facilitated the individual number, whereas controls contained fewest individuals (T*M*D: $F_{1,90}$ = 11.06, P = 0.001) (Table 5.15). Similar results were found for species richness: plots with a disturbed moss layer or dung deposition previously (spring) had an inhibited and later on (autumn) slightly increased number of species per plot (T*M: $F_{1,90}$ = 5.48, P = 0.021; T*D: $F_{1,90}$ = 13.32, P < 0.001).

In moss-disturbed plots more *C. dactylon* and *F. brevipila* were found with dung, whereas undisturbed plots with dung suppressed their abundance (T*M*D: *C. dactylon,*

$F_{1,90}$ = 5.90, P = 0.017; *F. brevipila,* $F_{1,90}$ = 4.37, P = 0.039). But over time, the presence of *C. dactylon* increased in all treatments except controls. Competitive species *P. angustifolia* and *C. arvense* also increased in time, independent of the treatment (*P. angustifolia,* $F_{1,90}$ = 11.60, P = 0.001; *C. arvense,* $F_{1,90}$ = 4.53, P = 0.036). In spring other graminoids, *C. hirta* and *B. hordeaceus* showed a lower abundance in dung plots (*C. hirta,* $F_{1,90}$ = 7.34, P = 0.008; *B. hordeaceus*, $F_{1,90}$ = 4.22, P = 0.043). Several herbs had significantly lower individual numbers in the presence of dung: *M. minima, E. cicutarium, V. lathyroides, C. semidecandrum, A. serpyllifolia*, whereas few *T. arvense* were exclusively found in plots with moss disturbance and without dung (*M. minima,* $F_{1,90}$ = 19.94, P < 0.001; *E. cicutarium,* $F_{1,90}$ = 14.25, P < 0.001; *V. lathyroides,* $F_{1,90}$ = 17.38, P < 0.001; *C. semidecandrum*, $F_{1,90}$ = 32.87, P < 0.001; *A. serpyllifolia,* $F_{1,90}$ = 7.80, P = 0.006; *T. arvense,* $F_{1,90}$ = 4.27, P = 0.042). For *V. arvensis* the effect of dung deposition was dependent on time: in spring dung plots contained fewer individuals than the controls, in autumn the opposite results were found ($F_{1,90}$ = 4.71, P = 0.033). Such a changing effect was also observed in the case of moss disturbance for *E. cicutarium*: in spring more individuals were found in intact moss plots, whereas 6 months later in autumn more individuals were found in moss-disturbed plots ($F_{1,90}$ = 5.70, P = 0.019).

The effect of dung deposition on the abundance of *M. falcata* and *M. stricta/M. ramosissima* was dependent on the moss-layer treatment: with disturbance, dung inhibited both species*,* whereas on intact moss plots with dung deposition more *M. falcata* and equal numbers of *M. stricta/M. ramosissima* individuals were found (*M. falcata*, $F_{1,90}$ = 4.87, P = 0.030; *M. stricta/M. ramosissima,* $F_{1,90}$ = 5.77, P = 0.018). Next to an inhibiting effect dung deposition had on several species, a few other species showed a higher abundance: *P. argentea*, *T. campestre, R. acetosella* (*P. argentea,* $F_{1,90}$ = 8.13, P = 0.005; *T. campestre* $F_{1,90}$ = 40.59, P < 0.001; *R. acetosella,* $F_{1,90}$ = 2.81, P = 0.097). Finally, as was found for seedlings, the number of *Crepis* sp. individuals was significantly higher in moss-disturbed plots ($F_{1,90}$ = 4.71, P = 0.033).

Table 5.15 Effects of Armerio-Festucetum dung deposition ('Dung') and disturbance of moss layer ('Moss') on species richness, total individual number and number of individuals per species in time ('Time') (results from mixed linear models). Level of significance; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, N.S. = not significant. Species with abundance ≤ 0.01 % of the total number of individuals didn't show any effects: *Agrostis capillaris, Psyllium arenarium, Bromus tectorum, Rumex* sp.*, Silene conica* and *Asparagus officinalis*.

	Abundance (% ind.)	Time	Dung	Moss	T*D	T*M	D*M	T*D*M
sum individuals		***	N.S.	N.S.	***	**	N.S.	**
sum species		N.S.	*	N.S.	***	*	N.S.	N.S.
Poa angustifolia	32.4	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cynodon dactylon	15.4	**	N.S.	N.S.	N.S.	N.S.	*	*
Cerastium arvense	9.6	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Veronica arvensis	9.5	*	N.S.	*	***	N.S.	N.S.	*
Trifolium campestre	4.7	***	***	N.S.	***	N.S.	N.S.	N.S.
Arenaria serpyllifolia agg.	4.5	N.S.	**	N.S.	N.S.	***	N.S.	**
Vicia lathyroides	4.4	**	***	***	N.S.	N.S.	N.S.	N.S.
Festuca rubra	3.5	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Geranium molle	2.4	***	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Potentilla argentea agg.	2.1	N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.
Cerastium semidecandrum	2.0	***	***	***	***	***	***	***
Medicago falcata (incl. x varia)	1.4	N.S.	N.S.	N.S.	N.S.	N.S.	*	N.S.
Medicago minima	1.3	N.S.	***	N.S.	N.S.	N.S.	N.S.	N.S.
Festuca brevipila	1.1	*	N.S.	N.S.	*	*	N.S.	*
Carex hirta	1.0	N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.
Euphorbia cyparissias	0.9	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Bromus hordeaceus	0.7	***	*	N.S.	*	N.S.	N.S.	N.S.
Vicia angustifolia	0.6	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Verbascum phlomoides	0.6	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Crepis sp.	0.5	N.S.	N.S.	*	N.S.	N.S.	N.S.	N.S.
Plantago lanceolata	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Rumex acetosella s.l.	0.4	**	~	N.S.	N.S.	N.S.	N.S.	N.S.
Koeleria macrantha	0.4	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Myosotis stricta	0.3	N.S.	*	*	N.S.	N.S.	N.S.	N.S.
Erodium cicutarium agg.	0.3	N.S.	***	N.S.	N.S.	*	N.S.	N.S.
Ononis repens	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Sedum acre	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Berteroa incana	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Myosotis ramosissima /stricta	0.2	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Festuca ovina agg.	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Armeria maritima ssp. e*longata*	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Chenopodium album agg.	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
unknown	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Petrorhagia prolifera	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Silene vulgaris s.l.	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Vulpia myuros	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Polygonum aviculare agg.	0.1	N.S.	N.S.	Moss	N.S.	N.S.	D*M	N.S.
Centaurea stoebe	0.1	*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Poaceae	0.1	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Myosotis ramosissima	0.04	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Fabaceae	0.04	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Calamagrostis epigejos	0.03	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Silene otites	0.03	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Trifolium arvense	0.03	N.S.	*	*	N.S.	N.S.	*	N.S.

Detrended correspondence analysis (DCA) (Fig. 5.11a) was used to analyse the species composition and development of the differently treated AF plots in time. Compared to the control, the three different treatments are situated relatively close together (low eigenvalues), indicating a relatively high similarity of species compositions. All autumn plots are positioned on the right side of the spring plots. This increase along the first axis might show the ruderalisation in time, which also fits with the above-mentioned results. The second axis could indicate the vegetation's species richness. In time, both treatments without dung show a decrease, whereas the two dung treatments moderately increase along the second axis. The central position of several graminoid competitors points out the ruderalised character of the plots (Fig. 5.11b).
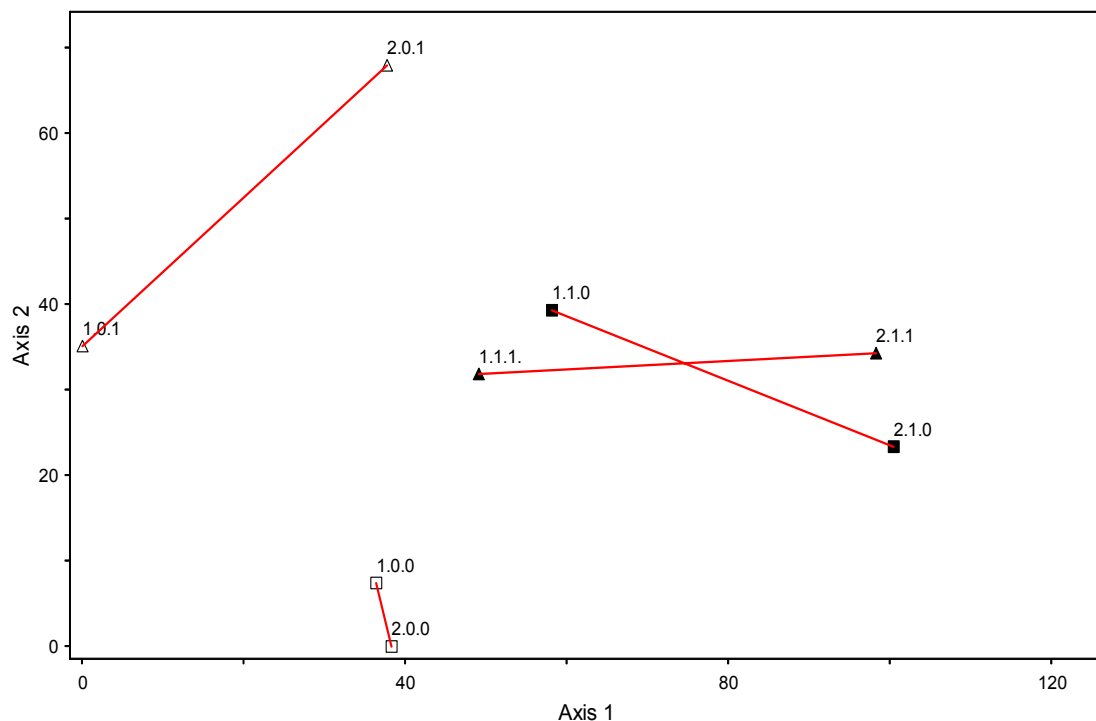
Figure 5.11a DCA of species composition of different treatments in time (used data: mean density per species). Eigenvalues and lengths of gradients: First axis, 0.116, 1.004; second axis, 0.039, 0.679; third axis (not shown), 0.009, 0.601. First number in treatment names indicates date of relevé: 1, spring 2006; 2, autumn 2006. Second number dung deposition: 1, with; 0, without dung. Third number moss layer: 1, intact; 0, disturbed. Fourth number dung beetle activity: 1, with; 0, without.
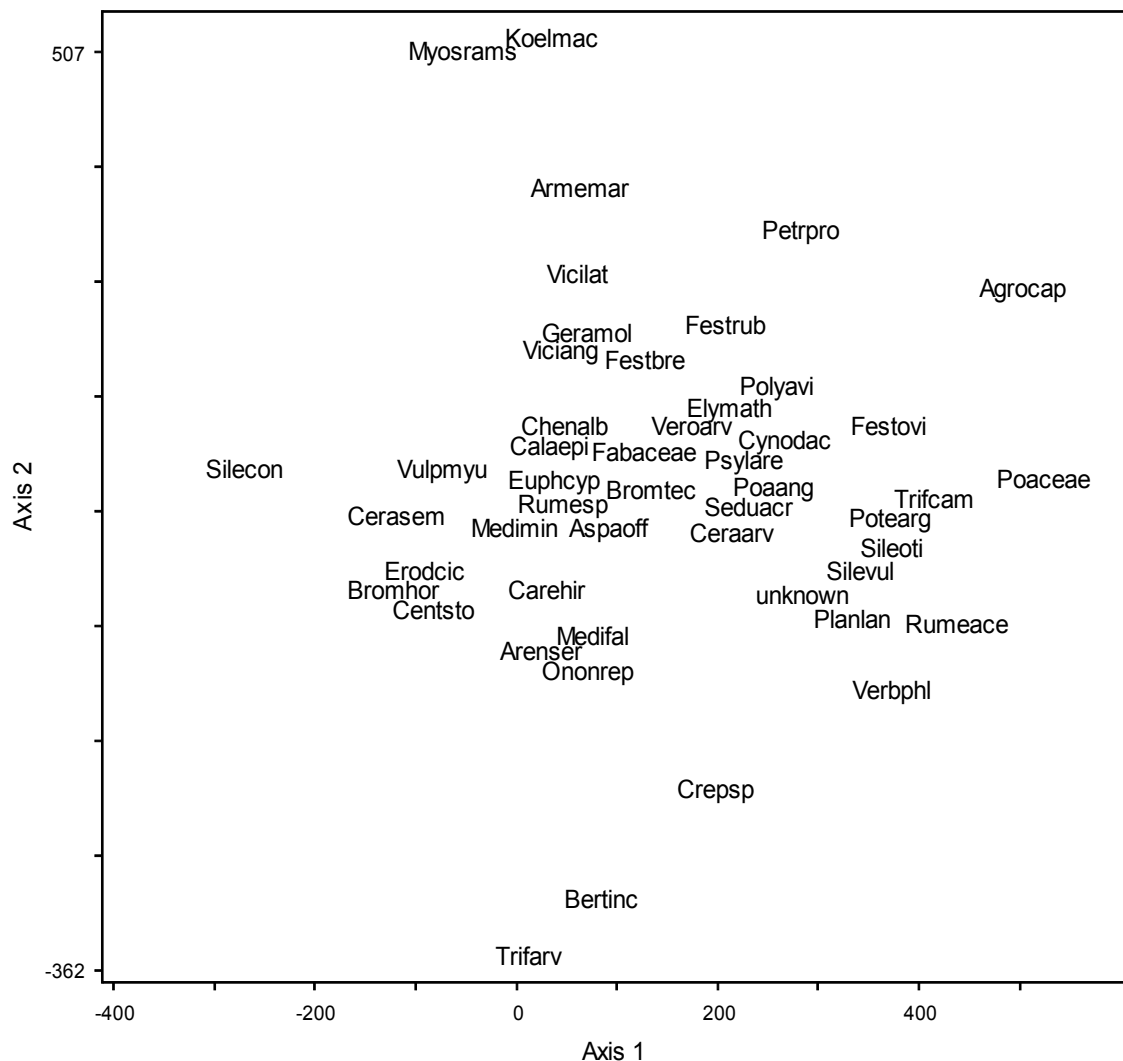
Figure 5.11b Species: Arenser *Arenaria serpyllifolia*, Armemar *Armeria maritima* ssp. *elongata*, Bertinc *Berteroa incana,* Bromhor *Bromus hordeaceus*, Carehir *Carex hirta*, Centsto *Centaurea stoebe,* Ceraarv *Cerastium arvense*, Cerasem *Cerastium semidecandrium,* Chenalb *Chenopodium album* agg., Crepsp Crepis sp., Cynodac *Cynodon dactylon,* Elymcam *Elymus athericus,* Erodcic *Erodium cicutarium,* Euphcyp *Euphorbia cyparissias,* Festbre *Festuca brevipila*, Festovi *Festuca ovina* agg., Festrub *Festuca rubra,* Geramol *Geranium molle,* Koelmac *Koeleria macrantha,* Medifal *Medicago falcata,* Medimin *Medicago minima*, Myosram *Myosotis ramosissima,* Myossp *Myosotis* sp., Myosstr *Myosotis stricta,* Ononrep *Ononis repens,* Petrpro *Petrorhagia prolifera,* Planlan *Plantago lanceolata,* Poaang *Poa angustifolia,* Poaceae, Polyavi *Polygonum aviculare* agg., Potearg *Potentilla argentea* agg.*,* Rumeace *Rumex acetosella* s.l., Seduacr *Sedum acre*, Sileoti *Silene otites,* Silevul *Silene vulgaris,* Trifarv *Trifolium arvense,* Trifcam *Trifolium campestre,* unknown, Verbphl *Verbascum phlomoides*, Veroarv *Veronica arvensis*, Viciang *Vicia angustifolia*, Vicilat *Vicia lathyroides*, Vulpmyu *Vulpia myuros*.

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Discussion

In the present study, the impact of (i) herbivore (dung deposition and moss disturbance) and (ii) dung beetle-initiated activities (dung removal and soil disturbance) on recruitment of target species and vegetation development was tested.

Species composition of dung-embedded seeds Grazing three well-developed target communities Kg, AS and AF resulted in endozoochorous seed transport of mostly (annual) herbs of which many are target species. Within the study area sheep were shown to consume more phytomass of herbs than graminoids (Süss and Schwabe 2007). The detected similarity between species composition of the grazed source and seed content of dung shows the importance of the quality of a source. The three dung types contained equally low seed numbers of graminoid competitor species.

Species-specific survival As predicted, small and/or hard-coated seeds have a higher recovery chance than larger and/or soft-coated seeds (e.g. Cocks 1988; Malo and Suárez 1995; Cosyns and Hoffmann 2005; Mouissie et al. 2005b). High numbers of viable seeds were, e.g., found for *Helianthemum nummularium*, *Trifolium campestre* and *Arenaria serpyllifolia*. Nevertheless, some irregularly shaped seeds, especially from the family of Poaceae, were detected as well. Probably for the same reason as mentioned above, no viable seeds of larger-seeded *Linum perenne* (feeding experiment) were detected after digestion. However, given that many of the extremely small *Jasione montana* seeds had been consumed, the lack of viable seeds was surprising. Presumably other germination requirements might not have been fulfilled for this acidophytic species.

Quantity of dung-borne seedlings As in many other field experiments (e.g. Sánchez and Peco 2002; Mouissie et al. 2005a; Eichberg et al. 2007), only a fraction of all viable dung-embedded seeds emerged under field conditions during the period in which dung samples were observed. Compared to the improved circumstances of germination tests (e.g. pellets were crushed, samples were watered frequently), field conditions can be harsh (dryness, embedded in dung pellets) which probably causes this disparity. Generally, species from which a high seed number was detected via a germination test also emerged frequently in the field (Kg, *Psyllium arenarium*; AS, *Helianthemum nummularium*; AF, *Potentilla argentea*). High seed contents and significant emergence rates of several target species indicate the contribution dung can

make to regeneration from the seed bank. Especially after dung decomposition the seed content of the soil seed bank, as detected in the top soil layer (0 – 1 cm) (Eichberg et al. (2006), could be increased by 75 % (Koelerion glaucae) up to 360 % (Armerio-Festucetum). Rabbit endozoochorously dispersed seeds could also build up the soil seed bank by 45 %, significantly promoting seedling emergence and species richness after disturbance in Mediterranean grasslands (Malo et al. 1995), whereas rabbit pellets could add 8 – 15 % of legume seeds (Russi et al. 1992a). However, not all endozoochorously dispersed seeds are able to build up a persistent seed bank; slow decomposition of dung pellets might therefore negatively affect the survival of these seeds.

Quality of dung-borne seedlings With all three dung types relatively more target species emerged from dung compared to their abundance in the grazing sources. *Helianthemum nummularium*, one of those target species, was previously absent in study area 1 and successfully emerged and established from AS dung.

In line with Eichberg et al. (2007), no graminoid competitor species emerged from Kg dung within plots of Koelerion glaucae. Eichberg and co-workers suggested that the extreme conditions (high temperatures) of this early successional community might prevent the germination of generalists. However, in ruderalised AF plots a few individuals of *C. hirta, Poa angustifolia* and *Cynodon dactylon* emerged from AS and AF dung. The potential impact of productivity differences will be discussed below (see *total vegetation*).

Treatment effects - Seedling emergence

Dung deposition in most cases suppressed the total seedling emergence, although it could also slightly favour it (AF autumn 2006, AS spring 2005, 2006). It seems that a compact layer of pellets affects micro-conditions in a similar way as does an intact *Hypnum* layer: physical interference and limitation of radiation prevent many seedlings from emergence. The relatively few dung-borne seedlings could not compensate this overall suppressing effect. The small increase in seedling emergence was found when emergence from the soil was low, additionally inhibited by dung. Since dung- and soil-borne seedlings emerged almost at the same rate, direct emergence from dung significantly contributed to the total rate. Malo and Suárez (1995) found a similar

inhibiting effect for cattle dung pats in a Mediterranean pasture. Dung deposition did, however, facilitate a greater species richness among emerging seedlings (Kg and AS). Cosyns et al. (2006) also found an increased small-scale species-richness after cattle dung deposition, due to decreased dominance of monocotyl species. Reduced competition might have stimulated more species to emerge.

On the level of individual species a varying effect of dung deposition was shown, determined by the number of seedlings emerging from dung and soil. Several species were facilitated since they showed a high emergence from the dung, e.g. *P. arenarium* (Kg), *H. nummularium* (AS), *T. campestre*, *P. argentea* (AF). Emergence of various annuals from the soil seed bank was inhibited, e.g. *C. canadensis*, *S. tridactylites* (Kg, AS)*, M. minima*, *V. lathyroides* (AF). Only emergence of *Rumex acetosella* from the soil seemed to be facilitated by dung deposition. This acidophytic species was possibly stimulated by the fertilizing effect dung could have on soil (Posse et al. 2000). By contrast, Williams and Haynes (1995) did not find a measurable phytomass response to sheep dung deposition.

After seedling emergence was initially suppressed by dung deposition, the intensive visitation of **dung beetles** in Kg plots stimulated emergence again. Dung removal and soil disturbance together activated the soil seed bank of especially *Oenothera biennis* and *Polygonum aviculare.* Both are disturbance species, probably with a light-requirement for germination (Gross and Kromer 1986). They were frequently detected in the soil seed bank of Kg (Eichberg et al. 2006). Nevertheless, species richness of emerging seedlings decreased in time. It may be that the natural reduction in time of seedling species richness (more species germinate in autumn and winter than in spring) is accelerated by dung beetles.

Moss disturbance facilitated seedling emergence from AS dung. Both the number of dung-borne seedlings and species richness increased if dung was established in moss-disturbed gaps. AF dung showed no difference. Disturbance probably improved germination conditions by increasing the soil-pellet contact. The denser vegetation of ruderalised AF plots in which AF dung was deposited could have prevented close contact between soil and pellets, as has been observed in degraded rangeland vegetation (Auman et al. 1998).

Disturbance also favoured total (soil- and dung-borne) seedling emergence and seedling species richness, with and without dung deposition. AF dung plots only temporarily showed such a difference. The facilitating effect is in line with the moss-disturbance experiments of Eichberg et al. (2007) in early successional Koelerion glaucae. Especially small-seeded species, e.g. *Sedum acre, Veronica arvensis*, *Arenaria serpyllifolia* emerged more frequently. Disturbance reduces the overall vegetation density (lower competition) and the newly created gaps stimulate species from the soil seed bank to emerge, enabling them to persist (Grace and Tilman 1992). Nevertheless, altered micro-conditions, e.g. increased temperature, could have inhibited seedling emergence as well; *E. athericus* (AS) and *G. molle* (AF) showed a lower emergence from moss-disturbed plots. The suppression of *E. athericus* could have been coincidence too: only three seedlings were detected. Within one year *Hypnum* moss overgrew dung pellets completely, which probably limited the chance of emergence for dung embedded seeds severely (Welch 1985).

Besides treatment effects, **time** had a strong impact on seedling emergence as well. Autumn and winter vs. spring germination was a distinguishing factor for species composition, as shown by DCA of KG seedling emergence (Exp.1a, Fig. 5.4a, b).

Total vegetation

The semi-ruderalised condition of AF plots in Exp. 1b seemed relatively stable, despite different treatments. Most competing species were only affected by time, although dung deposition suppressed *C. hirta* and *Festuca rubra* was probably stimulated by nutrients leaching out of dung (as found for *A. serpyllifolia* in Kg dung plots, Exp.1a). However, both treatments did work on several herbs. As a result, moss disturbance promoted overall plant density and species richness (periods 2 and 3); dung deposition also favoured species richness but suppressed density. An intact moss layer and deposition of dung showed a similar inhibiting effect on typical small-seeded soil seed bank species: *Cerastium semidecandrum, Saxifraga tridactylites* and *Conyza canadensis*. Additionally, disturbance of moss also facilitated other typical soil seed bank species, e.g. *A. serpyllifolia, V. arvensis*, *S. acre.* As mentioned above (seedling emergence section), only *R. acetosella*, an acidophytic species, was promoted by dung deposition. The abundance of *T. campestre* increased and *H. nummularium* was newly established

because of direct emergence from out of dung. The same processes affecting emergence and species richness of seedlings (dung-added seeds, activation/suppression of the soil seed bank, altered micro-site conditions and changed competition) work on total vegetation as well.

By contrast, in more ruderalised AF plots (exp.1c) moss disturbance and dung deposition initially both suppressed the overall plant density and species richness, which probably reduced competition. Six months later both treatments had moderately facilitated species richness. The temporal reduction of competitive species *C. hirta* and especially *C. dactylon* by dung deposition presumably allowed establishment of endozoochorous species, e.g. *P. argentea* and *T. campestre*. Despite that, most new species occurred only in relatively low individual numbers. The initially reduced competition (lower number of individuals) and/or leaching of dung nutrients secondary stimulated especially previously most dominant (more ruderal) species, *P. angustifolia, C. dactylon, Cerastium arvense.* Auman et al. (1998) found adjacent grasses to be stimulated by nutrients from sheep dung, which promoted an even more competitive environment that prevented seedling establishment. Welch (1985) also pointed out that vegetative colonization by species already present at the sites can be far more important than germination in the re-establishment of plant cover on dung. Despite temporal improvement, it seems that the rate of disturbance as applied in this experiment further facilitates ruderalisation in these more productive plots.

Olff and Ritchie (1998) state that the effect of herbivory on plant species richness depends on variation in habitat characteristics, e.g. soil fertility and water availability. In our dry and nutrient-poor investigation area a reduction of productivity is desirable since an increase of productivity from early to mid-successional stages reduces phytodiversity, although Koelerion glaucae could have a lower number of species too (Süss et al. 2007).

The specific impact of herbivore-formed gaps on species richness is presumably also related to productivity: plots with low and intermediate productivity showed an increase in species richness, whereas the same intensity of disturbance in more productive sites did not enhance species richness. Kondoh (2001) predicted an interaction between disturbance and productivity, together determining species richness. Intermediate disturbance does not always result in the highest species richness

(Intermediate-disturbance hypothesis; Connell 1978). Instead, high productivity allows a positive disturbance - diversity correlation, low productivity results in a negative correlation and a unimodal pattern is predicted with moderate productivity (Kondoh 2001). Consequently, more ruderalised Armerio-Festucetum stands would need a greater disturbance treatment to reduce the abundance of competitors and increase species richness, but such a predicted opposite effect of productivity under high- and low-disturbed conditions still needs to be tested (Kondoh 2001). Additional grazing by donkeys could greatly improve the phytodiversity of those stands. Donkeys can increase the rate of disturbance (more extensive bare ground cover) while reducing graminoids and litter and increasing the presence of herbs in more productive mid-successional stands (Süss and Schwabe 2007). Moreover, separate management of target plant communities on nutrient-poor soils is recommended (Mouissie et al. 2005a).

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Appendix 5.1 Effects of potential dung beetle activity (('Dung beetle') on seedling number, seedling species richness and number of seedlings per species in time ('Time') (results from mixed linear models) after deposition of Alio-Stipetum dung. Level of significance; * = P < 0.05, ** = P < 0.01, *** = P < 0.001, N.S. = not significant. Species with abundance = 0.1 % of the total number of seedlings didn't show any significant effects: *Artemisia campestris, Erophila verna, Silene conica, Veronica verna, Arabidopsis thaliana, Asparagus officinalis, Elymus athericus, Festuca rubra*, Poaceae and Asteraceae.

	Abundance (% ind)	Time	Dungbeetle	T*B
sum seedlings		***	N.S.	N.S.
sum species		***	N.S.	N.S.
Veronica arvensis	32.9	**	N.S.	N.S.
Helianthemum nummularium s.l.	11.6	***	N.S.	N.S.
Arenaria serpyllifolia agg.	6.8	**	N.S.	N.S.
Vicia lathyroides	6.7	***	N.S.	N.S.
Medicago falcata (incl. x varia)	5.6	***	N.S.	N.S.
Cerastium semidecandrum	5.5	***	N.S.	N.S.
Geranium molle	3.8	***	N.S.	N.S.
Poa angustifolia	3.7	N.S.	N.S.	N.S.
Rumex acetosella s.l.	3.1	N.S.	N.S.	N.S.
Trifolium campestre	2.9	***	N.S.	N.S.
Medicago minima	2.6	***	N.S.	N.S.
Erodium cicutarium	1.6	*	N.S.	N.S.
Centaurea stoebe	1.3	N.S.	N.S.	N.S.
Saxifraga tridactylites	1.3	N.S.	N.S.	N.S.
Myosotis stricta / M. ramosissima	1.8	*	N.S.	N.S.
Sedum acre	0.8	N.S.	N.S.	N.S.
unknown	0.8	N.S.	N.S.	N.S.
Chenopodium album agg.	0.7	N.S.	N.S.	N.S.
Conyza canadensis	0.7	N.S.	N.S.	N.S.
Plantago lanceolata	0.7	N.S.	N.S.	N.S.
Trifolium arvense	0.6	*	N.S.	N.S.
Salsola kali ssp. *tragus*	0.5	N.S.	N.S.	N.S.
Potentilla argentea agg.	0.4	N.S.	N.S.	N.S.
Cerastium arvense	0.4	N.S.	N.S.	N.S.
Fabaceae	0.4	**	N.S.	N.S.
Euphorbia cyparissias	0.3	**	N.S.	N.S.
Hypericum perforatum	0.2	N.S.	N.S.	N.S.
Koeleria macrantha	0.2	N.S.	N.S.	N.S.
Oenothera biennis s.l.	0.2	*	*	*
Vulpia myuros	0.2	N.S.	N.S.	N.S.
Achillea millefolium	0.2	N.S.	N.S.	N.S.
Carex hirta	0.2	N.S.	N.S.	N.S.
Trifolium repens	0.2	N.S.	N.S.	N.S.

Appendix 5.2 Effects of potential dung beetle activity (('Dung beetle') on individual nr, species richness and number of individuals * species^{-1} in time ('Time') (results from mixed linear models after deposition of Alio-Stipetum dung. Level of significance; * = P < 0.05, ** = P < 0.01, *** = P < 0.001, N.S. = not significant. Species with abundance ≤ 0.03 % of the total number of seedlings didn't show any significant effects: *Agrostis* sp., *Sisymbrium altissimum*, *Armeria maritima* ssp. *elongata*, *Asparagus officinalis, Helichrysum arenarium, Senecio vernalis*, Poaceae, Asteraceae.

	Abundance (% ind.)	Time	Dungbeetle	T*B
sum individuals		***	N.S.	N.S.
sum species		***	N.S.	N.S.
Poa angustifolia	22.2	**	N.S.	N.S.
Veronica arvensis	13.3	**	N.S.	N.S.
Elymus athericus	8.9	**	N.S.	**
Carex hirta	5.5	***	N.S.	N.S.
Medicago falcata (incl. M. x varia)	4.7	***	N.S.	N.S.
Cynodon dactylon	4.6	***	N.S.	N.S.
Arenaria serpyllifolia agg.	4.5	N.S.	N.S.	N.S.
Koeleria macrantha	4.1	*	N.S.	N.S.
Helianthemum nummularium	3.2	***	N.S.	N.S.
Medicago minima	3.0	*	N.S.	N.S.
Cerastium semidecandrum	3.0	*	N.S.	N.S.
Vicia lathyroides	2.9	***	N.S.	N.S.
Plantago lanceolata	1.8	N.S.	N.S.	N.S.
Geranium molle	1.8	***	N.S.	N.S.
Rumex acetocella s.l.	1.7	*	N.S.	N.S.
Festuca rubra	1.7	**	N.S.	N.S.
Trifolium campestre	1.1	***	N.S.	N.S.
Festuca ovina agg.	1.0	N.S.	N.S.	N.S.
Myosotis stricta / M. ramosissima	1.0	***	N.S.	N.S.
Sedu acre	0.9	N.S.	N.S.	N.S.
Achillea millefolium agg.	0.9	N.S.	N.S.	N.S.
Centaurea stoebe	0.8	N.S.	N.S.	N.S.
Erodium cicutarium	0.7	*	N.S.	N.S.
Ononis repens	0.6	N.S.	N.S.	N.S.
Calamagrostis epigejos	0.6	*	N.S.	N.S.
Euphorbia cyparissias	0.5	**	N.S.	N.S.
Saxifraga tridactylites	0.5	N.S.	N.S.	N.S.
Chenopodium album	0.5	N.S.	N.S.	N.S.
Potentilla argentea agg.	0.4	N.S.	N.S.	N.S.
Cerastium arvense	0.4	N.S.	N.S.	N.S.
Vulpia myuros	0.4	N.S.	N.S.	N.S.
Artemisia campestris	0.3	N.S.	N.S.	N.S.
Elymus repens	0.3	*	N.S.	N.S.
Oenothera biennis s.l.	0.2	***	N.S.	N.S.
Vicia angustifolia	0.2	*	N.S.	N.S.
Trifolium arvense	0.2	*	N.S.	N.S.
unknown	0.2	*	N.S.	N.S.
Salsola kali ssp. *tragus*	0.2	N.S.	N.S.	N.S.
Conyza canadensis	0.2	N.S.	N.S.	N.S.
Hypericum perforatum	0.2	N.S.	N.S.	N.S.
Koeleria glauca	0.2	N.S.	N.S.	N.S.
Veronica verna	0.1	N.S.	N.S.	N.S.
Trifolium repens	0.1	***	N.S.	N.S.
Fabaceae	0.1	*	N.S.	N.S.
Erophila verna	0.1	N.S.	N.S.	N.S.
Veronica praecox	0.1	N.S.	N.S.	N.S.
Arabidopsis thaliana	0.04	N.S.	N.S.	N.S.
Bromus tectorum	0.04	N.S.	N.S.	N.S.
Phleum arenarium	0.04	N.S.	N.S.	N.S.
Silene conica	0.04	N.S.	N.S.	N.S.

Chapter 6

General discussion

Helianthemum nummuralium successfully established from sheep dung.

Introduction

Today's fragmented landscapes cause isolation of many plant populations (Opdam 1990) and limits seed dispersal processes (Poschlod et al. 1996). The frequent extinction of such populations highlights the importance of dispersal and re-colonisation processes for their survival (Opdam 1990). Sheep can disperse large numbers of seeds (e.g. Welch 1985; Fischer et al. 1996; Pakeman et al. 2002), but especially preservation of target species and target communities is relevant from a nature conservation point of view. Very little is known about the dispersal of those particular species (Eichberg et al. 2005, 2007). Also, to further evaluate the contribution of sheep to dispersal and re-colonisation of target species in fragmented landscapes, more information regarding dispersal distances, arrival of seeds and their post-dispersal fate is needed. This study addressed the following research questions:

- Does the use of well-developed target communities as seed sources promote seed dispersal of especially target species?
- Which other factors affect seed attachment, retention and detachment to/from an animal coat?
- Does inter-area movement promote long-distance seed dispersal between different ecosystem fragments? How many seeds can arrive in the sink area?
- What is the post-dispersal fate of epi- and endozoochorously dispersed seeds? Does zoochory lead to recruitment of target species?
- Does sheep-induced disturbance and dung deposition promote colonisation of target species and fine-scale species richness?

Experiments were conducted in three different sandy grassland ecosystems, which reflect models for nutrient-poor open ecosystems.

Target communities as seed sources

Integrated grazing of nutrient-poor and -rich habitats might stimulate transport of seed species from nutrient-rich to -poor sites due to nutritional grazing differences (Mouissie et al. 2005a). Therefore, to stimulate high-quality seed dispersal in a desirable direction, consecutive grazing, initially of source areas with many target species and then of potentially less-developed sinks, was proposed. In the source paddocks (mostly well-

developed target communities Koelerion glaucae (Kg), Armerio-Festucetum trachyphyllae (AF), Allio-Stipetum capillatae (AS)) around half of the vascular plant species were target species. During the intra- and inter-area transfers conducted here, a total of 56 seed taxa were detected in sheep coats. The relative quality of epizoochorously transported seeds was slightly increased compared to most grazing sources (**Chapter 2**). Quantitatively, most of the detected seeds belonged to target species. Numerous burrs of the Red List species *Medicago minima* were present in investigated sheep coats. The proportion of target species and seeds was much higher than in other studies, where animals grazed larger areas without distinct sources and sinks. Of all the seeds found by Fischer et al. (1996), a third of the transported species and half of the detected seeds belonged to target vegetation types (Festuco-Brometea, Trifolio-Geranietea, Koelerio-Corynephoretea). Also Mouissie et al. (2005b) found many ubiquitous species to be dispersed epizoochorously via livestock.

Seeds recovered from dung were qualitatively similar to those in the grazing sources (same source paddocks as used for epizoochory investigations) (**Chapter 5**). In total, viable seeds of 59 taxa could be detected; half of them were target species and (annual) herbs. Also quantitatively, around half of the viable seeds belonged to habitat-typical herbs. Cosyns and Hoffmann (2005) showed that dung seed content of free-ranging horses was positively correlated with plant species abundance (cover) in a grazing area. As expected, the selection of a high-quality grazing source results in epi- and endozoochorous dispersal of large amounts of target species.

Estimation of the viable seed content of dung plays a crucial role in the evaluation of endozoochorous seed dispersal. Seedling emergence tests are frequently used to obtain such estimates, but emergence rates could differ depending on the method. The comparison I conducted between seedling numbers found by (a) the Ter Heerdt method (concentrated samples under controlled abiotic conditions, following Ter Heerdt et al. (1996)) and (b) a common garden experiment (unconcentrated samples under outdoor fluctuating abiotic conditions) showed relatively similar results (**Chapter 4**). Nevertheless, Ter Heerdt resulted in a higher (not significant) and faster overall emergence (experimental duration 5 months (TH) vs. 15 months (CG)); concentration especially promoted small-seeded winter annuals. Earlier studies had shown an

increased seedling emergence from concentrated soil samples (Ter Heerdt et al. 1996; Bossuyt et al. 2000). In common garden experiments, however, dormancy of several hard-coated species (*Helianthemum nummularium*, *Trifolium arvense, Trifolium campestre*) could be broken more frequently by strong (seasonal) temperature differences (Pritchard et al. 1988; Thanos et al. 1992). Finally, a few species were detected exclusively by one method, but low individual numbers (≤ 4) indicate this could have been a coincidence too.

Seed retention and long-distance seed dispersal

As in other studies on sheep epizoochory (Fischer et al. 1996; Mouissie et al. 2005b) a broad variety of seed species with and without surface structures was detected in the investigated sheep coats (**Chapter 2**). Nevertheless, not all species seem to have an equal attachment potential. Findings of Mouissie et al. (2005b) predict a minor role of seed surface structures for the attachment of seeds to sheep wool. However, when heavy seed species are also taken into account (Mouissie studied seeds ≤ 0.7 mg), the attachment probability seems to depend largely on the presence/absence of morphological seed structures. Generally, hooks or bristles did promote seed attachment, whereas seeds without morphological adaptations were negatively affected by seed mass. The overall detection of more high- than low-growing seed species shows the plant's seed-releasing height to be a determinant of attachment as well. Still, equal numbers of low- and high-growing species with morphological structures in low- and high-positioned sheep body parts again suggest the importance of those structures. Detected seed quantities seemed less affected by plant height; production of large seed numbers by certain plant species, e.g. low-growing *Medicago minima* with hooked burrs and high-growing *Verbascum phlomoides* with no seed structures, probably influenced the results. Moreover, differences in sheep behaviour (walking, grazing, lying down to ruminate or rest) could have stimulated contact between both low- and high-growing plants, but the lack of seed surface structure causes the position of the body part to negatively affect retention. Consequently, the highest seed quantities were found on the back, from where it is hard for seeds of any morphology to fall out of the coat.

Seed retention in an animal coat and the moment of detachment determine the dispersal distance and the actual seed arrival in the sink area. Other studies showed

inter-specific variation in retention times and detachment rates (Couvreur et al. 2004; Manzano and Malo 2006), at least partly explained by seed mass differences (Tackenberg et al. 2006). According to Römermann et al. (2005) seed mass and morphology are both important determinants of the retention potential in sheep wool. Similarly, an over-representation of medium- (0.5 – 2.0 mg) and heavy-weight (> 2.0 mg) seed species with well-developed appendages in sheep coat compared to visited vegetation suggested a low detachment rate for these two seed classes. In contrast, an equal or smaller amount of seeds without clear appendages in sheep coat indicated higher detachment rates for that group of seeds (**Chapter 2**; Wessels et al. 2008).

Intensity and duration of animal activity also seem to affect retention and detachment (**Chapter 2**). Retention times of naturally attached *Stipa capillata* and *Agrimonia procera* seeds were much shorter when the sheep walked from one area to another than during a stationary grazing period. Due to greater vibrations of the coat, walking a long distance shortens the retention time, compared to grazing. Nevertheless, no significant *Stipa* and *Agrimonia* seed losses were detected after walking a 3-km distance, whereas many seeds became detached in the sink area. Variation of activity duration (sheep can cover a 3-km distance within one hour, often grazing for several days) probably causes many more seeds to detach in a sink area than during a long-distance walk. In the grazing period, seed detachment could additionally be accelerated because of grooming behaviour. Especially seeds with morphological structures might irritate the animals and promote grooming (Kiviniemi 1996). In contrast to a grazing period, an inter-area transfer can be hectic: often no possibility for grooming exists (pers. observation).

Besides successful long-distance dispersal of *Stipa* and *Agrimonia* seeds (no sig. losses), also no significant reductions of total seed and species quantities were found after animals had walked a 3-km distance (**Chapter 2**). These first empirical data for naturally attached seeds proved sheep to be extremely effective dispersal vectors. More seeds can be dispersed over such a long distance than previously expected. Mouissie et al. (2005b) predicted that 1 % of all seeds would be transported over a distance > 2.9 km. Also experimentally attached seeds or dummies could underestimate dispersal distances and dispersed seed numbers (Shmida and Ellner 1983; Liddle and Elgar 1984; Fischer et al. 1996; Kiviniemi 1996). Assuming that seeds do detach from the coat

after arrival in the sink area, the applied grazing regime promotes the arrival of enormous amounts of seeds of target species in the sink area.

It took around 1 h for the sheep to walk a 3-km distance from one area to another. Seed retention in the gut is much longer, generally 1-3 days (Russi et al. 1992; Cosyns et al. 2005; Ramos et al. 2006). As a result, endozoochory could promote seed dispersal over significant distances, although this distance should be covered within three days after grazing took place. Because species-specific gut passage survival can also be tested, post-endozoochorous seed arrival in a sink area is largely predictable. Germination tests conducted here showed that, depending on plant community, 900 – 5000 viable seeds per 1000 g dung can be dispersed, half of which belong to target species (**Chapter 5**). One sheep produces ca. 700 g dry dung per day. Consequently, one inter-area transfer with a flock of 600 animals could result in endozoochorous dispersal of 200,000 – 1,000,000 seeds of target species.

Post-dispersal fate

To understand the importance of dispersal to the spatial patterns and dynamics of plant populations, post-dispersal processes should be considered (Nathan and Muller-Landau 2000). Landscape heterogeneity, especially differences in food availability/quality, initiates heterogeneous patterns of animal movement. Its effect on post-endozoochorous seed dispersal patterns was studied by Mack (1995) who used tagged seeds to follow their fate after digestion by the dwarf cassowary (*Casuarius bennetti*) in a rainforest ecosystem. Non-random dispersal patterns could be distinguished, mediated by movement and resting places. Even on bare sand fields sheep move around non-randomly (**Chapter 3**). Like excreted seeds, epizoochorously dispersed seeds were detected in non-random spatial patterns. Furthermore, heterogeneously distributed seedling emergence patterns of all frequently emerged study species were associated with trampling patterns (see Appendix 3.1). In general a higher trampling intensity positively affects the seed input and seedling emergence. Comparability among patterns shows the substantial role of non-random sheep abundance in the determination of heterogeneous recruitment patterns.

Eichberg et al. (2005) studied both epizoochorous dispersal and post-dispersal processes of *Jurinea cyanoides.* After dispersal, successful emergence took place in a

Koelerion glaucae stand, although relatively few individuals were detected. Epizoochorously dispersed seeds of nearly all 14 of the species investigated here successfully emerged on open sand fields as well (**Chapter 3**).

Differential seed detachment probably only partly explains the detected differences in seedling emergence (0 - 40 % of the original number of attached seeds). Heavy seeds with surface structures detach less easily from a sheep coat than seeds without such structures (**Chapter 2**; Wessels et al. 2008). Nevertheless, the three heaviest seed species with such structures had high detachment rates after 24 hours (40 - 80 %). Since all other species were much lighter in weight and/or did not have morphological dispersal structures, I assume that they detached frequently as well. Similarly, seed burial rates were probably high for most study species. Sheep trampling promoted seed burial of high numbers of large-seeded *Cynoglossum officinale* and *Medicago minima* (70%), although the long awn of *S. capillata* sometimes prevented complete burial. Smaller-sized seeds generally incorporate into the soil substrate more easily than larger seeds (Thompson et al. 1997). Seeds of the other study species were much smaller than those of the above-mentioned species. In contrast to Jakobsson and Eriksson (2000), who found evidence that increasing seed size could positively affect recruitment, here both small- (e.g. *Alyssum gmelinii, Phleum arenarium*) and large-seeded species (*C. officinale*) emerged and established in high numbers (Table 3.3). Consequently, recruitment in such open sand fields was probably not driven by seed size either. Finally, the absence of adult plants limited competition, so that both strongly (*C. officinale*) and weakly competitive species (*A. gmelinii, Silene conica*) could emerge.

However, the detected emergence differences among species suggest that differential burial responses (light vs. dark germination) could largely control recruitment in an early successional phase. As Eichberg et al. (2005) hypothesised, sheep trampling-induced seed burial stimulates seedling emergence of *J. cyanoides*. Unburied achenes are more vulnerable to granivores such as goldfinches (*Carduelis carduelis*), and newly emerged seedlings probably die off earlier because they dry out (Eichberg et al. 2005). On the other hand, equal seedling numbers of *Koeleria glauca* were detected in trampled and non-trampled plots (**Chapter 3**). Smaller seeds are less at risk for seed predators, especially if larger seeds are still available (Abramsky 1983). Besides, predominant dark germination largely explains the observed high emergence of *C.*

officinale. On the other hand, light reduction may have severely limited the emergence of *Jasione montana, Tragus racemosus* and *Scabiosa canescens*; unburied seeds of those species show much higher emergence rates than buried counterparts (germination test). Additionally, among poorly performing species, several typically occur in more consolidated stages of mid-successional communities, e.g. *Silene otites* and *S. canescens*.

As in other studies on post-endozoochorous processes (e.g. Welch 1985; Malo and Suárez 1995a; Cosyns et al. 2006), emergence of dung-embedded seeds from the three dung types (corresponding to grazed community) studied here under field conditions was low (max. 5 % of the viable seed content (Kg)). Gut passage of Fabaceae (e.g. *Trifolium campestre, T. arvensis*) and Cistaceae (*Helianthemum nummularium*) seeds probably increased their germination (Russi et al. 1992; Ramos et al. 2006). High rates were found in the field as well and allowed new establishment of *H. nummularium* in the study area. Qualitatively, relatively more target species emerged from Kg and AS dung in low and semi-productive Kg and AF stands, compared to their abundance among viable seeds. Only a minor increase of target species on AF dung plots, established in ruderalised AF, was detected. Furthermore, no graminoid competitors emerged from Kg, whereas several such taxa were found in the two more productive stands (**Chapter 5**). Results seem to confirm the hypothesis that more harsh abiotic conditions of early successional stands act as a "germination filter" for dung-embedded seeds. Habitat-typical species are better adapted to these extreme conditions and thus emerge more frequently than expected. On the other hand, germination of competitors is prevented (Eichberg et al. 2007). In more productive stands, conditions are less extreme, e.g. a higher amount of phytomass probably reduces temperature extremes. Cosyns et al. (2006) detected mostly common grassland species (many graminoids) from horse and cattle dung in highly productive grassland, although viable seeds of rare species were abundant.

However, seeds could become available after decomposition of dung. Estimated dung seed contents could increase the topsoil's seed content by 75 % (Koelerion glaucae) up to 360 % (Armerio-Festucetum) (Eichberg et al. 2006). Other studies observed a significant seed-bank contribution from rabbit dung (Malo et al. 1995),

indicating a future role of endozoochorously dispersed seeds in fine-scale species richness. Nevertheless, dung decomposition can be a long process in our study area (pers. observation) and fungi within the dung might reduce the persistence of dung-embedded seeds.

Micro-site availability

Sheep play an additional role in the recruitment of plant species, via the creation of suitable micro-sites. Herbivore behaviour such as trampling and scratching can remove vegetation and create bare soil patches that serve as regeneration sites for plant species (Bakker and Olff 2003). Eichberg et al. (2007) already demonstrated the negative impact *Hypnum cupressiforme* var. *lacunosum* can have on seedling emergence and fine-scale species richness. *Hypnum*, a dominant pleurocarpous moss species, could limit the amount of radiation, water, and seeds reaching the soil surface (Keizer et al. 1985). In the present study (**Chapter 5**), experimental moss disturbance in a half-ruderalised AF stand increased overall seedling emergence out of the soil and dung seed bank as well. Reduced competition could have stimulated the emergence of "fugitive" species (Tilman 1988). Overall, the increase of especially (target) herbs promoted fine-scale species richness. However, the most productive AF plots only temporarily showed such a positive response; initially suppressed graminoid competitors in a later stage increased in abundance.

Dung deposition affects micro-site conditions as well. The presence of dung pellets reduced seedling emergence. Emergence was probably physically suppressed (Eichberg et al. 2007). In the case of low-productive Kg and semi-productive AF plots, dung deposition positively affected small-scale species richness of emerging seedlings. By contrast, dung deposition in the most productive plots at first reduced competing species such as *Carex hirta* and *Cynodon dactylon,* but subsequently benefits from reduced competition and nutrients leaching out of the dung, as found for *Arenaria serpyllifolia* in early successional plots (**Chapter 5**).

Conclusion

In a fragmented landscape the conservation of target communities largely depends on long-distance seed dispersal and establishment of habitat-typical species. This study

provided evidence that sheep offer an efficient dispersal vector over long distances, which enables reconnection of separated plant populations and initiates the colonisation of new sites. A grazing regime with distinct source and sink areas and the use of well-developed target communities as seed sources promotes seed dispersal of high proportions of target species. Especially in early successional stages, epi- and endozoochorously dispersed target seeds can establish successfully, probably because of a higher availability of micro-sites. Through disturbance sheep can additionally promote the recruitment of target species. Sheep can mediate heterogeneous recruitment patterns, presumably further stimulating species richness. Conservation and restoration measures for inland sand ecosystems and other nutrient-poor habitats should consider sheep grazing as management tool. Restoration sites such as abandoned fields can be included as sink.

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Summary

The dispersal of seeds is crucial for the survival of many plant species. Fragmentation of the European cultural landscape and changes in land management, e.g. decrease of livestock numbers and lower mobility of livestock between different areas, have severely limited spatial dispersal processes, and thereby made a major contribution to the reduction of species richness of cultural landscapes. Reintroduction of extensive grazing regimes involving large domestic herbivores is often claimed to restore the connectivity between separated populations via endo- and epizoochorous dispersal of seeds.

This thesis aimed to investigate sheep-induced seed dispersal over long distances and its contribution to the recruitment of especially target species. The use of a sheep grazing regime which involves consecutive grazing of well-developed target communities, as a seed source, followed by less-developed sinks, could increase the quality of dispersed seeds (more target species). If recruitment takes place successfully, spatially isolated populations can be functionally re-connected or new sites colonised.

The study was carried out in three inland sand ecosystems, relatively isolated from each other in the landscape (Darmstadt region, Germany). The two larger areas "Ehemaliger August-Euler-Flugplatz von Darmstadt" and "Griesheimer Düne und Eichwäldchen" are both nature protection areas, grazed by sheep since 1999/2000. Animals walk a 3-km distance when transferring from one area to the other. Recently, for restoration purposes an abandoned agricultural field "Streitgewann" was also included in the grazing system. "Streitgewann" is situated between the first two areas and could function as a "stepping stone". Dispersal and post-dispersal processes within and between the above-mentioned areas were analysed. As seed sources mostly well-developed target communities Koelerion glaucae (Kg), Armerio-Festucetum trachyphyllae (AF) and Allio-Stipetum capillatae (AS) were used. All investigations employed three or four tamed male sheep.

First of all, species compositions of grazing sources and epizoochorously dispersed seeds (both intra- and inter-area transfers) were determined. The quantities and species composition of seeds detected in sheep coats before and after walking from one area to another were compared to test for potential seed losses. Additionally, the impact of seed surface structure, seed mass and plant seed-releasing height on attachment was tested.

Naturally attached seeds of *Stipa capillata* and *Agrimonia procera* were used to study retention times and detachment rates during different herbivore activities (long-distance walking, grazing). In total, 56 seed species were detected in investigated sheep coats. Half of the species in the three vegetation types were target species. In sheep coats target species were slightly over-represented; among them were seven Red List species. Quantitatively, most transported seeds belonged to target species, whereas almost no graminoid competitors were detected. No significant numbers of epizoochorously transported seeds dropped out of the sheep coats during 3-km inter-area transfers, whereas many seeds of *S. capillata* and *A. procera* detached in the sink area. Longer duration of the grazing period and grooming behaviour probably stimulate seed detachment. Furthermore, it was shown that attachment is determined by seed mass and seed morphological appendages. Seeds without well-developed seed structures are probably negatively affected by seed mass, whereas seeds with structures (e.g. hooks) seem to have an equal attachment probability, regardless of mass.

The fate of epizoochorously dispersed seeds was studied for 14 seed species. Most of them were endangered target species of inland sand ecosystems, for which epizoochorous dispersal was already shown in our previous investigations. Three 10 m x 10 m sand fields were established at a former agricultural field. Per field two sheep were present for 24 h; seeds were experimentally attached to their coats. The impact of sheep trampling on seedling emergence was also tested for two threatened species: *Jurinea cyanoides* (EU Fauna-Flora-Habitat directive species) and *Koeleria glauca.* Sheep trampling patterns, seed detachment rates and spatial dispersal patterns of the three largest-seeded species (*Stipa capillata, Medicago minima* and *Cynoglossum officinale*) were studied. Also, seedling emergence and survival of all included species were recorded over an 8-month period. The relatively brief sheep presence at the sand fields resulted in high detachment rates. Seedlings of almost all species emerged (up to 40 % of original seed number). Analysing the patterns of sheep trampling, seed shadow, and seedling emergence by use of Spatial Analysis by Distance Indices (SADIE), showed non-random distributions. Generally, a positive correlation between sheep abundance and the number of relocated seeds and emerged seedlings was found,

whereas individual species showed a variable trampling response. The seedling emergence of *J. cyanoides* increased after trampling, whereas *K. glauca* showed no effect.

Estimation of the potential contribution of herbivores to plant species dispersal via the endozoochorous pathway has mostly been based on results of seedling emergence tests. To check the reliability of such estimates, a comparison of viable seed contents in sheep dung by use of two methods was conducted. Dung was collected after a 6-day grazing period in one of the target communities (Allio-Stipetum). Following the Ter Heerdt method (TH), samples were concentrated and kept under controlled conditions (glasshouse or climate room, duration experiment 5 months). In the second seedling emergence test (common garden method, CG) unconcentrated samples were kept outdoors (15 months). Qualitative and quantitative similarities between the two methods were calculated by use of Sørenson similarity index (QS). Detected seeds showed a highly similar species composition (QS = 0.81) and content (QS = 0.69). Some more seedlings emerged via TH, and especially several small-seeded winter annuals (*Veronica arvensis, Arenaria serpyllifolia, Arabis glabra*) showed a higher emergence. More species and higher quantities of hard-coated seed species of Fabaceae and Cistaceae emerged outdoors (CG). In relation to each other, both methods offer a valuable means of estimating the potential seed input via dung deposition. If the main research interest is the species composition, CG should be used. TH, on the other hand, better estimates the overall viable seed content and uses less space and time.

Finally, the impact of endozoochorously transported seeds, the deposition of dung, disturbance by removal of the moss layer (*Hypnum cupressiforme*), and dung removal by the dung beetle *Typhaeus typhoeus* (Linnaeus, 1758) on fine-scale species richness was investigated (factorial experiment).. Sheep dung was collected after the same source paddocks used for epizoochory investigations were grazed (Kg, AF, AS). The species composition and viable seed content of dung-embedded seeds were analysed by use of seedling emergence tests. Treatments were established in the field in stands having different productivity (Kg < semi-ruderalised AF < ruderalised AF). From the three dung types (referring to vegetation types), viable seeds of 59 taxa were found,

whereas under field conditions, 23 dung-borne taxa were detected (60 % target species). Quantitatively, most seedlings belonged to target species (e.g. *Helianthemum nummularium*, previously absent in the sink area), whereas competing graminoids emerged only within more productive AF plots. Despite a lower seedling emergence, dung deposition did promote species richness in Kg and semi-ruderalised AF plots. The impact of dung deposition can be modified when dung beetles transport dung pellets into larvae chambers, situated below-ground (> 40 cm). As a result, several disturbance species, e.g. *Oenothera biennis* and *Polygonum aviculare*, emerged at high rates from the dung beetle-disturbed topsoil. Disturbance of the moss layer promoted seedling emergence from dung and soil seed bank in semi-ruderalised AF plots, and the emergence of especially herbs resulted in increased fine-scale species richness. The vegetation of the most productive AF plots responded differently to the two treatments (disturbance of moss layer and dung deposition) in comparison with semi-ruderalised AF plots. Phytodiversity and plant density were initially suppressed in both treatments and additionally dung deposition decreased the abundance of graminoid competitors *Carex hirta* and *Cynodon dactylon.* Nevertheless, the reduced competition and soil fertilising effect of dung presumably promoted those same competitors in a later stage. Increased competition probably limited species diversity. The effect of herbivore-induced disturbance and endozoochorously transported seeds on fine-scale species richness probably depends at least partly on the productivity of the established vegetation.

The present study has shown that a regime of sheep grazing, the use of well-developed target communities as seed sources and inter-area transfers between isolated habitats offers a good management measure for conservation and restoration of open inland sand ecosystems in fragmented landscapes. A large sheep flock (around 600 animals) and the presence of a high proportion of habitat-typical species in the selected grazing sources promote epi- and endozoochorous dispersal of millions of seeds of target species over long distances. Additionally, herbivore activity can increase the availability of micro-sites. By altering main determinants of recruitment (especially seed and micro-site availability), sheep play an important role in the establishment of target species and promote species-richness, especially in early and mid-successional stages.

Zusammenfassung

Die Ausbreitung von Diasporen ist entscheidend für das Überleben vieler Pflanzenarten. Die Fragmentation europäischer Kulturlandschaften und Änderungen im Land-Management, z.B. der Rückgang von Weidetier-Abundanzen und deren geringere Mobilität zwischen Gebieten, haben entscheidend die räumlichen Ausbreitungsprozesse gemindert und trugen zur Verminderng des Artenreichtums von Kulturlandchaften bei. Die Wiedereinführung eines extensiven Beweidungsregimes mit Haustieren und die dadurch bedingte endo- und epizoochore Ausbreitung von Diasporen von Fläche zu Fläche wird oft als entscheidend angesehen, um den Verbund ("connectivity") zwischen separierten Populationen zu gewährleisten.

Diese Arbeit hat zum Ziel, die Schaf-induzierte Ausbreitung von Diasporen über längere Distanzen und den Beitrag zur Etablierung insbesondere von Zielarten zu untersuchen. Die Etablierung eines Systems der Schafbeweidung, das die aufeinander folgende Beweidung gut entwickelter Leitbildflächen (Diasporen-„Source") mit anschließender Beweidung weniger entwickelter Flächen („Sink") verbindet, kann die Qualität der ausgebreiteten Diasporen (mehr Zielarten) steigern. Wenn die Etablierung erfolgreich war, können räumlich separierte Populationen wieder funktionell verbunden oder neue Flächen kolonisiert werden.

Die Untersuchungen wurden in Binnenland-Sandökosystemen durchgeführt, die relativ isoliert voneinander liegen (Region Darmstadt). Die zwei größeren Gebiete „Ehemaliger August-Euler-Flugplatz von Darmstadt" und „Griesheimer Düne und Eichwäldchen" sind beides Naturschutzgebiete, die seit 1999/2000 mit Schafen beweidet werden. Die Weidetiere legen eine Strecke von ca. 3 km zurück, wenn sie von einem Gebiet in das andere ziehen. Im Zusammenhang mit Restitutionsmaßnahmen wurde ein brach liegender Acker („Streitgewann") in das Beweidungsregime integriert. Die Fläche liegt zwischen den beiden zuerst genannten Naturschutzgebieten („Trittstein"). Ausbreitungs- und Nach-Ausbreitungsprozesse in und zwischen den oben genannten Gebieten wurden analysiert. Als „source" wurden gut entwickelte Zielgesellschaften des Koelerion glaucae (Kg), Armerio-Festucetum trachyphyllae (AF) und Allio-Stipetum capillatae (AS) genutzt. Für alle Untersuchungen wurden drei bis vier gezähmte Hammel verwendet.

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Zunächst wurden die Arten-Zusammensetzung der "Source"-Gebiete und die epizoochor ausgebreiteten Diasporen determiniert, sowohl für den Intra- als auch für den Inter-Gebietstransfer. Um mögliche Diasporen-Verluste zu quantifizieren, wurden die Mengen und Arten-Zusammensetzungen der Diasporen im Schaffell vor und nach dem Gebietstransfer bestimmt. Zusätzlich wurden die Oberflächenstruktur der Diasporen, das Diasporen-Gewicht und die Expositionshöhe der Diasporen auf der Pflanze (Höhe auf der Pflanze) mit der Anheftung im Schaffell korreliert. Durch natürliche Prozesse angeheftete Diasporen von *Stipa capillata* und *Agrimonia procera* konnten genutzt werden, um Rententionszeiten und Raten des Diasporen-Verlustes während verschiedener Aktivitäten (Fortbewegung bei Gebietswechsel bzw. bei Koppelbeweidung, Abfressen der Vegetation) zu berechnen. Insgesamt sind Diasporen von 56 Pflanzentaxa im Schaffell nachgewiesen worden. Die Hälfte der Taxa in den drei untersuchten Vegetationstypen waren Zielarten. Im Schaffell waren die Zielarten leicht überrepräsentiert; unter ihnen gab es sieben Rote-Liste-Arten. Quantitativ gehörten die meisten der transportierten Diasporen zu Zielarten, wohingegen praktisch keine konkurrenzstarken Graminoiden nachgewiesen wurden. Während der 3-km Gebietstransfers kam es nicht zu signifikanten Verlusten an epizoochor ausgebreiteten Diasporen, wohingegen viele Diasporen von *S. capillata* und *A. procera* im „Sink"-Gebiet ausgebreitet wurden. Eine längere Dauer der Weidezeit und Fellpflege mit Maul und Klauen fördern wahrscheinlich die Lösung von Diasporen aus dem Fell. Des weiteren wurde gezeigt, dass die Anheftung im Fell durch Diasporen-Gewicht und Diasporen-Strukturen (Anhänge) bestimmt wird. Der Erfolg der Anheftung wird bei Diasporen ohne gut entwickelte Strukturen (Anhänge wie Klettenstrukturen u.a.) wahrscheinlich durch das Diasporen-Gewicht bestimmt; bei solchen Diasporen mit gut entwickelten Anhangsstrukturen ist die Anheftungswahrscheinlichkeit nicht abhängig vom Diasporen-Gewicht.

Für 14 verschiedene Pflanzenarten wurde das Schicksal nach erfolgter epizoochorer Ausbreitung untersucht. Die meisten dieser Arten waren gefährdete Zielarten der Sandökosysteme, für die epizoochore Ausbreitung bereits in unseren vorherigen Untersuchungen gezeigt werden konnte. Drei 10 m x 10 m große Sandflächen wurden auf einer Ackerbrache etabliert. Pro Fläche hielten sich zwei Schafe mit experimentell im

Fell angehefteten Diasporen für 24 h auf. Außerdem wurde der Effekt des Schaftritts auf die Samenkeimung für zwei gefährdete Arten analysiert: *Jurinea cyanoides* (Art der EU Fauna-Flora-Habitat Direktive) und *Koeleria glauca.* Das räumliche Trittmuster, die Ausbreitungsrate der Diasporen und die räumliche Verteilung von drei Arten mit großen Diasporen (*Stipa capillata, Medicago minima* und *Cynoglossum officinale*) wurden untersucht. Das Keimlingsaufkommen und die Überlebensrate aller untersuchten Arten konnte für eine Periode von 8 Monaten verfolgt werden. Die relative kurze Präsenz der Schafe auf den Sandflächen führte trotzdem zu hohen Raten des Diasporen-Eintrags. Diasporen von fast allen Arten kamen zur Keimung (bis zu 40 % der ursprünglichen Diasporen-Anzahl). Die Analyse der räumlichen Verteilung des Schaftritts, der Diasporen-Verteilung und -Keimung auf der Fläche mit Hilfe von „Spatial Analysis by Distance Indices (SADIE)", zeigte eine nicht-randomisierte Verteilung. Generell konnte eine positive Korrelation zwischen der Abundanz der Weidetiere und der Zahl lokalisierter Diasporen auf dem Boden sowie dem Keimlingsaufkommen gefunden worden. Die Effekte des Schaftritts waren Arten-abhängig verschieden: *J. cyanoides* wurde gefördert, wohingegen *K. glauca* keine Effekte zeigte.

Die Abschätzung des potenziellen Beitrags von Herbivoren zur Ausbreitung von Pflanzenarten über den endozoochoren Pfad basiert zumeist auf Untersuchungen mit verschiedenen Keimungsmethoden. Um die Zuverlässigkeit dieser Methoden zu prüfen, wurde ein Vergleich von zwei Methoden zur Quantifizierung des Gehalts an lebensfähigen Diasporen im Schafdung durchgeführt. Der Dung wurde gesammelt nach einer Weideperiode von sechs Tagen in einer der Leitbildgesellschaften (Allio-Stipetum). Nach der Ter Heerdt-Methode (TH, 5 Monate) werden die Proben konzentriert und unter kontrollierten Bedingungen gehalten (Gewächshaus oder Klimaraum). Bei der zweiten Methode werden nicht-konzentrierte Proben unter Freilandbedingungen exponiert („common garden" CG, 15 Monate). Qualitative und quantitative Ähnlichkeiten zwischen den Methoden werden mit dem Sørenson-Index (QS) dargestellt. Die nachgewiesenen Diasporen zeigten für beide Methoden eine ähnliche Artenkombination (QS = 0.81) und Abundanz (QS = 0.69). Quantitativ keimten mehr Individuen bei TH; insbesondere einige kleinsamige Winterannuelle (*Veronica arvensis, Arenaria serpyllifolia, Arabis glabra*) zeigten hohe Abundanz. Bei CG keimten mehr Arten (auch mit höheren

Abundanzen), die hartschalige Diasporen haben (Fabaceae und Cistaceae). Im Vergleich sind beide Methoden sehr gut anwendbar, um die potenzielle Diasporenausbreitung via Dung zu quantifizieren. Wenn das Hauptinteresse einer Untersuchung die Artenzusammensetzung ist, ist CG eine optimale Methode; TH ermöglicht die beste Quantifizierung der Individuendichte und benötigt weniger Platz und Zeit.

Schließlich wurden die Einflüsse von endozoochor ausgebreiteten Diasporen, der Dung-Deposition, Störung in Moosbeständen (*Hypnum cupressiforme*), und Dung-Entnahme durch den Stierkäfer *Typhaeus typhoeus* (Linnaeus, 1758) auf die lokale Artenvielfalt untersucht. Schafdung wurde in den Habitaten gesammelt, die auch für die Epizoochorie-Untersuchungen genutzt wurden (Kg, AF, AS). Die Artenstruktur und die Abundanz im Dung wurde mit Keimungsmethoden analysiert. In einem feldökologischen Ansatz wurden faktorielle Experimente in einem Produktivitätsgradienten etabliert (Kg < semi-ruderalisiertes AF < ruderalisiertes AF). In den drei Dungtypen (bezogen auf die Vegetationseinheiten) konnten keimfähige Diasporen von 59 Taxa nachgewiesen werden, unter feldökologischen Bedingungen nur 23 Taxa (60 % Zielarten). Quantitativ waren die meisten Taxa Zielarten (z.B. *Helianthemum nummularium*, das im "Sink"-Gebiet nicht vorkommt), wohingegen konkurrenzstarke Graminoide nur in den produktiveren AF-Flächen keimten. Trotz eines geringeren Aufkommens an Keimlingen, förderte die Dung-Deposition den Artenreichtum in Kg und in semi-ruderalisierten AF-Untersuchungsflächen. Der Effekt der Dung-Deposition kann modifiziert werden, wenn Dungkäfer die Kotpillen in die Larven-Brutkammern transportieren (> 40 cm tief im Boden). Als ein Ergebnis stellten sich nach der Störung durch den Dungkäfer Störung-anzeigende Arten ein, z.B. *Oenothera biennis* und *Polygonum aviculare*, die mit hohen Individuenzahlen keimten. Die Störung der Moosdecke förderte das Aufkommen von Keimlingen aus dem Dungsubstrat und aus der Diasporen-Bank in den semi-ruderalisierten AF-Untersuchungsflächen; die Keimung insbesondere von krautigen Arten bedingte höheren Artenreichtum. Die produktivsten AF-Untersuchungsflächen zeigten im Vergleich zu den semi-ruderalisierten Flächen andersartige Reaktionen auf die beiden Behandlungen (Moos-Entfernung und Dung-Deposition). Phytodiversität und Individuenzahl wurden in beiden Behandlungen reduziert, und die Dung-Deposition

führte außerdem zu einer Abnahme der Abundanz der konkurrenzstarken Arten *Carex hirta* und *Cynodon dactylon.* Schließlich förderte wahrscheinlich die geringere Konkurrenz auf den Untersuchungsflächen bzw. der düngende Effekt der Faeces dieselben konkurrenzkräftigen Arten in einem späteren Stadium der Vegetationsentwicklung; letzteres führte zu einer geringeren Phytodiversität. Es zeigt sich, dass wahrscheinlich Störung und Dung-Applikation und ihre Auswirkung auf die Mikroskala-Phytodiversität zum Teil durch das Produktivitätsniveau der etablierten Vegetation bedingt werden.

Die vorliegende Arbeit hat gezeigt, dass ein extensives Beweidungsregime mit Schafen, die Nutzung gut entwickelter Leitbild-Flächen als Diasporen-Quellen und Inter-Gebietstransfers zwischen separierten Lebensräumen eine gute Management-Maßnahme für den Schutz und die Restitution von offenen Sandökosystemen in fragmentierten Landschaften sind. Eine große Schafherde (etwa 600 Tiere) und das Vorkommen eines hohen Anteils Habitat-spezifischer Arten in den "Source"-Gebieten fördern die epi- and endozoochore Ausbreitung von Millionen von Diasporen. Zusätzlich kann die Aktivität der Herbivoren die Verfügbarkeit von Kleinstandorten erhöhen. Durch die Änderung wichtiger Determinanten für die Etablierung von Pflanzenarten, insbesondere der Diasporen- und Mikrohabitat-Verfügbarkeit, spielen Schafe eine bedeutende Rolle für die Etablierung von Zielarten der Sandvegetation, insbesondere in frühen und mittleren Sukzessionsstadien.

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Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe. Ich habe noch keinen Promotionsversuch unternommen.

(Saskia Wessels)   Darmstadt, den 9-11-2007