

# How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits

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Römermann, C., Tackenberg, O. and Poschlod, P. 2005. How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. – *Oikos* 110: 219–230.

Dispersal is a process that determines many aspects in the life-history of plants. Up to now, however, it is difficult to quantify. Many studies rather assess it as a categorical trait, i.e. assuming a species is dispersed by a certain vector or not. Gradual differences in the dispersal potential between species are rarely considered.

In this paper we focus on the key process of epizoochory: the attachment potential of species to animal coats. We present two simple models (GLMs) how to quantify and to predict attachment potentials to sheep wool and to cattle hair from easily measurable seed traits. To calibrate the models, we investigated the attachment potential of seeds of 130 plant species on mechanically shaken coats of sheep and cattle and measured traits describing the seeds. We found that seed mass and seed morphology were correlated with attachment potentials. For sheep wool, the combination of the logarithm of seed mass and a constant for the different seed morphology types explained 85% of the variation of attachment potentials. For cattle hair, 71% were explained. To validate the models, they were applied to 36 additional species. Predicted and experimentally measured attachment potentials were correlated with  $r=0.84$  for sheep wool and  $r=0.61$  for cattle wool. Thus, the attachment potential of seeds to sheep or cattle coat can be assessed for a large set of species using the described models if seed mass and seed morphology are known.

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Dispersal, especially long-distance dispersal, has been consistently identified as an important process determining many aspects in the life history of plant species (Bonn and Poschlod 1998, Higgins and Richardson 1999, Nathan 2001), especially in fragmented landscapes (Poschlod et al. 1996a, Poschlod et al. 1998, Cain et al. 2000). Based on the theory of island biogeography (McArthur and Wilson 1967) and metapopulation dynamics (Hanski 1999), fragmentation is expected to result in reduced local population sizes and thereby increased extinction risk of local populations and a decreasing colonization due to isolation. It is therefore important to focus on dispersal processes of plants living in fragmented landscapes. Dispersal processes are how-

ever difficult to quantify (Nathan 2001). Hence, many studies rather assess dispersal as a categorical trait assuming a species is dispersed by means of a certain vector or not (Eriksson 1992, Rees 1993, Willson 1993, Hughes et al. 1994, Thompson et al. 2002). The classification systems most commonly used are based on diaspore morphology (Ridley 1930, Van der Pijl 1972, Müller-Schneider 1986, Sorensen 1986, Hughes et al. 1994, Cornelissen et al. 2003). It is assumed that e.g. species with hooked diaspores are adapted to external animal dispersal (= epizoochory, exozoochory, dispersal by adhesion), species with winged or plumed diaspores are classified as being wind-dispersed (anemochory), and species with fleshy fruits are predetermined for

Accepted 15 December 2004

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ISSN 0030-1299

internal animal dispersal (endozoochory). This classification is not evident, as several studies have shown that species with unspecialised or winged seeds are also e.g. epizoochorously dispersed (Fischer et al. 1996, Stender et al. 1997, Kiviniemi and Telenius 1998, Kiviniemi and Eriksson 1999, Heinken and Raudnitschka 2002).

As seed dispersal varies widely among plant species (Levin et al. 2003), gradual differences in the dispersal potential of species are likely to exist and have been proven by several studies e.g. for epizoochory by Fischer et al. (1996) and Kiviniemi (1996), for wind dispersal by Tackenberg et al. (2003) and for water dispersal by Poschlod et al. (1996b) and Boedeltje et al. (2003). In order to quantify these differences indicator traits have been developed for some dispersal types predicting a species' dispersal potential (Poschlod et al. 2004). Wind dispersal is regulated by falling velocity of the diaspores and height of release (Greene and Johnson 1989, Tackenberg et al. 2003). Water dispersal is related to specific density of the seeds, hence to seed mass and seed volume (Bill et al. 1999, Lopez 2001, Boedeltje et al. 2003). Endozoochorous dispersal is determined by specific gravity, hardness of the seed coat and seed size (Gardener et al. 1992).

Also the epizoochorous dispersal potential is driven by several processes and factors: one is the probability of seeds becoming attached to the fur of animals. Another key factor is the probability of them staying attached to the fur, i.e. the attachment potential (Fischer et al. 1996, Heinken and Raudnitschka 2002, Couvreur et al. 2004). Both processes are very difficult and time consuming to measure (Fischer et al. 1996, Couvreur et al. 2004) and easily measurable indicator traits predicting attachment potentials would be useful. Some studies have already described traits being related to the epizoochorous dispersal potential such as seed morphology and seed weight (Kiviniemi and Telenius 1998, Graae 2002, Heinken and Raudnitschka 2002, Couvreur et al. 2004), height of release (Graae 2002) and seed production (Willson 1993, Bruun and Fritzboeger 2002). There are, however, no studies going one step further, i.e. providing rules or algorithms on how to predict the epizoochorous dispersal ability from indicator traits.

In the current study we focus on one important process determining the dispersal ability of single diaspores: the attachment potentials of seeds to different fur types. Our aim is to find easily measurable traits being related to the attachment potential of diaspores and to predict attachment potentials from these traits. As large herbivores, which are long-distance dispersers, play major roles in agricultural and conservation management in Europe, we will develop two models: one for curly sheep wool and one for straight cattle hair.

## Materials and methods

### Species and diaspore selection

We measured attachment potentials of 130 plant species of the Northwest European flora (Appendix 1). As a first approach 120 species were selected randomly from the northwest European flora (area according to the boundaries given in Fitter et al. 1985; nomenclature according to the German standard list of Wißkirchen and Haeupler 1998). To include also species with seed morphologies being less abundant in the flora ten additional species were selected according to their seed morphology. Seeds were mainly collected in nature; rare species were obtained from botanical gardens and commercial seed suppliers. Generally all measurements were conducted on the diaspore, i.e. on the dispersal unit with all attached structures. For convenience all different diaspores (seeds or fruits) are referred to as seeds in this paper.

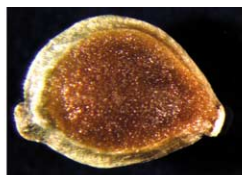
### Seed traits

Seed traits which are likely to determine seed attachment were examined, i.e. seed mass, seed dimensions (seed length, seed width, seed height) and seed morphology type (seed appendages).

Seed mass was measured by weighing three replicates of 100 seeds per species and calculating the mean weight for one single seed.

The three seed dimensions were measured on five replicate seeds per species using a binocular with a measurement ocular. Length, width and height were measured at the maximal extent of the respective dimension including all appendages.

Seed shape,  $V_s$ , (variance of seed dimension) was calculated according to the formula described in Bekker et al. (1998): the values of seed length, width and height were divided through length so that length is unity. The variance of these three values was calculated by dividing the summed squares of the deviation from the mean ( $\bar{x}$ ) by  $n - 3$ :  $V_s = \Sigma(x - \bar{x})^2 / n$ . The values range from 0 (perfectly spherical) to 0.2 (shaped like a slim needle or a thin disk). Seed morphology was described in five categories (Fig. 1; Klotz et al. 2002, Römermann et al. 2004a): "hooks", "elongated appendages", "flat appendages", "balloon structures" and "no appendages". The type "hooks" comprise all seeds with hooks, where hooks was meant as a functional term, therefore seeds with bristles that are directed downwards and that act as hooks were also included (e.g. *Bidens spec.*). "Elongated appendages" include all seeds having one or more appendages that prominently stick out from the seed surface in an elongated or stretched form and that are at least half as long as the respective dimension of the main part of the diaspore (i.e. bristles, awns, long hairs). "Flat



**No appendages:**  
*Ranunculus bulbosus* L.



**Flat appendages:**  
*Angelica sylvestris* L.



**Balloon structures:**  
*Carex alba* Scop.



**Elongated appendages:**  
*Centaurea stoebe* L.



**Hooks:**  
*Bidens cernua* L.



**Hooks:**  
*Daucus carota* L.



**Hooks:**  
*Agrimonia eupatoria* L.

Fig. 1. Examples for the classification of five different morphology types (proportions are not lifelike). The two last black and white pictures of seeds of *Daucus carota* L. and *Agrimonia eupatoria* L. were used to measure seed surface structure (=quotient of the perimeter of the intrinsic seed (=total extent of the seed) and the perimeter of the convex envelope around the seed (dashed line)).

appendages” comprise all structures that stick out of the more compact part of the dispersule with a flat, thin form and that at least double the seed surface (e.g. *Peucedanum* spec., *Acer* spec.). “Balloon structures” include all seeds with structures that are wrapped around the germinule in a more or less balloon like form, e.g. utricles of *Carex*-species or glumes of Poaceae. All seeds not belonging to one of the described categories were summarized in the category “no appendages”.

For this study every seed was categorized according to its main morphological type where the “main” type was that type which was likely to have the largest positive effect on the attachment potential (with effect of hooks > elongated appendages > flat appendages > balloon structures). For example seeds with elongated appendages and hooks (e.g. *Geum urbanum*) were classified as being “hooked” as hooks may play the most important role in the interaction between coat and seed. Awned grasses were classified as “elongated” as awns have an overruling effect on attachment potential compared to glumes which are categorized as open balloon structures.

To examine the effects of seed surface structures on attachment potentials on different coat types, we exemplarily developed a more detailed quantitative classification of the seed surface structure using image analyses for hooked diaspores. Pictures of five replicate seeds per species were taken under a binocular using the camera Axio Cam HRc and the program Axio Vision 3.1.2.1 (Carl Zeiss, Jena, Germany). The pictures were subsequently transformed into black and white pictures. Using the programme KS300 Version 3.0 (Carl Zeiss, Jena, Germany) the perimeter of the convex envelope around the seed and the perimeter of the intrinsic seeds including all appendages (and therefore resulting in a larger surface) were measured. Seed surface structure

was calculated by dividing the perimeter of the intrinsic seeds by the perimeter of the convex envelope around the seed (Fig. 1).

#### Attachment potential measurements

Attachment potentials (ATP) refer to the percentage of seeds still attached to a mechanically shaken animal coat after one hour (2400 swings). The experiments were carried out on sheep wool (Suffolk, wool length of about 3 cm, thick and curly) and on cattle hair (Fleckvieh cattle, wool length of about 8 cm, fine, smooth and straight to slightly undulated) using a machine that shakes the animal coats in a standardised way (Römermann et al. 2004b). For two selected species the temporal course of attachment rates measured in the lab-experiment using the machine fitted the field data measured by Fischer et al. (1996) in magnitude as well as in shape (O. Tackenberg, unpubl.). This indicates that the lab-experiment simulates the processes and mechanisms relevant under field conditions reasonably well.

Before starting the experiment the coat pieces (coat size of about 30 × 50 cm) were homogenised using a board with wooden pins (“comb”: board with 1.2 cm long wooden pins arranged in four lines with four centimetres distance between the pins). The board was moved two times each horizontally and vertically. Afterwards 100 seeds per species were distributed on the coat while lying in a horizontal position; for large-seeded species 60–80 seeds were taken to avoid neighbouring effects. Before installing the coat at the side of the machine the seeds were gently combed into the coat following the procedure described above. About 10 species were tested at the same time on the same coat depending on seed size. Generally, no more seeds were

applied than could adhere to the coat without interfering with each other. For every species the experiment was carried out on 3 replicates for both sheep wool and cattle hair.

## Data analysis

Analyses were done for each coat type separately.

As a first step we used non-parametric correlations (Spearman rank correlations) to investigate relationships between attachment potentials (AtP) and seed traits on a quantitative scale, and among seed traits themselves. For nominal traits we used one-way ANOVA with subsequent post-hoc LSD test; homogeneous variances and normal distribution were proved. Traits being correlated with attachment potentials but not inter-correlated with each other were included in a generalized linear model (GLM). Seed morphology was the main effect and  $\ln(\text{seed mass})$  was covariate. Regression model-1 was used as the magnitude of the random variation on the response variable (attachment potential) was much larger than that on the explanatory variables seed mass and seed morphology (Legendre and Legendre 1998). To achieve linear relationships between the parameters the attachment potentials (proportions) were arcsine-square root transformed and seed mass data were  $\ln$ -transformed before being analysed. Variables and residuals were normally distributed.

For the appendages type “hooks”, we set up a linear regression model considering seed surface structure and the logarithm of seed mass.

For all statistical analyses SPSS 11.0.1 (SPSS Inc., Chicago, USA) was used.

## Model validation

To validate the models, seed traits and attachment potentials were experimentally measured for another 36 species which were chosen according to seed availability (Appendix 2). Applying the respective models to both sheep wool and cattle hair the potential AtP were calculated. The so predicted AtP (from seed traits) were then compared with the measured AtP using

parametric correlations when pre-conditions were met. Otherwise non-parametric correlations were applied.

## Results

### Correlations between attachment potential and seed traits

For both sheep wool and cattle hair the best correlations with attachment potential were found for seed mass; negative relationships were detected (Table 1). The same relationships were identified for the seed dimensions seed length, seed width and seed height, though this can be attributed to the inter-correlation between seed dimensions and seed mass (Table 2). There was no relationship between seed shape and attachment potential (Table 1).

Figure 2 shows that different seed morphology types had different attachment potentials (sheep:  $F_{4,125} = 14.3$ ,  $p < 0.001$ ; cattle:  $F_{4,125} = 3.4$ ,  $p < 0.05$ ). When testing for differences in seed mass between the seed morphology types no significant differences were shown (Table 2). As seed mass and seed morphology are correlated with attachment potentials but not correlated with each other, both traits were used in the regression model.

### Regression model for attachment potential to sheep wool

The results of the GLM showed that both seed mass and seed morphology had an effect on attachment potentials (seed mass:  $F_{1,120} = 123.22$ ,  $p < 0.001$ ; seed morphology:  $F_{4,120} = 39.39$ ,  $p < 0.001$ ). The interaction between seed morphology and seed mass was not significant ( $F_{4,120} = 1.141$ ,  $p = 0.236$ ) indicating that the slopes of the regressions between seed mass and attachment potential to sheep wool did not differ between seed morphology types. The common regression slope being  $-0.132$  was significant ( $T = -17.686$ ,  $p < 0.001$ , Fig. 3) implying that there was a negative relationship between attachment potentials and seed mass. The attachment potentials adjusted by the covariate differed significantly between the morphology types ( $T = 54.78$ ,  $p < 0.001$ ) indicating the presence of an additive effect of seed

Table 1. Spearman rank correlations between attachment potential of seeds to sheep wool and cattle hair and seed traits.

Seed traits	N	Sheep		Cattle	
		$r_s$	p-value	$r_s$	p-value
Seed mass	130	-0.74	<0.001	-0.79	<0.001
Seed length	130	-0.45	<0.001	-0.57	<0.001
Seed width	130	-0.60	<0.001	-0.65	<0.001
Seed height	130	-0.50	<0.001	-0.55	<0.001
Seed shape (Vs)	130	-0.02	0.800	-0.10	0.268
Surface structure <sup>1</sup>	8	0.64	0.086	0.41	0.320

<sup>1</sup>seed surface structure was measured for hooked seeds only.

Table 2. Tests for possible inter-correlations within seed traits. As an index for the relation between the nominal trait seed morphology and seed mass, the test value of the ANOVA is given.

Seed trait 1	Seed trait 2	N	$r_s$	F	p-value
Seed mass	Seed length	130	0.73		<0.001
Seed mass	Seed width	130	0.78		<0.001
Seed mass	Seed height	130	0.68		<0.001
Seed mass	Seed morphology <sub>1</sub>	130		0.28	0.89
Seed mass	Surface structure <sub>1</sub>	8	-0.33		0.42

<sup>1</sup>seed surface structure was measured for hooked seeds only.

morphology on attachment potentials. Including different constants ( $C_{sheep}$ ) for each morphology type (estimated parameters from the GLM output in Table 3) we received one simple model equation to predict the attachment potential of seeds to sheep wool:

$$y = -0.132x + 0.843 + C_{sheep} \quad (1)$$

where  $y = \arcsin(\text{SQRT}(\text{AtP}(\%)_{sheep}/100))$ ,  $x = \ln(\text{seed mass (mg)})$ ,  $C_{sheep}$  = morphology type constants for sheep wool (Table 3). Due to the implemented arcsine function, AtP (%) sheep is set to 0 or to 100 when seed mass  $\geq 594$  mg or  $\leq 0.004$  mg for “no appendages” and “balloon structures”, when seed mass  $\geq 2914$  mg or  $\leq 0.02$  mg for “elongated appendages”, when seed mass  $\geq 9078$  mg or  $\leq 0.06$  mg for “hooks” and when seed mass  $\geq 77$  mg or  $\leq 0.0005$  mg for “flat appendages”. The regression was highly significant and explained 85% of the variation in attachment potentials ( $R^2 = 0.85$ ,  $F_{4,120} = 72.58$ ,  $p < 0.001$ , Fig. 3)!

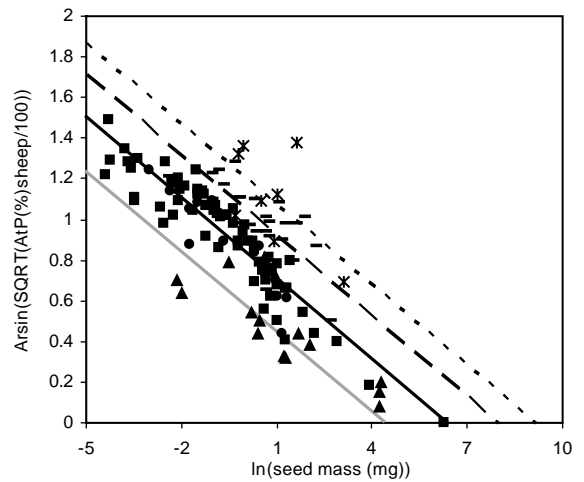
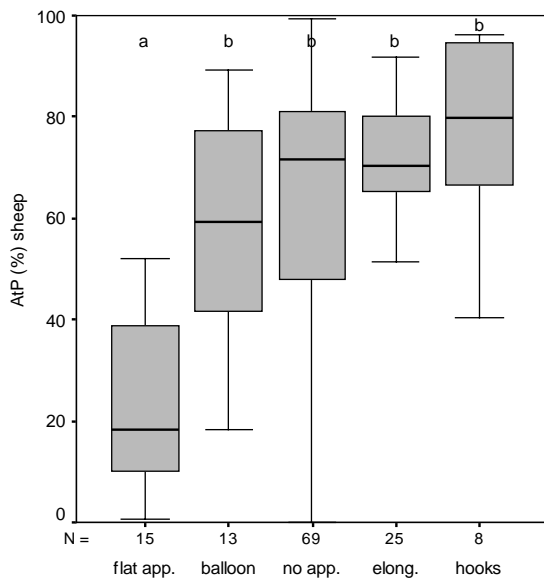


Fig. 3. Regressions of arcsine-square root transformed attachment potentials to sheep wool and  $\ln(\text{seed mass (mg)})$  with regard to the five different morphology types: ■ no appendages; \* hooks, — elongated appendages, ● balloon structures, ▲ flat appendages. For each morphology types, the regression lines are given (grey line: flat appendages, black line: no appendages, dashed line: elongated appendages, dotted line: hooks)

### Regression model for attachment potentials to cattle hair

Different to the model for sheep wool, the interaction between seed morphology and seed mass had a significant effect on attachment potentials ( $F_{4,120} = 3.74$ ,  $p < 0.01$ ; seed mass:  $F_{1,120} = 49.50$ ,  $p < 0.001$ ; seed morphology:  $F_{4,120} = 5.37$ ,  $p < 0.01$ ). The results of the GLM indicate that the intercepts and the slopes of the regression lines between seed mass and attachment

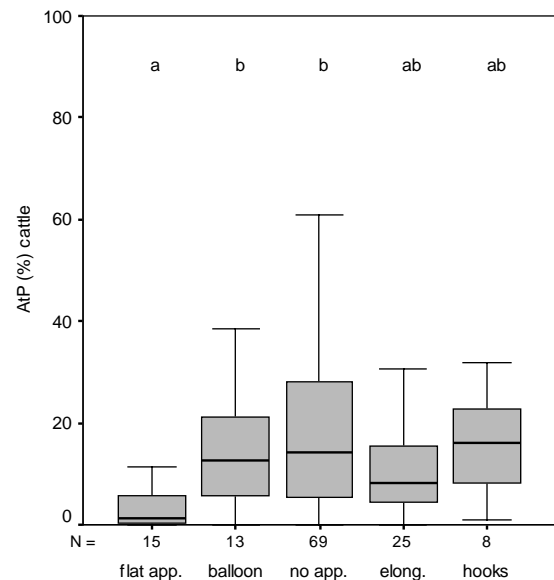


Fig. 2. Attachment potentials of seeds of different morphology types to sheep wool (left graph) and to cattle hair (right graph). Different letters (a, b) indicate significant differences (LSD post-hoc test) between the types.

Table 3. Estimated parameters (intercepts) of the different morphology classes (GLM output) for the sheep wool model. “No appendages” is the null-model.  $C_{sheep}$  represents derived constants for the five different morphology types for sheep wool (deviation of the intercept from the null-model).

	B	T	p-value	$C_{sheep}$
No app.	0.84			0
Hooks	1.21	6.43	<0.001	0.36
Elong. app.	1.05	6.87	<0.001	0.21
Flat app.	0.58	-7.72	<0.001	-0.27
Balloon	0.84	-1.00	0.321	0

potential to cattle hair differ between seed morphology types (Table 4). As parameter estimations for slopes and intercepts gave significant results only for the morphology type “flat appendages” (Table 4), two regression models were set up: one for all morphology types except “flat appendages” and one for the morphology type “flat appendages” (Fig. 4). The total model explained 71.6% of the variation in attachment potentials ( $R^2 = 0.716$ ,  $F_{2,126} = 33.63$ ,  $p < 0.001$ ).

Hence, depending on seed morphology, attachment potentials of seeds to cattle hair can be predicted applying the models

$$y = \begin{cases} -0.111x + 0.336 & \text{for morphology type } \neq \text{flat} \\ & \text{appendages} \\ -0.042x + 0.184 & \text{for morphology type} = \text{flat} \\ & \text{appendages} \end{cases} \quad (2)$$

where  $y = \arcsin(\text{SQRT}(\text{AtP}(\%)/100))$  and  $x = \ln(\text{seed mass}(\text{mg}))$ . Due to the implemented arcsine function, AtP (%) cattle is set to 0 when seed mass  $\geq 20$  mg for seeds without flat appendages and when seed mass  $\geq 100$  mg for seeds with flat appendages. It is set to 100 when seed mass  $< 0.00005$  mg.

### Model validations for sheep wool and cattle hair

For the 36 extra species, for sheep wool and cattle hair the experimentally measured attachment potentials and the predicted attachment potentials were highly significantly correlated (sheep wool:  $r = 0.84$ ,  $p < 0.001$ , cattle hair:  $r = 0.61$ ,  $p < 0.001$ , Fig. 5).

Table 4. Estimated parameters for slopes (m) and intercepts (B) of the different morphology classes (GLM output) for the cattle hair model. “No appendages” is the null-model. Derived slopes (m') and intercepts (B') for the regression lines of the different morphology types for cattle hair are given.

	m	T	p-value	B	T	p-value	m'	B'
No app.	-0.111			0.34			-0.111	0.34
Hooks	-0.067	1.06	0.292	0.44	1.77	0.08	-0.111	0.34
Elong. app.	-0.094	0.78	0.439	0.37	1.11	0.267	-0.111	0.34
Flat app.	-0.042	3.75	<0.001	0.18	-3.71	<0.001	-0.042	0.18
Balloon	-0.085	1.03	0.307	0.31	-0.65	0.517	-0.111	0.34

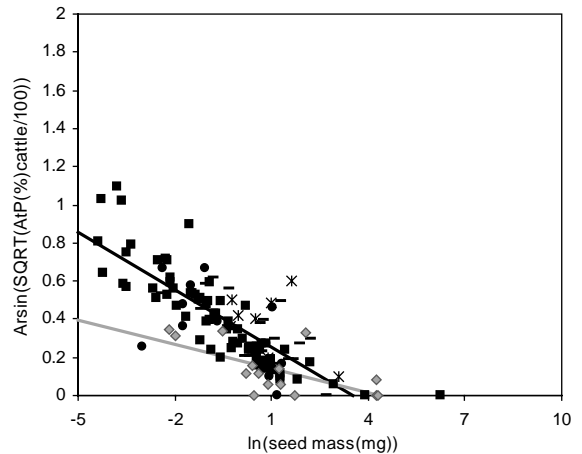


Fig. 4. Regressions of arcsine-square root transformed attachment potentials to cattle hair and  $\ln(\text{seed mass}(\text{mg}))$  with regard to the five different morphology types: ■ no appendages; ● hooks, ▲ elongated appendages, ◆ balloon structures, \* flat appendages. For all morphology types except flat appendages the common regression line is black; for flat appendages, the regression line is grey.

### Models for hooked seeds

Using the algorithm “ $\ln(\text{seed mass})/\text{surface structure}$ ” (i.e. the mass per different structured hooks) 79% of the variation in attachment potentials of hooked seeds can be explained for sheep wool ( $r = 0.79$ ,  $F_{1,7} = 9.81$ ,  $p < 0.001$ , Fig. 6). For cattle hair, the model was not significant ( $r = 0.53$ ,  $F_{1,7} = 2.37$ ,  $p = 0.175$ , Fig. 6).

### Discussion

The comparison of predicted and experimentally measured attachment potentials suggests that the models are applicable to other data sets. Simple measurable seed traits predict attachment potentials to sheep wool and cattle hair with a sufficient precision for most ecological questions focusing on large species sets.

### Attachment potentials to sheep wool and to cattle hair

Our results show that regardless of seed morphology (the classical dispersal syndrome, Van der Pijl 1972) nearly all species keep attached to shaken sheep wool

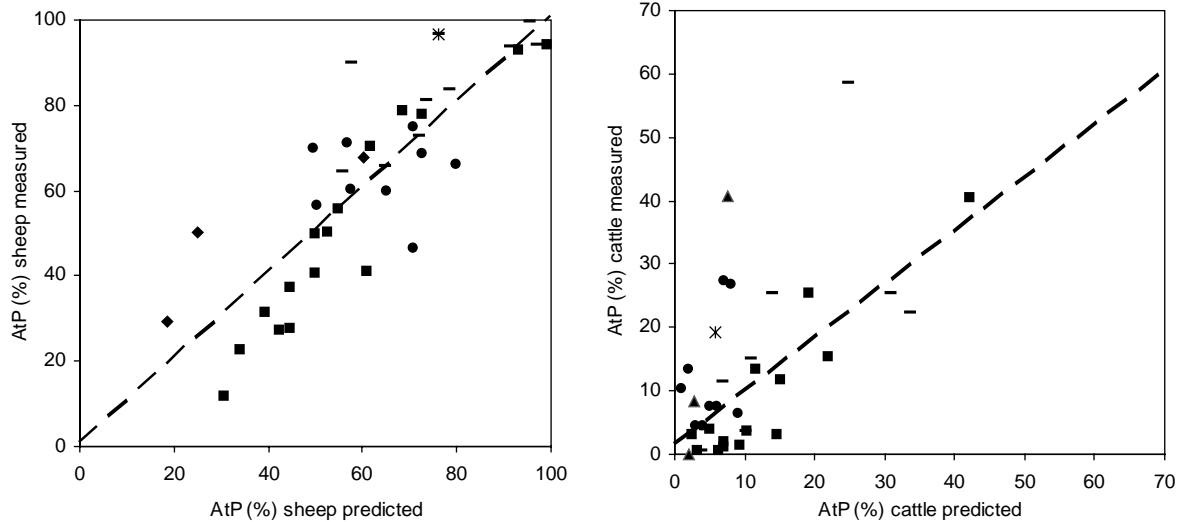


Fig. 5. Model validations: Correlations between measured attachment potentials AtP (%) and predicted attachment potentials (AtP (%) predicted) from the models for sheep wool (left graph) and for cattle hair (right graph). For sheep:  $r=0.84$ ,  $p < 0.001$ ,  $N=36$ . For cattle:  $r=0.61$ ,  $p < 0.001$ ,  $N=36$ . Different morphology types: ■ no appendages; \* hooks, — elongated appendages, ● balloon structures, ▲ flat appendages.

and cattle hair for at least one hour which is accordant to several hours under natural conditions (O. Tackenberg, pers. comm.). Differences in the attachment potentials of species depend on the seed traits seed mass and seed morphology and on the coat type of the dispersal vector, i.e. curly sheep wool or soft, straight cattle hair.

In curly sheep wool attachment potentials are predicted from both seed mass and seed morphology. Hooked and elongated morphology types have higher

attachment potentials than expected from seed mass alone. Their regression lines lie above, or to the right of that for no appendages, which is why they have positive values for  $C_{sheep}$ . Differently, seeds with flat appendages have lower attachment potentials than expected from seed mass alone as the regression line lies below, or to the left of that for no appendages; the value for  $C_{sheep}$  is negative.

In straight cattle hair seed mass is the main predictor; seed morphology plays a minor role with flat morphology types having a negative effect on attachment potentials of small or medium sized seeds only. Above a certain threshold (about 10 mg), regardless of seed morphology, seeds do not keep attached to cattle hair at all.

While adhesive appendages have positive effects on the attachment potentials only in sheep wool, flat appendages decrease the attachment potentials in both coat types. Flat appendages probably hinder the seeds to penetrate into the coat; they rather stay on the coat surface compared to seeds of other morphology types. Adhesive appendages need probably structured coat types to compensate for large seed weights and to increase the attachment potential. This is also underlined by detected differences in the interaction between seed structures of hooked seeds and coat types: while the addition of the parameter seed structure explained differences in attachment potentials in sheep wool, it did not explain differences in cattle hair.

Our findings are consistent with those of other studies indicating that adhesive appendages can at least partly overcome the attachment difficulties of larger-sized seeds (Kiviniemi and Telenius 1998, Couvreur et al. 2004); complex interactions exist between e.g. hooked seeds and animal coats (Gorb and Gorb 2002). Other

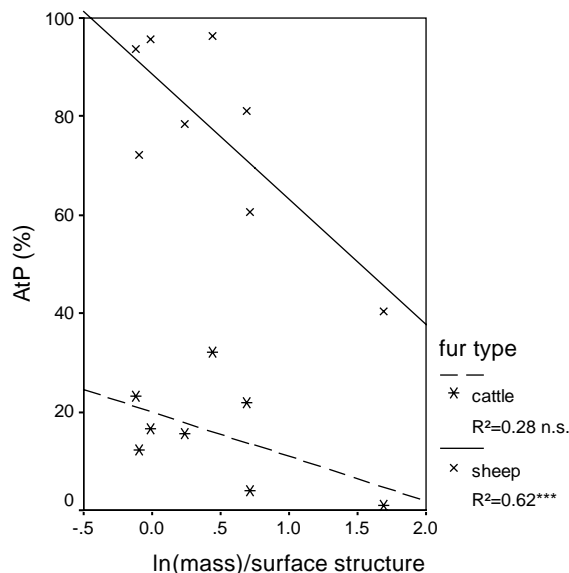


Fig. 6. Prediction of attachment potentials (AtP) for sheep wool and cattle hair for seeds with hooks ( $N=8$ ) using the seed parameters seed mass and seed surface structure (linear regression: sheep:  $r=0.79$ ;  $p < 0.001$ ; cattle:  $r=0.53$ ,  $p=0.175$ ).

appendages may even decrease attachment potentials (Couvreur et al. 2004). Hughes et al. (1994) have shown that seeds above a certain weight are not dispersed by epizoochory, though they related this to a higher weight range (> 100 mg).

### Model applicability and conclusions

As the models for both sheep wool and cattle hair explained to a high extent the variation in attachment potentials of the different species, we recommend applying the models to large data sets. However, the figures of the validations (Fig. 5) illustrate some trends in the deviation from the model: both models slightly overestimate the attachment potential of species with no appendages; species with elongated appendages are to some extent underestimated. These trends may occur because plant species used for model validation were not chosen randomly. To downsize the models' inaccuracy, it should be used for large data sets on ordinal scales only.

The application of the model is restricted to comparisons of attachment potentials. The epizoochorous dispersal potentials cannot be compared between species as many other factors play important roles in epizoochory, too (Kiviniemi and Eriksson 1999). The probability of seeds becoming attached to the coat of animals is an important process, though it has not been quantified yet. Both the probability to become attached and to keep attached to the coat of animals are determined by several factors as seed production (Willson 1993, Bruun and Fritzboeger 2002), height of release (Fischer et al. 1996, Graae 2002, Heinken and Raudnitschka 2002), duration of dissemination (Fischer et al. 1996, Heinken and Raudnitschka 2002) and species abundance in the vegetation (Stender et al. 1997). Some of these traits are already available from literature or from databases (Fitter and Peat 1994, Hodgson et al. 1995, Klotz et al. 2002). For the process of becoming attached to the coat indicator traits need to be defined. To predict the total epizoochorous dispersal potential of a plant species, rules or thresholds should be defined considering all significant traits.

However, the evaluation of successful dispersal includes also other processes, e.g. post-dispersal processes as species establishment (Eriksson and Eriksson 1998, Eriksson and Jakobsson 1999). Though large seeds have relatively low attachment potentials (this study) and are generally produced in lower numbers (Coomes and Grubb 2003, reviewed by Moles et al. 2004), they are better recruiters (Turnbull et al. 1999, Jakobsson and Eriksson 2000). Differently, small seeds having high attachment potentials (this study) are generally produced in high numbers which also enhances dispersal (Hughes et al. 1994, Weiher et al. 1998); their establishment, however, is hampered in many habitats with dense vegetation (Turnbull et al. 1999, Jakobsson and Eriksson

2000, Jensen and Gutekunst 2003, Kahmen 2004). Consequently, dispersal of very few large diaspores can be relatively efficient, whereas small seeds need to be effectively dispersed in higher numbers to increase the chance of successful establishment. Hence, despite differences in attachment potentials, the total dispersal success might be comparable between large and small seeded species.

As we have shown that for curly sheep wool and for straight and soft cattle hair attachment potentials are driven by similar factors but with different properties, the application to other animal species might be possible but is not evident. Couvreur et al. (2004) has shown that attachment potentials were very similar in the coats of horses, rabbits and Holstein cattle. Also attachment potentials in the coats of wild boar, sheep and Galloway cattle were comparable. Therefore, we propose to apply the cattle-model to the first group of species having soft, straight hair. The sheep-model could be applied to the other group including curled or more structured coat types. However, the derived values of attachment potentials need to be considered with caution and should also be taken as a rough indication of attachment potentials.

*Acknowledgements* – We thank M. Bernhardt, Dr. I. Kühn, Dr. K. Neugebauer, F. Schurr and Dr. K. Thompson for helpful discussions, D. Krutinat for machine construction, S. Bonn and E. Talmon for coat supply, H. Fridl, A. Krämer, I. Lauer, M. Ratzinger, S. Reidinger, C. Richter, Dr. C. Rütger and S. Schurm for technical support. Research was supported by the European Commission (LEDA-project, EVR1-CT-2002-40022).

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Subject Editor : Ove Eriksson

**Appendix 1.** Species list of the 130 investigated species. Given are attachment potentials of seeds in sheep wool (AtP (%) sheep) and cattle hair (AtP(%) cattle) and the seed traits mass, length, width, height, shape and main morphological type (no- no appendages, el- elongated appendages, ho- hooks, ba- balloon structures, flat- flat appendages).

Species name	AtP (%) sheep	AtP (%) cattle	Seed mass (mg)	Seed length (cm)	Seed width (cm)	Seed height (cm)	Seed shape	Morph type
<i>Acer campestre</i> L.	0.7	0.7	68.9	30.6	11.2	0.5	0.1	flat
<i>Acer pseudoplatanus</i> L.	2.2	0.0	70.2	32.8	11.5	0.5	0.1	flat
<i>Achillea millefolium</i> agg.	83.2	28.0	0.1	1.7	0.7	0.3	0.2	no
<i>Agrimonia eupatoria</i> L.	40.3	1.0	22.2	7.0	4.3	4.1	0.3	ho
<i>Agrostis capillaris</i> L.	89.2	6.25	0.0	1.7	0.4	0.3	0.2	ba
<i>Alopecurus pratensis</i> L.	89.3	33.8	0.4	7.1	2.9	1.1	0.2	el
<i>Amaranthus retroflexus</i> L.	72.8	22.7	0.6	1.2	1.0	0.6	0.3	no
<i>Andromeda polifolia</i> L.	63.0	8.0	0.3	1.1	0.7	0.6	0.3	no
<i>Anemone nemorosa</i> L.	63.4	7.0	2.2	4.6	2.0	1.1	0.2	el
<i>Anemone ranunculoides</i> L.	61.0	2.7	3.2	4.2	2.2	1.6	0.2	el
<i>Angelica sylvestris</i> L.	52.2	1.3	1.8	5.3	3.4	0.8	0.2	flat
<i>Anthyllis vulneraria</i> L. s.l.	32.4	2.7	3.7	4.0	2.3	1.5	0.2	ba
<i>Arenaria serpyllifolia</i> agg.	92.0	42.0	0.1	0.5	0.5	0.3	0.3	no
<i>Atriplex oblongifolia</i> Waldst. & Kit.	18.3	0.0	3.2	4.5	3.5	1.2	0.2	ba
<i>Betula pendula</i> Roth	41.3	11.3	0.1	3.8	2.5	0.3	0.2	flat
<i>Bidens cernua</i> L.	93.7	23.3	0.8	6.7	1.8	0.4	0.1	ho
<i>Bidens frondosa</i> L.	81.1	21.9	2.7	9.1	3.0	0.8	0.1	ho
<i>Bidens tripartita</i> L.	78.3	15.7	1.6	7.6	2.2	0.6	0.1	ho
<i>Biscutella laevigata</i> L.	9.7	0.3	3.7	6.4	4.6	0.6	0.2	flat
<i>Brachypodium pinnatum</i> agg.	77.7	8.3	3.0	8.8	1.8	0.9	0.1	el
<i>Briza media</i> L.	60.8	14.3	0.5	2.4	1.5	1.2	0.3	ba
<i>Bromus erectus</i> Huds.	69.0	3.7	5.2	8.3	1.2	1.0	0.1	el
<i>Bromus ramosus</i> agg.	71.7	7.3	6.5	11.8	1.9	0.8	0.1	el
<i>Bupleurum falcatum</i> L.	33.7	2.0	2.2	3.7	1.2	1.1	0.2	no
<i>Calluna vulgaris</i> (L.) Hull	91.6	72.3	0.0	0.7	0.4	0.3	0.3	no
<i>Cardamine pratensis</i> agg.	72.7	4.0	0.6	1.5	1.0	0.4	0.3	no
<i>Carex alba</i> Scop.	33.3	19.7	2.8	3.6	2.0	2.0	0.3	ba
<i>Carex sylvatica</i> Huds.	65.3	7.0	1.5	5.2	1.4	1.2	0.2	el
<i>Centaurea cyanus</i> L.	51.4	3.7	4.7	6.7	2.2	1.3	0.2	el
<i>Centaurea scabiosa</i> L. s.l.	58.6	8.3	9.3	8.5	2.0	1.0	0.1	el
<i>Centaurea stoebe</i> L. s.l.	71.3	13.7	1.9	5.1	1.4	1.0	0.2	el
<i>Cerastium glomeratum</i> Thuill.	92.7	50.3	0.0	0.4	0.4	0.3	0.3	no
<i>Chaerophyllum aromaticum</i> L.	36.7	2.7	2.0	10.8	0.8	0.7	0.1	no
<i>Corydalis solida</i> (L.) Clairv.	45.8	7.0	2.0	2.2	2.1	1.4	0.3	no
<i>Cochlearia officinalis</i> agg.	57.7	5.7	0.4	1.4	1.1	0.6	0.3	no
<i>Daucus carota</i> L.	95.7	16.7	1.0	3.6	2.8	1.2	0.3	ho
<i>Deschampsia flexuosa</i> (L.) Trin.	88.7	30.7	0.4	4.8	1.0	0.9	0.2	el
<i>Echium vulgare</i> L.	23.0	1.7	2.8	2.6	1.6	1.6	0.3	no
<i>Eleocharis uniglumis</i> (Link) Schult.	28.7	2.3	1.8	2.3	1.4	0.9	0.2	no
<i>Elymus caninus</i> (L.) L.	70.3	15.0	2.1	25.9	1.7	1.1	0.1	el
<i>Epilobium tetragonum</i> L. s.l.	87.7	26.3	0.1	2.8	2.8	2.8	0.3	el
<i>Erica tetralix</i> L.	88.0	51.9	0.0	0.4	0.3	0.2	0.3	no
<i>Festuca diffusa</i> Dumort.	67.7	4.3	1.2	7.0	1.0	0.6	0.1	el
<i>Festuca ovina</i> agg.	80.2	12.0	0.8	5.9	1.0	0.7	0.1	el
<i>Fraxinus excelsior</i> L.	4.0	0.0	73.6	31.0	5.2	0.5	0.1	flat
<i>Galeopsis bifida</i> Boenn.	16.0	0.7	3.7	3.0	2.2	1.5	0.3	no
<i>Galeopsis tetrahit</i> L.	38.0	1.3	3.6	2.9	2.5	1.6	0.3	no
<i>Galium mollugo</i> agg.	72.3	17.0	0.5	1.4	1.0	0.8	0.3	no
<i>Galium odoratum</i> (L.) Scop.	96.3	32.0	5.1	3.7	3.7	3.7	0.3	ho
<i>Galium verum</i> agg.	77.3	14.3	0.4	1.3	1.2	0.8	0.3	no
<i>Geranium pusillum</i> Burm.	65.3	7.0	1.0	2.9	1.3	1.3	0.2	no
<i>Geum reptans</i> L.	80.3	11.7	0.8	21.7	1.4	1.1	0.1	el
<i>Geum urbanum</i> L.	60.6	4.0	2.5	7.2	1.4	0.6	0.1	ho
<i>Helianthemum nummularium</i> s.l. (L.) Mill.	68.3	11.7	1.0	1.6	1.3	0.9	0.3	no
<i>Helictotrichon pubescens</i> (Huds.) Pilg.	65.3	5.3	2.0	10.4	1.0	0.8	0.1	el
<i>Hesperis matronalis</i> L.	46.4	4.0	1.7	2.3	1.3	1.3	0.3	no
<i>Holcus lanatus</i> L.	78.8	38.0	0.4	2.2	0.7	0.5	0.2	ba
<i>Humulus lupulus</i> L.	46.7	0.3	2.4	16.3	6.9	1.9	0.2	flat
<i>Hypericum humifusum</i> L.	80.0	29.0	0.0	0.6	0.4	0.2	0.2	no

## Appendix 1. (Continued)

Species name	AtP (%) sheep	AtP (%) cattle	Seed mass (mg)	Seed length (cm)	Seed width (cm)	Seed height (cm)	Seed shape	Morph type
<i>Hypericum perforatum</i> L.	78.8	31.3	0.1	1.0	0.5	0.5	0.2	no
<i>Hypochaeris radicata</i> L.	91.7	28.3	0.7	21.3	10.7	0.7	0.3	el
<i>Impatiens noli-tangere</i> L.	26.0	0.7	6.2	4.0	2.1	1.4	0.2	no
<i>Jasione laevis</i> Lam.	69.3	24.0	0.1	1.1	0.5	0.3	0.2	no
<i>Jasione montana</i> L.	95.0	78.7	0.0	0.6	0.3	0.1	0.2	no
<i>Juncus atratus</i> Krock.	92.2	36.0	0.0	0.6	0.2	0.2	0.2	no
<i>Juncus compressus</i> Jacq.	99.3	73.7	0.0	0.4	0.2	0.2	0.2	no
<i>Juncus effusus</i> L.	90.3	30.3	0.0	0.5	0.2	0.2	0.2	no
<i>Lamium album</i> L.	56.3	5.7	1.4	2.7	1.4	0.9	0.2	no
<i>Lamium maculatum</i> L.	41.7	2.0	2.0	3.3	1.4	1.1	0.2	no
<i>Laserpitium latifolium</i> L.	13.7	10.3	7.8	7.5	6.1	3.0	0.2	flat
<i>Lathyrus pratensis</i> L.	17.8	3.0	9.1	3.1	2.6	2.3	0.3	no
<i>Lathyrus sylvestris</i> L.	3.3	0.0	49.9	4.7	3.8	3.3	0.3	no
<i>Leonurus cardiaca</i> L.	60.3	7.7	0.8	2.4	1.2	0.8	0.2	no
<i>Lepidium campestre</i> (L.) R. Br.	39.7	3.7	2.7	2.4	1.5	1.2	0.2	no
<i>Leucanthemum vulgare</i> agg.	36.0	9.3	0.1	2.2	0.8	0.7	0.2	flat
<i>Lolium multiflorum</i> Lam.	69.0	22.7	3.5	9.9	1.6	1.0	0.1	el
<i>Lotus corniculatus</i> L.	60.2	8.7	1.1	1.6	1.3	1.0	0.3	no
<i>Luzula luzuloides</i> (Lam.) Dandy & Wilm.	76.7	23.7	0.3	1.4	0.7	0.6	0.2	no
<i>Lycopus europaeus</i> L.	89.7	61.0	0.2	1.6	1.1	0.5	0.3	no
<i>Matricaria discoidea</i> DC.	85.3	25.5	0.1	1.7	0.6	0.4	0.2	no
<i>Melica nutans</i> L.	47.8	7.0	2.3	2.7	1.3	0.8	0.2	no
<i>Melilotus officinalis</i> (L.) Lam.	52.2	3.3	2.2	2.2	1.5	1.1	0.3	no
<i>Mentha aquatica</i> L.	86.0	43.3	0.1	1.0	0.6	0.5	0.3	no
<i>Molinia caerulea s.str.</i> (L.) Moench	55.6	5.7	1.4	4.6	1.1	1.0	0.2	ba
<i>Oenothera biennis s.l.</i> L.	71.6	17.3	0.5	2.1	1.5	0.9	0.3	no
<i>Oxyria digyna</i> (L.) Hill	50.0	11.0	0.6	4.7	3.4	0.9	0.2	flat
<i>Papaver argemone</i> L.	84.2	20.7	0.1	0.9	0.6	0.5	0.3	no
<i>Peucedanum ostruthium</i> (L.) Koch	26.7	1.3	1.2	4.3	3.0	0.8	0.2	flat
<i>Phalaris arundinacea</i> L.	78.0	19.0	0.3	3.7	1.8	0.4	0.2	el
<i>Phleum phleoides</i> (L.) H. Karst.	82.6	38.3	0.1	1.6	0.5	0.4	0.2	ba
<i>Pimpinella major</i> (L.) Huds.	60.8	20.3	1.3	2.4	1.2	0.9	0.2	no
<i>Pimpinella saxifraga</i> L.	77.0	31.0	0.4	1.7	0.9	0.7	0.2	no
<i>Pinus rotundata</i>	18.3	0.0	5.5	14.7	5.5	0.2	0.1	flat
<i>Plantago lanceolata</i> L.	40.3	6.0	1.3	2.9	1.3	0.9	0.2	no
<i>Plantago major s.l.</i> L.	82.4	25.0	0.3	1.6	0.9	0.4	0.2	no
<i>Plantago media</i> L.	74.6	22.7	0.4	2.0	1.1	0.5	0.2	no
<i>Poa angustifolia</i> L.	75.5	21.2	0.2	2.6	0.7	0.6	0.2	ba
<i>Poa trivialis s.l.</i> L.	77.4	30.0	0.2	2.6	0.7	0.5	0.2	ba
<i>Primula veris</i> L.	75.3	11.3	0.7	1.9	1.2	0.9	0.3	no
<i>Prunella laciniata</i> (L.) L.	58.0	6.0	0.8	2.2	1.1	0.7	0.2	no
<i>Puccinellia maritima</i> (Huds.) Parl.	59.3	12.7	0.2	2.6	0.7	0.6	0.2	ba
<i>Ranunculus acris</i> L.	49.8	6.3	1.7	3.5	2.4	0.8	0.2	no
<i>Ranunculus bulbosus</i> L.	51.7	5.7	4.1	3.5	2.6	1.0	0.2	no
<i>Ranunculus repens</i> L.	45.0	5.7	1.9	3.7	2.2	0.9	0.2	no
<i>Reseda luteola</i> L.	81.2	26.0	0.2	0.9	0.8	0.6	0.3	no
<i>Rhinanthus glacialis</i> Personnat	10.3	2.0	3.4	4.4	3.5	0.9	0.2	flat
<i>Rhinanthus minor</i> L.	18.3	2.3	1.5	4.3	3.2	0.6	0.2	flat
<i>Rosa micrantha</i> Borrer ex Sm.	0.0	0.0	524.5	15.8	9.0	9.0	0.3	no
<i>Rumex acetosella s.l.</i> L.	77.8	21.3	0.4	1.4	1.0	0.9	0.3	no
<i>Rumex crispus</i> L.	41.7	1.0	2.6	5.3	3.3	3.3	0.3	ba
<i>Salvia pratensis</i> L.	49.4	2.3	2.7	2.2	1.8	1.4	0.3	no
<i>Sanguisorba minor s.l.</i> Scop.	37.2	1.0	3.7	3.4	2.0	1.7	0.3	no
<i>Saponaria officinalis</i> L.	50.2	5.3	1.6	1.9	1.6	0.7	0.2	no
<i>Scrophularia umbrosa</i> Dumort.	76.0	28.3	0.1	0.8	0.5	0.4	0.3	no
<i>Selinum carvifolia</i> (L.) L.	23.0	0.0	1.6	4.3	2.6	1.1	0.3	flat
<i>Senecio incanus</i> ssp. <i>carniolicus</i> (Willd.) Braun-Blanq.	69.3	12.0	0.8	9.2	6.5	6.1	0.3	el
<i>Setaria pumila</i> (Poir.) Roem. & Schult.	58.0	5.7	1.6	4.5	2.1	1.4	0.2	ba
<i>Silene vulgaris s.l.</i> (Moench) Garcke	69.2	14.0	0.7	1.4	1.2	0.9	0.3	no
<i>Stellaria graminea</i> L.	81.4	23.0	0.3	1.1	0.8	0.5	0.3	no
<i>Stellaria media</i> agg.	73.2	15.0	0.4	1.1	1.1	0.6	0.3	no
<i>Succisa pratensis</i> Moench	79.2	4.3	1.4	6.2	2.2	1.6	0.2	el

Appendix 1. (Continued)

Species name	AtP (%) sheep	AtP (%) cattle	Seed mass (mg)	Seed length (cm)	Seed width (cm)	Seed height (cm)	Seed shape	Morph type
<i>Taraxacum</i> sect. <i>ruderalia</i> Kirschner, H. Ollg. & Stepanek	72.3	12.3	0.7	9.1	7.4	7.1	0.2	ho
<i>Thymus pulegioides</i> s.l. L.	74.3	16.0	0.2	0.8	0.7	0.4	0.3	no
<i>Tofieldia calyculata</i> (L.) Wahlenb.	78.3	46.3	0.0	0.9	0.3	0.2	0.2	no
<i>Tragopogon pratensis</i> s.l. L.	23.0	0.0	14.8	57.0	23.0	23.0	0.2	el
<i>Verbascum lychnitis</i> L.	87.0	33.7	0.1	1.0	0.7	0.5	0.3	no
<i>Veronica chamaedrys</i> s.str. L.	83.0	26.0	0.2	1.5	1.2	0.4	0.2	no
<i>Veronica officinalis</i> L.	72.3	42.7	0.1	1.1	0.8	0.3	0.2	no
<i>Vicia cracca</i> agg.	15.3	0.3	18.6	2.8	2.6	2.3	0.3	no
<i>Vulpia myuros</i> (L.) C. C. Gmel.	84.6	15.3	0.5	11.2	0.7	0.6	0.1	el

**Appendix 2.** Species list of the additional 36 species. Given are experimentally measured (AtP (%)) and calculated attachment potentials (AtP(%) predicted) of seeds to sheep wool and to cattle hair. Traits to calculate the predicted attachment capacity (seed mass and morphology type with no- no appendages, el- elongated appendages, ho- hooks, ba- balloon structures, flat- flat appendages) are given.

Species	Sheep wool		Cattle hair		Model parameter	
	AtP (%)	AtP (%) predicted	AtP (%)	AtP (%) predicted	Seed mass (mg)	Morph type
<i>Alopecurus geniculatus</i> L.	93.67	91.31	58.67	24.81	0.19	el
<i>Alopecurus myosuroides</i> Huds.	65.67	64.85	11.33	5.50	2.42	el
<i>Arrhenatherum elatius</i> (L.) P. Beauv. ex J. Presl & C. Presl	69.67	49.57	10.33	7.82	1.60	ba
<i>Biscutella didyma</i> L.	50.33	25.02	8.33	2.83	1.45	flat
<i>Bromus racemosus</i> L.	64.33	55.75	0.67	2.47	4.91	el
<i>Calamagrostis epigejos</i> (L.) Roth	94.00	97.06	22.33	34.63	0.07	el
<i>Coronopus squamatus</i>	50.33	52.53	3.67	9.23	1.28	no
<i>Dipsacus pilosus</i> L.	22.67	34.03	0.67	2.21	5.30	no
<i>Doronicum clusii</i> agg.	83.67	78.39	25.33	12.75	0.77	el
<i>Erysimum cheiri</i> (L.) Crantz	27.67	44.58	1.00	5.70	2.34	no
<i>Festuca arundinacea</i> Schreb.	71.33	56.74	4.33	11.41	0.93	ba
<i>Festuca filiformis</i> Pourr.	68.67	72.64	13.33	21.85	0.26	ba
<i>Festuca trichophylla</i> (Ducros ex Gaudin) K. Richt.	56.67	50.50	4.33	8.25	1.49	ba
<i>Fumana procumbens</i> (Dunal) Gren. & Godr.	31.33	39.31	4.00	3.78	3.50	no
<i>Gentiana asclepiadea</i> L.	67.67	60.32	40.67	7.63	0.09	flat
<i>Glyceria maxima</i> (Hartm.) Holmb.	66.00	80.01	7.67	28.24	0.14	ba
<i>Gypsophila muralis</i> L.	93.00	93.14	40.33	44.35	0.03	no
<i>Holcus mollis</i> L.	75.00	70.98	7.67	20.58	0.30	ba
<i>Hyoseris radiata</i> L.	81.11	73.54	15.00	9.71	1.19	el
<i>Knautia arvensis</i> s.str. (L.) Coult	27.00	42.48	0.67	4.90	2.74	no
<i>Lactuca perennis</i> L.	40.67	49.89	1.33	7.97	1.56	no
<i>Melampyrum sylvaticum</i> L.	11.67	30.77	3.00	1.42	6.90	no
<i>Mercurialis annua</i> L.	37.33	44.54	2.00	5.68	2.34	no
<i>Oenanthe fistulosa</i> L.	29.33	18.70	0.00	2.11	2.59	flat
<i>Phleum pratense</i> s.str. L.	59.67	65.07	27.33	16.41	0.49	ba
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	99.67	95.61	25.33	31.52	0.10	el
<i>Poa pratensis</i> s.str. L.	46.33	70.94	26.67	20.55	0.30	ba
<i>Potentilla recta</i> L.	78.67	68.44	25.33	18.71	0.37	no
<i>Prunella vulgaris</i> L.	41.00	60.96	3.00	13.82	0.67	no
<i>Rumex acetosa</i> L.	60.33	57.67	6.33	11.92	0.86	ba
<i>Sanicula europaea</i>	96.67	75.96	19.30	4.48	2.99	ho
<i>Scabiosa canescens</i> Waldst. & Kit.	72.67	72.06	3.67	8.89	1.35	el
<i>Teesdalia nudicaulis</i> (L.) R. Br.	78.00	72.55	15.33	21.78	0.26	no
<i>Trifolium pratense</i> L.	55.67	54.96	13.33	10.46	1.06	no
<i>Trifolium repens</i> L.	70.40	61.63	11.67	14.22	0.64	no
<i>Trifolium stellatum</i> L.	90.00	57.74	4.00	3.03	4.22	el