Seed Science Research (2004) **14**, 147–159 DOI: 10.1079/SSR2004164

An experimental assessment of seed adhesivity on animal furs

Martine Couvreur*, Bart Vandenberghe, Kris Verheyen and Martin Hermy

Laboratory for Forest, Nature and Landscape Research, University of Leuven, Vital Decosterstraat 102, B-3000 Leuven, Belgium

Abstract

Epizoochory is widely recognized as an effective long-distance seed dispersal mechanism. Nevertheless, few studies have focused on the investigation of its influencing factors. One of the key aspects of epizoochory is the adhesive interaction between seeds and furs. We describe a new method to quantify experimentally and standardize the adhesivity of seeds to animal fur, as a measure of epizoochorous dispersal potential. The method excludes the impact of animal behaviour and environmental factors, and allows the ranking of species according to their adhesivity score. We measured adhesivity scores for 66 species on the furs of seven mammals. Deep furs with long, rough, undulated hairs implanted at a large angle were most suited for seed adhesion, while seeds adhered less well to shallow furs with short, smooth, straight hairs implanted at small angles. Seeds with specialized adhesive appendages had higher adhesivity scores than seeds with unspecialized appendages and seeds without appendages. However, an interaction effect between certain seed and fur types exists. Although seed morphology is a good predictor for seed adhesivity on fur, less well-adhering seed types often still have relatively high adhesivity scores. Therefore, it is likely that nearly all species are, to some extent, able to disperse epizoochorously.

Keywords: adhesive seed dispersal, adhesivity score, epizoochory, mammalian fur, methodology, seed traits

Introduction

Dispersal of plant seeds in the fur of animals (epizoochory) is presumed to be one of the key factors in historical and actual long-distance seed transport, but is far from being fully understood (Bonn and Poschlod, 1998; Higgins and Richardson, 1999; Higgins *et al.*, 2003). In the past, seed dispersal mechanisms were mainly derived from morphological characteristics of seeds (cf. Grime *et al.*, 1988; Hughes *et al.*, 1994). However, the idea that seeds are merely dispersed by one process, i.e. the process they are morphologically adapted for, is no longer tenable. It is now recognized that seeds may disperse by several mechanisms (Higgins *et al.*, 2003).

To identify these mechanisms, observational studies in the field are extremely valuable, because they provide evidence for the occurrence of a certain dispersal mode in combination with certain plant species. In the case of epizoochory, such field studies comprise inspection of the epizoochorous seed loads of animals (see Agnew and Flux, 1970; Shmida and Ellner, 1983; Fischer *et al.*, 1996; Stender *et al.*, 1997; Mrotzek *et al.*, 1999; Heinken, 2000; Graae, 2002; Heinken and Raudnitschka, 2002; Couvreur *et al.*, unpublished data). However, to unravel the process behind these observations, more directed experiments are indispensable. For instance, field experiments in which marked seeds are attached to living animals allow control of the attachment procedure, but have the disadvantage that the influence of environmental (e.g. vegetation, weather) and behavioural factors (e.g. animal movement, grooming, wallowing) cannot be entirely separated from the dispersal and detachment process (see Shmida and Ellner, 1983; Sorensen, 1986; Fischer *et al.*, 1996; Kiviniemi, 1996; Stender *et al.*, 1997). Even if these experiments are conducted in laboratory conditions, the behavioural aspects of the animals still interfere with the behaviour of the seeds [e.g. noticeable or irritating seeds can induce grooming behaviour (Kiviniemi and Telenius, 1998)]. The use in the field of man-made constructions, such as dummies, can allow the researcher to control the behavioural factor, but not the vegetational or other environmental influences (see Bullock and Primack, 1977; Fischer *et al.*, 1996; Heinken *et al.*, 2001; Castillo-Flores and Calvo-Irabien, 2003). To fully understand the process of seed dispersal, it is therefore necessary to study the affecting

*Correspondence
Fax: +32 16 32 97 60
Email: martine.couvreur@agr.kuleuven.ac.be

factors separately, i.e. to raise the level of experimental control. Until now, few studies include such highly controlled experiments. However, they provide missing pieces of the puzzle, since only an integration of field observations and experimental data, which isolate the different influencing factors, can result in a full understanding of the dispersal process.

One of the most obvious aspects of epizoochorous seed dispersal is the adhesive interaction between seeds and furs. Experimental quantification of this interaction requires a standardized seed attachment procedure, in which environmental factors and animal behaviour are controlled. To our knowledge, no such experiments are described in the literature. Only Lacey (1981) mentioned a limited experiment with *Daucus carota* seeds and prepared mammalian furs, and Gorb and Gorb (2002) measured the contact separation force of burrs to assess the mechanical interlocking ability of four plant species. As such, there is a considerable gap in our knowledge with respect to this key aspect of epizoochorous seed dispersal.

In this study, we investigate the adhesive interaction of different seed types with the furs of different mammals. A useful quantitative measure of seed adhesivity to fur, as a key aspect of epizoochorous dispersal potential, should allow species to be ranked on an ordinal scale with regard to their adhesive properties. Besides the possibility of comparing the epizoochorous dispersal potential among species, the advantage of such a ranking is the feasibility of comparing the relative dispersal potential of species with regard to several dispersal modes, at least if comparable methods for these other dispersal modes exist (see also Tackenberg *et al*., 2003). In an attempt to develop such a method in the context of epizoochory, we designed a standardized method to quantify seed adhesivity to samples of animal furs under controlled conditions. The following research questions were addressed:

- Does seed adhesivity differ among different fur types?
- Which fur traits enhance the adhesivity of seeds?
- Is seed morphology predictive for the adhesive behaviour of seeds?
- Can all types of seed appendages enhance adhesivity to fur?
- Is there an interaction between fur type and seed morphology with respect to adhesivity?

Materials and methods

Species selection and seed characterization

Diaspores of 66 plant species were collected in the field (usually seeds or fruits, but further referred to as seeds; see Appendix 1). The selected species covered a broad range of morphological seed features, and had either been reported in the literature as dispersing epizoochorously (see Appendix 1), or chosen because of their commonness and availability in the western European landscape.

Because intra-specific variation in seed size occurs frequently, and since accurate measurements are relatively scarce in the literature, eight morphological traits relevant for adhesive dispersal were carefully recorded (see Appendix 1): (1) type of adhesive appendage: hooks (hooked appendages), bristles (straight appendages), awns (organ hypothesized to anchor seeds into the soil, present on diaspores of many grass species), hairs (pappus hairs or hairs covering the seed surface), stems or remnants of the perianth, no appendages; (2) seed-surface texture rank: smooth, slightly rough, rough, hairy, sticky; (3) rank of appendage density (no appendages, 1 appendage, low density, high density). The continuous variables – (4) appendage length, (5) seed length (excluding appendages), (6) seed width, and (7) seed thickness – were measured as the average of 15 randomly chosen seeds, while (8) seed weight was calculated by dividing the weight of 50 seeds by 50. To assign all species to one of the appendage type categories, a limited number of simplifications were necessary. Seeds with more than one type of appendage were assigned the type of the most noticeable one, e.g. for *Anthoxanthum odoratum*, the awn was chosen as most prominent adhesive appendage, while the hairs present on the dispersal unit were incorporated in the surface texture rank. For *Juncus effusus* diaspores, the stem was considered the adhesive appendage, while the surface texture category was described as 'rough' because of the presence of spiny tepala.

Fur preparation and characterization

Prepared fur samples of seven mammalian species were collected, among which are some important wild animals in our region – roe deer (*Capriolus capriolus*), wild boar (*Sus scrofa*) and rabbit (*Oryctolagus cuniculus)* – as well as some common domesticated animals in agriculture and nature management – horse (*Equus caballus*), sheep (*Ovis aries)* (a meat race) and two races of cattle (*Bos taurus*): Holstein cattle (short-haired) and Galloway cattle (long-haired). Most of these animals have already been reported in the literature to be important seed dispersers (see Appendix 1).

Because intra-specific variations in fur traits, e.g. the contrast between summer and winter fur, are sometimes even more pronounced than some inter-specific differences, we recorded seven fur traits to obtain an objective fur description. We measured: (1)

https://doi.org/10.1079/SSR2004164 Published online by Cambridge University Press

the length of the individual hairs and (2) the depth of the fur (without straightening the hairs). Additionally, a rank order was assigned to (3) the thickness of the individual hairs, (4) the density of the hair implantation, (5) the roughness of the fur, (6) the hair undulation and (7) the angle between hair and skin (Appendix 2).

Comparison of the furs with those of living animals indicated that the prepared fur samples were somewhat softer or less greasy than the fur of living animals. Therefore, in order to imitate the original roughness, the fur samples were rubbed with a small amount of moist loamy sand, which was brushed out again after drying.

Adhesivity tests

To estimate the seed adhesivity on the different fur samples, a simple test was designed, in which both seed application and fur manipulation were standardized. To facilitate manipulation of the furs, they were clasped between two wooden boards, one of which had a gap of 25 × 25 cm, thus leaving a 25 × 25 cm zone of fur uncovered. To put the seeds on this test zone, the construction was placed on a horizontal surface, the test zone facing upwards. For each test, 50 seeds of a certain species were dropped perpendicularly on the fur, from a height of 15 cm above the test zone. Care was taken to spread the seeds more or less evenly over the test zone so that they would not hamper each others' attachment. Subsequently, the wooden construction was carefully lifted upwards, rotated to an upside-down position above a collection box and turned back to its original position, slowly and without irregular movements. The rotation of the construction was always in the direction of the hair implantation, to avoid retrapping falling seeds in the fur. The seeds that fell off were counted and those that were still attached were removed. This test was repeated five times for each seed–fur combination. The proportion of attached seeds was then averaged for the five tests, resulting in an 'adhesivity score' between 0 and 1 for each seed–fur combination.

Data analysis

For all seed species, the adhesivity score on each of the seven furs was calculated, as well as the 'global adhesivity score' (the mean adhesivity score on all furs). The data were then analysed to reveal the differences between the seven animal furs, the importance of the fur traits and the role of the seed traits. Only if the assumptions for the use of parametric statistics were not met, non-parametric statistics were used and, unless mentioned otherwise, all statistical analyses were performed using SPSS 10 (SPSS, 1999). For multiple comparisons between groups, a least significant difference (LSD) correction with alpha = 0.05 was performed (Siegel and Castellan, 1988).

First, the seven fur samples were compared using Spearman rank correlation coefficients (Siegel and Castellan, 1988) between the adhesivity scores on the different furs. Additionally, the mean adhesivity scores of the furs were tested for significant differences between the furs with a Kruskal–Wallis test, followed by multiple comparisons (Siegel and Castellan, 1988). To visualize the position of the furs in a two-dimensional space, we applied principal component analysis (PCA) on the adhesivity scores, using the program CANOCO 4.5 (ter Braak and Smilauer, 2003). The fur traits were then plotted as 'supplementary environmental variables' on the ordination diagram.

Secondly, the role of the seed traits was examined. Spearman rank correlation coefficients were calculated between the values of the seed traits and the adhesivity scores (individual and global). This was done for the complete set of species and for the set of species without adhesive appendages, to separate the influence of the presence of adhesive appendages from the influence of the other seed traits. For the nominal variable 'appendage type', a one-way ANOVA with *post-hoc* multiple comparisons (LSD) was performed to test whether the global adhesivity scores differed between seeds with different appendage type categories.

Then the seed species were clustered into more homogeneous groups on the basis of the seed traits, using Gower's similarity coefficient and the 'increase in sum of squares' method, using the program Clustan Graphics 5.08 (Clustan Ltd, 2001). The resulting seed clusters were then characterized in function of the seed traits, using Kruskall–Wallis tests in combination with multiple comparisons for the continuous and ordinal seed traits, and a Pearson chi^2 association test for the nominal variable (Siegel and Castellan, 1988). The most distinctive trait was incorporated in the cluster names.

Subsequently, to check whether the seed clustering could account for the difference in seed adhesivity, a multivariate analysis of variance (MANOVA) was used, with seed clusters as factor and adhesivity on the different furs as dependent variables. In addition, a between-subjects univariate test (one-way ANOVA) and *post-hoc* multiple comparisons (LSD) were performed to reveal significant differences in adhesivity scores between the clusters on individual furs. To homogenize the variances, the variables 'adhesivity on horse' and 'adhesivity on rabbit' were square root-transformed, while for the other furs the assumption of homogeneity of variances between the seed clusters was fulfilled.

Finally, discriminant analysis (DA) (Dillon and Goldstein, 1984) was used to examine the degree to which the division of the seed species by the cluster analysis, which resulted solely from the seed traits, matched the pattern of adhesivity to the furs. The adhesivity scores on the different furs were used as predictor variables and the cluster division as the grouping variable in the DA. The percentage of seed species correctly assigned to a seed traits-based cluster indicates the strength of the association of the seed characteristics with the adhesivity scores. The DA-ordination plot, based on adhesivity scores, was compared to a NMDS (non-metric multidimensional scaling; Doyle, 1973) ordination plot, based solely on the seed traits. For this NMDS ordination, the Gowers' proximity matrix computed in Clustan Graphics 5.08 was used.

Results

The adhesivity scores of the 66 seed species on the different fur samples ranged from 0.000 to 0.876. The global adhesivity ranged from 0.003 to 0.629, with a mean of 0.27.

Comparison of furs and role of fur traits

The adhesivity scores were highly positively correlated among the furs (*r*s ranging from 0.62 to 0.92, $P < 0.001$). However, the correlation was somewhat lower if wild boar was one of the compared furs (data not shown). The adhesivity scores differed significantly between the furs (Kruskal–Wallis test: $\chi^2 = 156.88$; df = 6; $P < 0.001$) (Table 1). The adhesivity scores on the furs of horse, rabbit and Holstein cattle were significantly lower than those on wild boar, sheep and Galloway cattle. Roe deer had an intermediate position, with adhesivity scores not significantly higher than Holstein cattle nor lower than those on wild boar and sheep. The adhesivity scores recorded on Galloway cattle were still significantly higher than those on sheep and wild boar. This ranking was also reflected in the position of the furs along the first axis of the PCA-ordination plot based on the adhesivity scores (% of explained variance, axis 1: 79.3%; axis 2: 7.4%) (Fig. 1). The fur traits (Appendix 2) positively correlated with PCA-axis 1 were hair length, fur depth, fur roughness, hair undulation and hair/skin angle. Hair thickness and fur density were positively and negatively correlated, respectively, with the second axis (explaining much less of the total variance than axis 1).

Table 1. Mean seed adhesivity scores ($n = 66$) on the seven furs (Kruskal–Wallis test: $\chi^2 = 156.88$; df = 6; $P < 0.001$). Different letters indicate significant differences between groups. The global adhesivity scores, calculated as the average of the mean adhesivity scores of all furs together, ranged from 0.003 to 0.629, with a mean of 0.27

Fur	Mean	Range
Horse	0.12 a	0.000–0.464
Rabbit	0.14 a	0.000–0.628
Holstein	0.19 ab	0.000–0.496
Roe deer	0.26 bc	0.000–0.720
Wild boar	0.35 c	0.000–0.596
Sheep	0.37 c	0.000–0.788
Galloway	0.50 d	0.004–0.876

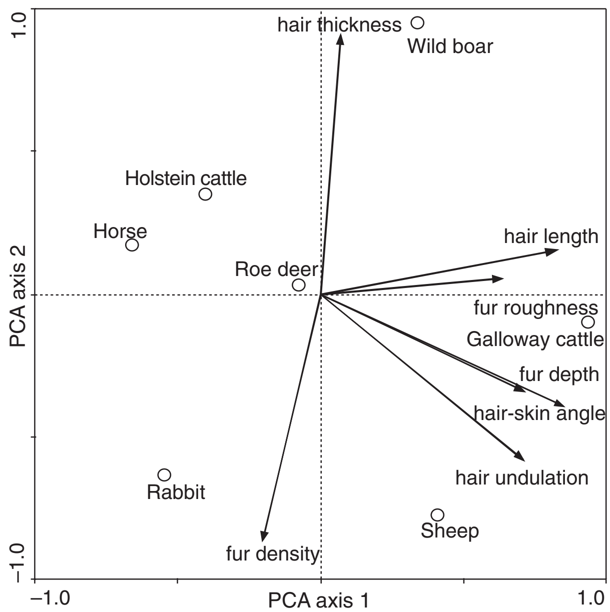

Figure 1. Principal component analysis (PCA) of the seven fur samples, based on the adhesivity scores of 66 seed species (79.3% of the total variance is explained by axis 1 and 7.4% by axis 2). The fur traits were plotted as 'supplementary environmental data'.

Role of seed traits and functional seed groups

The adhesivity scores (Appendix 1, Table 2) were consistently significantly negatively correlated with seed length, seed width, seed thickness and seed weight, especially if only the seed species without adhesive appendages were considered. The surface texture, on the other hand, was only weakly positively correlated with adhesivity on some furs, if all seed species were included in the analysis. The appendage length and density showed a weak, but significant, positive correlation with adhesivity, except for wild boar fur. The appendage types associated with the highest global adhesivity scores (Table 3) were awns, followed by hooks and then bristles. Hairs seemed to be intermediately efficient, and stems or perianth remnants even less efficient than no appendages.

Table 2. Spearman rank correlations between seed adhesivity scores on different furs and seed traits

	Seed length	Seed width	Seed thickness	Seed weight	Surface texture	Appendage length	Appendage density
Horse[1]	–0.30*	–0.57***	–0.54***	–0.69***	0.31*	0.33**	0.29*
Rabbit[1]	–0.32*	–0.54***	–0.42***	–0.61***	0.38**	0.33**	0.34**
Holstein cattle[1]	–0.43***	–0.58***	–0.50***	–0.68***	0.26*	0.26*	0.28*
Roe deer[1]	–0.48***	–0.70***	–0.57***	–0.79***	0.20ns	0.26*	0.26*
Wild boar[1]	–0.57***	–0.67***	–0.49***	–0.74***	0.14ns	–0.08ns	–0.09ns
Sheep[1]	–0.32**	–0.52***	–0.38**	–0.59***	0.41**	0.35**	0.35**
Galloway cattle[1]	–0.30*	–0.55***	–0.42***	–0.63***	0.31*	0.29*	0.29*
Global adhesivity[1]	–0.39**	–0.63***	–0.50***	–0.72***	0.33**	0.31*	0.31*
Horse[2]	–0.59***	–0.75***	–0.80***	–0.84***	0.23ns		
Rabbit[2]	–0.69***	–0.71***	–0.59***	–0.80***	0.22ns		
Holstein cattle[2]	–0.73***	–0.70***	–0.67***	–0.83***	0.21ns		
Roe deer[2]	–0.81***	–0.81***	–0.70***	–0.93***	0.08ns		
Wild boar[2]	–0.75***	–0.80***	–0.64***	–0.84***	0.18ns		
Sheep[2]	–0.79***	–0.74***	–0.60***	–0.85***	0.23ns		
Galloway cattle[2]	–0.61***	–0.71***	–0.58***	–0.82***	0.11ns		
Global adhesivity[2]	–0.81***	–0.85***	–0.68***	–0.96***	0.17ns		

[1] All seed species included in the analysis (n = 66).
[2] Only seed species without adhesive appendages included (n = 37).
*** $P \leqslant 0.001$; ** $P \leqslant 0.01$; * $P \leqslant 0.05$; ns, not significant.

Table 3. Global seed adhesivity scores in different classes of seed appendage type. A one-way ANOVA (F = 8.66, df = 5, P < 0.001) was calculated to test the differences between the classes. Values are group averages, and groups that differ significantly are indicated with different letters

Appendage type	n	Global adhesivity	Standard deviation
Stem, perianth remnants	9	0.155 a	0.101
No appendages	37	0.233 a	0.120
Hairs	10	0.329 b	0.182
Bristles	2	0.414 bc	0.086
Hooks	4	0.464 bc	0.015
Awns	4	0.530 c	0.080

Three seed clusters resulted from the cluster analysis based on the seed traits (cluster members in Appendix 1). All traits except seed thickness and seed weight differed significantly between at least two of the clusters (Table 4). The first seed cluster was characterized by rather long, broad seeds with one appendage (stem or perianth remnants). The second cluster contained, on average, rather long, narrow seeds with a rough surface texture, and a low to high density of appendages (hairs, awns, bristles or hooks). Finally, the third cluster comprised the rather short, narrow, smooth textured seeds without appendages. The three clusters were named, respectively, SUA (seeds with unspecialized appendages), SSA (seeds with specialized appendages) and SWA (seeds without appendages).

The effect of seed cluster on adhesivity for all furs together was highly significant (MANOVA, Pillai's Trace, F = 3.31, df = 14, P = 0.0002). For most furs, the adhesivity of seed cluster SSA was significantly higher than that of clusters SUA and SWA (one-way ANOVA and multiple comparisons, see Table 5). Two furs, however, behaved differently. The adhesivity on Galloway differed significantly between all three clusters, cluster SWA taking an intermediate position between SUA and SSA. For wild boar, the adhesivity of cluster SWA was as high as that of cluster SSA.

Discriminant analysis (DA), based on the adhesivity data, separated the three seed clusters derived from the cluster analysis (Wilks' λ = 0.308; χ^2 = 70.6, df = 14, P < 0.001). The correspondence between the DA ordination plot, based on the adhesivity scores (Fig. 2b), and the NMDS ordination plot, based on the seed traits (Fig. 2a), illustrates this. The DA correctly classified 77.3% of the 66 seed species into the three seed clusters (Table 6). Most

Table 4. Overview of the seed traits associated with the three seed clusters (SUA, seeds with unspecialized appendages; SSA, seeds with specialized appendages; SWA, seeds without appendages; n = number of seed species in the clusters)

	Test statistic	SUA (n=9)	SSA (n=20)	SWA (n=37)
Seed length (mm)	^{kw} 13.99***	9.23 a	4.37 a	3.06 b
Seed width (mm)	^{kw} 6.40*	3.2 a	1.12 b	1.42 ab
Seed thickness (mm)	^{kw} 3.75 ns	2.14 a	0.83 a	0.90 a
Seed weight (mg)	^{kw} 4.54 ns	9.84 a	1.76 a	2.01 a
Surface texture (rank)	^{kw} 7.72*	2.11 ab	3.15 a	1.86 b
Appendage length (mm)	^{kw} 58.57***	2.62 a	5.02 a	0.00 b
Appendage density (rank)	^{kw} 61.57***	1.00 a	2.20 a	0.00 b
Appendage type	^{chi}132***	–5.0/7.8/ –0.5/–1.4/–0.3/–0.5	–11.2/–2.7/ 2.8/7.0/1.4/2.8	16.3/–5.0/ –2.2/–5.6/–1.1/–2.2

^{kw}Kruskal–Wallis test. Values are group averages and groups that differ significantly are indicated with different letters.
^{chi} Pearson χ^2 association test. Values are the differences between the observed and expected values for the different appendage types (first line: no appendages/stem or remnants of perianth; second line: awn/hairs/bristles/hooks). A positive value indicates an overrepresentation of that appendage type in the cluster.
*** $P \leqslant 0.001$; ** $P \leqslant 0.01$; * $P \leqslant 0.05$; ns, not significant.

Table 5. Overview of the seed adhesivity scores (AS) of the different seed clusters on the seven furs (SUA, seeds with unspecialized appendages; SSA, seeds with specialized appendages; SWA, seeds without appendages; n = number of seed species in the clusters). A one-way ANOVA was used to test the differences between the clusters. Values are group averages and groups that differ significantly are indicated with different letters

	F	SUA	SSA	SWA
n		9	20	37
Horse	10.51***	0.04 a	0.29 b	0.08 a
Rabbit	17.14***	0.05 a	0.23 b	0.08 a
Holstein	9.04***	0.09 a	0.29 b	0.15 a
Roe deer	9.36***	0.14 a	0.41 b	0.21 a
Wild boar	5.40**	0.21 a	0.39 b	0.36 b
Sheep	19.58***	0.22 a	0.57 b	0.29 a
Galloway	16.86***	0.32 a	0.66 c	0.46 b
Global AS	15.80***	0.15 a	0.40 b	0.23 a

*** $P \leqslant 0.001$; ** $P \leqslant 0.01$; ns, not significant.

species of clusters SSA and SWA were correctly classified (75% and 89.2%, respectively), while only 33.3% of the species in cluster SUA were correctly classified. Wrongly assigned species of the clusters SUA and SSA were almost all assigned to cluster SWA, while wrongly assigned species of cluster SWA were mainly assigned to cluster SUA. This intermediate position of cluster SWA was not reflected in the cluster analysis, where cluster SWA was separated from both other clusters on a higher hierarchical level.

Discussion

General

This study provides detailed experimental information on the adhesivity of a wide variety of seed types on to prepared furs of seven mammals. Our method allows species to be ranked on an ordinal scale, on the basis of their adhesivity scores. Both the 'global' adhesivity score (the average of the adhesivity scores on all tested furs) and the adhesivity scores on individual furs can be used for this purpose, since the ranking of the species showed relatively small differences between different furs. The adhesivity score, reflecting the epizoochorous dispersal potential, continually varies among species, ranging from extremely low to extremely high. In contrast to the formerly established idea that 'the' dispersal mechanism can be derived directly from the morphological properties of a seed (Grime *et al.*, 1988; Hughes *et al.*, 1994), it is thus likely that even species adapted to other dispersal modes or unspecialized species can disperse epizoochorously. Recently, species have been recognized to disperse in many different ways (Higgins *et al.*, 2003; Tackenberg *et al.*,

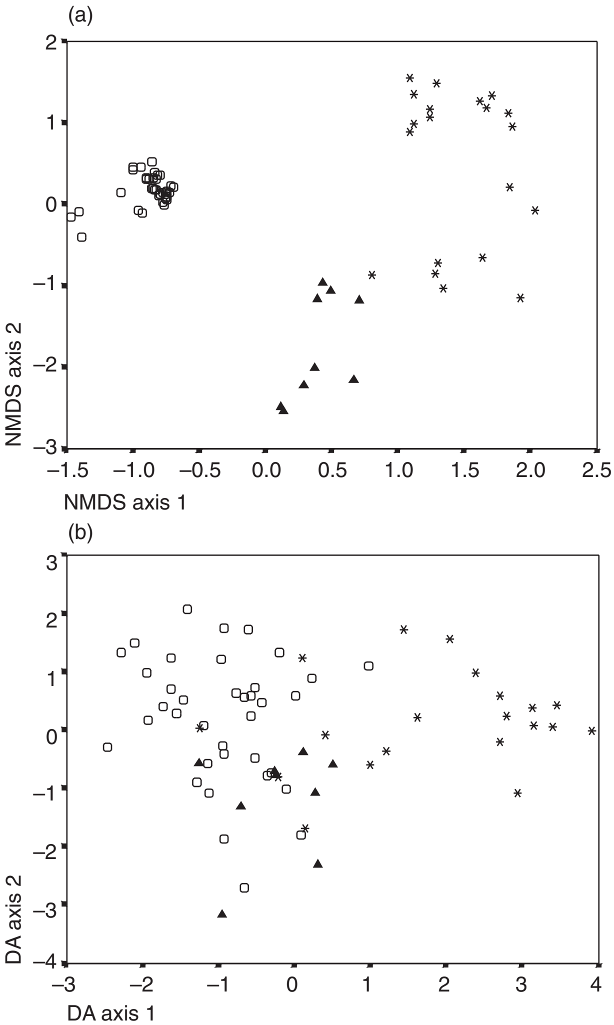

Figure 2. Ordination of the 66 seed species by (a) non-metric multidimensional scaling (NMDS) of the Gowers' proximity matrix, based on eight different seed traits, and (b) discriminant analysis (DA) based on adhesivity scores (86.9% of the total variance is explained by axis 1 and 13.1% by axis 2). The three seed type clusters are represented by different symbols: triangles, cluster SUA (seeds with unspecialized appendages); stars, cluster SSA (seeds with specialized appendages); squares, cluster SWA (seeds without appendages).

2003). Questions regarding the relative efficiency of certain dispersal modes for a range of species are answerable after characterization and comparison of the relative dispersal potentials of the species on an ordinal scale, on the basis of indicator values of dispersal potential for different dispersal modes (Tackenberg *et al*., 2003). Efforts to establish a species ranking with respect to wind dispersal potential and, to a more limited extent, water dispersal potential have already been made by Tackenberg *et al*. (2003) and Lopez (2001), respectively. This paper provides a method for species ranking in terms of epizoochorous dispersal potential.

Methodology

The adhesivity test method was chosen for its simplicity (e.g. in comparison with the method of Gorb and Gorb, 2002), and preferred to other explored methods, such as one involving pushing the fur softly on to the seeds and then lifting it up. In the latter method, standardization of the applied force on to the furs was complicated by the weight differences between the furs, and damage to fragile seeds (e.g. *Cirsium oleraceum)* was inevitable. Seed dropping on to the fur might have resulted in a somewhat conservative assessment of the adhesivity of seeds with adhesive adaptations, since the heaviest part of such seeds, which is usually not the most adhesive, touches the fur first when falling. In addition, the results may vary with intra-species variation in seed and fur characteristics (see also Kiviniemi, 1996), which can depend on genetic factors, on the seed position in the inflorescence of a plant, on the season, or on the age, sex and health or body part of an animal (see also Agnew and Flux, 1970; Mrotzek *et al*., 1999).

Possibilities abound for extending the test method used in this paper. For example, after the first rotation of the construction, followed by counting of the attached seeds, the construction could be tilted once again. This procedure could demonstrate that once seeds are attached to the fur, they are less likely to fall off rapidly. In other words, it would explain why the epizoochorous dispersal curve is very steep at the beginning, but exhibits a relatively fat tail, because

Table 6. Cross-tabulation of the number of seed species in the seed clusters (rows) and the predicted groups from the discriminant analysis (DA, columns). The last column shows the percentage of correctly classified species of each cluster

Cluster	DA group 1	DA group 2	DA group 3	Total	% Correctly assigned
SUA	3	0	6	9	33.3
SSA	1	15	4	20	75.0
SWA	3	1	33	37	89.2
Total	7	16	43	66	77.3

https://doi.org/10.1079/SSR2004164 Published online by Cambridge University Press

attached seeds tend to stay attached. Other variations of the tilt-method, such as shaking of the fur construction, could imitate animal movement. In addition, the effect of weather conditions could be investigated by using dry, moist and wet furs. Special adaptations, such as mucus-containing seed coats, could then be validated. For instance, *Plantago lanceolata* and *Prunella vulgaris* do not behave differently from other similarly shaped species in the present study, but might perform better on wet furs.

Fur traits and seed traits influencing adhesivity

The fur traits positively associated with high adhesivity scores were hair length, fur roughness, fur depth, hair undulation, and angle between hair and skin (Fig. 1). Galloway cattle, sheep and wild boar proved to be most suited for seed adherence, followed by roe deer, and finally Holstein cattle, rabbit and horse (Table 1). This is in agreement with observations of other authors who compared fur impact on seed adhesion, e.g. Heinken and Raudnitschka (2002) for wild boar and roe deer; Kiviniemi (1996) and Kiviniemi and Telenius (1998) for fallow deer and short-haired domestic cattle; Shmida and Ellner (1983) for sheep and goat.

The three seed clusters, based on eight seed traits (Table 4), had different adhesivity scores (Table 5). Cluster SSA [seeds with specialized appendages (awns, hairs, bristles, hooks)], scored significantly better than the two similarly scoring clusters, SUA [seeds with unspecialized appendages (stems or remnants of the perianth)] and SWA (seeds without appendages). This was true for all furs, except those of Galloway, on which cluster SWA had a score intermediate between SUA and SSA, and wild boar, where cluster SWA scored as high as SSA. Our results suggest that unspecialized appendages, such as stems, do not contribute to, or might even hamper seed adherence. However, the larger length of the seeds in cluster SUA, in comparison with cluster SWA seeds, may also explain their low adhesivity scores. Nevertheless, the seeds in cluster SSA, with specialized adhesive appendages (awns, hooks and bristles), adhered very well, although they were not differently sized from seeds in cluster SUA. (Tables 3 and 4). The negative impact of seed length, seed width, seed thickness and seed weight on adhesivity was also higher if only the species without adhesive appendages were considered (Table 2). Our results suggest that specialized adhesive appendages can, at least partly, overcome the adhesive dispersal difficulties of larger-sized and heavy seeds (see also Kiviniemi and Telenius, 1998). Only in the case of wild boar did the advantage of appendage-bearing seeds seem to be absent (Table 5). Apparently, fur density and hair thickness have an opposite effect on certain seed types (interaction-effect of fur type and seed type) (Fig. 1). For instance, seeds with specialized adhesive appendages adhered better to the dense, thin-haired fur of sheep than on the thick-haired, not-dense fur of wild boar, while the reverse was true for seeds without appendages. In the fur of wild boar, many small seeds without appendages (e.g. *Lychnis flos-cuculi*, *Silene conica*, *Myosotis scorpioides*, *Lycopus europaeus*, *Glyceria maxima*) adhered better than seeds with very specialized adhesive appendages (e.g. *Torilis japonica*, *Bidens frondosa*, *Erodium cicutarium*, *Geum urbanum* and *Daucus carota*). The wild boars' thick hairs, implanted at low densities, apparently allow good penetration and retention of small, unappendaged seeds, but offer relatively poor grip to seeds with sophisticated adhesive appendages [see also Mrotzek *et al*. (1999) and Heinken and Raudnitschka (2002)]. In contrast, the dense undulated fur of sheep, as well as the other furs, seemed better suited for attachment of seeds with specialized appendages.

The high degree of predictability of the adhesivity scores starting from the seed clusters (Fig. 2, Table 6) indicates that seed morphology is a good predictor for adhesivity on fur. Seeds with unspecialized appendages, however, behave more like unappendaged seeds than like seeds with specialized appendages (Fig. 2). However, the predictive potential of seed morphological traits for adhesivity to fur, does not imply that one seed morphological aspect determines 'the' seed dispersal mechanism of a plant. Wind-dispersal adaptations, for instance, also provide some seed adhesivity to fur. Unspecialized appendages do not appear to aid seed adherence, and the functionality of specialized adhesive appendages depends on the fur type. In addition, it is important to realize that the adhesivity scores of the clusters SWA and SUA are still about half those of cluster SSA. This suggests that it is likely that even seeds without epizoochorous adaptations can disperse successfully by epizoochory. The fact that even seeds with very low adhesivity scores (*Galeopsis tetrahit*, *Anthriscus sylvestris*, *Heracleum sphondylium*, *Angelica sylvestris*, *Alnus glutinosa*) have been observed to disperse epizoochorously in other studies (see Appendix 1), further adds to the evidence that many more species than previously thought occasionally disperse in the fur of mammals. Possibly, some of these species could adhere successfully by means of remains of other rough plant parts on the seeds.

However, full understanding of the process of epizoochory requires an integration of knowledge about all influencing factors. For instance, the chance of a seed reaching an animal's fur also depends on the abundance in the vegetation (Stender *et al*., 1997) and on plant traits, such as the height of seed exposure (Fischer *et al*., 1996; Stender *et al*., 1997; Heinken, 2000), the duration of the disseminating period (Fischer *et al*., 1996; Heinken, 2000), the degree of seed exposure and the ease of release from the parent plant. The latter occurs in the case of many wind-dispersed herbs in dry, sunny weather (Tackenberg *et al*., 2003) and might also influence epizoochory. Other key elements in epizoochorous dispersal are animal presence and behaviour (Fischer *et al*., 1996). Animal behaviour can also interact with seed traits. For instance, pronounced adhesive structures that promote seed attachment to fur may actually reduce the probability of successful dispersal by increasing grooming behaviour, especially if the seeds are accessible and noticeable to the animals (Sorensen, 1986; Kiviniemi, 1996).

Conclusions and consequences

The adhesivity scores, as a measure of epizoochorous seed dispersal potential, suggest that a continuum in adhesive capacity exists among all types of seeds, and that, for most species, seed morphology is probably not a limiting factor for epizoochorous dispersal. Species with high adhesivity scores probably have a higher potential to achieve long-distance dispersal through epizoochory. Although it remains arbitrary to define a threshold in this context, we propose that seed species with a global adhesivity score higher than 0.3 have a reasonable chance of being dispersed over long distances in fur, at least if they are sufficiently abundant in the vegetation. Species such as *Juncus effusus, Eupatorium cannabinum, Torilis japonica* and *Urtica dioica*, for instance, with a global adhesivity score between 0.3 and 0.4, have been observed frequently in animal fur (Appendix 1).

Although we demonstrated the existence of an interaction-effect between seed morphology and fur type, which was best illustrated by comparing the fur of wild boar with other furs, our results indicate that specialized seed appendages, such as awns, hooks and bristles, considerably enhance adhesivity to fur. Seeds with unspecialized appendages, such as stems, did not perform better than unappendaged seeds.

Long-haired, deep, rough, undulating furs, with a large angle between hairs and skin, proved to be most suited for dispersing seeds over large distances. This does not mean that animals with smooth, short-haired, shallow furs do not participate in epizoochorous seed dispersal. Smooth-furred small mammals, such as rabbits and mice, for instance, probably contribute considerably to epizoochory on a local scale (see also Kiviniemi and Telenius, 1998), especially in view of their high relative abundance in our landscapes. Domesticated large herbivores with smooth, straight, short hairs, such as horse and Holstein cattle, are also expected to contribute to epizoochory on a rather local scale. Roe deer, with somewhat longer and rougher fur, takes an intermediate position with respect to seed adhesivity, but might be of considerable importance, being the most abundant wild large mammal in the western European landscape. Also, wild boar might be an important long-distance seed disperser, taking into account its high adhesivity scores and large home range (Briedermann, 1990). However, the two furs with the highest adhesivity scores belong to sheep and Galloway cattle. Therefore, the increasing importance of the latter animals in nature management seems a positive step from a plant dispersal point of view.

Acknowledgements

This research was supported financially by a Research Assistant grant from the Fund for Scientific Research, Flanders (FWO). We are grateful to Bert Delanoeije for the practical help.

References

Agnew, A.D.Q. and Flux, J.E.C. (1970) Plant dispersal by hares (*Lepus capensis* L.) in Kenya. *Ecology* **51**, 735–737.

Bonn, S. and Poschlod, P. (1998) *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Wiesbaden, Quelle and Meyer Verlag.

Briedermann, L. (1990) *Schwarzwild* (2nd edition) Berlin, Deutscher Landwirtschaftsverlag.

Bullock, S.H. and Primack, R.B. (1977) Comparative experimental study of seed dispersal on animals. *Ecology* **58**, 681–686.

Castillo-Flores, A.A. and Calvo-Irabien, L.M. (2003) Animal dispersal of two secondary-vegetation herbs into the evergreen rain forest of south-eastern Mexico. *Journal of Tropical Ecology* **19**, 271–278.

Clustan Ltd (2001) Clustangraphics 5.08. Edinburgh, Clustan Ltd.

Dillon, W.R. and Goldstein, M. (1984) *Multivariate analysis: Methods and applications*. New York, John Wiley and Sons.

Doyle, P. (1973) Nonmetric multidimentional scaling – users guide. *European Journal of Marketing* **7**, 82–88.

Fischer, S.F., Poschlod, P. and Beinlich, B. (1996) Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* **33**, 1206–1222.

Gorb, E. and Gorb, S. (2002) Contact separation force of the fruit burrs in four plant species adapted to dispersal by mechanical interlocking. *Plant Physiology and Biochemistry* **40**, 373–381.

Graae, B.J. (2002) The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Science Research* **12**, 113–121.

Grime, J.P., Hodgson, J.G. and Hunt, R. (1988) *Comparative plant ecology*. London, Unwin Hyman Ltd.

Heinken, T. (2000) Dispersal of plants by a dog. *Botanische*

Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie **122**, 449–467.

Heinken, T. and Raudnitschka, D. (2002) Do wild ungulates contribute to the dispersal of vascular plants in central European forests by epizoochory? A case study in NE Germany. *Forstwissenschaftliches Centralblatt* **121**, 179–194.

Heinken, T., Lees, R., Raudnitschka, D. and Runge, S. (2001) Epizoochorous dispersal of bryophyte stem fragments by roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *Journal of Bryology* **23**, 293–300.

Higgins, S.I. and Richardson, D.M. (1999) Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist* **153**, 464–475.

Higgins, S.I., Nathan, R. and Cain, M.L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* **84**, 1945–1956.

Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgerson, L. and Westoby, M. (1994) Predicting dispersal spectra – a minimal set of hypotheses based on plant attributes. *Journal of Ecology* **82**, 933–950.

Kiviniemi, K. (1996) A study of adhesive seed dispersal of three species under natural conditions. *Acta Botanica Neerlandica* **45**, 73–83.

Kiviniemi, K. and Telenius, A. (1998) Experiments on adhesive dispersal by wood mouse: seed shadows and dispersal distances of 13 plant species from cultivated areas in southern Sweden. *Ecography* **21**, 108–116.

Lacey, E.P. (1981) Seed dispersal in wild carrot (*Daucus carota*). *The Michigan Botanist* **20**, 15–20.

Lambinon, J., De Langhe, J.E., Delvosalle, L. and Duvigneaud, J. (1998) *Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden*. Meise, Nationale Plantentuin van België.

Lopez, O.R. (2001) Seed flotation and postflooding germination in tropical terra firme and seasonally flooded forest species. *Functional Ecology* **15**, 763–771.

Mrotzek, R., Halder, M. and Schmidt, W. (1999) Die Bedeutung von Wildschweinen für die Diasporenausbreitung von Phanerogamen. *Verhandlungen der Gesellschaft für Ökologie* **29**, 437–443.

Shmida, A. and Ellner, S. (1983) Seed dispersal on pastoral grazers in open Mediterranean chaparral, Israel. *Israel Journal of Botany* **32**, 147–159.

Siegel, S. and Castellan, N.J. (1988) *Non-parametric statistics for the behavioural sciences*. New York, McGraw-Hill.

Sorensen, A.E. (1986) Seed dispersal by adhesion. *Annual Review of Ecology and Systematics* **17**, 443–463.

SPSS (1999) SPSS 10.0. Chicago, SPSS Inc.

Stender, S., Poschlod, P., Vauk-Hentzelt, E. and Dernedde, T. (1997) Die Ausbreitung von Pflanzen durch Galloway-Rinder. *Verhandlungen der Gesellschaft für Ökologie* **27**, 173–180.

Tackenberg, O., Poschlod, P. and Bonn, S. (2003) Assessment of wind dispersal potential in plant species. *Ecological Monographs* **73**, 191–205.

ter Braak, C.J.F. and Smilauer, P. (2003) *CANOCO reference manual and user's guide to Canoco for Windows, software for canonical community ordination (version 4.5)*. Ithaca, New York, Microcomputer Power.

Appendix 1

Overview of the 66 study species, with a description of their diaspores (further referred to as seeds) (column 2), seed traits (columns 3–10), seed cluster number [1, seeds with unspecialized appendages (SUA); 2, seeds with specialized appendages (SSA); 3, seeds without appendages (SWA)] (column 11), adhesivity scores on the furs of seven animal species (columns 12–18) and global adhesivity score (the average adhesivity of the seven furs) (column 19). Botanical nomenclature follows Lambinon *et al*. (1998). At least 38 of the plant species have been observed to disperse epizoochorously, and at least five of the animal species have been reported as epizoochorous dispersal vectors (indicated by a reference number after the species name)

	Seed traits										Adhesivity scores							
	Diaspore description	Appendage type	Seed surface texture	Appendage density	Appendage length (mm)	Seed length (mm)	Seed width (mm)	Seed thickness (mm)	Seed weight (mg)	Seed cluster	Horse[8]	Rabbit	Holstein cattle	Roe deer[7]	Wild boar[4,7]	Sheep[1,2]	Galloway cattle[3,8]	Mean adhesivity score
Achillea millefolium[7]	5	1	1	1	1.88	4.46	0.62	0.63	0.4	1	0.028	0.052	0.112	0.292	0.372	0.360	0.448	0.238
Agrostis canina[3]	3	2	1	1	1.54	2.09	0.31	0.31	0.02	2	0.424	0.628	0.476	0.720	0.584	0.724	0.848	0.629
Alisma plantago-aquatica	2	0	1	0	0	1.69	0.93	0.20	0.2	3	0.056	0.024	0.232	0.200	0.436	0.360	0.576	0.269
Alnus glutinosa[7,8]	2	0	3	0	0	2.85	2.15	0.82	1.2	3	0.016	0.020	0.040	0.064	0.264	0.200	0.340	0.135
Alopecurus pratensis[2,4,5]	3	2	4	1	4.31	4.79	1.80	0.76	0.4	2	0.356	0.440	0.308	0.660	0.496	0.724	0.784	0.538
Angelica sylvestris[2]	2	0	3	0	0	4.68	3.40	0.91	2	3	0.036	0.016	0.240	0.044	0.144	0.124	0.256	0.123
Anthoxanthum odoratum[2,3]	3	2	4	2	7.72	3.17	1.12	1.00	0.6	2	0.276	0.416	0.324	0.436	0.596	0.744	0.844	0.519
Anthriscus sylvestris[2,8]	2	0	1	0	0	7.43	1.08	1.08	5.2	3	0.008	0.004	0.012	0.004	0.188	0.136	0.272	0.089
Arrhenatherum elatius[2,8]	3	2	4	1	4.29	7.90	1.50	1.50	1.8	2	0.268	0.288	0.312	0.344	0.364	0.676	0.780	0.433
Bellis perennis[3]	2	0	4	0	0	1.40	0.64	0.11	0.02	3	0.360	0.112	0.432	0.624	0.488	0.448	0.616	0.440
Bidens frondosa[8]	2	5	5	2	3.12	7.23	2.17	0.68	3	2	0.288	0.336	0.400	0.356	0.340	0.716	0.716	0.450
Bromus sterilis[7]	3	5	5	1	24.23	16.05	1.28	1.28	8.75	2	0.080	0.432	0.116	0.444	0.528	0.788	0.876	0.466
Caltha palustris	1	0	1	0	0	2.65	1.22	1.22	1.9	3	0.000	0.006	0.013	0.031	0.200	0.088	0.344	0.097
Capsella bursa-pastoris[2,3,4,7]	1	0	1	0	0	0.87	0.44	0.44	0.1	3	0.260	0.472	0.308	0.552	0.448	0.420	0.548	0.430
Centaurea jacea[2,4]	2	0	1	0	0	3.29	1.25	1.25	2.3	3	0.004	0.024	0.028	0.072	0.320	0.148	0.352	0.135
Centaurea nigra[8]	4	3	1	2	0.35	3.51	1.27	1.27	2.4	2	0.000	0.036	0.200	0.080	0.304	0.240	0.288	0.164
Chelidonium majus	1	0	1	0	0	1.30	0.77	0.77	0.6	3	0.012	0.088	0.084	0.260	0.420	0.232	0.412	0.215
Cirsium oleraceum	4	3	1	3	15.92	4.31	1.53	0.96	4.5	2	0.020	0.000	0.020	0.040	0.000	0.000	0.280	0.051
Crepis biennis	4	3	2	3	5.76	4.70	0.60	0.60	1.4	2	0.060	0.124	0.148	0.176	0.436	0.444	0.644	0.290
Daucus carota[1,2,4]	2	4	5	3	1.00	2.78	1.30	0.78	0.8	2	0.228	0.340	0.428	0.404	0.444	0.748	0.732	0.475
Erodium cicutarium	2	5	5	1	7.85	4.81	0.91	0.91	1	2	0.464	0.272	0.488	0.528	0.424	0.640	0.576	0.485
Eupatorium cannabinum[3,8]	4	3	2	3	4.26	2.66	0.33	0.33	0.4	2	0.208	0.124	0.312	0.544	0.272	0.304	0.528	0.327
Fallopia japonica	6	1	2	1	3.01	9.92	4.87	4.87	2.2	1	0.060	0.016	0.072	0.016	0.104	0.112	0.348	0.104
Festuca pratensis[3,8]	3	0	1	0	0	6.38	1.34	0.77	2.4	3	0.040	0.012	0.020	0.136	0.376	0.228	0.520	0.190
Filipendula ulmaria[4]	2	0	2	0	0	3.01	1.23	0.58	0.8	3	0.008	0.016	0.128	0.140	0.436	0.216	0.500	0.206
Fraxinus excelsior	2	1	2	1	2.44	42.35	8.51	0.37	59.2	1	0.000	0.000	0.000	0.000	0.008	0.008	0.004	0.003
Galeopsis tetrahit[4]	2	0	1	0	0	3.17	2.20	1.66	5.5	3	0.000	0.000	0.000	0.044	0.156	0.022	0.267	0.070
Galinsoga ciliata[8]	4	3	4	3	1.04	2.40	0.40	0.40	0.2	2	0.356	0.536	0.496	0.612	0.524	0.756	0.772	0.579

	Seed traits										Adhesivity scores							
	Diaspore description	Appendage type	Seed surface texture	Appendage density	Appendage length (mm)	Seed length (mm)	Seed width (mm)	Seed thickness (mm)	Seed weight (mg)	Seed cluster	Horse[8]	Rabbit	Holstein cattle	Roe deer[7]	Wild boar[4,7]	Sheep[1,2]	Galloway cattle[3,8]	Mean adhesivity score
Geum urbanum[2, 4–8]	2	5	4	1	3.16	3.76	1.36	0.72	1.5	2	0.236	0.372	0.232	0.432	0.436	0.688	0.784	0.454
Glyceria fluitans[3,8]	3	0	2	0	0	5.71	1.05	1.05	0.6	3	0.056	0.060	0.112	0.100	0.296	0.344	0.680	0.235
Glyceria maxima	3	0	2	0	0	3.56	0.48	0.76	0.2	3	0.096	0.192	0.108	0.268	0.500	0.336	0.492	0.285
Heracleum sphondylium[2]	2	0	2	0	0	9.47	7.28	0.34	3.8	3	0.048	0.040	0.040	0.088	0.152	0.148	0.196	0.102
Juncus effusus[3,4,8]	7	1	3	1	3.13	1.91	1.25	1.25	0.4	1	0.212	0.160	0.172	0.368	0.348	0.420	0.536	0.317
Knautia arvensis	2	3	4	3	1.12	4.83	2.41	1.49	5.6	2	0.000	0.008	0.004	0.052	0.144	0.092	0.336	0.091
Leucanthemum vulgare[2]	2	0	3	0	0	2.46	0.78	0.78	0.8	3	0.076	0.040	0.140	0.064	0.476	0.344	0.504	0.235
Lychnis flos-cuculi	1	0	2	0	0	0.55	0.55	0.55	0.1	3	0.204	0.168	0.360	0.476	0.536	0.424	0.652	0.403
Lycopus europaeus[4,8]	2	0	2	0	0	1.43	1.04	0.48	0.4	3	0.072	0.152	0.208	0.224	0.512	0.412	0.504	0.298
Lysimachia vulgaris	1	0	2	0	0	1.71	1.05	1.05	0.4	3	0.028	0.032	0.060	0.200	0.396	0.288	0.564	0.224
Lythrum salicaria[8]	1	0	1	0	0	0.90	0.28	0.28	0.02	3	0.364	0.188	0.472	0.580	0.456	0.472	0.644	0.454
Myosotis scorpioides	2	0	2	0	0	0.87	0.87	0.59	0.2	3	0.160	0.144	0.168	0.384	0.512	0.368	0.540	0.325
Myosoton aquaticum	1	0	1	0	0	1.61	1.13	1.13	0.5	3	0.030	0.050	0.120	0.230	0.340	0.230	0.510	0.216
Myrrhis odorata	2	0	3	0	0	18.15	2.42	2.42	25	3	0.000	0.000	0.000	0.000	0.028	0.032	0.084	0.021
Oenothera biennis	1	0	2	0	0	1.67	1.02	1.02	0.6	3	0.028	0.064	0.040	0.176	0.428	0.300	0.456	0.213
Papaver rhoeas[2,4]	1	0	2	0	0	0.54	0.54	0.54	0.02	3	0.256	0.056	0.484	0.552	0.492	0.464	0.604	0.415
Phalaris arundinacea[8]	3	3	1	2	1.05	3.11	0.93	0.93	0.2	2	0.172	0.180	0.200	0.468	0.480	0.520	0.620	0.377
Phragmites australis	3	3	1	3	5.88	2.95	0.78	0.78	0.2	2	0.456	0.152	0.404	0.564	0.448	0.616	0.760	0.486
Plantago lanceolata[3,8]	1	0	1	0	0	2.61	1.19	1.19	1.8	3	0.000	0.004	0.240	0.084	0.332	0.328	0.404	0.199
Polygonum hydropiper	2	0	2	0	0	3.56	1.85	1.25	2.2	3	0.004	0.020	0.016	0.040	0.220	0.212	0.364	0.125
Prunella vulgaris[4]	2	0	1	0	0	1.64	0.91	0.91	0.6	3	0.068	0.032	0.036	0.164	0.472	0.340	0.392	0.215
Pulicaria dysenterica	4	3	1	3	3.27	1.47	0.22	0.22	0.1	2	0.400	0.540	0.444	0.588	0.332	0.672	0.752	0.533
Ranunculus acris	2	1	2	1	0.42	3.62	2.40	1.02	2.4	1	0.000	0.000	0.016	0.060	0.236	0.116	0.336	0.109
Rhinanthus minor	1	0	2	0	0	4.59	3.56	0.63	3.2	3	0.004	0.008	0.004	0.020	0.204	0.064	0.376	0.097
Rumex hydrolapathum	6	1	2	1	3.48	4.99	3.84	3.84	5.8	1	0.008	0.020	0.136	0.032	0.124	0.128	0.188	0.091
Rumex obtusifolius[2,5,8]	6	1	3	1	3.98	4.42	3.50	3.50	3	1	0.036	0.088	0.212	0.252	0.272	0.348	0.348	0.222
Scrophularia nodosa[4]	1	0	2	0	0	0.77	0.39	0.39	0.2	3	0.232	0.200	0.372	0.444	0.500	0.428	0.648	0.403
Scutellaria galericulata	2	0	3	0	0	1.38	1.38	1.38	0.6	3	0.016	0.060	0.092	0.248	0.368	0.396	0.412	0.227
Senecio jacobea[8]	4	3	4	3	4.36	1.74	0.49	0.49	0.3	2	0.160	0.240	0.300	0.432	0.332	0.640	0.604	0.387
Silene conica	1	0	2	0	0	0.93	0.74	0.74	0.4	3	0.068	0.072	0.204	0.264	0.520	0.356	0.652	0.305
Silene dioica[4]	1	0	2	0	0	1.12	1.12	1.12	0.8	3	0.004	0.076	0.272	0.124	0.400	0.416	0.412	0.243
Sparganium erectum	5	1	2	1	3.39	7.19	3.08	3.08	14.6	1	0.004	0.000	0.004	0.016	0.084	0.172	0.252	0.076
Symphytum officinale	2	0	1	0	0	4.22	2.60	2.60	7.2	3	0.000	0.004	0.000	0.012	0.044	0.056	0.224	0.049
Tanacetum vulgare[3,4,8]	5	1	2	1	1.89	4.16	0.74	0.74	0.6	1	0.036	0.108	0.100	0.252	0.328	0.332	0.464	0.231
Torilis japonica[2,4]	2	4	5	3	0.12	3.15	1.66	1.18	2	2	0.076	0.304	0.196	0.240	0.332	0.628	0.692	0.353

Trifolium dubium	1	0	2	0	0	2.48	2.11	1.08	2	3	0.027	0.093	0.040	0.053	0.347	0.387	0.400	0.192
Urtica dioica[2,4,6,7,8]	2	0	3	0	0	1.85	1.14	0.71	0.3	3	0.176	0.288	0.176	0.316	0.552	0.556	0.684	0.393
Verbascum thapsus	1	0	2	0	0	0.72	0.38	0.38	0.2	3	0.136	0.144	0.280	0.496	0.488	0.516	0.460	0.360

[1]Shmida and Ellner (1983); [2]Fischer *et al*. (1996); [3]Stender *et al*. (1997); [4]Mrotzek *et al*. (1999); [5]Heinken (2000); [6]Graae (2002); [7]Heinken and Raudnitschka (2002); [8]Couvreur *et al*. (unpublished).
Diaspore description: 1, seed; 2, fruit; 3, fruit with bracts; 4, fruit with pappus; 5, fruit with remnants of perianth; 6, fruit with stem and remnants of perianth; 7, capsule with stem and remnants of perianth.
Appendage type: 0, no appendages; 1, stem or remnants of perianth; 2, awn; 3, hairs; 4, bristles; 5, hooks.
Surface texture: 1, smooth; 2, slightly rough; 3, rough; 4, hairy; 5, sticky.
Appendage density: 0, no appendage; 1, one appendage; 2, low density (2–50); 3, high density (>50).

Appendix 2.

Overview of the fur traits of the different fur samples

Fur sample	Hair length (mm)	Fur depth (mm)	Hair thickness (rank)	Fur density (rank)	Fur roughness (rank)	Hair undulation (rank)	Hair–skin angle (rank)
Horse	15	2	3	3	2	1	1
Rabbit	32	13	2	4	1	1	2
Holstein cattle	20	2	3	2	2	1	1
Roe deer	55	15	4	4	4	2	2
Wild boar	100	25	5	1	5	1	3
Sheep	80	40	1	5	6	4	5
Galloway cattle	70	20	3	2	3	3	4

Received 5 January 2004
accepted after revision 17 February 2004