EPIZOOCHORY BY THE RED FOX (*VULPES VULPES*) IN RELATION TO SEED AVAILABILITY: FIELD EXPERIMENTS WITH A FOX DUMMY

FRØSPREDNING I PELS HOS RØDREV (*VULPES VULPES*) SETT I FORHOLD TIL TILGJENGELIG FRØMENGDE I VEGETASJONEN: EN EKSPERIMENTELL TILNÆRMING

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MASTEROPPGAVE 30 STP. 2006

PREFACE

This thesis, written at the Department of Ecology and Natural Resource Management at the Norwegian University of Life Sciences, is the final 30 credits of my studies for the Master degree in Natural Resource Management.

In autumn 2003, I participated in a plant/animal-interaction class in South Africa. Back home in Norway the opportunity came to study these interactions, and there were no doubts in my mind that this was the right topic for my Master thesis.

The fieldwork was conducted on university grounds and on the land of Per Arne Bjerklund, to whom I wish to share my gratitude for letting me use his land.

I would like to thank my two supervisors, Mikael Ohlson and Knut Anders Hovstad, for their support, advice and inspiration during my work with this thesis. A special thanks to Knut Anders for his invaluable aid with the statistics. I would also like to thank Jon Gunnar Dokk for constructing the fox carrier, Anveig N. Wist for helping with fieldwork and to Åsmund Fjellbakk at the County Governor in Østfold and Jens Galby for providing the two foxes used in this study. Thanks also to my boyfriend Ole R. Sandven, for reading and commenting on my thesis.

Last, but not least, I would like to give thanks to my parents for letting me use their car during field work, it could not have been done without it. I would also like to show my sincere appreciation for all support, emotionally and financially, that I have received from them over the years.

Ås, 12th May 2006

Silje Borvik

ABSTRACT

Red fox (*Vulpes vulpes*) was evaluated as an epizoochorous seed disperser of meadow plant species. Seed attachment efficiencies and seed retention efficiencies of different plant species were examined with the help of a fox dummy.

Red fox fur provided epizoochorous seed dispersal for 20 of 34 species in the studied hay meadow, with 4500 seeds found attached to the dummy after 10 replicate walks of 52 m each. Six species were overrepresented in fox fur compared to seed availability in vegetation. The grass *Deschampsia cespitosa* was most overrepresented in the fur and showed thus the highest attachment efficiency. A minimal adequate model confirmed that attachment efficiency was greatly improved by the presence of hooks, hairs, awns and/or wings on seeds. Pappus, seed weight, seed shape and plant height, explained to little of the variation between species to be included in the model.

Seed retention efficiencies of different plant species were tested by attaching seeds to the fox dummy and subsequently recording how long distances the seeds stayed attached to the fur. Depending on species, 3 – 58 % of seeds remained on the dummy after 500 meters, with *Trifolium arvense*, *Agrimonia eupatoria* and *Geum rivale* retaining the highest number of seeds. A minimal adequate model found a negative relationship between seed retention and distance moved, and the model showed that retention efficiency was improved if seeds had hooks, hairs, awns and/or pappus. Winged appendages, seed weight and seed shape, explained too little of the variation between species to be included in the model. Seed retention efficiency by red fox was habitat-specific, with grazing meadows providing better seed retention than forest habitats.

It is concluded that red fox should be regarded a potentially important seed disperser, enhancing the probability for meadow plants to obtain long-distance dispersal in the cultural landscape.

SAMMENDRAG

I denne studien ble det vurdert hvorvidt frø fra forskjellige engplanter fester seg i pels hos rødrev (*Vulpes vulpes*), og hvor lange distanser ulike arter klarer å holde seg fast i pelsen. Dette ble undersøkt ved hjelp av en reveattrapp, bestående av en revepels og en trillevogn.

Av 34 arter på den undersøkte engen festet 20 arter seg i rødrevpelsen, med totalt 4500 frø etter 10 gjentak à 52 m. Seks arter var overrepresentert på reveattrappen i forhold til tilgjengelig frømengde i vegetasjonen. Graset sølvbunke (*Deschampsia cespitosa)* var mest overrepresentert på reven, og var dermed den arten som hadde høyest evne til å feste seg i revepelsen. Den statistiske analysen viste at evnen til å feste seg i revepels økte betydelig om et frø hadde kroker, hår, snerp og/eller vinger. Frøvekt, frøfasong, plantehøyde og om frø hadde pappus, forklarte for lite av variasjonen mellom arter til å ha avgjørende betydning.

Hvor lenge frø av forskjellige arter klarte å holde seg fast i revepels, ble testet ved å feste frø til reveattrappen og registrere hvor lange distanser frøene klarte å holde seg fast i revepelsen. Avhengig av art hang fortsatt 3 – 58 % av frøene fast i pelsen etter 500 meter. *Trifolium arvense*, *Agrimonia eupatoria* og *Geum rivale* hadde flest frø igjen på revepelsen etter denne distansen. Det funnet en negativ sammenheng mellom distanse og antall frø som fortsatt hang fast i revepelsen. Sannsynligheten for å ha mange frø igjen i revepelsen etter de ulike distansene, økte for frø med kroker, hår, snerp og/eller pappus. Frøvekt, frøfasong og om frø hadde vinger, forklarte for lite av variasjonen mellom arter til å ha avgjørende betydning. Frøspredning i rødrevpels var habitatspesifikk. Flere frø hang fortsatt fast i revepelsen etter at reveattrappen ble beveget gjennom beiteengvegetasjon enn etter at den ble beveget gjennom skogvegetasjon.

Det ble konkludert at rødrev øker sannsynligheten for at planter oppnår langdistansespredning, og at rødrev derfor bør betraktes som en potensielt viktig frøspreder av engplanter i kulturlandskapet.

CONTENTS

1 INTRODUCTION

Plants are for the most part rooted to one spot with a limited ability for movement, so they disperse through their offspring as fruits, seeds or related structures (Gurevitch et al. 2002). Seed dispersal is thus an fundamental and obligatory phase in the life-cycle of plants, and its function is to spread seeds to new unoccupied habitats in order to reduce the probability of competition between siblings and parents, inbreeding, insect and pathogen infestations and extinction in ephemeral habitats (Macdonald & Smith 1990; Howe & Westley 1997; Howe & Miriti 2000; Fenner & Thompson 2005). Seed dispersal can influence the abundance and distribution of species, both on local and regional landscape scales (Kiviniemi & Eriksson 1999). Long-distance seed dispersal give plants a chance of reaching new habitats, and it is the key to survival for many species in the modern fragmented landscape (Opdam 1990). Most seeds do not obtain long-distance dispersal, but if small proportions of seeds are dispersed far, this can lead to an increase in spread rates of many orders of magnitude (Higgins & Richardson 1999).

Plants rely on physical forces or animals to disperse their seeds (Howe & Westley 1997), and all plant species are probably dispersed by more than one agency (Fischer et al. 1996). Epizoochorous dispersal is the external transport of plant seeds on animals (Couvreur et al. 2005b), and it may seem an attractive option for plants, since no nutritional or energetic reward is provided to the vector (Sorensen 1986). However, most epizoochorous seeds are dispersed within a few meters from the mother plant, due to low removal rates (Verkaar 1990; Fenner & Thompson 2005). Still, adhesive dispersal is considered a most significant factor in plant metapopulation dynamics, as it enhances the probability of occasional seeds reaching suitable sites in the fragmented landscape and it gives seeds a greater probability for long-distance transport than provided by most other mechanisms. (Kiviniemi & Telenius 1998; Takahashi & Kamitani 2004; Fenner & Thompson 2005; Mouissie et al. 2005). In the uttermost consequence, if able to stay undetected or ungroomable, epizoochorously dispersed seeds may remain on the vector until the animal sheds its coat or dies (Sorensen 1986). Several studies have demonstrated that mammals are important seed dispersal vectors (Agnew & Flux 1970; Fischer et al. 1996; Graae 2002; Heinken et al. 2002).

Epizoochory is, as opposed to seed dispersal by animals (“synzoochory”) and in animals (“endozoochory”), a continuous process where attachment and detachment can take place within every meter moved by the vector (Bullock & Primack 1977). To say anything about potential dispersal distances for epizoochorous dispersed seeds, it is important to investigate both the attachment and the detachment processes. The attachment process determines the number of seeds and which species that get attached, and the detachment process determines how long seeds of different plant species stay attached to the animal coat before dropping off.

Three different methods have primarily been used to investigate the epizoochorous attachment process empirically, namely use of live animal (Fischer et al. 1996; Graae 2002; Couvreur et al. 2004a), examination of the furs of shot animals (Agnew & Flux 1970; Heinken et al. 2002; Schmidt et al. 2004) and use of fur/cloth attached to some kind of movable device (Bullock & Primack 1977; Fischer et al. 1996; Mouissie et al. 2005). Epizoochory by living wild mammals is very difficult to study, and methodology is scarce (Heinken et al. 2006). However, a dummy constructed of animal fur can be used to mimic the natural appearance of a given animal (Fischer et al. 1996; Castillo-Flores & Calvo-Irabien 2003). Compared to live or shot animals, dummies are advantageous when it is important to control for animal behaviour in order to obtain comparable results. Use of a dummy gives the opportunity to compare attached seeds with seed availability, because the researcher has full knowledge of where the dummy has been walked.

A common method to investigate the detachment process of different plant species has been to attach seeds to a vector and subsequently counting the remaining seeds after a period of time or after walking a given distance (Sorensen 1986; Kiviniemi & Eriksson 1999; Couvreur et al. 2005b). Different methodological strategies, such as use of paint and use of non-resident seeds, have been used to separate the detachment process from the attachment process (Bullock & Primack 1977; Sorensen 1986; Kiviniemi 1996; Graae 2002). Recently, several studies have tested the epizoochorous properties of different plant species in controlled environments, attaching seeds to coats that are subsequently mechanically shaken, in order to find the seed characteristics that determine seed retention in different fur types (Couvreur et al. 2004b; Romermann et al. 2005; Tackenberg et al. 2006).

In this study, I chose to examine red fox (*Vulpes vulpes*) as a possible epizoochorous seed-dispersing agent. Red fox was chosen because it is common in the study area and because it occurs in a wide range of habitats (Bjärvall & Ullström 1997). Mobility and lack of specific habitat requirements are two of the key factors determining its success (Harris & Woollard 1990). Red foxes have relatively long and soft fur. Fur type is known to be important as regard seed retention, with long and undulated fur providing better seed retention than short and straight fur (Couvreur et al. 2005b). It is therefore likely that red fox can provide good seed retention for meadow plant species. The relatively large red fox populations, their fur quality, mobility, and habitat use, make red foxes potentially important as seed dispersal vectors. An American study tested red fox fur as a potential vector for a rare plant species (Laughlin 2003), but no study has, to my knowledge, considered red fox as an epizoochorous seed disperser of European plant species.

My study was carried out in different cultural landscape habitats. Cultural landscapes in northern Europe have undergone extensive changes following the transition from traditional to modern land-use regimes (Stoate et al. 2001; Eriksson et al. 2002; Antrop 2004). These large-scale landscape changes bring on great consequences for biodiversity, as a large part of northern Europe's plant species richness is directly or indirectly associated with traditionally managed meadows (Norderhaug et al. 2000; Eriksson et al. 2002; Pykala et al. 2005). Today, only fragments are left of the species rich hay meadows in Norway, often just as narrow strips around cultivated land (Kielland-Lund et al. 1999). Typical consequences of fragmentation and habitat loss are isolation and reduced population sizes, making survival of viable populations and seed dispersal to new habitats harder (MacArthur & Wilson 1967; Hanski 1999).

The main aim of this study was to evaluate the red fox as an epizoochorous seed disperser of meadow plant species in cultural landscapes. By the use of a fox dummy, I aimed to reveal why different plant species had certain attachment efficiencies, i.e. the relationship between the number of seeds found in fur and the number of seeds available in vegetation. In addition, I attempted to uncover potential seed dispersal distances in the fur of red fox for different plant species. In order to do this, I ask the following questions:

- How many seeds of a species get attached to the fox fur compared to the number of seeds available in vegetation?
- How long distances are seeds of different plant species able to stay attached to fox fur?
- Which seed traits regulate seed attachment efficiency and seed retention efficiency in fox fur?
- Does plant height affect seed attachment efficiency in fox fur?
- Will retention time differ between habitat types?

2 MATERIAL AND METHODS

The study was carried out in three parts, a pilot study, an attachment experiment with a seed source analysis, and a detachment experiment. Nomenclature for vascular plants follows Lid et al. (1994). For convenience, all diaspores (seeds or fruits) are referred to as ‘seeds’ in this thesis.

2.1 Study area

2.1.1 Pilot study

The pilot study was performed in a grazing meadow in Ås Municipality (6615461N 599065E[1]), in the county of Akershus, southeastern Norway (Figure 1).

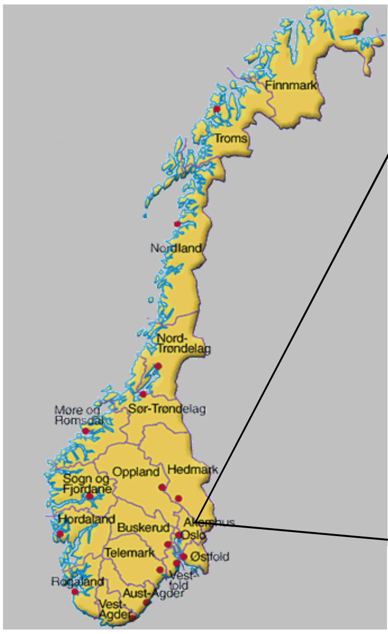

Figure 1 The pilot study area in Ås Municipality, Akershus County. The exact study location is indicated by ‘S’. Scale 1:5000 ©Norkart A/S

The meadow, size c. 80x190 m, was situated about 60 m above sea level. Vegetation about 20 cm tall, and was dominated by vegetative grasses. Some few and scattered herbs, such as *Taraxacum spp*., *Trifolium pratense* and *Urtica dioica* were present. The study was carried out in the first week of June 2005, prior to the seed dispersal of the naturally occurring species.

2.1.2 Attachment study

The attachment study was performed in a moist hay meadow in Stunner Nordre in Ski Municipality in the county of Akershus, southeastern Norway (6625113N 607950E). The meadow, c. 30x50 m, was situated between groves and cultivated land, about 150 m above sea level (Figure 2). *Agrostis capillaris*, *Anthoxanthum odoratum*, *Deschampsia cespitosa*, *Luzula multiflora* and *Potentilla erecta* were abundant species, but also *Prunella vulgaris, Rhinanthus minor* and *Achillea millefolium* were

1 All coordinates are in 22 EU89 UTM zone 32

rather frequent. A more detailed description of the vegetation can be found in the results (Table 2) and in Appendix 1.

Mowing had traditionally been carried out once a year, normally in the beginning of August, and the meadow had never been fertilised (pers. comm. Per Arne Bjerklund). Owing to my fieldwork, the mowing was delayed by one week in 2005. In the year 2000 biodiversity registrations, this area was listed as the greatest valued old hay meadow in Ski Municipality (Stokland 2000).

Figure 2 The study area in Ski Municipality, Akershus County. The exact study location is indicated by ‘S’. Scale 1:5000 ©Norkart A/S

2.1.3 Detachment study

The detachment study was performed in two different locations; in a grazing meadow close to Lake Årungen in Ås Municipality (N 6617661 598900E) and in forest habitat in Nordskogen, also in Ås Municipality (6615936N 599211E) (Figure 3).

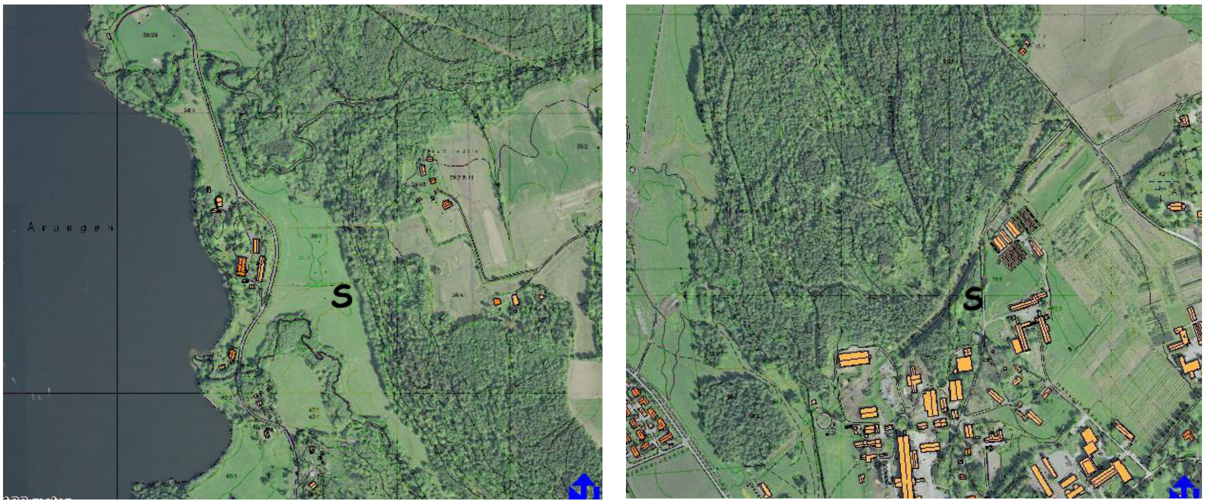

Figure 3 The study areas used in the detachment study, Ås Municipality, Akershus County. Left) The grazing meadow. Right) The forest area. The exact study locations are indicated by ‘S’. Scale 1:5000 ©Norkart A/S

The grazing meadow, c. 120x140 m, was situated between a forest and other grazing areas, about 50 m above sea level. Vegetation consisted mainly of short vegetative grasses (5-8 cm) and some *U. dioica*. The forest habitat was a clear-cut area, size c. 40x70 m, situated in a mixed forest, about 80 m above sea level. Being in an early successional phase, many low herbs and grasses, and higher shrubs, such as *Rubus idaeus,* were present. Leftover branches and stumps had not been removed from the ground after the clear-cutting.

2.2 The fox

A fox dummy was constructed in order to examine the seed attachment and detachment processes in red fox fur. In the pilot study, an adult fox in its winter coat was used, whilst a 4.0 kg juvenile fox shot around mid-July 2005 was used in the attachment and detachment experiments. Guard hair length of the juvenile fox was 3.5 – 4.5 cm, while the undercoat was 2.5 cm long. The only holes in the skin were a large hole in the rear end, holes through the eyes and cuts down the legs. I attached the fox to a wheeled carrier, designed for the purpose to get the fox through the vegetation while imitating normal walking behaviour as much as possible (Figure 4).

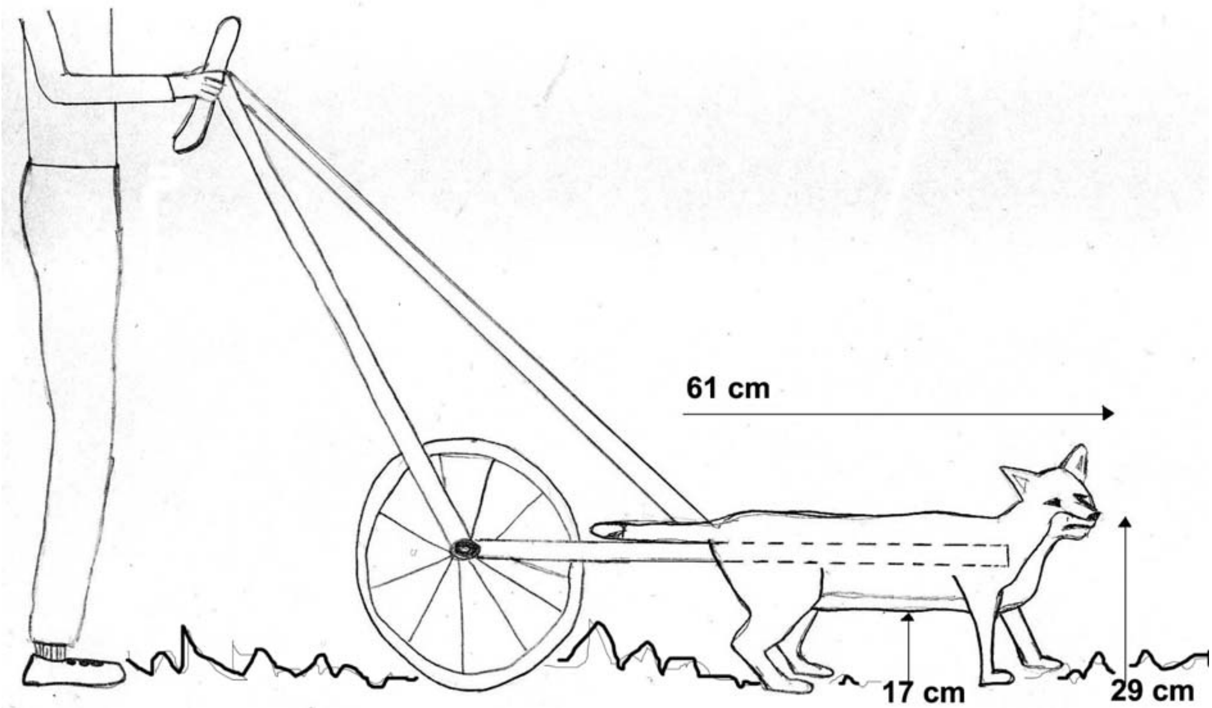

Figure 4 Fox dummy constructed in order to measure the attachment and detachment of different seeds in fox fur.

The carrier consisted of a wheel, a handle and a narrow plank to which the fox was being attached. The hollow fox was stuffed with newspapers and thick sticks were put inside head and neck in order to keep them stiff. To ensure that the fox was kept stable, the foxtail was tied to the carrier, and was thus not included in the seed-dispersing unit. Henceforth, the fox dummy (the fox + the carrier) will mainly be referred to as “the dummy”.

2.3 Pilot study

2.3.1 Pre-study examination

A pre-study examination was carried out in order to find out how to remove seeds efficiently from the fox fur. Several techniques were tested, and the method that proved most efficient was pushing the dummy over a tub and gently remove the seeds, see Graae (2002). After shaking the fur over the tub, I went through the fox fur by hand. Five minutes were used on each side of the dummy. I avoided removing the fox from the carrier by using this method, and the examination showed that all attached seeds were retrieved in the tub.

2.3.2 Pilot study

In order to practice in using the dummy and to improve the methodology, a pilot study was conducted in the first week of June 2005. The pilot study was carried out as a detachment study, by attaching seeds to the dummy and subsequently walking the dummy given distances. In the pilot study, the following species were used: *Hypochoeris maculata*, *Pimpinella saxifraga*, *Anthriscus sylvestris*, *Knautia arvensis*, *Festuca rubra*, *Angelica sylvestris* and *Plantago lanceolata*. These species were chosen because they represented different seed types and because the seeds were available. Seeds used in the pilot study were mostly collected from local plant populations, but some species were obtained from commercial seed suppliers. Seeds of *P. lanceolata* produce sticky mucilage when wet (Grime et al. 1988), so seeds of this species were applied to the dummy both as dry and wet.

Five different distances were walked, i.e. 5 m, 10 m, 50 m, 100 m and 200 m, with five replicates per species per distance. In each walk, ten seeds of four species were evenly placed on both sides of the dummy with a pair of tweezers and the dummy was walked a given distance. Wet and dry *P. lanceolata* was never placed in the same walk, and the order of distances was randomised. The seed-collecting tub was located at the starting point, so the dummy was always returned to this spot to have the remaining seeds removed. After a distance had been walked, the remaining seeds were collected, put back in their glass container and counted. Rainy weather created some minor problems, which made it obvious that the upcoming experiments needed to be carried out in dry weather. Results from the pilot study were used to improve the accomplishment of the attachment and detachment experiments (Section 3.1, Figure 6).

2.4 Attachment study and seed source analysis

An attachment study and a seed source analysis were carried out to examine the importance of epizoochorous seed dispersal of meadow plants in cultural landscapes.

Every fourth meter of the long side of the study meadow was marked, indicating the starting points of eight right-angled transects of 26 meters in length (Figure 5). Five of the transects were randomly chosen to be part of the attachment experiment.

The vegetation of the meadow was surveyed in the first week of August 2005, and six plots of 1 m^2 (1x1 m) were examined in each transect, giving thirty plots in total. The plots were placed along the

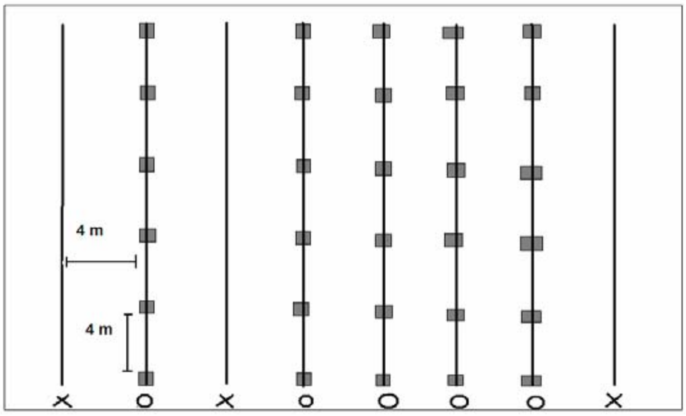

Figure 5 Design of the attachment study. Straight lines indicate transects, while filled squares indicate the 30 vegetation analysis plots. 'O' indicates transects used in the attachment experiment, while 'X' indicates transects not used.

transects with four meters in between (Figure 5). A wooden frame was put down to mark the outer edges of the plots, and the number of ramets with flowers and/or fruits was recorded in each plot. Due to difficulties in separating them, *Agrostis stolonifera* and *A. capillaris* were recorded as one species, and are from now on referred to as *A. capillaris*. Care was taken to avoid trampling of the vegetation.

The attachment study with the dummy was carried out on August 9 and 10. Vegetation was always dry when walking the dummy. The dummy was walked through a transect and back, a total of 52 meters, with a walking speed of about 3 km/h. Seeds that had attached themselves to the dummy were removed as described in Section 2.3.1, and put in a lidded glass container. All seeds were dried over night at room temperature, and stored for later identification and counting. All transects were walked twice – once going on the right side of the plots (A) and once going on the left side of the plots (B), thus ensuring that the fur never touched the same vegetation twice. The order of transects and A/B walked, was completely randomised.

The seed source analysis was carried out from August 8 to 10. Ramets from the meadow were collected in order to asses the seed availability (number of seeds in the plant populations). Thirty fertile ramets of the plants that had been registered in the five studied transects, were collected at random from the unused transects (Figure 5). Due to several factors, only eight ramets were collected of *Lathyrus linifolius* and *Scutellaria galericulata* was not collected at all. Each ramet was put in a separate envelope, and all envelopes were dried at 105 ̊C in 24 hours.

Ramet seed number was estimated by counting the seeds of a minimum of ten ramets of each species (with the exception of *L. linifolium* and *S. galericulata*). Korsmo et al. (2001) was used as a reference to distinguish mature seeds. To increase the precision of the mean, I strived to reduce the standard error to <20 % of the mean. This was done by counting the seeds in up to 25 samples for the species found on the dummy, see Appendix 3 and 4. Counted seeds created a seed herbarium collected *in situ* (Mouissie et al. 2005). Identification of the seeds found on the dummy was based on this local seed herbarium.


The hay meadow in Stunner Nordre, used in the attachment study (Photo: Silje Borvik).

Seed traits that are likely to influence seed attachment and detachment processes were examined. Seed weight, seed length and seed width were measured for all species found in the five transects (Appendix 5). Seeds from the seed herbarium collected *in situ* were used for these measurements. Seed weight was calculated by using a Precisa 2005A SCS-weight, weighing ten replicates with 1, 10, 20 or 50 seed(s). Ten replicates could not be accomplished for all species, due to low seed numbers (Appendix 5). Seed width and seed length was calculated by measuring ten individual seeds of each species, using a measuring ocular. Seeds were classified according to six dummy variables, hook, hair/bristle, awn, pappus, wing and shape (0= round, 1= not round). A seed was categorised as round if 'seed length/seed width < 2', and if the seed was considered not to be flat. Seeds could be described by several variables, taking into account that many seeds have more than one appendage type, e.g. *Geum rivale* that is both hooked and haired (Table 2). Plant heights were the mean calculated from the minimal and maximal values given by Lid et al. (1994).

2.5 Detachment

A detachment experiment was carried out in August and September 2005, in order to examine how long different seeds can stay attached to fox fur. The experiment was performed in two separate locations, in a grazing meadow and in a forest habitat. Methodology was the same in both sites, but fewer species were tested in the forest habitat. Seeds used in the experiment were primarily collected from local plant populations, but some species were acquired from commercial seed suppliers.

Seed retention efficiency was tested for four distances, i.e. 10 m, 50 m, 100 m and 500 m. The experiment was separated into four groups of eight species (Table 1). All species were walked each distance six times. Four species with ten seeds each were attached to the dummy at a time and walked a given distance. The species of each walk was chosen by randomisation, as was the order of distances walked. The design of the experiment is shown in Appendix 2. Walks were only carried out when vegetation was dry.

Seeds were attached to only one side of the dummy, with a dropping distance of 5 cm. Seeds touching other seeds were relocated, in order to make each seed independent with respect to detachment. Walking speed was the same as in the attachment study, about 3 km/h, and different paths were taken each time to avoid trampling of the vegetation. After each distance had been walked, the remaining seeds were removed as discussed in Section 2.3.1, and counted at the study location.

Table 1 Species used in the detachment study. G = grazing meadow. F= forest habitat. Observers were Silje Borvik (S.B.), Knut Anders Hovstad (K.A.H.) and Anveig Nordtug Wist (A.N.W.). All experiments were carried out in August and September 2005.

Group	Observers	Date	Species
G1	K.A.H. & A.N.W.	15.08-19.08	Ranunculus acris, Geum rivale, Rumex acetosa, Cirsium palustre, Festuca rubra, Anthoxanthum odoratum, Agrostis capillaris, Carex pallescens.
G2	S.B	30.08-01.09	Luzula multiflora, Bistorta vivipara, Prunella vulgaris, Leucanthemum vulgare, Phleum pratense, Vicia cracca, Rhinanthus minor, Deschampsia cespitosa.
G3	K.A.H. & A.N.W.	02.09-07.09	Trifolium pratense, Trifolium arvense, Pimpinella saxifraga, Anthriscus sylvestris, Knautia arvensis, Dactylis glomerata, Agrimonia eupatoria, Centaurea scabiosa.
F	S. B.	09.09-12.09	R. acetosa, L. multiflora, B. vivipara, L. vulgare, R. minor, G. rivale, A. odoratum

2.6 Statistics

Only parametric tests were used in this thesis, but specific methods were applied to adjust for heterogeneous variances and non-normal distributions. For all statistical analysis, SAS 9.1.3 was used, and all graphs were produced using Sigmaplot 9.0.

2.6.1 Attachment

The thirty plots from the vegetation analysis were considered restricted random sampling plots, treating the meadow as a homogenous unit (Appendix 6). Dispersal efficiency for seeds (Q_{SEED}) was defined as number of seeds found in the fur divided by seed availability (1000 seeds m^{-2}). Dispersal efficiency for ramets (Q_{RAMET}) was defined as number of seeds found in the fur divided by ramet availability (ramets m^{-2}). The transformation $\log_{10}(y+1)$ were used to normalise the distributions of Q_{SEED} and Q_{RAMET}, and log-transformed values are from now on referred to as log Q_{SEED} and log Q_{RAMET}.

Statistical testing was only preformed on log Q_{SEED}. Log Q_{SEED} was approximately normal distributed, but with unequal variances in the different species. To account for heterogeneity of variance, differences in log Q_{SEED} between species were analysed in a weighted ANOVA using PROC MULTTEST to model the variance within each species as described by Westfall et al. (1999). Degrees of freedom for the error term were determined by the Satterthwaite approximation (Westfall et al. 1999). P-values of multiple comparisons between species were corrected using PROC MULTTEST (SAS 2004), to a false discovery rate of less than 5 % (Westfall et al. 1999). The false discovery rate is a useful multiple comparison procedure in situations with a large number of comparisons where the more common Tukey and Bonferroni procedures have very low power (Verhoeven et al. 2005).

2.6.2 Attachment model

The relation between attachment and plant and seed traits was analysed in a robust regression using the Huber M-estimator and PROC ROBUSTREG (SAS 2004). The relations between the response variable log Q_{SEED} and explanatory variables were assumed linear, and the analysis was restricted to eight main effects (plant height, seed weight, hook, hair/bristle, awn, pappus, wing and shape) to avoid overfitting. Model simplification followed the procedure described by Crawley (2002). With this method, simplification from the full model proceeds via stepwise removal and re-insertion until a minimal adequate model containing only significant terms ($P<0.05$) remains.

2.6.3 Detachment

Detachment data were analysed as two distinct datasets since 'observer' seemed to decide a considerable part of the variation between species (see results Figure 9 and 11); dataset 1 with the species from groups G1 and G3 (Table 1), and dataset 2 with species from groups G2 and F (Table 1).

Detachment was recorded as the proportion of ten initially attached seeds remaining on dummy after a given distance. Proportionate data like these are best analysed in a generalised linear model (GLM) with a binomial error distribution and a logit link function (Crawley 2002), which ensures that predicted proportions can not be greater than one or less than zero. Species, distance and the interaction, were included as independent variables, and the model was analysed using PROC GENMOD (SAS 2004). The contribution of the main effects and the interaction to model fit were tested by likelihood ratio tests. To account for overdispersion, deviance was used as a scale parameter and F-tests were used rather than chi-square tests (Crawley 2002). Multiple comparisons to find differences between species followed the same procedure as in Section 2.6.1.

2.6.4 Detachment model

A GLM (see Section 2.6.3 for details) was used to explore whether different variables could predict the probability of a seed staying attached to the dummy. Type 3 analysis was used due to an unbalanced number of observations in each group. The relations between the response variable 'proportion of seeds remaining on the dummy' and explanatory variables were assumed linear, and the analysis was restricted to eight main effects (distance, seed weight, hook, hair, awn, pappus, wing and shape) to avoid overfitting. Model building followed the same procedure as in the regression model for attachment (Section 2.6.2). Due to the logit link function, the predicted y given by direct insertion into the model has to be back-transformed using the transformation '1/(1+ (1/e^y))' (Crawley 2002).

2.6.5 Seed retention in different habitats

A two-way ANOVA was used to test whether seed retention differed between grazing meadow and forest habitat for the species in dataset 2. Interaction effects between habitat and species and between habitat and distance were also tested.

3 RESULTS

3.1 Pilot study

The general trend was a decrease in number of attached seeds with increasing distance walked, and all species in the pilot study had a minimum of 50 % of the seeds remaining after 200 m (Figure 6). However, six out of seven study species showed an increase in number of seeds remaining between some distances. This was in particular the case between the two shortest distances (Figure 6, Appendix 7). Moreover, on several occasions, seeds of different species than applied for a given walk were found on the dummy. Taken together, this showed that seeds remained on the dummy for larger periods than intended, and it also showed the need for more thorough searches for seeds in the fur between each replicate walk. In addition, stochastic variations due to small sample sizes may be the reason for some of observed increase. To avoid this kind of "increase" effect in the attachment and detachment studies, I consequently used larger sample sizes and searched the fur more thoroughly.

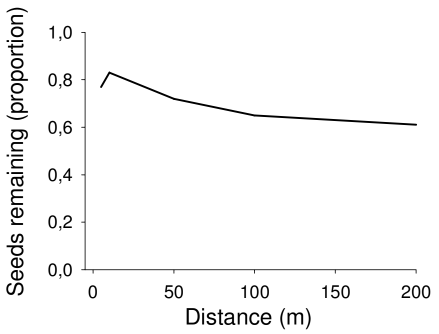

Figure 6 Proportion of seeds remaining on fox dummy after walks of 5m, 10m, 50m, 100 m and 200 m. The graph shows the general trend for all seven species of the pilot study combined.

Soaked *P. lanceolata* had a flatter detachment curve and a larger number of seeds remaining after 50, 100 and 200m than all other species (Appendix 7). *F. rubra* had the fewest number of seeds remaining after 200m (Appendix 7).

3.2 Attachment study

3.2.1 Plant species and seed numbers on dummy

In total, 34 species with seeds were observed in the vegetation plots. A total of 4500 seeds from twenty of these species were found on the fox dummy (Table 2). A few species contributed the majority of the seeds, while most species attached only a small amount of seeds to the dummy (Figure 7). Most of the attached seeds were from the Poaceae, with *D. cespitosa* contributing 84.2 %, followed by *A. capillaris* with 6.2 % (Table 2). Of the non-poaceaeous species, *Rumex acetosa* and *Ranunculus acris* had the largest number of seeds found on the dummy, 2.9 % and 1.9 %, respectively (Table 2). Only one seed of the species *B. vivipara* and *Viola canina* were found attached to the dummy (Table

2). Fourteen of the fertile species on the study meadow, including *T. pratense* and *K. arvensis*, did not attach seeds to the dummy (Table 2).

Table 2 Characteristics of fertile species found in transects at the hay meadow. 'Seeds on dummy' are the total number of seeds found on dummy after ten replicate walks. The number of walks of which a species was found is also given. Whether a species was over- or underrepresented on dummy compared to seed availability in meadow is indicated by +/-. 'Plant height' is the mean value given by Lid et al. (1994). All other characteristics were found by counting and measuring seeds found in the hay meadow. Seeds were classified according to six variables; hook, hair/bristle, awn, pappus, wing and shape (0= round, 1= not round). *Leucanthemum vulgare* was divided into two groups, small (s) and large (l) seeds. (a) Species found on dummy. (b) Species not found on dummy.

Species	Seed found on dummy	Found in no. walks	+/-	Plant height (cm)	Seed weight (mg)	Hook	Hair	Awn	Pappus	Wing	Shape
(a) Species found on dummy											
Agrostis canina	16	6	-	40	0.07	0	0	1	0	0	1
Agrostis capillaris	281	10	-	47.5	0.09	0	0	0	0	0	1
Anthoxanthum odoratum	35	8	+	30	0.61	0	1	1	0	0	1
Bistorta vivipara	1	1	-	17.5	3.93	0	0	0	0	0	0
Carex pallescens	72	10	-	40	1.08	0	0	0	0	0	1
Carex panicea	4	4	-	35	2.47	0	0	0	0	0	0
Cirsium palustre	4	3	-	125	1.16	0	0	0	1	0	1
Deschampsia cespitosa	3709	10	+	70	0.26	0	1	0	0	0	1
Festuca ovina	25	6	+	27.5	0.40	0	0	1	0	0	1
Festuca rubra	5	4	-	45	1.12	0	0	1	0	0	1
Geum rivale	40	6	+	30	1.00	1	1	0	0	0	1
Leucanthemum vulgare (s)	8	1	+	45	0.33	0	0	0	0	0	1
L. vulgare (l)	1	1	+	45	0.82	0	0	0	0	0	1
Luzula multiflora	58	9	-	30	0.42	0	0	0	0	0	0
Nardus stricta	4	3	-	22.5	0.68	0	0	1	0	0	1
Poa pratensis	3	2	-	55	0.32	0	1	0	0	0	1
Potentilla erecta	5	4	-	20	0.42	0	0	0	0	0	0
Ranunculus acris	87	10	+	47.5	1.11	1	0	0	0	0	1
Rhinanthus minor	10	4	-	20	1.66	0	0	0	0	0	1
Rumex acetosa	131	10	-	50	0.90	0	0	0	0	1	1
Viola canina	1	1	-	12.5	0.66	0	0	0	0	0	0
(b) Species present in transects, but not found on dummy											
Achillea millefolium	0	0	-	35	0.13	0	0	0	0	0	1
Achillea ptarmica	0	0	-	40	0.17	0	0	0	0	0	1
Carex nigra	0	0	-	30	0.63	0	0	0	0	0	1
Cirsium helenioides	0	0	-	100	1.76	0	0	0	1	0	1
Galium boreale	0	0	-	27.5	0.76	1	0	0	0	0	0
Galium uliginosum	0	0	-	22.5	0.17	0	0	0	0	0	0
Hieracium umbellatum	0	0	-	42.5	0.38	0	0	0	1	0	1
Hypericum maculatum	0	0	-	60	0.02	0	0	0	0	0	1
Knautia arvensis	0	0	-	55	5.31	0	1	0	0	0	1
Phleum pratense	0	0	-	70	0.65	0	0	0	0	0	0
Prunella vulgaris	0	0	-	15	0.56	0	0	0	0	0	0
Solidago virgaurea	0	0	-	52.5	0.17	0	0	0	0	0	1
Trifolium pratense	0	0	-	32.5	1.99	0	1	0	0	0	1
Vicia cracca	0	0	-	50	10.50	0	0	0	0	0	0

The dispersal unit found in the fur was not always a single seed. *A. capillaris* and *L. multiflora* were frequently found with small branches and flower heads.

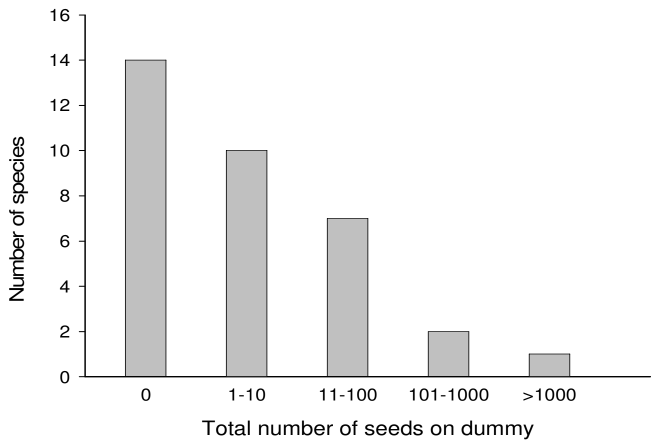

Figure 7 Number of species with 0, 1-10, 11-100, 101-1000 and >1000 seeds found on dummy after ten repeats.

3.2.2 Attachment efficiency of different species

The species found on the fox dummy differed significantly in attachment efficiency (F=43.5, DF=21.3, P<0.001) (Figure 8a and 8b, Table 3). Adjusting for number of fertile ramets and adjusting for number of seeds in the vegetation, gave somewhat different sequences of species (Figure 8a and 8b). *D. cespitosa* showed the highest attachment efficiency (Figure 8a and8b, Table 3 and 4). Of the species that did attach to the fox dummy, *B. vivipara* and *V. canina*, which only contributed with one seed each, had the lowest attachment efficiency (Figure 8a and 8b, Table 3 and 4). *D. cespitosa* attached 3709 seeds to the dummy, while *Festuca ovina* and G. *rivale* contributed with only 25 and 40 seeds, respectively. However, 'seeds/ramet' and 'ramet/m^2' differed greatly between the species found on the meadow (Appendix 3), and when adjusted for number of seeds available in the vegetation, no difference was found between *D. cespitosa* and the two species (*F. ovina*: F=0.68, DF=9.33, P=0.64) (*G. rivale*: F=0.71, DF=9.33, P=0.63) (Appendix 8). The results for some species, e.g. *G. rivale* and *L. vulgare*, were considerably more variable than for the other species, resulting in few significant differences when compared with other species (Appendix 8).

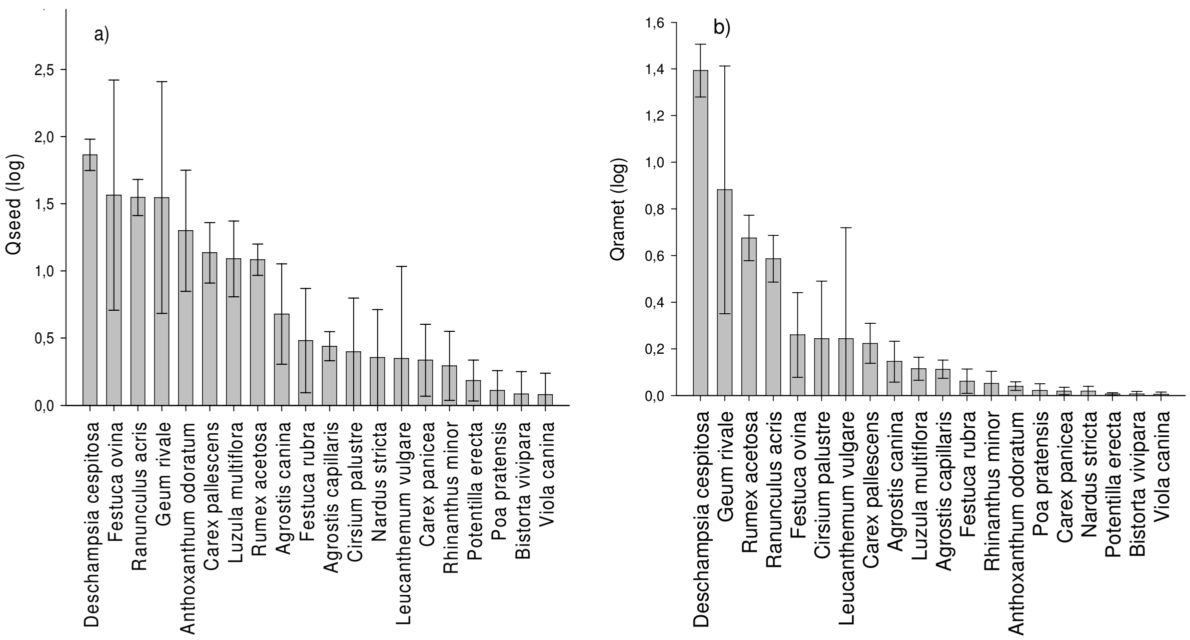

Figure 8 Histograms of Q_{SEED} and Q_{RAMET} for the species found on dummy in the attachment experiment. Q-values represent the attachment efficiency of the different species (mean ± 95CI, *n*=10). (a) Attachment efficiency in relation to the number of seeds in the vegetation, log Q_{SEED}. (b) Attachment efficiency in relation to the number of fertile ramets in vegetation, log Q_{RAMET}.

Table 3 Seed attachment efficiency, Q_{SEED}, for species found on dummy. Q_{SEED} is the number of seeds found on dummy divided by seed density in the vegetation (1000 seed m^{-2}). The log-values for Q_{SEED} are given in mean value. Mean, SE mean, median, minimum and maximum values are given for the non-transformed Q_{SEED}-values.

Species	Log Q_{SEED}	Mean	SE mean	Min	Max	Median
Agrostis canina	0.7	8.3	2.7	0.0	20.7	7.8
Agrostis capillaris	0.4	2.0	0.4	0.5	4.4	1.6
Anthoxanthum odoratum	1.3	38.2	9.1	0.0	76.4	43.6
Bistorta vivipara	0.1	0.6	0.6	0.0	6.1	0.0
Carex pallescens	1.1	17.0	4.1	2.4	40.1	13.0
Carex panicea	0.3	2.4	1.0	0.0	5.9	0.0
Cirsium palustre	0.4	6.4	3.6	0.0	32.1	0.0
Deschampsia cespitosa	1.9	78.4	10.8	38.3	131.3	61.3
Festuca ovina	1.6	349.2	150.5	0.0	1257.2	139.7
Festuca rubra	0.5	6.2	2.8	0.0	25.0	0.0
Geum rivale	1.5	537.3	391.9	0.0	4029.6	134.3
Leucanthemum vulgare	0.3	311.6	311.6	0.0	3116.0	0.0
Luzula multiflora	1.1	16.4	4.2	0.0	45.3	12.8
Nardus stricta	0.4	4.5	2.5	0.0	22.6	0.0
Poa pratensis	0.1	0.5	0.4	0.0	3.6	0.0
Potentilla erecta	0.2	0.8	0.4	0.0	3.1	0.0
Ranunculus acris	1.5	38.3	6.3	13.2	74.8	33.0
Rhinanthus minor	0.3	2.1	1.2	0.0	10.7	0.0
Rumex acetosa	1.1	12.1	1.7	3.7	25.0	12.5
Viola canina	0.1	0.5	0.5	0.0	5.4	0.0

Table 4 Ramet dispersal efficiency, Q_{RAMET}, for species found on dummy. Q_{RAMET} is the number of seeds found on dummy divided by ramet density in the vegetation (ramets m^{-2}). The log-values for Q_{RAMET} are given in mean value. Mean, 1SE of the mean, median, minimum and maximum values are given for the non-transformed Q_{RAMET} values.

Species	Log Q_{RAMET}	Mean	SE	Min	Max	Median
Agrostis canina	0.1	0.5	0.2	0.0	1.2	0.4
Agrostis capillaris	0.1	0.3	0.1	0.1	0.7	0.2
Anthoxanthum odoratum	0.0	0.1	0.0	0.0	0.2	0.1
Bistorta vivipara	0.0	0.0	0.0	0.0	0.1	0.0
Carex pallescens	0.2	0.8	0.2	0.1	1.8	0.6
Carex panicea	0.0	0.0	0.0	0.0	0.1	0.0
Cirsium palustre	0.2	1.7	0.9	0.0	8.6	0.0
Deschampsia cespitosa	1.4	25.8	3.5	12.6	43.1	20.1
Festuca ovina	0.3	1.3	0.5	0.0	4.6	0.5
Festuca rubra	0.1	0.2	0.1	0.0	0.7	0.0
Geum rivale	0.9	40.0	29.2	0.0	300	10.0
Leucanthemum vulgare	0.2	27.0	27.0	0.0	270	0.0
Luzula multiflora	0.1	0.3	0.1	0.0	0.9	0.3
Nardus stricta	0.0	0.0	0.0	0.0	0.2	0.0
Poa pratensis	0.0	0.1	0.0	0.0	0.4	0.0
Potentilla erecta	0.0	0.0	0.0	0.0	0.1	0.0
Ranunculus acris	0.6	3.1	0.5	1.1	6.1	2.7
Rhinanthus minor	0.1	0.1	0.1	0.0	0.7	0.0
Rumex acetosa	0.7	4.0	0.6	1.2	8.3	4.1
Viola canina	0.0	0.0	0.0	0.0	0.1	0.0

3.2.3 Regression model for attachment

The minimal adequate model for attachment included ‘hook’, ‘hair’, ‘awn’ and ‘wing’ as significant explanatory parameters (Table 5). The non-significant parameters ‘plant height’, ‘seed weight’, ‘shape’ and ‘pappus’ were excluded from the model.

Table 5 Parameter estimates for the minimal adequate model for attachment. The relation between attachment and plant and seed traits was analysed using robust regression.

Parameter	Estimate	95% confidence limit	χ^2	P-value
Intercept	0.1433	0.0688 – 0.2177	14.22	0.0002
Hook	0.7072	0.4872 – 0.9273	39.68	<0.0001
Hair	0.3285	0.1661 – 0.4909	15.71	<0.0001
Awn	0.5410	0.3662 – 0.7158	36.78	<0.0001
Wing	0.9412	0.5758 – 1.3065	25.49	<0.0001
Scale	0.6110			

3.3 Detachment study

3.3.1 Seed retention in grazing meadow

Species and their characteristics are given in Tables 1, 2 and 6. Seed retention differed significantly between the species ($F_{15, 320}$= 18.2, P<0.0001) (Appendix 9), and between distances ($F_{3, 320}$= 98.8, P<0.0001). The response among the species did not differ significantly at different distances (interaction species x distance, $F_{45, 320}$= 1.2, P=0.22).

Table 6 Seed characteristics for six of the species tested in the detachment experiment. Seeds were classified according to six variables; hook, hair/bristle, awn, pappus, wing and shape (0= round, 1= not round). Characteristics are taken from literature (Grime et al. 1988; Peat & Fitter 2005; Romermann et al. 2005). Characteristics for the other species used in the detachment experiment are shown in Table 2.

Species	Seed weight (mg)	Hook	Hair	Awn	Pappus	Wing	Shape
Agrimonia eupatoria	22.1	1	1	0	0	0	0
Anthriscus sylvestris	4.68	0	0	0	0	0	1
Centaurea scabiosa	7.5	0	0	0	0	0	0
Dactylis glomerata	0.51	0	0	1	0	0	1
Pimpinella saxifraga	1.20	0	0	0	0	0	0
Trifolium arvense	0.39	0	1	0	0	0	1

Trifolium arvense, *Agrimonia eupatoria* and *G. rivale* had the best seed retention after 500 meters (Figure 9 and 10). All three species had haired and/or hooked appendages, but there were large weight variations between the species. However, the haired seeds of *K. arvensis* had the poorest seed retention of all species on all distances (Figure 10, Appendix 9). The two species with pappus, *Cirsium palustre* and *Centaurea scabiosa*, showed intermediate seed retention efficiency (Figure 9 and 10), and differed significantly both from the species with highest seed retention efficiency and from the species with the lowest seed retention efficiency (Appendix 9). *R. acetosa* was the only species in the study with a winged appendage and had intermediate seed retention efficiency (Figure 9 and 10, Appendix 9).

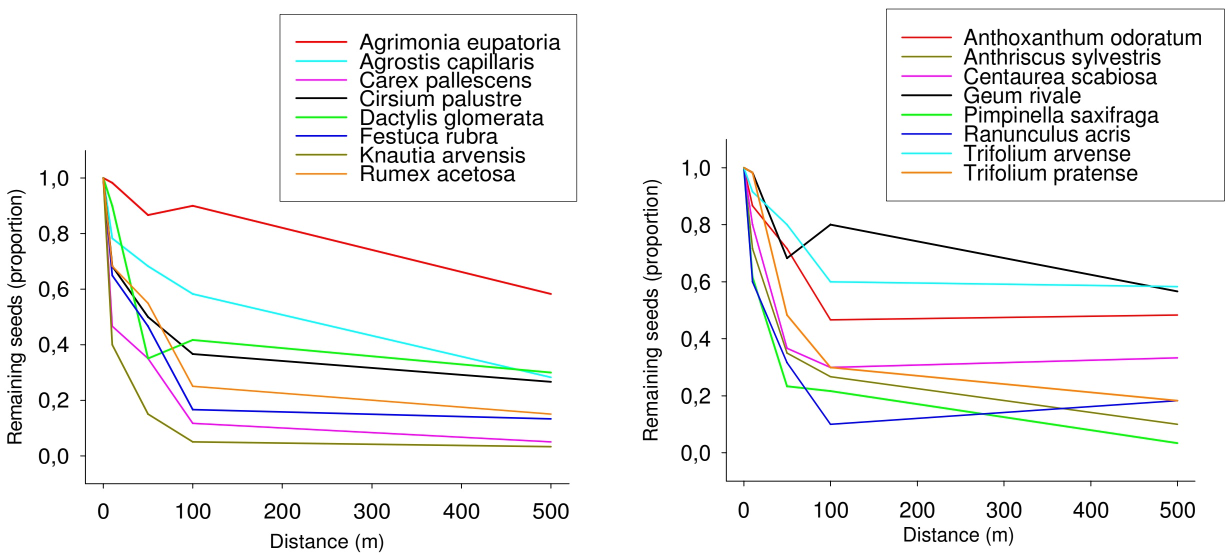

Figure 9 Mean number of seeds remaining after distances 10 m, 50 m, 100 m and 500 m for the 16 species examined in dataset 1 of the detachment experiment.

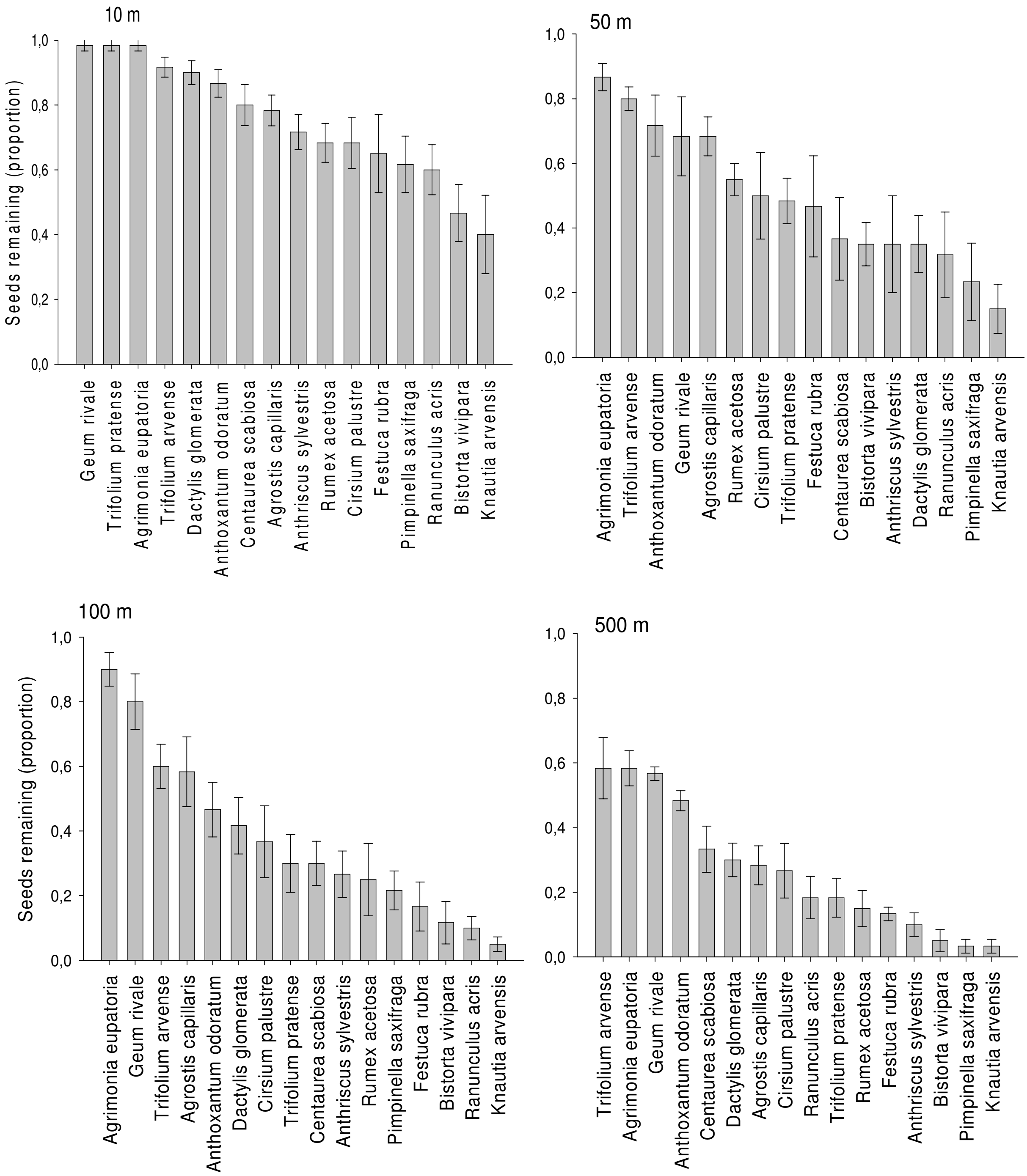

Figure 10 Seeds remaining after 10 m, 50m, 100m and 500m in grazing meadow, for the 16 species of dataset 1 (mean ± 1SE, *n*=6).

3.3.2 Detachment model

The minimal adequate model for detachment included ‘distance’, ‘hook’, ‘hair’, ‘awn’ and ‘pappus’ as significant explanatory parameters (Table 7). The non-significant parameters ‘seed weight’, ‘shape’ and ‘wing’ were excluded from the model.

Table 7 Minimal adequate model for detachment. The proportion of ten initially attached seeds remaining on dummy after a given distance, were analysed in a generalised linear model with a binomial error distribution and a logit link function. The set of explanatory variables were tested by likelihood ratio tests using the F statistic to find the minimal adequate model with 376 degrees of freedom. Distance is a class variable with four levels and '500 m' as baseline. Deviance was used as a scale parameter to account for overdispersion. Due to the logit link function, the predicted y given by direct insertion into the model has to be back-transformed using the transformation '1/(1+ (1/e^y)).

Parameter	Estimate	95% confidence limit	F-statistic	P-value
Intercept	-1.759	-2.089 – -1.428		
Hook	0.824	0.474 – 1.174	21.65	<0.001
Pappus	0.595	0.188 – 1.002	8.15	0.0043
Hair	0.944	0.663 – 1.225	44.56	<0.001
Awn	0.473	0.135 – 0.811	7.52	0.0061
Distance			59.33	<0.001
10 m	2.283	1.901 – 2.665		
50 m	1.059	0.704 – 1.413		
100 m	0.512	0.153 – 0.860		
500 m (baseline)	0			
Scale	1.778			

3.3.3 Seed retention in different habitats

Seed retention did not differ significantly between the species ($F_{3, 160}$= 1.9, P= 0.127), but a highly significant difference was found between the habitats ($F_{1, 160}$= 157.1, P<0.001), with grazing meadow providing better seed retention than forest habitat (Figure 11). Difference in seed retention between the two habitats increased with increasing distance (interaction habitat x distance, $F_{3, 160}$=16.2, P<0.001), and the response among the species did not differ significantly between the habitats (interaction species x habitat, $F_{3, 160}$= 2.3, P=0.078).

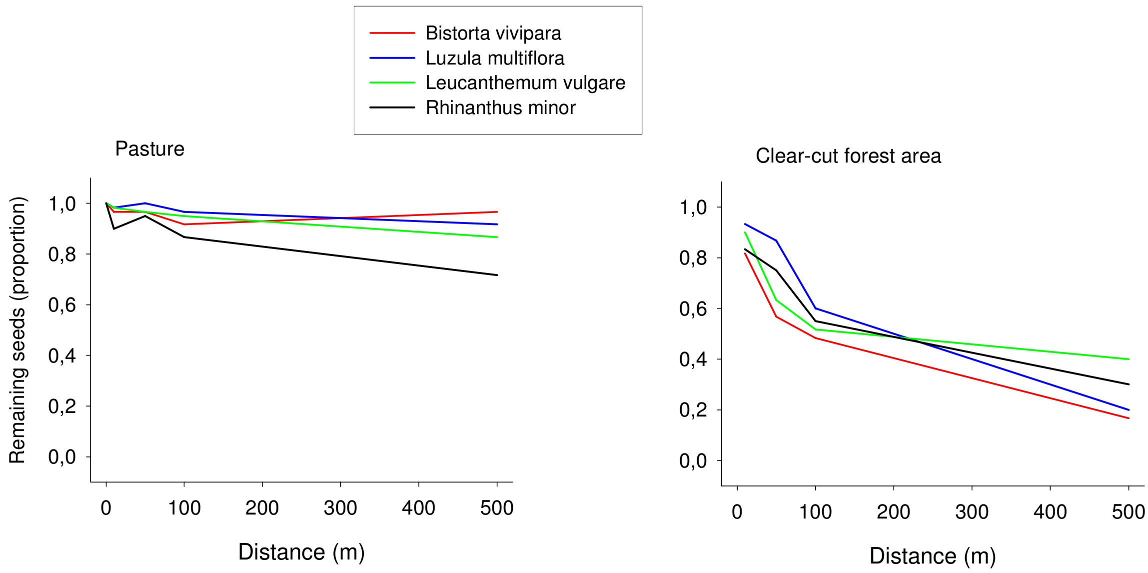

Figure 11 Mean number of seeds remaining attached to the fox dummy after distances 10 m, 50 m, 100 m and 500 m, for *B. vivipara*, *L. vulgare*, *L. multiflora* and *R. minor* in grazing meadow (pasture) and forest habitat.

4 DISCUSSION

I draw four main conclusions from my study:

1. Red fox fur provided epizoochorous seed dispersal for species in the cultural landscape.
2. The parameters 'hook', 'hair', 'awn' and 'wing' gave the best model to predict seed attachment to fox fur.
3. The parameters 'distance', 'hook', 'hair', 'awn' and 'pappus' gave the best model to predict seed retention in fox fur.
4. Seed retention efficiency by red fox was habitat-specific.

4.1 Seed attachment to fox dummy

A total of 4500 seeds from 20 different species were found on the fox dummy after ten replicate walks of 52 m each. My study supports the view that the majority of the seeds getting attached to animal fur typically belongs to a small number of plant species (Agnew & Flux 1970; Constible et al. 2005; Couvreur et al. 2005a). Fisher et al. (1996) observed that most of the attached seeds to sheep (*Ovis aries*) belonged to the Poaceae, which was also the case in my study. The small and hairy seeds of the grass *D. cespitosa* contributed with only 19.1 % of seed availability in my study meadow, but with as much as 82.4 % of the seeds found on the fox dummy. Seeds of *D. cespitosa* seem to be well adapted for epizoochorous seed dispersal by medium-sized mammals, as this species previously have been found in abundance on shot roe deer (*Capreolus capreolus*), shot wild boar (*Sus scrofa*) and on a domestic dog (*Canis lupus familiaris*) (Graae 2002; Heinken & Raudnitschka 2002; Heinken et al. 2006). In addition to *D. cespitosa*, only five species were overrepresented in the fur compared to seed availability in the meadow (Table 2). Of these, *L. vulgare* was the only one that lacked hooks, hairs or awns, suggesting that such appendages greatly improve seed attachment efficiency. Even though the smooth-seeded *A. capillaris* had the second-largest amount of seeds on the dummy, this species was greatly underrepresented compared to seed availability (Table 2, Appendix 3).

Graae (2002) compared the number of seeds found on a German Wirehaired Pointing dog with the number of ramets in the vegetation, but not with the number of available seeds. As seed number per ramet can vary greatly within and among species (Appendix 3), and because the difference between Q_{SEED} and Q_{RAMET} may be substantial, it is necessary to know the number of available seeds in the vegetation to make a realistic estimate of the dispersal efficiency of a given animal (Table 3 and 4, Figure 8a and 8b). In addition to my study, the study by Mouissie et al. (2005) is, to my knowledge, the only other assessment of epizoochorous seed dispersal in relation to seed availability. Mouissie et al. (2005) found that the seeds of *Nardus stricta* attached best to the sheep- and cattle (*Bos taurus*) dummies, followed by *F. ovina* and *F. rubra*. In my study, however, *N. stricta* attached quite few seeds to the dummy, and had lower seed attachment efficiency than both *F. ovina* and *F. rubra* (Figure

8a). The discrepancy between my study and the study by Mouissie et al. (2005) may be due to patchiness of species in the vegetation, different seeds ripening processes at different study locations or properties of the dummies.

Fischer et al. (1996) found that pace of movement, as well as the period of movement, had a great influence on the number of seeds as well as which species that attached on the dummy. A real fox would therefore maybe be able to get more species attached in the fur than would the fox dummy. However, red fox behaviour, e.g. grooming and movement pattern, may reduce the number of seeds found on real foxes compared to what was found on the fox dummy (Sorensen 1986).

4.2 Plant/seed characteristics and seed dispersal

Adhesive structures such as hooks, hairs and awns improved the chance of a species getting and staying attached to the fox fur (Table 5 and 7). A number of studies have observed that seeds with adhesive structures are among the best retained in animal coats (Kiviniemi & Eriksson 1999; Graae 2002; Heinken & Raudnitschka 2002; Romermann et al. 2005; Tackenberg et al. 2006).

Seeds with pappus, generally assumed wind-dispersed, showed intermediate retention efficiency on the fox dummy (Table 7, Figure 9 and 10). Kiviniemi and Eriksson (1999) observed that a species with pappus, *Hieracium pilosella*, retained just as well in cattle fur as the hooked and haired seeds of *G. rivale*. I found no relationship between pappus and seed attachment efficiency (Table 5), but seeds of *C. palustre* were found on fox dummy on several walks (Table 2). The idea that seeds are exclusively dispersed by the one single process they are supposed to be morphologically adapted for, has been rejected by Higgins et al. (2003). My results showing that several species without appendages/adaptations for epizoochorous seed dispersal, e.g. *A. capillaris*, *Carex pallescens* and *L. multiflora* (Table 2), were found in the fox fur, clearly support the view by Higgins et al. (2003). Several authors conclude that almost all plant species can be transported epizoochorously, and that a binary classification of seeds dispersal in animal furs is artificial since differences in seed attachment are gradual (Fischer et al. 1996; Couvreur et al. 2004b; Tackenberg et al. 2006). Thus, seeds without adhesive structures may be dispersed on the coats of animals, but probably only rarely. This seems true for the smooth- and round-seeded *B. vivipara* and *V. canina,* which had the lowest attachment efficiency of all species found on the dummy, with only one seed getting attached (Table 2 and Figure 8a and 8b). Seeds of *A. capillaris* and *L. multiflora* were frequently found in flower heads and branches on the dummy. Several authors have observed the same for some plant species, including *A. capillaris* (Graae 2002; Mouissie et al. 2005). Branches and flower heads that are easily detached from the parent plant can probably act as appendages, increasing the epizoochorous dispersal efficiency of smooth-seeded species.

I found no relationship between seed weight and attachment- and retention efficiency (Table 5 and 7), however several studies have observed such negative relationships (Romermann et al. 2005; Tackenberg et al. 2006). Contrary to these authors, Couvreur et al. (2005b) found seed weight to be positively correlated with retention in fur of Galloway cattle. Other studies have found little difference between small and large seeds in attachment- and retention efficiency (Graae 2002; Takahashi & Kamitani 2004; Mouissie et al. 2005). The seed size of a species represents the amount of maternal investment in an individual offspring, with larger seeds giving more vigorous seedlings (Howe & Westley 1997; Leishman et al. 2000). Normally there will be a trade-off between seed dispersal distances and seed weight, with larger seeds resulting in shorter dispersal distances (Augspurger 1986; Howe & Westley 1997). However, selection for large seeds may bring with it selection for altered dispersal devices that compensate for the reduced attachment efficiency, and this can blur the negative effects of weight (Willson & Traveset 2000). Several authors have found that even though small seeds are more efficiently transported than larger seeds, large seeds carrying appendages can still remain attached to animal furs for considerable periods (Kiviniemi & Telenius 1998; Couvreur et al. 2004b). A fundamental trade-off between seed number and seed size is generally assumed. However, dispersal of a few large seeds may be more efficient than dispersal of many small seeds, due to better recruitment potential of the larger seeds (Turnbull et al. 1999; Jakobsson & Eriksson 2000). Hence, despite possible differences in attachment efficiency, the dispersal- and recruitment success might be comparable for large- and small-seeded species (Romermann et al. 2005).

There was no relationship between seed shape and attachment- and retention efficiency in my study (Table 5 and 7). Tackenberg et al. (2006) found a significant effect of seed shape in regards of seed retention in sheep fleece, but found no such effect in cattle hair. Romermann et al. (2005) detected no such relationship between seed shape and attachment efficiency. Seed shape is not defined similarly in all studies, this discrepancy in parameter classification may account for some of the variation between studies. However, coats of some animals may allow attachment of seeds that would not get attached on other animals (Romermann et al. 2005; Tackenberg et al. 2006).

I found no relationship between plant height and attachment efficiency (Table 5). It may seem somewhat surprising that low-growing species such as *P. erecta* and *V. canina* were able to attach seeds to the dummy (Table 2). However, all species found on the studied meadow can reach a maximal height of at least 20 cm (Lid et al. 1994), enabling contact with the fox fur (see Figure 4). Seeds from plants taller than the fox dummy (>30 cm) may have fallen on the back of the dummy due to shaking of the plant. Mouissie et al. (2005) detected a negative relationship between plant height and seed attachment, while other studies have found a positive association (Fischer et al. 1996; Graae 2002). Vector species and vector behaviour seem to be of prime importance for determining how tall plants must be for achieving effective seed dispersal.

In the attachment experiment, a distance of 52 meters was walked before seeds were removed from the fox fur and counted. Epizoochorously dispersed seeds are picked up and dropped within every meter moved by the vector, and in uniform monocultures a dynamic equilibrium will soon establish between loading and loss of seeds (Bullock & Primack 1977). A higher number of seeds than found on the end of a walk will thus achieve seed dispersal. Obviously, seeds with poor retention in fox fur drop off faster than species with good retention. In species rich stands, there will be species with good and with poor seed retention efficiency, so some species will drop more seeds off the fox fur than others do, and the differences between species in number of seeds found on the dummy will therefore increase with increasing distances. However, most seeds were found on the back of the dummy, reducing seed detachment (Fischer et al. 1996; Kiviniemi 1996; Graae 2002). The differences in seed retention for the plant species will therefore probably not determine the variations in attachment efficiency.

The minimal adequate models for predicting seed attachment and seed retention had quite large confidence intervals, leading to large errors for the predicted values (Table 5 and 7). The large confidence intervals were caused by large variations in attachment and retention efficiency for individual species within each parameter group. For example, *K. arvensis* has hairs that in general improved both attachment- and retention efficiency. However, no seeds of this species were found on the dummy in the attachment experiments (Table 2) and it had the lowest seed retention efficiency (Figure 9). It may have been to early in the season for this species to have fully mature seeds, but seed size was only marginally smaller than given by Grime et al. (1988) (Appendix 5), indicating fully grown and mature seeds. Many of the factors determining whether a plant is able to disperse its seeds epizoochorously, are probably undetectable by the human eye or hard to measure. Gorb and Gorb (2002) found functional differences in contact separation force between species with hooked appendages, and how easily a seed is detached from the parent plant can most likely explain much of the variation in seed attachment. There can also be a vast number of factors interacting to give a species a certain attachment- and retention efficiency, but such relations were not included in the statistical model due to the limited size of the dataset. The best indicator of attachment- and retention efficiency will therefore not be relatively subjective chosen parameters such as ‘hook’ or ‘hair’, but the individual species, i.e. the total combination of attributes that makes a species. However, if a species have characteristics such as hooks or hairs, the chance of becoming and staying attached increases considerably, but large variations must be expected.

The seed characteristic ‘wing’ was included in the minimal adequate model for attachment, but not in the corresponding model for detachment (Table 5 and 7). An obvious weakness of the model is that only one species in my study, *R. acetosa*, had a winged appendage. This parameter thus defines this one species and not necessarily other species with winged appendages.

4.3 Seed retention in different habitats

The grazing meadow provided better seed retention than the forest habitat, and the difference between the two habitats increased with increasing distance (Figure 11). The tall vegetation and branches in the forest area probably swept more seeds off the fox dummy than did the mere effect of movement in the grazing meadow. My results are supported by Mouissie et al. (2005), who found seed detachment to accelerate when a vector moved through vegetation. However, Couvreur et al. (2005b) did not find significant differences in seed retention between different vegetation structures in their study with horse (*Equus caballus*) and cattle. The discrepancy between studies may be due to dissimilar vegetation structures giving different dynamic equilibriums of sweeping away seeds and protecting seeds underneath hairs (Couvreur et al. 2005b). Also, unlike Couvreur et al. (2005b), all species used in my comparison of habitats, were without appendages. Seeds with appendages may get more easily entangled in the fur than seeds with such appendages, when in contact with vegetation. In addition, the forest habitat had a rougher ground surface than did the grazing meadow, making it more difficult to navigate the fox dummy smoothly. This can have lead to a bumpier ride for the seeds than a real fox would have given, thus resulting in more seeds getting detached than may have been expected.

4.4 Red fox and seed dispersal efficiency

The red fox dummy provided seed dispersal for meadow plants in the cultural landscape, this is however not synonymous with real red foxes being true seed dispersal vectors. To draw such conclusions, shot foxes need to be examined, in order to quantify the actual number of seeds that are attached in their furs. However, use of shot animals to study epizoochory have many weaknesses and would not necessarily provide a realistic picture (Heinken et al. 2006). Population sizes, habitat use, home ranges and dispersal distances of red fox, can indicate whether these animals are true epizoochorous seed dispersers.

Red fox is a widespread and abundant mammal, yet surprisingly little is known of red fox populations in Norway (Bjärvall & Ullström 1997; Frafjord 2005). A rough population estimate gives a spring population of about 50 000 animals, and an autumn population of about 120 000 animals (pers. comm. Olav Hjeljord). Meadows are frequently used by red foxes (Cavallini & Lovari 1991; Dell'Arte & Leonardi 2005), and a Finnish study documented that fox abundance was highest in landscapes with about 20-30 % agricultural land (Kurki et al. 1998). The large population sizes and habitat use of red foxes indicate that seeds, from meadows similar to the one I have examined, will have a good chance of coming in contact with fox fur.

I found that 3-58 % of attached seeds remained after 500 m walks in a grazing meadow. The seed depletion curves had leptokurtic distributions, i.e. distributions with more acute peaks around the mean, and thicker tails than the normal distribution (Kiviniemi & Eriksson 1999). The depletion curves probably had this shape because the seeds that were not well attached fell of with the first movements of the vector, while seeds that were properly attached tended to stay attached (Couvreur et al. 2004b). The tail of the depletion curves determines the long-distance dispersal of seeds, but it is difficult to measure (Sorensen 1986; Kiviniemi 1996; Bullock & Clarke 2000). The central tendency (mean) and the tail of a dispersal curve can vary independently (Cain et al. 2000), making it difficult to extrapolate the data to find potential seed dispersal distances. Nevertheless, most species in my study would probably be able to stay attached for far greater distances than the documented 500 meters. How long a seed will stay attached to a vector is dependent on several factors, including animal behaviour (Sorensen 1986; Kiviniemi & Telenius 1998; Westcott et al. 2005). I used a dummy that excluded all effects of animal behaviour. In addition, all seeds were attached to the vertical side of the dummy. If a real fox had been used or the seeds had been attached to the back of the dummy, somewhat different seed dispersal distances would be expected (Fischer et al. 1996; Kiviniemi 1996; Graae 2002).

Dispersal distances for epizoochorously dispersed seeds are dependent on how far the vector moves while retaining the seeds (Westcott et al. 2005). Maximum potential dispersal distances are thus limited by the home ranges of adult foxes and by the natal dispersal distances of juvenile foxes (Stiles 2000). Red fox home ranges can be as large as 10-20 km^2, but are in most cases smaller than 3 km^2 (Frafjord 2004). Natal dispersal can greatly increase potential seed dispersal distances. For example, Allen and Sargeant (1993) found marked foxes up to 302 km from tagging locations.

Effective seed dispersal is not only dependent on dispersal distances, but also on seed production and recruitment (Willson 1993). The presence of seeds in fox fur is not conclusive evidence of successful dispersal, because the germination ability of attached seeds are unknown and because it is unknown whether seeds will end up in suitable locations (Bruun & Fritzboger 2002; Couvreur et al. 2005a). Organisms that actively move around in the landscape and thereby increase habitat connectivity, are termed “mobile links” (Lundberg & Moberg 2003; Couvreur et al. 2004a). According to Sorensen (1986), most epizoochorous seeds do probably not achieve directed dispersal, but are rather dispersed to random habitats. Nevertheless, due to the habitat selection of the vectors, seeds caught in animal fur have a reasonable chance of getting detached in a similar habitat to that occupied by the parent plant (Kiviniemi & Eriksson 1999). Even though red foxes use a wide range of habitats, red foxes can still to some extent be regarded mobile links, dispersing seeds between fragments, since seed dispersal by wind and other mechanisms is much closer too random (Purves & Dushoff 2005).

Some species, such as *D. cespitosa*, are more efficient at achieving seed dispersal in the fur of red fox than others. Seeds with adhesive appendages on are particularly likely to be dispersed epizoochorously by red fox. Once seeds are attached to the fox, most species are able to stay in the fur for considerable distances, at least in habitats with low vegetation. I conclude that red fox should be regarded a potentially important seed disperser, enhancing the probability for plants to obtain long-distance dispersal and of reaching new habitats in fragmented cultural landscapes.

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Appendix 1 List of additional species in the hay meadow of the attachment study. (a) Species present in at least one plot, but not observed with mature seeds. (b) Species outside the plats and transects. The list may be incomplete.

(a) Species without mature seeds
Betula pubescens
Equisetum arvense
Equisetum sylvaticum
Filipendula ulmaria
Lathyrus linifolius
Mentha arvensis
Rubus idaeus
Salix aurita
Scutellaria galericulata
Sorbus aucuparia
Trifolium campestre
Vaccinium vitis-idaea
Viola palustris
(b) Species outside plots and transects
Calluna vulgaris
Campanula rotundifolia
Carex echinata
Carex flava
Carex rostrata
Centaurea jacea
Elymus caninus
Eriophorum vaginatum
Euphrasia sp.
Juncus conglomeratus
Menyanthes trifoliata
Parnassia palustris
Peucedanum palustre
Potentilla palustris
Salix myrsinifolia
Trichophorum alpinum

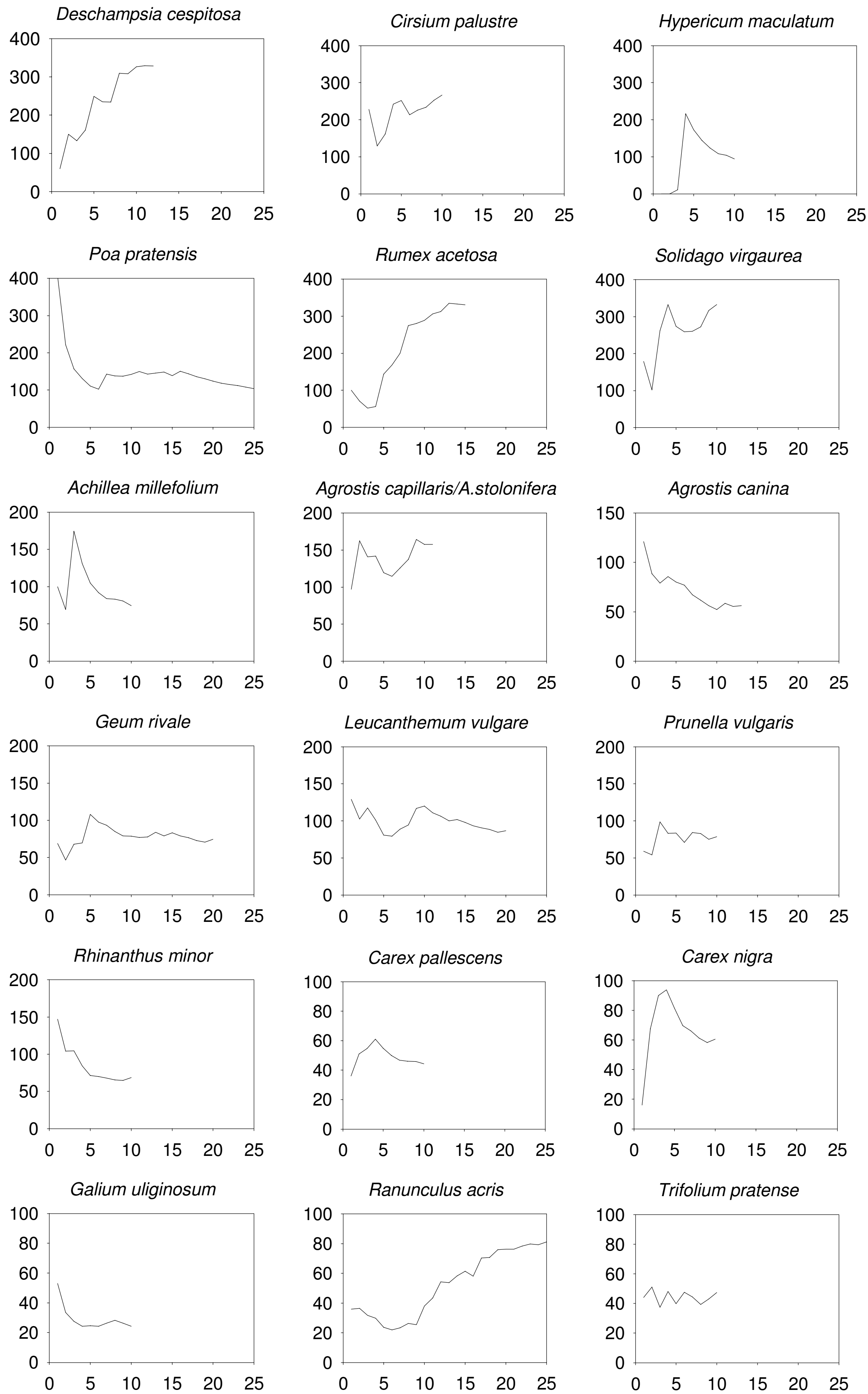
Appendix 2 The design scheme used for the four detachment groups in the detachment study. Series 3-6 follow the same pattern as shown here for series 1 and 2. The letters ‘A’ to ‘H’ represent the eight different species in each detachment group. The pilot study followed a corresponding design, only with five series and the distances 5 m, 10 m, 50 m, 100 m and 200 m.

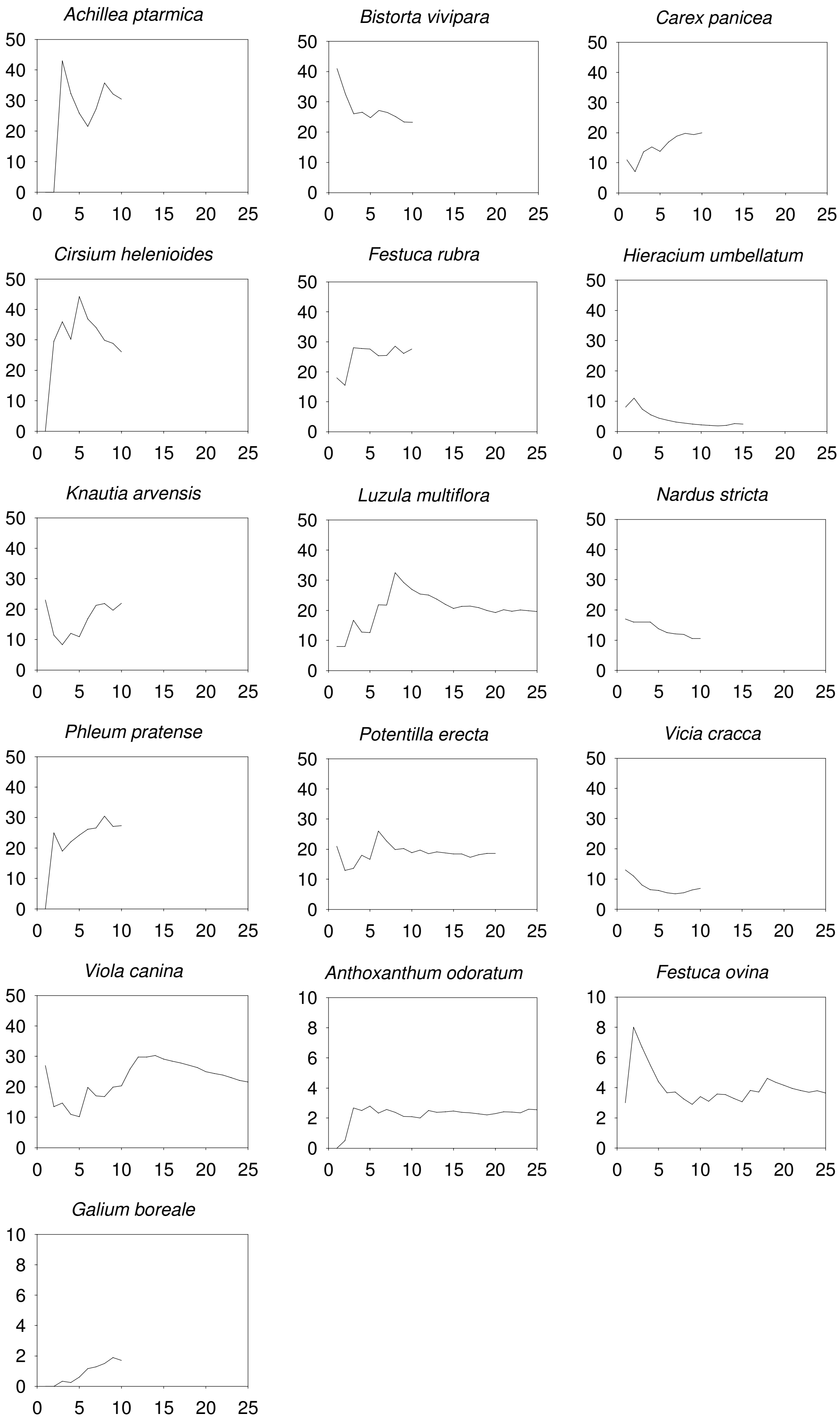
Series	Set	Distance (m)	Seeds	A	B	C	D	E	F	G	H
1	1	10	ABCF								
1	2	10	DEGH								
1	1	50	ACDE								
1	2	50	BFGH								
1	1	100	BCEF								
1	2	100	ADGH								
1	1	500	BCFG								
1	2	500	ADEH								
2	1	10	ABDG								
2	2	10	CEFH								
2	1	50	DFGH								
2	2	50	ABCE								
2	1	100	ABCG								
2	2	100	DEFH								
2	1	500	BCGH								
2	2	500	ADEF								

Appendix 3 Mean number of seeds per fertile ramet for the species found in at least one of 30 plots in the vegetation. 'N' gives the number of samples counted for each species. 'Minimum' and 'Maximum' give the lowest and highest number of seeds found in any sample. Standard error and total number of seeds counted are also given, as is the number of seeds found per m^2 in the vegetation.

Species	N	Total number of seeds counted	Seeds per ramet (mean)	SE Mean	Minimum	Maximum	Seeds in vegetation (m^{-2})
Achillea millefolium	10	745	74.5	35.970	0	385	27
Achillea ptarmica	10	304	30.4	15.118	0	129	7
Agrostis canina	13	731	56.2	11.089	10	122	193
Agrostis capillaris	11	1732	157.5	28.778	29	379	14302
Anthoxanthum odoratum	25	64	2.6	0.469	0	8	92
Bistorta vivipara	10	232	23.2	3.296	9	41	164
Carex nigra	10	604	60.4	14.384	10	135	379
Carex pallescens	10	443	44.3	5.941	26	80	424
Carex panicea	10	200	20.0	3.190	3	32	169
Cirsium helenioides	10	261	26.1	10.544	0	100	12
Cirsium palustre	10	2668	266.8	47.590	20	483	62
Deschampsia cespitosa	12	3942	328.5	63.801	60	837	4730
Festuca ovina	25	91	3.6	1.083	0	20	7
Festuca rubra	10	276	27.6	4.994	7	53	80
Galium boreale	10	17	1.7	0.578	0	5	1
Galium uliginosum	10	243	24.3	4.928	6	53	126
Geum rivale	20	1489	74.5	14.244	8	262	7
Hieracium umbellatum	15	36	2.4	1.174	0	14	0.1
Hypericum maculatum	10	938	93.8	82.377	0	832	50
Knautia arvensis	10	219	21.9	5.943	0	48	7
Lathyrus linifolius	8	0	0.0	0.000	0	0	0
Leucanthemum vulgare	20	1733	86.7	15.813	0	298	3
Luzula multiflora	25	491	19.6	4.780	0	108	353
Mentha arvensis	10	0	0.0	0.000	0	0	0
Nardus stricta	10	106	10.6	1.778	0	17	89
Phleum pratense	10	273	27.3	6.225	0	58	63
Poa pratensis	25	2592	103.7	24.153	0	406	560
Potentilla erecta	20	372	18.6	3.685	0	73	639
Prunella vulgaris	10	787	78.7	19.164	7	188	289
Ranunculus acris	25	2028	81.1	12.778	0	266	227
Rhinanthus minor	10	684	68.4	12.298	20	147	465
Rumex acetosa	15	4954	330.3	56.043	15	800	1079
Scutellaria galericulata	0	0	0	0	0	0	0
Solidago virgaurea	10	3327	332.7	72.587	24	672	11
Trifolium pratense	10	473	47.3	10.617	4	86	24
Vicia cracca	10	69	6.9	1.479	2	13	2
Viola canina	25	540	21.6	4.606	0	81	185
Viola palustris	0	0	0.0	0.000	0	0	0

Appendix 4 Species-specific relationships between sample size (horizontal axes) and the mean number of seeds per fertile ramet (vertical axes). Note different scale on the vertical axes. Continues on next page.




Achillea ptarmica
Bistorta vivipara
Carex panicea
Cirsium helenioides
Festuca rubra
Hieracium umbellatum
Knautia arvensis
Luzula multiflora
Nardus stricta
Phleum pratense
Potentilla erecta
Vicia cracca
Viola canina
Anthoxanthum odoratum
Festuca ovina
Galium boreale

Appendix 5 Seed weight. seed width and seed length of species found in the transects in the hay meadow. All values, except *Phleum pratense,* are for the complete seed dispersing unit. Two sets of values are given for *Leucanthemum vulgare* as two distinct seed sizes was found. The number of replicates measured is only given for seed weight, as number of replicates for seed width and seed length is 10 for all species. 'N' gives number of replicates, while 'm' gives number of seeds in each replicate. The lowest and highest weight/width/length found is given in the 'min' and 'max' columns. The column 'lit' gives the values found in the literature: Grime et al. (1988)[1] and Korsmo et al. (2001)[2].

	Seed Weight (mg)							Seed Width (mm)					Seed Length (mm)				
Species	m	n	Mean	SE mean	min	max	Lit	Mean	SE mean	Min	Max	Lit	Mean	SE mean	Min	Max	Lit
Achillea millefolium	10	10	0.13	0.0035	0.11	0.14	0.16[1]	0.7	0.0269	0.5	0.8	1.1[1]	1.8	0.0371	1.6	2.0	2.1[1]
Achillea ptarmica	10	10	0.17	0.0047	0.14	0.19	0.2[2]	0.9	0.0249	0.8	1.0	1[2]	1.9	0.0690	1.7	2.5	2[2]
Agrostis canina	10	10	0.07	0.0029	0.05	0.08	0.05[1]	0.4	0.0213	0.3	0.5	0.4[1]	2.3	0.1790	1.6	3.3	1.3[1]
Agrostis capillaris	20	10	0.09	0.0055	0.07	0.12	0.06[1]	0.4	0.0200	0.3	0.5	0.5[1]	1.7	0.0605	1.4	1.9	1.9[1]
Anthoxanthum odoratum	10	5	0.61	0.0478	0.50	0.79	0.45[1]	0.9	0.0394	0.8	1.1	1.3[1]	6.8	0.2970	4.7	7.8	4.3[1]
Bistorta vivipara	10	10	3.93	0.1420	3.12	4.80		2.1	0.0932	1.6	2.4		3.4	0.1360	2.7	4.1	
Carex nigra	10	10	0.63	0.0350	0.40	0.84	0.81[1]	1.4	0.0699	1.0	1.7	1.1[1]	2.1	0.0667	1.7	2.4	2.7[1]
Carex pallescens	10	10	1.08	0.0192	1.01	1.20		1.1	0.0340	1.0	1.3		3.1	0.0909	2.6	3.6	
Carex panicea	10	10	2.47	0.0361	2.24	2.63	1.88[1]	1.9	0.0521	1.6	2.1	2.1[1]	3.0	0.1070	2.5	3.6	3.7[1]
Cirsium helenioides	10	10	1.76	0.1780	1.16	2.69	1.5[2]	1.1	0.0401	0.8	1.2	1.5[2]	22.5	0.5010	20.1	25.2	3.5[2]
Cirsium palustre	10	10	1.16	0.0341	0.92	1.30	2.00[1]	0.9	0.0690	0.6	1.3	1.6[1]	12.2	0.1850	11.3	12.9	12.0[1]
Deschampsia cespitosa	10	10	0.26	0.0102	0.21	0.32	0.31[1]	0.7	0.0427	0.4	0.8	0.9[1]	2.5	0.1150	2.0	3.0	2.9[1]
Festuca ovina	10	9	0.40	0.0109	0.35	0.43	0.35[1]	0.8	0.0269	0.6	0.9	1.1[1]	3.7	0.1130	3.2	4.5	4.3[1]
Festuca rubra	10	10	1.12	0.2820	1.01	1.25	0.79[1]	0.9	0.0233	0.8	1.0	1.1[1]	6.7	0.1440	6.1	7.6	7.3[1]
Galium boreale	10	1	0.76	n.a.	0.76	0.76		1.2	0.0814	0.8	1.8		1.9	0.0898	1.5	2.5	
Galium uliginosum	10	10	0.17	0.0050	0.15	0.20		0.7	0.0153	0.6	0.7		0.9	0.0180	0.8	1.0	
Geum rivale	10	10	1.00	0.0294	0.86	1.15		1.1	0.0619	0.8	1.5		7.9	0.3530	6.0	9.5	
Hieracium umbellatum	10	3	0.38	0.0300	0.35	0.44		0.6	0.0153	0.6	0.7		7.2	0.2240	6.3	8.4	
Hypericum maculatum	50	2	0.02	0.0010	0.02	0.02		0.3	0.0153	0.3	0.4		0.7	0.0180	0.6	0.8	
Knautia arvensis	10	10	5.31	0.1020	4.91	6.00	4.0[2]	2.0	0.0715	1.7	2.2	2.1[2]	5.1	0.1270	4.1	5.5	5.5[2]
L. vulgare (small)	10	10	0.332	0.0113	0.28	0.40	0.33[1]	0.7	0.0269	0.5	0.8	0.5[1]	2.0	0.0394	1.8	2.2	2.4[1]
L. vulgare (large)	10	10	0.822	0.0184	0.71	0.90		1.1	0.0267	1.0	1.1		5.1	0.1350	4.2	5.6	
Luzula multiflora	10	10	0.42	0.0099	0.38	0.48		0.7	0.0221	0.6	0.8		1.3	0.0359	1.2	1.5	
Nardus stricta	10	9	0.68	0.0201	0.58	0.76	0.38[1]	0.7	0.0291	0.5	0.8	0.9[1]	10.1	0.3450	8.5	12.2	10.4[1]
Phleum pratense	10	10	0.65	0.0120	0.58	0.69	0.45[1]	1.0	0.0277	0.9	1.1	1.2[1]	1.7	0.0365	1.6	2.0	3.5[1]
Poa pratensis	10	10	0.32	0.0107	0.24	0.37	0.25[1]	0.7	0.0133	0.6	0.7	0.7[1]	2.9	0.1180	2.5	3.5	2.9[1]
Potentilla erecta	10	10	0.42	0.0130	0.34	0.49	0.58[1]	1.0	0.0547	0.7	1.3	1.1[1]	1.5	0.0269	1.3	1.6	1.6[1]
Prunella vulgaris	10	10	0.56	0.0186	0.48	0.65	0.73[1]	0.9	0.0307	0.7	1.0	1.0[1]	1.7	0.0213	1.6	1.8	2.0[1]
Ranunculus acris	10	10	1.11	0.0471	0.95	1.36	1.90[1]	2.0	0.1050	1.5	2.6	2.0[1]	2.7	0.1290	2.1	3.6	3.0[1]
Rhinanthus minor	10	10	1.66	0.0627	1.26	1.93	2.84[1]	3.2	0.0827	2.9	3.7	3.8[1]	4.1	0.0933	3.7	4.8	4.9[1]
Rumex acetosa	10	10	0.90	0.0198	0.78	1.02	0.74[1]	3.1	0.2270	2.2	4.6	2.3[1]	4.8	0.2440	3.6	6.0	3.2[1]
Solidago virgaurea	10	10	0.17	0.0062	0.14	0.21	0.52[1]	0.5	0.0200	0.4	0.6	0.8[1]	2.6	0.0696	2.4	3.2	7.8[1]
Trifolium pratense	10	10	1.99	0.0351	1.80	2.11	1.35[1]	2.2	0.1160	1.8	2.8	1.5[1]	5.7	0.2620	4.3	6.9	2.1[1]
Vicia cracca	1	10	10.50	0.5300	7.90	12.90	14.3[1]	2.3	0.0452	2.2	2.6	2.6[1]	2.5	0.0657	2.2	2.9	2.8[1]
Viola canina	10	10	0.66	0.0149	0.57	0.72		1.0	0.0153	1.0	1.1		1.8	0.0371	1.7	2.0	

Appendix 6 Correlations of seeds found on dummy, between and within transects. This was done in order to check whether variation is larger between or within transects. Pearson’s correlation values are given to the left, P-values to the right.

Transect		1A	1B	2A	2B	3A	3B	4A	4B	5A	5B
		P-values									
1A	Pearson’s correlation		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
1B		0.86		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2A		0.77	0.81		0.00	0.00	0.00	0.00	0.00	0.00	0.00
2B		0.95	0.91	0.90		0.00	0.00	0.00	0.00	0.00	0.00
3A		0.97	0.86	0.85	0.97		0.00	0.00	0.00	0.00	0.00
3B		0.78	0.76	0.78	0.83	0.82		0.01	0.00	0.00	0.00
4A		0.45	0.75	0.63	0.60	0.54	0.42		0.00	0.00	0.00
4B		0.82	0.92	0.90	0.91	0.84	0.83	0.67		0.00	0.00
5A		0.80	0.93	0.88	0.90	0.83	0.89	0.64	0.95		0.00
5B		0.71	0.74	0.70	0.71	0.72	0.65	0.58	0.73	0.73	

Appendix 7 Mean and 1SE of the mean for 'proportion of seeds remaining' after walks of 5 m, 10 m, 50 m, 100 m and 200 m, for the seven species tested in the pilot study.

Distance	5 m		10 m		50 m		100 m		200 m	
Species	Mean	1SE	Mean	1SE	Mean	1SE	Mean	1SE	Mean	1SE
Angelica sylvestis	8.6	0.51	8.8	0.37	8.0	0.71	6.2	1.46	5.8	0.92
Anthriscus sylvestris	7.0	0.84	8.8	0.37	7.4	0.51	6.2	0.97	6.8	1.02
Festuca rubra	8.4	0.93	7.6	0.60	6.4	0.60	6.0	0.71	5.0	0.95
Hypochoeris maculata	7.4	0.81	9.4	0.24	6.6	0.98	5.8	1.02	6.4	0.98
Knautia arvensis	6.8	0.37	8.4	1.12	6.2	0.80	7.0	1.26	5.4	1.17
Pimpinella saxifraga	8.0	0.84	8.2	0.58	7.6	1.03	6.0	0.95	5.4	0.68
Plantago lancelata (dry)	7.4	0.68	7.2	0.37	6.2	0.86	6.4	1.29	6.0	0.71
P. lanceolata (wet)	8.2	0.80	7.6	1.44	9.0	0.45	8.4	0.81	8.0	0.55

Appendix 8 Multiple comparisons of seed attachment efficiency (log Q_{SEED}) of the species found attached to the fox dummy. *Leucanthemum vulgare* is included in two versions, both as small (s) and large (l) seeds. Significance of all multiple comparisons was corrected using PROC MULTTEST to a false discovery rate (FDR) of less than 5 %. Comparisons with P ≤0.05 after correction for multiple comparisons, are indicated with *. Continues on pages x and xi.

Species 1		Species 2	DF	t	Corrected P	
Agrostis canina	vs	Agrostis capillaris	10.5	1.21	0.3812	
Agrostis canina	vs	Anthoxanthum odoratum	17.4	-2.07	0.1012	
Agrostis canina	vs	Bistorta vivipara	12.4	2.84	0.0377'	*
Agrostis canina	vs	Carex pallescens	14.6	-2.05	0.1107	
Agrostis canina	vs	Carex panicea	16.3	1.46	0.2706	
Agrostis canina	vs	Cirsium palustre	17.9	1	0.4766	
Agrostis canina	vs	Deschampsia cespitosa	10.7	-5.91	0.0008	*
Agrostis canina	vs	Festuca ovina	12.3	-1.85	0.1572	
Agrostis canina	vs	Festuca rubra	18	0.72	0.619	
Agrostis canina	vs	Geum rivale	12.3	-1.8	0.1684	
Agrostis canina	vs	Leucanthemum vulgare(l)	14.6	0.94	0.5038	
Agrostis canina	vs	Leucanthemum vulgare(s)	13.9	0.81	0.5785	
Agrostis canina	vs	Luzula multiflora	16.7	-1.71	0.1835	
Agrostis canina	vs	Nardus stricta	18	1.23	0.3595	
Agrostis canina	vs	Poa pratensis	11.7	2.77	0.044	*
Agrostis canina	vs	Potentilla erecta	11.9	2.4	0.0747	
Agrostis canina	vs	Ranunculus acris	11.2	-4.27	0.0055	*
Agrostis canina	vs	Rhinanthus minor	15.9	1.66	0.1993	
Agrostis canina	vs	Rumex acetosa	10.7	-2.02	0.1296	
Agrostis canina	vs	Viola canina	12.1	2.88	0.0363	*
Agrostis capillaris	vs	Anthoxanthum odoratum	10	-3.63	0.0156	*
Agrostis capillaris	vs	Bistorta vivipara	15.4	3.49	0.0115	*
Agrostis capillaris	vs	Carex pallescens	13	-5.52	0.0006	*
Agrostis capillaris	vs	Carex panicea	11.8	0.7	0.6268	
Agrostis capillaris	vs	Cirsium palustre	10.3	0.19	0.9187	
Agrostis capillaris	vs	Deschampsia cespitosa	17.9	-17.61	<.0001	*
Agrostis capillaris	vs	Festuca ovina	9.29	-2.55	0.0682	
Agrostis capillaris	vs	Festuca rubra	10.4	-0.2	0.9187	
Agrostis capillaris	vs	Geum rivale	9.28	-2.49	0.0738	
Agrostis capillaris	vs	Leucanthemum vulgare(l)	9.52	0.35	0.8427	
Agrostis capillaris	vs	Leucanthemum vulgare(s)	9.44	0.24	0.9016	
Agrostis capillaris	vs	Luzula multiflora	11.6	-4.21	0.0059	*
Agrostis capillaris	vs	Nardus stricta	10.6	0.44	0.7896	
Agrostis capillaris	vs	Poa pratensis	16.5	3.52	0.0103	*
Agrostis capillaris	vs	Potentilla erecta	16.2	2.68	0.0401	*
Agrostis capillaris	vs	Ranunculus acris	17.2	-12.63	<.0001	*
Agrostis capillaris	vs	Rhinanthus minor	12.1	1.03	0.474	
Agrostis capillaris	vs	Rumex acetosa	17.9	-7.96	<.0001	*
Agrostis capillaris	vs	Viola canina	15.9	3.67	0.0087	*
Anthoxanthum odoratum	vs	Bistorta vivipara	11.4	4.94	0.0021	*
Anthoxanthum odoratum	vs	Carex pallescens	13.1	0.64	0.6549	
Anthoxanthum odoratum	vs	Carex panicea	14.7	3.59	0.0105	*
Anthoxanthum odoratum	vs	Cirsium palustre	17.7	2.92	0.0275	*
Anthoxanthum odoratum	vs	Deschampsia cespitosa	10.2	-2.38	0.0787	
Anthoxanthum odoratum	vs	Festuca ovina	13.6	-0.54	0.7221	
Anthoxanthum odoratum	vs	Festuca rubra	17.6	2.69	0.0383	*
Anthoxanthum odoratum	vs	Geum rivale	13.6	-0.5	0.7505	
Anthoxanthum odoratum	vs	Leucanthemum vulgare(l)	16.2	2.44	0.0597	
Anthoxanthum odoratum	vs	Leucanthemum vulgare(s)	15.5	2.24	0.0813	
Anthoxanthum odoratum	vs	Luzula multiflora	15.1	0.77	0.5986	
Anthoxanthum odoratum	vs	Nardus stricta	17.1	3.21	0.0169	*
Anthoxanthum odoratum	vs	Poa pratensis	10.9	4.9	0.0028	*
Anthoxanthum odoratum	vs	Potentilla erecta	11	4.58	0.0035	*
Anthoxanthum odoratum	vs	Ranunculus acris	10.6	-1.03	0.474	
Anthoxanthum odoratum	vs	Rhinanthus minor	14.3	3.79	0.0079	*
Anthoxanthum odoratum	vs	Rumex acetosa	10.2	0.9	0.5308	
Anthoxanthum odoratum	vs	Viola canina	11.2	4.99	0.002	*
Bistorta vivipara	vs	Carex pallescens	16.7	-7.4	<.0001	*
Bistorta vivipara	vs	Carex panicea	15	-1.55	0.2366	
Bistorta vivipara	vs	Cirsium palustre	12	-1.42	0.2925	
Bistorta vivipara	vs	Deschampsia cespitosa	16.1	-17.15	<.0001	*
Bistorta vivipara	vs	Festuca ovina	9.68	-3.32	0.0271	*
Bistorta vivipara	vs	Festuca rubra	12.2	-1.84	0.1586	
Bistorta vivipara	vs	Geum rivale	9.67	-3.26	0.0275	*
Bistorta vivipara	vs	Leucanthemum vulgare(l)	10.2	-0.71	0.6268	
Bistorta vivipara	vs	Leucanthemum vulgare(s)	10	-0.74	0.619	
Bistorta vivipara	vs	Luzula multiflora	14.6	-6	0.0003	*
Bistorta vivipara	vs	Nardus stricta	12.7	-1.34	0.319	

Bistorta vivipara	vs	Poa pratensis	17.7	-0.22	0.9062	
Bistorta vivipara	vs	Potentilla erecta	17.8	-0.86	0.5443	
Bistorta vivipara	vs	Ranunculus acris	17.2	-13.4	<.0001	*
Bistorta vivipara	vs	Rhinanthus minor	15.5	-1.34	0.3137	
Bistorta vivipara	vs	Rumex acetosa	16.1	-9.62	<.0001	*
Bistorta vivipara	vs	Viola canina	17.9	0.04	0.986	
Carex pallescens	vs	Carex panicea	17.4	4.49	0.0017	*
Carex pallescens	vs	Cirsium palustre	14.1	3.15	0.0226	*
Carex pallescens	vs	Deschampsia cespitosa	13.6	-5.69	0.0005	*
Carex pallescens	vs	Festuca ovina	10.2	-0.95	0.5038	
Carex pallescens	vs	Festuca rubra	14.3	2.87	0.0337	*
Carex pallescens	vs	Geum rivale	10.2	-0.9	0.5308	
Carex pallescens	vs	Leucanthemum vulgare(l)	11.2	2.35	0.0787	
Carex pallescens	vs	Leucanthemum vulgare(s)	10.8	2.1	0.1144	
Carex pallescens	vs	Luzula multiflora	17.1	0.25	0.8955	
Carex pallescens	vs	Nardus stricta	15.1	3.63	0.0093	*
Carex pallescens	vs	Poa pratensis	15.6	7.52	<.0001	*
Carex pallescens	vs	Potentilla erecta	15.9	6.92	<.0001	*
Carex pallescens	vs	Ranunculus acris	14.7	-3.11	0.0241	*
Carex pallescens	vs	Rhinanthus minor	17.7	4.86	0.0008	*
Carex pallescens	vs	Rumex acetosa	13.6	0.4	0.8027	
Carex pallescens	vs	Viola canina	16.2	7.57	<.0001	*
Carex panicea	vs	Cirsium palustre	15.7	-0.25	0.8955	
Carex panicea	vs	Deschampsia cespitosa	12.2	-10.21	<.0001	*
Carex panicea	vs	Festuca ovina	10.8	-2.68	0.0539	
Carex panicea	vs	Festuca rubra	16	-0.6	0.676	
Carex panicea	vs	Geum rivale	10.7	-2.62	0.0578	
Carex panicea	vs	Leucanthemum vulgare(l)	12.1	0.03	0.986	
Carex panicea	vs	Leucanthemum vulgare(s)	11.7	-0.05	0.986	
Carex panicea	vs	Luzula multiflora	18	-3.79	0.0055	*
Carex panicea	vs	Nardus stricta	16.7	-0.08	0.9793	
Carex panicea	vs	Poa pratensis	14	1.44	0.2819	
Carex panicea	vs	Potentilla erecta	14.2	0.96	0.498	
Carex panicea	vs	Ranunculus acris	13.2	-7.9	<.0001	*
Carex panicea	vs	Rhinanthus minor	18	0.22	0.9062	
Carex panicea	vs	Rumex acetosa	12.3	-5	0.0016	*
Carex panicea	vs	Viola canina	14.6	1.61	0.2179	
Cirsium palustre	vs	Deschampsia cespitosa	10.5	-6.89	0.0003	*
Cirsium palustre	vs	Festuca ovina	12.8	-2.41	0.0713	
Cirsium palustre	vs	Festuca rubra	18	-0.29	0.8799	
Cirsium palustre	vs	Geum rivale	12.7	-2.36	0.0757	
Cirsium palustre	vs	Leucanthemum vulgare(l)	15.2	0.19	0.9187	
Cirsium palustre	vs	Leucanthemum vulgare(s)	14.4	0.11	0.9694	
Cirsium palustre	vs	Luzula multiflora	16.2	-2.77	0.0363	*
Cirsium palustre	vs	Nardus stricta	17.8	0.16	0.9336	
Cirsium palustre	vs	Poa pratensis	11.4	1.32	0.3299	
Cirsium palustre	vs	Potentilla erecta	11.5	0.98	0.4969	
Cirsium palustre	vs	Ranunculus acris	11	-5.33	0.0013	*
Cirsium palustre	vs	Rhinanthus minor	15.3	0.43	0.7899	
Cirsium palustre	vs	Rumex acetosa	10.5	-3.22	0.0271	*
Cirsium palustre	vs	Viola canina	11.7	1.45	0.2848	
Deschampsia cespitosa	vs	Festuca ovina	9.33	0.68	0.6382	
Deschampsia cespitosa	vs	Festuca rubra	10.6	6.7	0.0004	*
Deschampsia cespitosa	vs	Geum rivale	9.33	0.71	0.6268	
Deschampsia cespitosa	vs	Leucanthemum vulgare(l)	9.6	4.66	0.0051	*
Deschampsia cespitosa	vs	Leucanthemum vulgare(s)	9.5	4.21	0.0087	*
Deschampsia cespitosa	vs	Luzula multiflora	12	4.96	0.0017	*
Deschampsia cespitosa	vs	Nardus stricta	10.9	7.87	0.0001	*
Deschampsia cespitosa	vs	Poa pratensis	17	18.28	<.0001	*
Deschampsia cespitosa	vs	Potentilla erecta	16.8	17.2	<.0001	*
Deschampsia cespitosa	vs	Ranunculus acris	17.7	3.51	0.0099	*
Deschampsia cespitosa	vs	Rhinanthus minor	12.5	10.94	<.0001	*
Deschampsia cespitosa	vs	Rumex acetosa	18	9.28	<.0001	*
Deschampsia cespitosa	vs	Viola canina	16.5	17.82	<.0001	*
Festuca ovina	vs	Festuca rubra	12.5	2.26	0.0856	
Festuca ovina	vs	Geum rivale	18	0.03	0.986	
Festuca ovina	vs	Leucanthemum vulgare(l)	16.6	2.27	0.0777	
Festuca ovina	vs	Leucanthemum vulgare(s)	17.2	2.15	0.0908	
Festuca ovina	vs	Luzula multiflora	10.9	1.03	0.474	
Festuca ovina	vs	Nardus stricta	12	2.55	0.0578	
Festuca ovina	vs	Poa pratensis	9.53	3.28	0.0275	*
Festuca ovina	vs	Potentilla erecta	9.57	3.11	0.0337	*
Festuca ovina	vs	Ranunculus acris	9.44	0.04	0.986	
Festuca ovina	vs	Rhinanthus minor	10.6	2.78	0.0464	*
Festuca ovina	vs	Rumex acetosa	9.33	1.09	0.4528	
Festuca ovina	vs	Viola canina	9.61	3.34	0.0267	*

Festuca rubra	vs	Geum rivale	12.5	-2.21	0.0911	
Festuca rubra	vs	Leucanthemum vulgare(l)	14.9	0.41	0.7982	
Festuca rubra	vs	Leucanthemum vulgare(s)	14.1	0.31	0.8687	
Festuca rubra	vs	Luzula multiflora	16.5	-2.49	0.0557	
Festuca rubra	vs	Nardus stricta	17.9	0.47	0.7688	
Festuca rubra	vs	Poa pratensis	11.6	1.75	0.1843	
Festuca rubra	vs	Potentilla erecta	11.7	1.39	0.3044	
Festuca rubra	vs	Ranunculus acris	11.1	-5.09	0.0017	*
Festuca rubra	vs	Rhinanthus minor	15.6	0.79	0.5873	
Festuca rubra	vs	Rumex acetosa	10.6	-2.92	0.0383	*
Festuca rubra	vs	Viola canina	11.9	1.87	0.1572	
Geum rivale	vs	Leucanthemum vulgare(l)	16.6	2.23	0.0813	
Geum rivale	vs	Leucanthemum vulgare(s)	17.2	2.11	0.0954	
Geum rivale	vs	Luzula multiflora	10.9	0.98	0.4969	
Geum rivale	vs	Nardus stricta	12	2.5	0.0617	
Geum rivale	vs	Poa pratensis	9.53	3.21	0.0295	*
Geum rivale	vs	Potentilla erecta	9.56	3.04	0.0363	*
Geum rivale	vs	Ranunculus acris	9.43	0	1	
Geum rivale	vs	Rhinanthus minor	10.6	2.73	0.05	*
Geum rivale	vs	Rumex acetosa	9.33	1.04	0.474	
Geum rivale	vs	Viola canina	9.6	3.27	0.0275	*
Leucanthemum vulgare(l)	vs	Leucanthemum vulgare(s)	17.9	-0.06	0.986	
Leucanthemum vulgare(l)	vs	Luzula multiflora	12.4	-2.15	0.0996	
Leucanthemum vulgare(l)	vs	Nardus stricta	14.2	-0.08	0.9793	
Leucanthemum vulgare(l)	vs	Poa pratensis	9.97	0.64	0.657	
Leucanthemum vulgare(l)	vs	Potentilla erecta	10	0.42	0.7973	
Leucanthemum vulgare(l)	vs	Ranunculus acris	9.79	-3.68	0.0169	*
Leucanthemum vulgare(l)	vs	Rhinanthus minor	11.8	0.09	0.9793	
Leucanthemum vulgare(l)	vs	Rumex acetosa	9.6	-2.3	0.0911	
Leucanthemum vulgare(l)	vs	Viola canina	10.1	0.73	0.619	
Leucanthemum vulgare(s)	vs	Luzula multiflora	11.9	-1.93	0.1432	
Leucanthemum vulgare(s)	vs	Nardus stricta	13.5	0	1	
Leucanthemum vulgare(s)	vs	Poa pratensis	9.82	0.67	0.642	
Leucanthemum vulgare(s)	vs	Potentilla erecta	9.86	0.47	0.7706	
Leucanthemum vulgare(s)	vs	Ranunculus acris	9.67	-3.31	0.0271	*
Leucanthemum vulgare(s)	vs	Rhinanthus minor	11.4	0.16	0.9336	
Leucanthemum vulgare(s)	vs	Rumex acetosa	9.51	-2.04	0.1299	
Leucanthemum vulgare(s)	vs	Viola canina	9.93	0.75	0.619	
Luzula multiflora	vs	Nardus stricta	17.1	3.16	0.0185	*
Luzula multiflora	vs	Poa pratensis	13.6	6.02	0.0003	*
Luzula multiflora	vs	Potentilla erecta	13.8	5.53	0.0006	*
Luzula multiflora	vs	Ranunculus acris	12.8	-2.86	0.0368	*
Luzula multiflora	vs	Rhinanthus minor	17.8	4.09	0.0034	*
Luzula multiflora	vs	Rumex acetosa	12	0.04	0.986	
Luzula multiflora	vs	Viola canina	14.1	6.11	0.0002	*
Nardus stricta	vs	Poa pratensis	12	1.24	0.3632	
Nardus stricta	vs	Potentilla erecta	12.2	0.86	0.5474	
Nardus stricta	vs	Ranunculus acris	11.5	-6.12	0.0005	*
Nardus stricta	vs	Rhinanthus minor	16.3	0.27	0.8879	
Nardus stricta	vs	Rumex acetosa	10.9	-3.8	0.012	*
Nardus stricta	vs	Viola canina	12.4	1.38	0.3044	
Poa pratensis	vs	Potentilla erecta	18	-0.68	0.6314	
Poa pratensis	vs	Ranunculus acris	17.8	-14.13	<.0001	*
Poa pratensis	vs	Rhinanthus minor	14.4	-1.21	0.3721	
Poa pratensis	vs	Rumex acetosa	17.1	-10.14	<.0001	*
Poa pratensis	vs	Viola canina	17.9	0.27	0.8879	
Potentilla erecta	vs	Ranunculus acris	17.7	-13.19	<.0001	*
Potentilla erecta	vs	Rhinanthus minor	14.6	-0.72	0.619	
Potentilla erecta	vs	Rumex acetosa	16.9	-9.2	<.0001	*
Potentilla erecta	vs	Viola canina	18	0.93	0.5038	
Ranunculus acris	vs	Rhinanthus minor	13.6	8.5	<.0001	*
Ranunculus acris	vs	Rumex acetosa	17.7	5.11	0.0006	*
Ranunculus acris	vs	Viola canina	17.5	13.88	<.0001	*
Rhinanthus minor	vs	Rumex acetosa	12.6	-5.5	0.0008	*
Rhinanthus minor	vs	Viola canina	15	1.39	0.2963	
Rumex acetosa	vs	Viola canina	16.6	10.02	<.0001	*

Appendix 9 Multiple comparisons of seed retention efficiency for the 16 species in dataset 1. Significance of all multiple comparisons was corrected using PROC MULTTEST to a false discovery rate (FDR) of less than 5 %. Comparisons with P≤ 0.05 after correction for multiple comparisons, are indicated with *. Continues on page xiii.

Species 1		Species 2	DF	Chi-square	Corrected P	
Carex pallescens	*vs*	Geum rivale	1	37.03	<.0001	*
Carex pallescens	*vs*	Agrostis capillaris	1	25.08	<.0001	*
Carex pallescens	*vs*	Ranunculus acris	1	1.21	0.3224	
Carex pallescens	*vs*	Rumex acetosa	1	6.96	0.0147	*
Carex pallescens	*vs*	Centaurea scabiosa	1	12.19	0.0012	*
Carex pallescens	*vs*	Pimpinella saxifraga	1	0.04	0.8631	
Carex pallescens	*vs*	Anthoxanthum odoratum	1	32.51	<.0001	*
Carex pallescens	*vs*	Trifolium arvense	1	44.87	<.0001	*
Carex pallescens	*vs*	Dactylis glomerata	1	16.8	0.0001	*
Carex pallescens	*vs*	Anthriscus sylvestris	1	3.51	0.0882	
Carex pallescens	*vs*	Cirsium palustre	1	12.14	0.0012	*
Carex pallescens	*vs*	Trifolium pratense	1	13.48	0.0006	*
Carex pallescens	*vs*	Knautia arvensis	1	2.06	0.1852	
Carex pallescens	*vs*	Festuca rubra	1	3.34	0.0943	
Carex pallescens	*vs*	Agrimonia eupatoria	1	46.41	<.0001	*
Geum rivale	*vs*	Agrostis capillaris	1	7.58	0.0107	*
Geum rivale	*vs*	Ranunculus acris	1	31.01	<.0001	*
Geum rivale	*vs*	Rumex acetosa	1	20.42	<.0001	*
Geum rivale	*vs*	Centaurea scabiosa	1	15.45	0.0002	*
Geum rivale	*vs*	Pimpinella saxifraga	1	32.76	<.0001	*
Geum rivale	*vs*	Anthoxanthum odoratum	1	4.45	0.0537	
Geum rivale	*vs*	Trifolium arvense	1	1.07	0.3541	
Geum rivale	*vs*	Dactylis glomerata	1	10.61	0.0025	*
Geum rivale	*vs*	Anthriscus sylvestris	1	24.85	<.0001	*
Geum rivale	*vs*	Cirsium palustre	1	16.13	0.0002	*
Geum rivale	*vs*	Trifolium pratense	1	4.37	0.0556	
Geum rivale	*vs*	Knautia arvensis	1	45.56	<.0001	*
Geum rivale	*vs*	Festuca rubra	1	25.68	<.0001	*
Geum rivale	*vs*	Agrimonia eupatoria	1	0.7	0.4354	
Agrostis capillaris	*vs*	Ranunculus acris	1	18.83	<.0001	*
Agrostis capillaris	*vs*	Rumex acetosa	1	7.63	0.0106	*
Agrostis capillaris	*vs*	Centaurea scabiosa	1	3.39	0.0926	
Agrostis capillaris	*vs*	Pimpinella saxifraga	1	20.08	<.0001	*
Agrostis capillaris	*vs*	Anthoxanthum odoratum	1	0.9	0.3918	
Agrostis capillaris	*vs*	Trifolium arvense	1	5.68	0.0271	*
Agrostis capillaris	*vs*	Dactylis glomerata	1	0.74	0.4286	
Agrostis capillaris	*vs*	Anthriscus sylvestris	1	12.04	0.0012	*
Agrostis capillaris	*vs*	Cirsium palustre	1	3.85	0.0737	
Agrostis capillaris	*vs*	Trifolium pratense	1	0.01	0.9203	
Agrostis capillaris	*vs*	Knautia arvensis	1	33.53	<.0001	*
Agrostis capillaris	*vs*	Festuca rubra	1	12.95	0.0008	*
Agrostis capillaris	*vs*	Agrimonia eupatoria	1	13.46	0.0006	*
Ranunculus acris	*vs*	Rumex acetosa	1	2.83	0.1207	
Ranunculus acris	*vs*	Centaurea scabiosa	1	6.92	0.0148	*
Ranunculus acris	*vs*	Pimpinella saxifraga	1	0.67	0.4426	
Ranunculus acris	*vs*	Anthoxanthum odoratum	1	26.23	<.0001	*
Ranunculus acris	*vs*	Trifolium arvense	1	38.77	<.0001	*
Ranunculus acris	*vs*	Dactylis glomerata	1	11.09	0.0019	*
Ranunculus acris	*vs*	Anthriscus sylvestris	1	0.73	0.4286	
Ranunculus acris	*vs*	Cirsium palustre	1	6.82	0.0155	*
Ranunculus acris	*vs*	Trifolium pratense	1	9.08	0.005	*
Ranunculus acris	*vs*	Knautia arvensis	1	6.08	0.0222	*
Ranunculus acris	*vs*	Festuca rubra	1	0.63	0.4498	
Ranunculus acris	*vs*	Agrimonia eupatoria	1	40.24	<.0001	*
Rumex acetosa	*vs*	Centaurea scabiosa	1	0.93	0.3864	
Rumex acetosa	*vs*	Pimpinella saxifraga	1	5.11	0.0371	*
Rumex acetosa	*vs*	Anthoxanthum odoratum	1	13.09	0.0007	*
Rumex acetosa	*vs*	Trifolium arvense	1	23.56	<.0001	*
Rumex acetosa	*vs*	Dactylis glomerata	1	3.15	0.1035	
Rumex acetosa	*vs*	Anthriscus sylvestris	1	0.65	0.4461	
Rumex acetosa	*vs*	Cirsium palustre	1	0.83	0.4101	
Rumex acetosa	*vs*	Trifolium pratense	1	3.62	0.0835	
Rumex acetosa	*vs*	Knautia arvensis	1	14.41	0.0004	*
Rumex acetosa	*vs*	Festuca rubra	1	0.79	0.4196	
Rumex acetosa	*vs*	Agrimonia eupatoria	1	28.62	<.0001	*
Centaurea scabiosa	*vs*	Pimpinella saxifraga	1	9.33	0.0046	*
Centaurea scabiosa	*vs*	Anthoxanthum odoratum	1	7.5	0.0111	*
Centaurea scabiosa	*vs*	Trifolium arvense	1	16.43	0.0001	*
Centaurea scabiosa	*vs*	Dactylis glomerata	1	0.77	0.4225	

Centaurea scabiosa	*vs*	Anthriscus sylvestris	1	3.04	0.1095	
Centaurea scabiosa	*vs*	Cirsium palustre	1	0.01	0.9203	
Centaurea scabiosa	*vs*	Trifolium pratense	1	1.67	0.2355	
Centaurea scabiosa	*vs*	Knautia arvensis	1	20.43	<.0001	*
Centaurea scabiosa	*vs*	Festuca rubra	1	3.41	0.0926	
Centaurea scabiosa	*vs*	Agrimonia eupatoria	1	22.98	<.0001	*
Pimpinella saxifraga	*vs*	Anthoxanthum odoratum	1	26.5	<.0001	*
Pimpinella saxifraga	*vs*	Trifolium arvense	1	37.55	<.0001	*
Pimpinella saxifraga	*vs*	Dactylis glomerata	1	13.32	0.0007	*
Pimpinella saxifraga	*vs*	Anthriscus sylvestris	1	2.4	0.1549	
Pimpinella saxifraga	*vs*	Cirsium palustre	1	9.23	0.0047	*
Pimpinella saxifraga	*vs*	Trifolium pratense	1	11.47	0.0016	*
Pimpinella saxifraga	*vs*	Knautia arvensis	1	2.45	0.1516	
Pimpinella saxifraga	*vs*	Festuca rubra	1	2.26	0.1677	
Pimpinella saxifraga	*vs*	Agrimonia eupatoria	1	41.58	<.0001	*
Anthoxanthum odoratum	*vs*	Trifolium arvense	1	2.15	0.1764	
Anthoxanthum odoratum	*vs*	Dactylis glomerata	1	3.02	0.1097	
Anthoxanthum odoratum	*vs*	Anthriscus sylvestris	1	18.31	<.0001	*
Anthoxanthum odoratum	*vs*	Cirsium palustre	1	8.27	0.0077	*
Anthoxanthum odoratum	*vs*	Trifolium pratense	1	0.25	0.6384	
Anthoxanthum odoratum	*vs*	Knautia arvensis	1	40.67	<.0001	*
Anthoxanthum odoratum	*vs*	Festuca rubra	1	19.48	<.0001	*
Anthoxanthum odoratum	*vs*	Agrimonia eupatoria	1	9.28	0.0046	*
Trifolium arvense	*vs*	Dactylis glomerata	1	9.37	0.0046	*
Trifolium arvense	*vs*	Anthriscus sylvestris	1	29.6	<.0001	*
Trifolium arvense	*vs*	Cirsium palustre	1	17.66	<.0001	*
Trifolium arvense	*vs*	Trifolium pratense	1	2.24	0.1681	
Trifolium arvense	*vs*	Knautia arvensis	1	52.4	<.0001	*
Trifolium arvense	*vs*	Festuca rubra	1	31.12	<.0001	*
Trifolium arvense	*vs*	Agrimonia eupatoria	1	3.97	0.0695	
Dactylis glomerata	*vs*	Anthriscus sylvestris	1	6.2	0.0213	*
Dactylis glomerata	*vs*	Cirsium palustre	1	0.94	0.3864	
Dactylis glomerata	*vs*	Trifolium pratense	1	0.46	0.5193	
Dactylis glomerata	*vs*	Knautia arvensis	1	25.24	<.0001	*
Dactylis glomerata	*vs*	Festuca rubra	1	6.74	0.0159	*
Dactylis glomerata	*vs*	Agrimonia eupatoria	1	17.09	0.0001	*
Anthriscus sylvestris	*vs*	Cirsium palustre	1	2.92	0.1154	
Anthriscus sylvestris	*vs*	Trifolium pratense	1	5.84	0.0251	*
Anthriscus sylvestris	*vs*	Knautia arvensis	1	9.81	0.0037	*
Anthriscus sylvestris	*vs*	Festuca rubra	1	0.01	0.9203	
Anthriscus sylvestris	*vs*	Agrimonia eupatoria	1	33.48	<.0001	*
Cirsium palustre	*vs*	Trifolium pratense	1	1.83	0.2135	
Cirsium palustre	*vs*	Knautia arvensis	1	20.4	<.0001	*
Cirsium palustre	*vs*	Festuca rubra	1	3.28	0.0967	
Cirsium palustre	*vs*	Agrimonia eupatoria	1	23.83	<.0001	*
Trifolium pratense	*vs*	Knautia arvensis	1	20.8	<.0001	*
Trifolium pratense	*vs*	Festuca rubra	1	6.17	0.0214	*
Trifolium pratense	*vs*	Agrimonia eupatoria	1	8.21	0.0078	*
Knautia arvensis	*vs*	Festuca rubra	1	9.61	0.0041	*
Knautia arvensis	*vs*	Agrimonia eupatoria	1	54.93	<.0001	*
Festuca rubra	*vs*	Agrimonia eupatoria	1	34.44	<.0001	*