

Epizoochorous and post-dispersal processes in a rare plant species: *Jurinea cyanoides* (L.) Rchb. (Asteraceae)

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Abstract

We used *Jurinea cyanoides* as a model plant species to ask the question whether sheep play a dual role in enabling the establishment of a rare species (1) by epizoochorous transport of diaspores and (2) by influencing post-dispersal processes. We carried out two field experiments in sand grassland (*Jurinea*–*Koelerietum glaucae*) in the northern upper Rhine valley, Germany. In the first one, we attached diaspores to the fleeces of sheep and assessed retention time, seed shadow, seedling emergence and establishment. In the second one, diaspore displacement by sheep trampling was investigated.

It could be shown that establishment of *J. cyanoides* is possible after sheep-epizoochorous dispersal, but is severely limited by several factors. First, retention time is mostly short (only 18% of the diaspores remained in the fleeces > 2 h). Thus, the seed shadow is concentrated around the place of attachment (mostly < 5 m distance, maximum 17 m). Second, seedling emergence of dispersed achenes is severely limited by above-ground granivory (99%). Third, establishment is limited by seedling mortality (68%) due to summer drought. The seedlings germinated from achenes that had been incorporated into the soil (or into deeper parts of the bryophyte layer). The second experiment showed that sheep trampling significantly enhanced the incorporation of achenes into the soil compared with controls. Our study gives evidence that sheep can play a dual role: diaspore transport and facilitation of establishment by trampling.

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Keywords: Establishment of seedlings; Granivory; Pappus; Seed dispersal by sheep; Seed retention time; Trampling effects

Introduction

In the increasingly fragmented cultural landscape, investigations on diaspore dispersion of rare species and (re-)colonisation of habitats have become of urgent significance (Opdam, 1990; Poschlod et al., 1996; Saunders et al., 1991). The importance of grazing by sheep as a measure for nature conservation is increas-

ingly recognised (Hellström et al., 2003; Poschlod et al., 1998; Schwabe and Kratochwil, 2004). Although the notable potential of sheep as an epizoochorous diaspore vector has been described in detail (Fischer et al., 1996; Milton et al., 1990; Ridley, 1930; Shmida and Ellner, 1983), our knowledge about the impact of sheep on both diaspore transport and post-dispersal processes is still very limited. We chose *Jurinea cyanoides* as a model species.

Generally, the pappus of Asteraceae species is seen as an adaption to wind dispersal. However, there are many

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examples in the Asteraceae where wind dispersal structures of the pappus are not “optimised” and there might be strategies of dispersal by different processes (anemo- and zoochory). In the cases of, e.g., *Cirsium arvense* (Bakker, 1960; Wagenitz, pers. comm.) and *Senecio leucanthemifolius* (Coleman and Abbott, 2003), wind dispersal is rather imperfect, as the pappus disperses even without achenes. On the other hand, many Asteraceae species with pappus-bearing achenes were detected in sheep fleece in various ecosystem types (Fischer et al., 1996; Milton et al., 1990; Ridley, 1930; Shmida and Ellner, 1983). In our study area, *Centaurea stoebe* with a small, stiff and scabrid pappus is one of the most common sheep-epizoochorously dispersed species. There is evidence that the pappus of *J. cyanoides* favours epizoochory by means of the scabrid pappus bristles (Frank and Klotz, 1990; Klotz, pers. comm.). In natural habitats, this is with high probability an important dispersal mechanism especially as the achenes are relatively heavy and wind dispersal may be restricted. If epizoochory is an effective dispersal mechanism, the achenes have to be retained in the fleece for some time after they became attached. There are only a few studies dealing with retention times of diaspores in sheep fleece (Fischer et al., 1996; Liddle and Elgar, 1984; Lodge and Hamilton, 1981; Shmida and Ellner, 1983). It has been shown by several authors that the degree of adherence to animal fur and the retention time depends on diaspore morphology (Carlquist and Pauly, 1985; Couvreur et al., 2005; Kiviniemi, 1996; Sorensen, 1986). But in the special case of sheep wool (curly, matted, greasy), diaspore morphology is less significant (Fischer et al., 1996). So far there are no data available on the retention time of achenes of *J. cyanoides* in sheep fleece.

We hypothesise that sheep grazing has also effects on post-dispersal processes, especially via trampling. Such processes could be: escape from granivory, creation of safe sites, altered germination conditions or establishment success. Little attention has been directed towards the effect of livestock trampling on post-dispersal diaspore fate (exceptions are Liddle and Elgar, 1984; and recently Rotundo and Aguiar, 2004).

To our knowledge, as yet there exists no experimental study dealing with the establishment success of an epizoochorously dispersed plant species. The lack of investigations might be attributable to the methodological difficulties of locating epizoochorously dispersed diaspores within the vegetation. In the case of our model species, the shiny and comparatively large pappus can easily be located, and experimental sites were chosen for absence of the model species.

In the present study we are focussing on the following questions:

(A) *Epizoochorous processes*: (1) How long is the retention time of achenes of *J. cyanoides* in sheep fleece after experimental diaspore attachment? (2) How far do

sheep transport the diaspores? Is the seed shadow clumped at distinct parts of the paddock (e.g., resting places)? (B) *Post-dispersal processes*: (3) What is the post-dispersal fate of above-ground diaspores? (4) (a) Does sheep-epizoochorous dispersal enable *J. cyanoides* to set seedlings and establish itself in formerly unsettled habitats? (b) Does the mortality rate of these seedlings differ from seedlings in existing populations of *J. cyanoides*? (5). What is the effect of sheep trampling on the horizontal and vertical displacement of diaspores?

Summarising aspects of A and B: Do sheep play a dual role in enabling the establishment of a rare plant species?

“Establishment” often is defined as reaching a phase of independence from the diaspore reserves, as indicated by the development of a photosynthetic surface of a seedling (e.g., Harper, 1977). As desiccation and frost effects are the main factors restricting seedling survival on bare ground in open habitats (e.g., Ryser, 1990), we define “establishment” as the survival of a young plant for one summer and one winter after seedling emergence.

Materials and methods

Species description

The herbaceous perennial Asteraceae, *J. cyanoides*, has its main occurrence in the steppes of central Eurasia (Meusel and Jäger, 1992). Small populations of *J. cyanoides*, which are highly disjunct from the main area, occur mainly in the river areas of Rhine-Main and Elbe (Internet1, 1999; Meusel and Jäger, 1992). In the northern upper Rhine valley, *J. cyanoides* is a local character species of the Jurineo cyanoidis–Koelerietum glaucae, an endangered pioneer community of open, calcareous drift sand areas. Due to its rare and threatened occurrence in Central Europe, *J. cyanoides* is one of the few appendix species of the flora–fauna–habitat directive of the European Union (Ssymank et al., 1998).

J. cyanoides propagates both generatively and vegetatively, the latter by root shoots, building up clones. The flower and fruit set is sumptuous on our study sites, although often many of the fruits are not well developed. *J. cyanoides* flowers from June to August (occasionally October) and disperses diaspores from August to October (occasionally November). The achenes of *J. cyanoides* are obpyramidal in shape, slightly ribbed, glabrous and bearing a pappus with bristles of various length and forward-pointing teeth.

The achene body length (without pappus) is 0.6 ± 0.05 cm (mean \pm SD; $n = 100$), the longest pappus

bristle measures 1.1 ± 0.1 cm and the achene weight (with pappus) is 7.6 ± 2.0 mg (dried at 40°C) at two sites in our study area. At one site we measured a mean achene number per capitule of 47 ± 13 (mean \pm SD; $n = 50$) with a maximum of 88, and a mean exposure height of achenes of 40 ± 7 cm (mean \pm SD; $n = 50$) with a maximum height of 56 cm above ground. The exposure height is much lower if there is a higher grazing pressure and individuals flower after the removal of the apical meristem by grazing (Klotz, pers. comm.).

The few existing investigations on seed banks of Jurineo–Koelerietum stands indicate that *J. cyanoides* does not form a persistent seed bank (Krolupper and Schwabe, 1998; Sautter, 1994).

Study area

The study area is located in the northern upper Rhine valley in Hesse, Germany ($8^\circ 39' \text{E}$, $49^\circ 53' \text{N}$; districts Darmstadt and Darmstadt-Dieburg). It is characterised by calcareous sand, dating from the late and post-glacial age. The mean annual temperature is 9°C and the mean annual rainfall is 700 mm (Süss et al., 2004).

Two experiments were carried out at the nature conservation area “Ehemaliger August-Euler-Flugplatz von Darmstadt”, which has been grazed extensively by sheep since 1999 (site 1) (Zehm and Zimmermann, 2004). About two-thirds of all experimental paddocks were covered by the Jurineo cyanoidis–Koelerietum glaucae (with a high portion of open ground) and one-third was covered by ruderalised stages with a closed cover of grass species (mainly *Cynodon dactylon*) and bryophytes (mainly *Hypnum cupressiforme* var. *lacunosum*). There is no historic or current report on the existence of *J. cyanoides* at this site, neither in the vegetation nor in the seed bank. The soil seed bank of a permanent plot of 25 m^2 in the centre of one of the experimental paddocks was assessed in 1997 and 2001 (Kraft n.p.; Eichberg et al., 2006). For the time of examination an immigration from the nearest existing populations of *J. cyanoides* can be excluded.

Additionally, seedling-mortality rates in existing populations of *J. cyanoides* were investigated at two sites: a small open pine forest area of 4 ha (site 2) and a sandy grassland of 1 ha (site 3), situated under an overhead power cable.

Experimental design

In November 2002, experiment 1 was carried out to investigate transport processes (retention time, dispersal distance) and post-dispersal processes (diaspore and seedling fate). Two adjacent paddocks were prepared (each 475 m^2 ; P1/P2). After a pre-specified number of

diaspores had been attached manually to the fleeces of four sheep, the paddocks were grazed by two sheep each for 3 days.

In October 2003, experiment 2 (based on results of experiment 1) was carried out to investigate the effectiveness of diaspore incorporation into the soil by sheep trampling. Two adjacent paddocks were set up (each 140 m^2 ; P3/P4). After a specific number of diaspores had been manually placed on the ground, the paddocks were grazed by two sheep each for 24 h and compared to controls (C3/C4).

Diaspore material

The achenes used in our experiments were collected from large populations of *J. cyanoides* in the study area, in years with a high fruit set (2001 and 2002). The former were kept in cold storage ($5\text{--}8^\circ\text{C}$) until the investigations started. Only the most well-developed (thickest) achenes were used. Their capacity to develop seedlings was assessed under controlled conditions: 3×25 achenes of each year were kept in autoclaved sandy soil from site 2 at varying temperatures and in varying light conditions. In all, $47 \pm 11\%$ (mean \pm SD) of the achenes set seedlings, with no significant difference between the material from the 2 years ($p > 0.05$; *t*-test).

Experiment 1

Retention time (Question 1)

In November 2002, we attached 4×180 achenes of *J. cyanoides* manually to the fleeces of four tamed Rhoen sheep wethers directly adjacent to the paddocks. In order to represent different modes of epizoochorous diaspore uptake, the achenes were attached at three body parts of the sheep: back-shoulder, flank-belly and thigh-hind leg. The flank-belly area and the thigh-hind leg area represent both the uptake of diaspores into the fleece as the sheep brush against the plants while walking by and the uptake through resting on the ground. The back-shoulder area represents the uptake of diaspores by rolling. At each body part an area of $12\text{ cm} \times 14\text{ cm}$ on both sides of the sheep's bodies was marked with colour. Each of these six patches per sheep was stocked with 30 achenes by means of forceps, covering both superficial and deeper parts of the fleece (“fleece partings”). The hair length in these patches was 10–11 cm.

The retention time of the attached achenes of *J. cyanoides* was determined by repeated counting of the achenes that remained in the fleeces. The examinations were carried out 2, 3, 4, 20, 24, 28, 44, 52, 69 (end of grazing time on the experimental paddocks), 142, 311 h and 7 months (shearing day) after attachment.

Dispersal distance and seed shadow (Question 2)

After grazing time the paddocks were searched systematically for visually detectable achenes of *J. cyanoides*. Every achene was marked with a plastic stick. Distances from these achenes to the centre of the place of diaspore attachment were measured.

Post-dispersal fate of above-ground diaspores (Question 3)

The fate and displacement of marked achenes were observed approximately every 14 days.

Seedling emergence and establishment success at site 1 (Question 4a)

Seedling emergence and establishment were investigated for 19 months from November 2002 to June 2004 fortnightly. Seedlings were protected by chicken fences (height: 50 cm; mesh width: 25 mm) to prevent damage by rabbits, which were highly abundant in 2003, as well as by sheep, which grazed on the paddocks again in 2003. The vegetation period 2003 was characterised by an extraordinarily hot and dry summer (Internet2, 2003; Zehm and Zimmermann, 2004). Therefore, three summer rainfalls, such as usually occur, were simulated (14, 14 and 28 mm) in August 2003 (application of distilled water with a measuring cup). For the nearest weather station (Frankfurt a. M., airport) the maximum daily precipitation during August in the time period 1991–2002 was 33 mm (in August 2003: 4 mm); three stronger rainfalls occurred in August 1999 (17, 16 and 20 mm) (Internet3, 2003).

Seedling-mortality rates at sites 2 and 3 (Question 4b)

On both sites two plots (each 2 m²) were set up according to the following criteria: (1) high number of seedlings of *J. cyanoides*; (2) seedlings of *J. cyanoides* existing both on open patches and on patches with bryophyte cover. Seedlings present at the beginning of the investigations and also newly emerging seedlings were marked with plastic sticks. Their emergence and fate were registered every fortnight as at site 1. Examinations in the surrounding areas of the plots verified that the seedling emergence waves of the plots

were representative. Examinations of the plots were carried out from March/April 2003 to June 2004. Livestock grazing on seedlings of *J. cyanoides* was excluded. Rabbit impact was negligible at these sites.

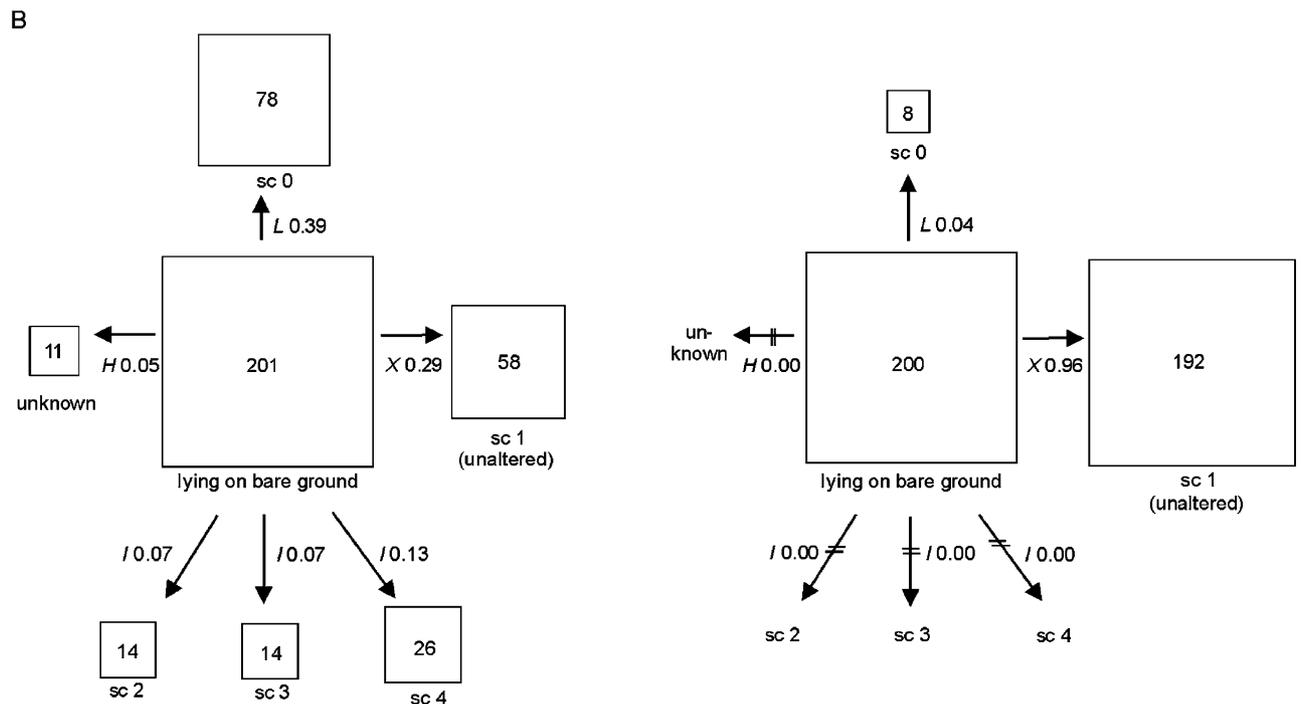
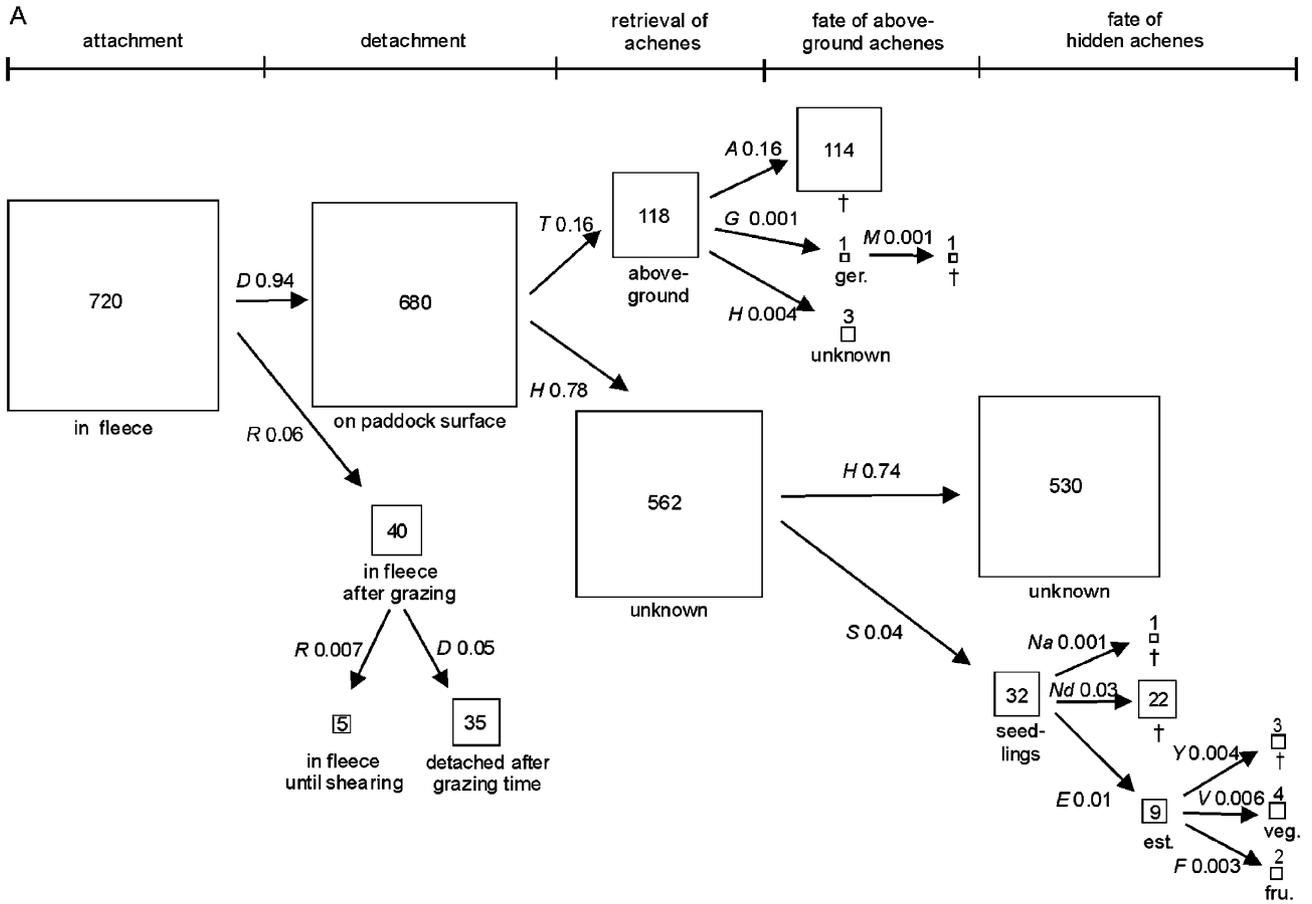
Experiment 2

Effects of trampling on horizontal and vertical diaspore displacement (Question 5)

At both paddocks (P3/P4) 20 plots (each 10 cm × 10 cm) with an open ground percentage of at least 50% were selected by means of a random systematic design with a minimum distance between plots of 10 cm. Adjacent to both paddocks 20 ungrazed control plots of equal size were established (C3/C4). In all 80 plots, five (six in one case) achenes were spread on the open ground patches, with the achene bodies placed in a lateral position. The achenes were sprinkled with a small amount of tap water, thus creating a contact between sandy soil and achenes, which persisted even after re-drying. This treatment was used to prevent a random drifting by wind (it corresponds to October rainfalls). After the grazing time visible diaspores were counted per plot and their vertical and horizontal position was determined. The coverage of diaspores by soil was estimated in the following five classes: 0 (0% cover), 1 (1–50%), 2 (51–99%), 3 (100%, excl. pappus), 4 (100%, incl. pappus). Achenes that could not be retrieved by above-ground survey were sought out by sieving the cryptogam layer and the soil (mesh width: 2 mm). In a preliminary investigation of 50 sheep hoofprints, a maximum depth of 6 cm was measured. Therefore, soil monoliths with a depth of 8 cm and a contour of 10 cm × 10 cm (plot), 30 cm × 30 cm (surrounding zone 1) and 50 cm × 50 cm (surrounding zone 2) were examined successively. Retrieved achenes were checked for destructive trampling effects.

For statistical analysis the grazed plots (P3+P4) and controls (C3+C4) were pooled. Trampling effects (differences between grazed plots and controls) were tested by Fisher's exact test, using STATISTICA, release 6.0 (StatSoft). To estimate the degree of association the Phi (Φ) coefficient was used.

Fig. 1. Overview of dispersal and post-dispersal processes of achenes of *Jurinea cyanoides* after attachment to sheep fleece (A: experiment 1) and placement on the ground (B: experiment 2; left: grazed; right: control). Figures denote number of achenes (boxes) and probabilities based on the total number of attached/spread achenes (arrows). Box sizes are proportional to underlying achene numbers. (A) † = dead achenes/plant individuals; ger. = germinated achenes; est. = established plant individuals; fru. = fruiting plant individuals; veg. = plant individuals in vegetative stage (pre-generative). Key to processes: *D* = detachment; *R* = remaining in fleece; *T* = retrieval on paddock ground; *H* = hidden; *A* = achene death; *G* = germination; *M* = death of germinated achenes; *S* = seedling emergence; *Na/Nd* = seedling death due to accidental injury (*Na*)/drought (*Nd*); *E* = establishment; *Y* = death of young plant individuals (observations until October 2004); *V* = vegetative growth without fruit set (October 2004); *F* = fruit set (October 2004). (B) Soil covering classes (sc): 0 = 0% cover; 1 = 1–50%; 2 = 51–99%; 3 = 100% (excl. pappus); 4 = 100% (incl. pappus). Key to processes: *X* = remaining fixed on soil surface in lateral position; *I* = incorporation into the soil; *H* = hidden; *L* = release of the achenes from fixed position.



Nomenclature

The nomenclature follows [Wisskirchen and Haeupler \(1998\)](#) for vascular plant species and [Koperski et al. \(2000\)](#) for bryophytes.

Results

In [Fig. 1](#), the results of experiments 1 ([Fig. 1A](#)) and 2 ([Fig. 1B](#)) are displayed as an overview. In the following, we explain the details stepwise.

(1) Retention time

The retention time of achenes of *J. cyanoides* in sheep fleece was mostly very short: 82% achene detachment within 2 h, 13% detachment within 2–52 h and only 5%

of achenes remaining >52 h could be recorded on average ([Table 1](#); [Fig. 2](#)). One animal shook its body soon after reaching the paddock, causing a high portion of the achenes to fall out. In rainy weather (as in the case of our experiment), sheep were observed shaking their bodies frequently during grazing time. About 1% of the attached achenes remained in the fleeces until shearing day ([Fig. 1A](#)).

(2) Dispersal distance and seed shadow

In all, 17% of the 680 achenes that had fallen out during grazing time could be retrieved as ungerminated diaspores on the soil surface (on bare ground or sites with bryophytes) of the paddocks ([Table 1](#); [Fig. 1A](#)). The seed shadow was narrow in extent: most achenes were found at a distance of less than 5 m to the centre of the place of diaspore attachment. Only 1% of the

Table 1. Results of experiment 1 (sheep-epizoochorous dispersal and post-dispersal processes) n = number of achenes.

Paddock no.	P1 <i>n</i>	P2 <i>n</i>	Sum	P1 %	P2 %	Mean
(1) Retention time						
Attachment	360	360	720	100	100	100
Detachment within 0–2 h	302	285	587	84	79	82
Detachment within 2–52 h	44	50	94	12	14	13
Detachment within 52 h–7 months	12	22	34	3	6	5
No detachment	2	3	5	1	1	1
(2) Retrieval and dispersal distance						
Detachment on paddocks	346	334	680	100	100	100
Retrieval of above-ground achenes in <10 m distance	81	33	114	23	10	17
Retrieval of above-ground achenes in >10 m distance	2	2	4	1	1	1
Unknown fate	263	299	562	76	90	83
(3) Germination and predation of retrieved achenes						
Retrieval rate	83	35	118	100	100	100
Death by granivory	79	34	113	95	97	96
Other causes of death	1	0	1	1	0	1
Germination	1	0	1	1	0	1
Unknown fate	2	1	3	2	3	3
(4) Seedling emergence of germinated achenes						
Germinated achenes	1	0	1	100	—	—
Death after germination (no seedling emergence)	1	0	1	100	—	—
(5) Seedling emergence of hidden achenes						
Hidden achenes	263	299	562	100	100	100
Seedling emergence on microsites with bryophyte cover	5	11	16	2	4	3
Seedling emergence on bare-ground microsites	13	3	16	5	1	3
Unknown fate	245	285	530	93	95	94
(6) Establishment of hidden achenes						
Seedlings	18	14	32	100	100	100
Seedling death by desiccation	16	6	22	89	43	66
Establishment on microsites with bryophyte cover	1	5	6	6	36	21
Establishment on bare-ground microsites	1	2	3	6	14	10
Unknown fate	0	1	1	0	7	4

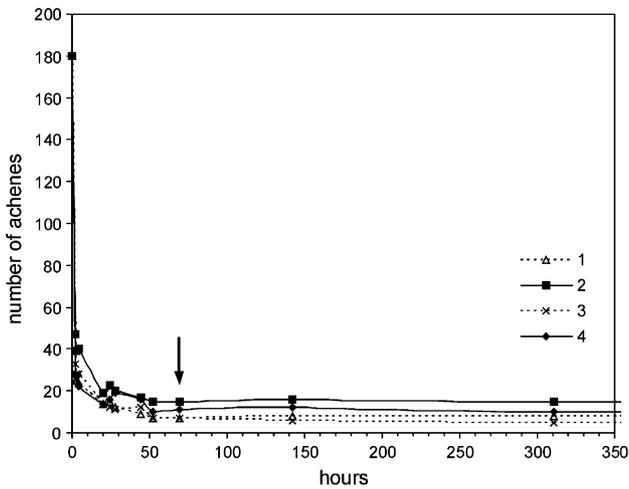


Fig. 2. Retention times of achenes of *Jurinea cyanoides* in the fleeces of four grazing sheep (1–4) after manual attachment on three body parts (180 achenes per sheep; for further explanations see text). The arrow indicates the end of the grazing time on experimental paddocks. The data points from the last date of survey (7 months after diaspore attachment) are not displayed here.

achenes were retrieved at a distance of more than 10 m. The maximum distance was 17 m (highest possible distance of dispersal within the paddocks: 41 m). At the resting places of the sheep no achenes could be found.

(3) Post-dispersal fate of above-ground diaspores

Above-ground secondary dispersal of the 118 marked achenes was essentially negligible. With the exception of three achenes (3%) that could not be retrieved and whose fate is unknown, all achenes remained close to their marking sticks and had been moved at most a few centimetres as long as they remained intact (2–15 weeks).

The fate of the other 115 achenes was almost exclusively determined by predation (P1: 98%; P2: 100%; Fig. 3). The achenes were cracked and showed no traces of gnawing (Fig. 4). The major loss by predation (P1: 89%; P2: 59%) occurred within 4 weeks after grazing in the time period 05.11.02–05.12.02 (Fig. 3). Predation happened at the place where the achene had been deposited.

The germination rate of above-ground achenes was very low: out of 115 above-ground achenes only one germinated (emergence of the radicle) in the time period 19.12.02–04.01.03 within the bryophyte layer. This achene did not reach the seedling stage (emergence of the cotyledons) and died in February 2003. Thus, no establishment of above-ground achenes could be observed (Fig. 1A).

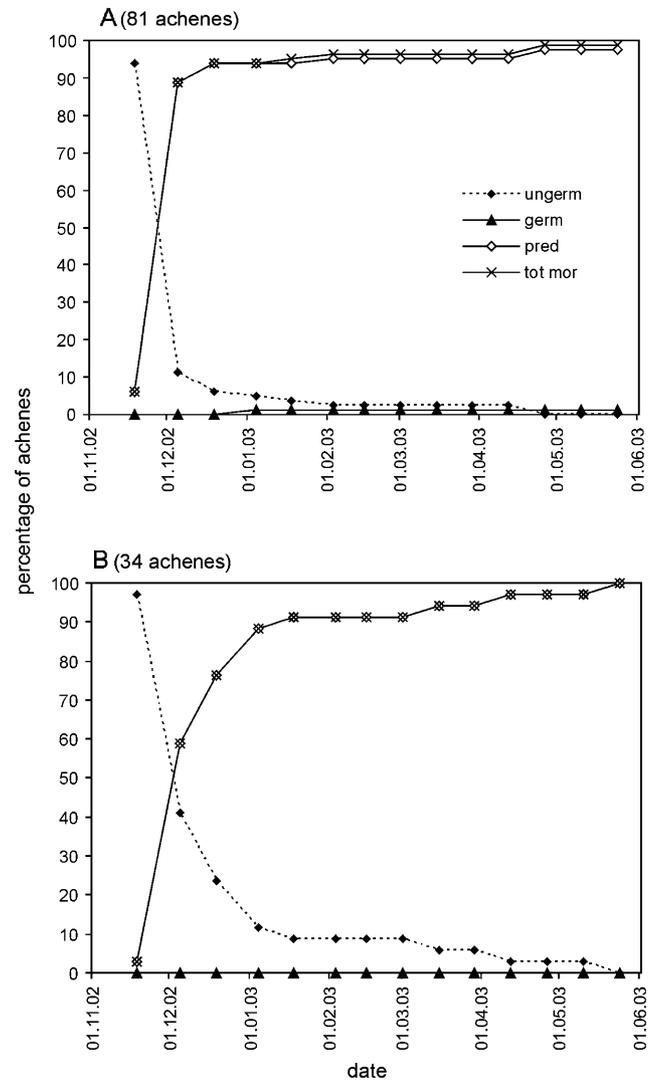


Fig. 3. Post-dispersal fate of above-ground achenes of *Jurinea cyanoides* on two experimental paddocks (A: P1; B: P2). ungerm: ungerminated, intact achenes; germ: germinated achenes; pred: achenes lost by predation; tot mor: total mortality. In (B), predation and total mortality match each other. Achenes with unknown fate are excluded from this diagram (cf. Table 1).

(4a) Seedling emergence and establishment success at site 1

A total of 32 (P1: 18; P2: 14) seedlings of *J. cyanoides* were detected: these correspond to 5% of the achenes detached on the paddocks (Table 1; Fig. 1A). Thus, seedling emergence rate in the field reached only one-tenth of the seedling emergence rate under controlled conditions (cf. chapter “Diaspore material”). All seedlings were located in non-ruderalised areas, mainly in proximity to the place of diaspore attachment. There is evidence that the seedlings germinated from achenes that had been incorporated into the soil or into deeper

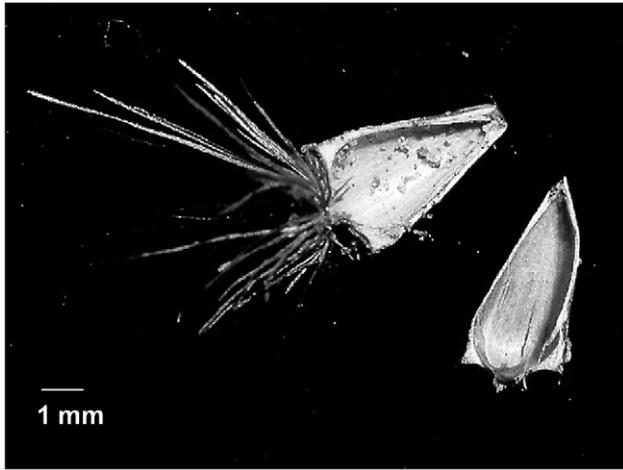


Fig. 4. Remains of achenes of *Jurinea cyanoides* after post-dispersal granivory (photo: A. Kratochwil).

parts of the bryophyte layer: none of the seedlings emerged from marked diaspores, but all were located among them, at places where intensive searching had been done before. Furthermore, the freshly emerged cotyledons of most seedlings apparently had penetrated the soil surface. Nearly all seedlings emerged in March/April 2003. No further seedlings emerged in the second vegetation period. Contrary to site 1, on all four plots of sites 2 and 3 new seedlings of *J. cyanoides* occurred in 2004.

Seedling mortality was moderate to high (P1: 89%; P2: 46%; seedlings with unknown fate excluded; Table 1) and occurred mainly in April/May and July/August 2003 (Fig. 5). Mortality was obviously caused by drought, as seedling leaves dried out gradually before death and dying occurred exclusively in dry periods. We also observed traces of herbivory on the seedlings, but these attacks did not lead to seedling death.

Nine individuals of *J. cyanoides* showed successful establishment: this corresponds to 1% of the total number of achenes detached on the paddocks and 28% of the recorded seedlings (Fig. 1A). On the date of the last survey in June 2004 one of these plants had died by desiccation and another two died suddenly in July and September 2004, probably due to root herbivory. In September 2004, one individual showed a first rooted shoot and two other individuals reached (early) fruit ripeness stage. Individuals that were able to establish themselves were located at an average distance of 4.2 ± 3.1 m (mean \pm SD) and a maximum distance of 7.9 m from the centre of the place of diaspore attachment. No further seedling death occurred after watering in August 2003 within that summer. The fate of a high percentage of the attached achenes remained unknown (74%; Fig. 1A).

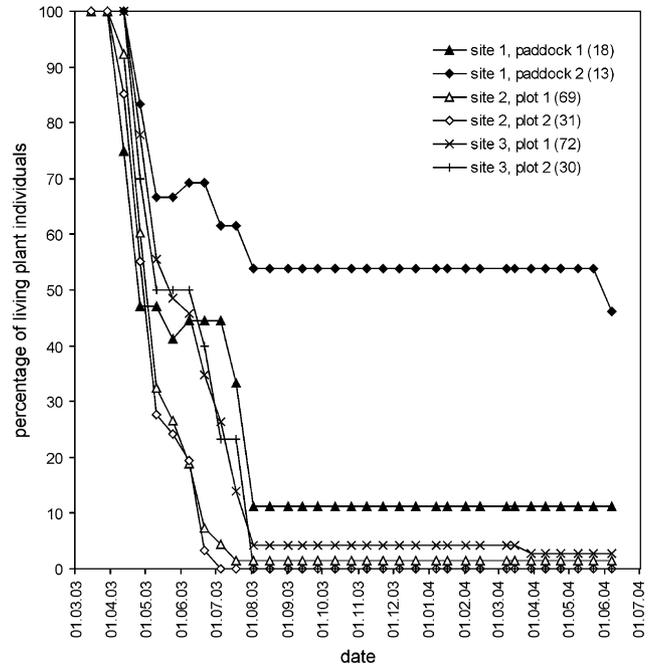


Fig. 5. The fate of seedlings of *Jurinea cyanoides*: living individuals on all three study sites as a percentage of the cumulative number of seedlings recorded in the time period 15.03.03–07.06.03 on each plot (final numbers in parentheses).

(4b) Comparison of seedling-mortality rates at site 1 with mortality rates in existing populations of *J. cyanoides* (sites 2 and 3)

We compared the fate of seedlings that were recorded in the time period 15.03.03–07.06.03 until establishment was reached (29.03.04): 31 seedlings on site 1 (P1: 18; P2: 13; one of the 32 seedlings that emerged died back owing to accidental injury and is not counted here); 100 seedlings on site 2 (plot 1: 69; plot 2: 31) and 102 seedlings on site 3 (plot 1: 72; plot 2: 30). The mean seedling mortality in the existing populations of *J. cyanoides* (site 2: 99%; site 3: 99%) was 1.5-fold higher than on the paddocks (site 1: 68%).

The three individuals that could establish themselves at sites 2 and 3 grew in the shelter of bigger perennial plants (*Artemisia campestris*) or abiotic structures (a tree stump). In the existing populations of *J. cyanoides*, where no watering was carried out, the mortality rate was already at a standstill at the time of watering in August 2003 and did not increase further within that summer (Fig. 5).

(5) Effects of trampling on diaspores

Table 2 shows the results of the assessment of horizontal and vertical diaspore displacement. In all, 93% (P3) and 96% (P4) of the spread achenes could be retrieved on the grazed sites and 100% on the ungrazed

Table 2. Results of experiment 2 (diaspore displacement by sheep grazing)

Treatment	Paddock			Control			<i>p</i>	Φ
	P3	P4	Mean	C3	C4	Mean		
Paddock/control no.	P3	P4	Mean	C3	C4	Mean		
No. of spread achenes	100	101		100	100			
Retrieval percentage	93	96	95	100	100	100		
A								
Intact	100	100	100	100	100	100	—	—
B								
A	49	40	45	98	100	99	***	0.61
B	20	29	25	2	0	1	***	0.36
C	14	18	16	0	0	0	***	0.30
D	14	13	14	0	0	0	***	0.27
C								
0	41	41	41	3	5	4	***	0.45
1	31	30	31	97	95	96	***	0.68
2	9	6	8	0	0	0	***	0.20
3	8	7	8	0	0	0	***	0.20
4	12	15	14	0	0	0	***	0.27

Note: Figures are percentages of retrieved achenes. *p* = significance of grazing effect (Fisher's exact test; two-tailed; performed with numbers of achenes); ****p* < 0.001; Φ = Phi coefficient of association. (a) Diaspore condition after grazing; (b) types of diaspore displacement (cf. Fig. 6): A = unaltered position; B = horizontal displacement (achene displaced out of the 10 cm × 10 cm plot); C = entering (located within hoofprint); D = covering (covered with loose sand); types B, C and D partly occur in combination; (c) soil covering classes: 0 = 0% cover; 1 = 1–50%; 2 = 51–99%; 3 = 100% (excl. pappus); 4 = 100% (incl. pappus).

sites (C3/C4). From the similar values in Table 2 for P3/P4 and C3/C4, a high reproducibility of the results can be inferred.

- (a) No destructive effects of trampling on achene bodies could be found, as all achenes remained visibly intact.
- (b) Different types of diaspore displacement were distinguished (Fig. 6). Whereas 98% (C3) and 100% (C4) of the achenes had been retrieved at the end of the grazing time in an (almost) unaltered position (type A) on control sites, this was true only for 49% (P3) and 40% (P4) of the grazed sites (difference significant at *p* < 0.001; Φ = 0.61; Fisher's exact test). Horizontal displacement (achene displaced out of the 10 cm × 10 cm plot: type B) was significantly higher on grazed plots (*p* < 0.001; Φ = 0.36). Among the retrieved achenes two types of trampling-induced soil incorporation could be observed: "entering" (pressing into the soil: type C; on average 16%) and "covering" (covering with loose soil: type D; on average 14%). The fraction of completely buried achenes could not be classified clearly (C and/or D) and corresponds to soil class 4 (see (c)).
- (c) On control plots no incorporation of achenes into the soil (coverage with sand > 50%) could be observed (Fig. 1B). Complete incorporation of diaspores (incl. pappus) amounts to 12% (P3) and 15% (P4) on grazed sites (*p* < 0.001; Φ = 0.27). We

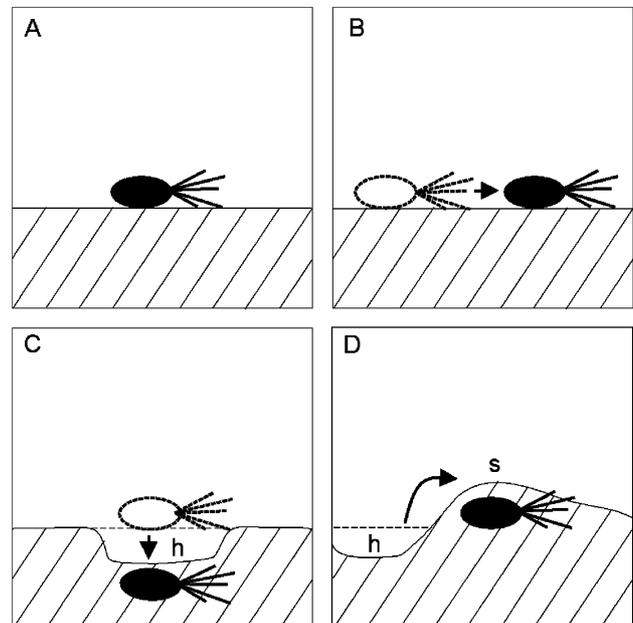


Fig. 6. Types of positions of diaspores after sheep grazing; (A) unaltered position; (B) horizontal displacement; (C) incorporation into soil by direct trampling pressure ("entering"); (D) incorporation into soil by trampling-induced covering with loose sand ("covering"). Types B, C and D can occur in combination. h: hoofprint; s: sand heap; striped: soil.

did not carry out thorough investigations on burial depth of achenes, but for 58% of the buried achenes rough estimations were done, which indicate that

burial depth by sheep trampling is small (up to 2 cm). Six achenes found in soil samples of surrounding zone 1 showed a complete incorporation after horizontal displacement on grazed plots. No achenes could be retrieved from soil samples of surrounding zone 2.

Discussion

(A) Epizoochorous processes (Questions 1 + 2)

The retention times of achenes in sheep fleece and post-dispersal achene distribution give evidence that *J. cyanoides* is dispersed mainly over short distances by sheep: most achenes quickly fall out of the fleece and the seed shadow is concentrated in the vicinity of the place of diaspore attachment. There is no evidence for directed dispersal, as neither achenes nor seedlings could be detected at specific paddock areas, e.g., the resting places of the sheep. On average 18% of the achenes were dropped within 2 h–7 months and may contribute to inter-population transfer, if sheep flocks are moving. Given that extensive grazing by moving sheep flocks is an appropriate management measure for Jurineo–Koelerietum stands, dispersal distance by sheep in a given time could be relatively high and could partly compensate for the short retention times.

Our results indicate that epizoochory could be another dispersal mode, in addition to wind dispersal, for *J. cyanoides*. Generally, there is evidence for an evolutionary reduction of the pappus in the Asteraceae (Zohary, 1950). This is an indication for a change from wind dispersal to other dispersal modes (Häffner, 2000), since a well-developed pappus is seen as a primordial feature (Zohary, 1950). Within the genus *Jurinea* and closely related groups the pappus function exhibits a high plasticity (Häffner, 2000). The outermost pappus bristles of *Jurinea* are shorter than the inner ones, and shortness of pappus bristles can be interpreted as an apomorphic feature (Häffner, 2000). Scabrid pappi, with teeth-like appendages, might function as structures that easily become entangled with sheep hair (cf. Frieb, 1901; Kronfeld, 1885; Ridley, 1930). There is evidence that only a slight morphological modification of the achene is necessary to change between anemo- and epizoochory (Sorensen, 1986; Willson and Traveset, 2000). Different modes of dispersal can exist in one plant species and one fruit type (Vander Wall, 1992; Vickery et al., 1986) or in different, more specialised fruit types (phenomenon of heterocarpy; e.g., Baker and O'Dowd, 1982; Brändel, 2004; Imbert, 2001; Mandák, 2003; Sorensen, 1978, 1986; Zohary, 1950).

(B) Post-dispersal processes

Post-dispersal fate of above-ground diaspores (Question 3)

The fact that secondary horizontal displacement of achenes of *J. cyanoides* was very short in distance, if it occurred at all, can be explained by “agglutination” of achenes with the sandy soil due to rainy weather during grazing time.

The results on the post-dispersal fate of achenes of *J. cyanoides* show that above-ground granivory can strongly diminish the plants' reproductive success and the colonisation potential. Cavers (1983) pointed out that within the life cycle of many plant species mortality is highest in the stage of the diaspore.

We do not have direct observations of the achene predator in our study, but the observed traces of granivory give some evidence that the main predators have been *Carduelis* species. On site 1 the achenes were cracked. This type of predation is typical of birds, especially *Carduelis* species. Groups of goldfinches (*C. carduelis*) were regularly present in the investigation area in autumn and winter. Achenes of Asteraceae species play an important role in the foraging strategies of goldfinches (*C. carduelis*); foraging takes place not only in the stratum of the infructescences but also in the soil litter stratum (Glutz von Blotzheim, 1997).

Seedling emergence and establishment success at site 1 (Question 4a)

Our experiment showed that establishment of *J. cyanoides* after sheep-epizoochorous dispersal is possible, although several factors restrict establishment. We found a strong limitation of establishment of seedlings of *J. cyanoides*, which was due to summer drought. Frost effects played no obvious role, as all plant individuals that had survived in 2003 re-sprouted in 2004. But other factors can be important for the survival of established individuals of *J. cyanoides* exceeding 1 year, as is indicated by the sudden death of two plant individuals, probably due to below-ground herbivory. For many species the conditions for establishment are tougher than those for germination (Turnbull et al., 2000). Establishment success under natural dispersal conditions might be even lower, because only well-developed achenes were used in our experiment.

The successful colonisation of *J. cyanoides* on site 1 implies that the occurrence of this species is diaspore limited. This is a typical phenomenon for low-productivity ecosystems (Foster et al., 2004; Turnbull et al., 2000).

A longer-term establishment is achieved if individuals that had become established on a previously unsettled site are able to build a self-sustaining population. In the

case of *J. cyanoides*, the ability to reproduce by vegetative growth (cf. “Results”) and the perennial life history are advantageous features for a successful colonisation. In our study area there are examples of *Jurinea* populations that persist for relatively long times with a low level of shoots: e.g., natural monument “Seeheimer Düne”: 22 shoots (year 1995); 130 shoots (1998); 149 shoots (2003) (Zehm, Kleine-Weischede, Beil n.p.).

Comparison of seedling-mortality rates at site 1 with mortality rates in existing populations of *J. cyanoides* (sites 2 and 3)

The higher seedling-mortality rate of *J. cyanoides* at sites 2 and 3 (99%) compared with site 1 (68%) could be attributable to several facts. First, watering, which occurred exclusively at site 1, must be taken into account. However, seedling-mortality rate had already stagnated at the time of watering (August) in the existing populations (Fig. 5). Second, sheep impact during the experimental grazing period could have facilitated establishment, e.g., by trampling (see below). Third, seedlings in the existing *Jurinea* populations might originate from diaspores with a broader vitality spectrum than the pool used in our experiment.

Despite the extremely hot and dry conditions in 2003, a small number of seedlings were able to establish themselves without watering in the neighbourhood of perennial plants or abiotic structures (on average 1%). Thus, nurse-plant effects such as shading or reduction of wind velocity might facilitate the establishment of *J. cyanoides*. This is what has been found for various plant species in dry, nutrient-poor, open habitats, e.g., by Wood and Del Moral (1987) in subalpine ecosystems, by Ryser (1990) in limestone grassland and by Maun (1994) in coastal dune ecosystems.

Effects of trampling on diaspores (Question 5)

In our investigations, grazing had significant effects on the horizontal and vertical displacement of diaspores situated on the ground within a short period of time. Secondary processes of diaspore displacement can influence diaspore fate in many aspects and are more likely to form distribution patterns of plants than is the primary dispersal of diaspores (Chambers and MacMahon, 1994).

Rotundo and Aguiar (2004) could show that sheep trampling increases seedling emergence of the perennial grass species *Bromus pictus* in the Patagonian steppes significantly by burial. Hach et al. (2005) recorded increased seedling establishment in sheep and donkey hoofprints in our study area. Harper (1977) reports two cases of increased seedling establishment of some species in the hoofprints of pigs in arable land and cattle in permanent grassland, whereas Stammel and Kiehl (2004) showed that hoofprints of cattle in calcareous

fen pastures have no importance as special regeneration niches. Burial of diaspores becomes more important in dry ecosystems with fast-drying upper soil layers (Rotundo and Aguiar, 2004).

In view of the high losses of achenes of *J. cyanoides* due to above-ground predation, which occurred relatively quickly in our study (within a few weeks), we assume that the percentage of complete burial into the soil by trampling (14%) has a considerable effect on population dynamics of *J. cyanoides* in grazed habitats. Although the impact of rainfall could also be an effective mechanism of seed burial, this process needs much more time (cf. Fenner, 1985), especially in low-precipitation steppe areas.

The incorporation of diaspores into the soil and the vertical movement of diaspores within the soil depend on both diaspore morphology (Bekker et al., 1998; Chambers et al., 1991) and the size of soil particles. Chambers et al. (1991) state that when the soil-particle size is small (0.5–1.0 mm), the only diaspores to be incorporated into the soil are either small (length with accessory structures: 1.0–1.9 mm) or have adhesive diaspore coats, while large diaspores (3.3–8.3 mm) drift above ground, without being incorporated. Thus, especially for a species like *J. cyanoides*, with comparatively big diaspores and an inflexible, persistent pappus, trampling-induced burial provides a considerable advantage on sandy soils (the soils of our study area consist predominantly of fine- to medium-grained sand; Bergmann, 2004). As Pemadasa and Lovell (1975) could show, small-seeded species are more subject to factors inhibiting germination with increasing soil depth than big-seeded species. Deep burial enforces dormancy (Harper, 1977; Maun, 1994; Pemadasa and Lovell, 1975). As the burial depth of achenes of *J. cyanoides* after grazing is obviously slight (up to 2 cm), soil incorporation by sheep trampling might offer an ideal spatial position of dispersed achenes: deep enough to escape predation to a certain degree, but not too deep to suppress germination.

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