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The effects of seed traits and fabric type on the retention of seed on different types of clothing

Michael Ansong*, Catherine Pickering

Environmental Futures Research Institute, Griffith University, Gold Coast, Queensland 4222, Australia

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Abstract

People can intentionally or unintentionally transport seed of a diversity of species over long distances, facilitating plant invasions. To better understand factors affecting unintentional human-mediated seed dispersal, we quantified the effects of seed traits and fabric type on the retention potential of weed seed on clothing. First, we compared seed retention among 33 species of weeds that differ in seed morphology using three fabrics. We then compared seed retention for 10 different fabrics using seed from five species of weeds. Retention potential, calculated as the percentage seed retained on fabric after shaking for fixed periods of time, was compared using Linear Mixed Models. Across the 33 species, seed of most species fell off fabric soon after shaking commenced: 17 species had low retention potentials (<20% of the seed remain attached after 5 min of shaking), 10 species had moderate seed retention (20–50% seed retained), and only five species had high retention potentials (>50% seed retained). Retention potentials varied among fabrics, with seed more tightly attaching to fabrics with “woolly” or “fleecy” characteristics such as fleece, knitted wool, double weave wool nylon blend (hiking socks) and ribbed cotton/nylon (sports socks), than to smoother fabrics such as canvas, fine nylon weave, denim and drill cotton. The weight, length and presence of attachment structures affected how long seed remain attached. The effect of these traits varied among fabrics. Seed with structures such as hairs, awns and pappus remained attached for longer on fabrics like fleece and wool, but not on smoother fabrics. These results support the observation that people wearing clothing made of different fabrics are likely to disperse different combinations of weed seed, depending, at least in part, on seed traits. Unintentional human mediated seed dispersal via clothing is therefore a very selective example of epizoochory favouring some weeds more than others.

Zusammenfassung

Berabsichtigt oder unbeabsichtigt können Personen Samen von verschiedenen Pflanzenarten über weite Strecken transportieren und so Invasionen erleichtern. Um die Faktoren besser zu verstehen, die die unbeabsichtigte vom Menschen vermittelte Samenausbreitung beeinflussen, quantifizierten wir die Einflüsse von Samenmerkmalen und Gewebetyp der Bekleidung auf das Retentionspotential von Unkrautsamen. Zunächst verglichen wir für drei Gewebearten das Retentionspotential von 33 Unkrautarten, die sich hinsichtlich der Samenmorphologie unterscheiden. Danach untersuchten wir das Retentionsverhalten von fünf Samenarten auf zehn Gewebearten. Die Gewebeproben wurden für eine bestimmte Zeit geschüttelt und das Retentionspotential als der prozentuale Anteil der noch vorhandenen Samen berechnet. Die Samen der meisten Arten fielen schnell ab: 17 Arten hatten geringe Retentionspotentiale (<20% der Samen verblieben nach 5 Minuten Schütteldauer), zehn Arten hatten mittleres Retentionspotential (20–50% verblieben) und nur bei fünf Arten verblieben mehr als 50% der Samen auf dem Stoff. Die

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*Corresponding author. Tel.: +61 7 55529483; fax: +61 7 5552 8067.
E-mail addresses: michael.ansong@griffithuni.edu.au, boatans@gmail.com (M. Ansong).

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Retentionspotentiale variierten mit dem Gewebetyp, wobei die Samen fester an Stoffen mit Woll- oder Fleecestruktur (Fleece, gestrickte Wolle, doppelt gewirktes Wolle-Nylon-Gemisch (Wandersocken) oder Baumwoll-Nylon-Gemisch (Sportsocken)) hängen blieben als an glatteren Stoffen (Segeltuch, feines Nylongewebe, Jeansstoff und Baumwolldrillich). Gewicht und Länge der Samen sowie das Vorhandensein von Haftstrukturen bestimmten, wie lange die Samen haften blieben. Der Effekt dieser Merkmale variierte mit der Gewebeart. Samen mit Haaren, Grannen und Pappi hafteten länger an Fleece und Wolle aber nicht an glatteren Geweben. Diese Ergebnisse unterstützen die Beobachtung, dass Personen, die Bekleidung aus unterschiedlichen Stoffen tragen wahrscheinlich unterschiedliche Kombinationen von Samen transportieren, was zumindest teilweise von der Samenart abhängt. Unbeabsichtigte Samenausbreitung mit der Bekleidung des Menschen ist deshalb ein Beispiel dafür, dass bei der Epizoochorie manche Arten stärker als andere begünstigt werden.

Keywords: Biological invasion; Epizoochory; Human-mediated seed dispersal; Tourism impact; Long distance dispersal; Recreational ecology

Introduction

Dispersal is a key ecological process where plants disseminate propagules (hereafter referred to as seed) far from the source/parents (Howe & Smallwood, 1982; Willson & Traveset, 2000). An important dispersal mechanism is via human-mediated seed dispersal, where people intentionally or unintentionally carry and disperse seed (Ansong & Pickering, 2013a,b; von der Lippe & Kowarik, 2007; Wichmann et al., 2009). This includes seed on clothing, which is a special case of epizoochory, where seed is dispersed on the outside of animals (Cousens, Dytham, & Law, 2008; Pickering, Mount, Wichmann, & Bullock, 2011). With more people travelling and travelling to more remote locations, humans can unintentionally transport seed from a range of species, including weeds, over long distances (Ansong & Pickering, 2013c; Auffret & Cousins, 2013a). This type of long distance dispersal facilitates biological invasions in urban, rural and remote natural areas (Pickering & Mount, 2010; Pyšek, Jarosik, & Pergl, 2011; Ware, Bergstrom, Müller, & Alsos, 2012).

Clothing is an important type of dispersal vector as people can unintentionally carry a range of weed seed on their clothing over long distances (Ansong & Pickering, 2014a; Chown et al., 2012). Seed on clothing can be carried thousands of kilometres, with people travelling to very remote locations, such as Antarctica, found to have weed seeds attached to their clothing (Chown et al., 2012; Whinam, Chilcott, & Bergstrom, 2005). The number of seed attaching to individual items of clothing can be substantial, with over 600 seeds attached to individual socks after 5 min walks through weedy roadsides in a national park in Australia (Mount & Pickering, 2009). A recent review of seed dispersal from clothing found that seed from 450 species have been recorded attached to clothing, 87% of which are considered weeds (Ansong & Pickering, 2014b). Many of these weeds are known to have a range of negative environmental impacts including out-competing native species and altering ecosystem structures and processes. They also reduce the economic value of natural and agricultural areas and increase management costs (Richardson, 2011; Weber, 2003).

Seed dispersal via clothing, as in all epizoochory, involves several steps: seed must first become attached to the clothing, then remain attached (retained) during transportation, and finally be deposited in new sites. Characteristics of the seed and the clothing affect each stage (Ansong & Pickering, 2014b; Ansong, Pickering, & Arthur, 2015). Differences in the size and morphology of seed, for instance, affect the potential for seed to disperse from clothing (Ansong & Pickering, 2014b; Bullock & Primack, 1977). The amount and type of seed dispersed is also affected by where on the body the clothing is worn, if it is covered by other clothing and the behaviour of the person wearing the clothing (Ansong & Pickering, 2015; Mount & Pickering, 2009). The adhesive quality of fabrics is also important, with differences in the number and type of seed retained on clothing such as socks depending on the type of fabric used to make the sock (Bullock & Primack, 1977; Whinam et al., 2005). Previous research has found that seed detach faster from drill cotton trousers than some types of sports socks (Pickering et al., 2011) and that sports and hiking socks vary in the types of seed that attach (Mount & Pickering, 2009). Understanding the importance of seed traits and fabric on seed dispersal from clothing is important when implementing strategies to minimise the spread of invasive species by humans.

Despite its potential importance as a dispersal mechanism, there is still limited research directly assessing seed retention on different types of clothing (Ansong & Pickering, 2014b). Most of the research has been observational or natural experiments where seed were collected from clothing in natural settings or obtained as part of other activities, and the number and types of seed quantified (see Ansong & Pickering, 2014b; Auffret & Cousins, 2013b; Chown et al., 2012). A few studies have used manipulative experiments to assess different factors affecting human-mediated dispersal including types of clothing, species of weed and distances travelled (Ansong & Pickering, 2013c; Bullock & Primack, 1977; Pickering et al., 2011). The literature on seed dispersal from clothing is therefore sparse compared to that assessing seed dispersal from other vectors such as animal fur and feathers. For instance, there are several manipulative experiments conducted under controlled conditions that have quantified the effect of seed traits on seed dispersal for more traditional examples of epizoochory including seed dispersed from the fur of horses, cattle and sheep (Bläß, Ronnenberg, Tackenberg, Hensen, & Wesche, 2010; Couvreur, Couvreur, Vandenberghe, Verheyen, & Hermy, 2004; Couvreur, Verheyen, & Hermy, 2005; Römermann, Tackenberg, & Poschlod, 2005; Tackenberg, Römermann, Thompson, & Poschlod, 2006; Will, Maussner, & Tackenberg, 2007).

Where manipulative experimental methods were used to assess seed retention on clothing, the probability of seed detachment was found to be a function of time/distance since attachment, with most seed dispersed close to where they became attached to clothing (Ansong & Pickering, 2013c; Ansong et al., 2015; Pickering et al., 2011). Across the 14 species assessed to date, species with attachment structures such as barbs and hooks (e.g., *Acaena novae-zelandiae*, *Acetosella vulgaris*, *Anthoxanthum odoratum, Bidens pilosa*, *Dactylis glomerata*, *Festuca rubra* and *Heteropogon contortus*) have seed that remained attached to clothing for longer distances (>5 km walks) than species without these types of structures (e.g., *Cynodon dactylon* and *Rumex acetosella*) (Ansong & Pickering, 2013c; Ansong et al., 2015; Pickering et al., 2011). With so few species tested, however, there has been limited capacity to generalise from these results.

To better assess some of the key aspects of human-mediated seed dispersal from clothing, we quantified the importance of seed traits (length, weight and attachment structures) and different types of fabric on seed retention potential. This was done using similar experimental methods used to assess seed retention potential on animal fur using a shaking machine under laboratory conditions. Specifically we assessed: (1) What is the retention potential of different types of weed seed on common types of fabrics used in outdoor clothing? (2) What seed traits influence the proportion of seed retained? *and* (3) How does the retention potential of seed vary among different types of fabrics? Answering these questions will enhance our capacity to generalise about the factors that affect human-mediated seed dispersal on clothing and develop recommendations about how to minimise how we may unintentionally contribute to biological invasions.

Materials and methods

Study species

The retention potential of 33 widely distributed weed species that represent a diversity of seed shapes and sizes were assessed (Table 1, Appendix A: Table A1). These species are now found well beyond their natural distributions including a range of habitats where they occur as weeds in agriculture fields, disturbed sites such as roadsides, and a range of natural ecosystems (Weber, 2003). They all have the potential to produce large numbers of seed that remain viable in seed banks for several years post dispersal (Weaver, 2001; Weber, 2003). Seed from many of these weeds have been found attached to clothing in previous studies covering a range of habitats and countries (Ansong & Pickering, 2014b) and many are considered to be internationally important environmental weeds (Weber, 2003). For our experiments, mature seed from the 33 species were collected from roadsides and other disturbed sites on the Gold Coast in south-eastern Queensland, Australia, in October 2013. The seed were then carefully stored in boxes at room temperature in a laboratory to ensure that adhesive structures such as hairs and awns were not damaged.

The seed of the 33 species differed in a range of traits, including length (0.5–61.0 mm), width (0.3–5.9 mm), weight (0.06–23.09 mg) and the presence of adhesive structures such hairs, awns, barbs and pappus (Table 1). For the experiments, data on seed traits were obtained directly from subsamples of the seed collected, including seed length, width and weight. The length (mm) of seed was measured as the longest axis of the seed including all appendages, while width (mm) was recorded perpendicular to length including all appendages with five replicates per species. Seed weight (mg) was obtained by weighing six replicates of 50 seed per species, from which a mean value per seed was calculated for each species following the protocols of Römermann et al. (2005). Based on visual observations of the seed, we also assigned seed to two categories based on their morphology: those with structures that could aid in attachment such hairs, awns and pappus, and those without such structures (Table 1).

Quantifying retention potential

We quantified the relative retention potential of seed on different fabrics by determining the proportion of seed remaining attached to a fabric after shaking for a specified time using a machine that simulated the type of shaking that occurs when people walk. This 'shaking machine' (Appendix A: Fig. A1) is based on those used by other researchers to quantify and compare seed retention on different types of fur (Bläß et al., 2010; Römermann et al., 2005; Tackenberg et al., 2006; Will et al., 2007). The speed of the machine was set to an average of 33 cycles/hits per minute throughout the experiments. See Appendix A for details of the experimental setup and the machine.

Seed and fabric combinations were randomly allocated to different locations on the shaking machine, with a total of 40 combinations possible per run of the machine. At the start of each run, $12 \times 14\,\text{cm}^2$ sections of fabric were clipped to the inner side of a series of 10 plastic storage boxes ($16 \times 14 \times 16\,\text{cm}^3$) fastened to the sample stage of the shaking machine. Seed were then gently attached in a centrally marked area of $10 \times 10\,\text{cm}^2$ of the fabrics using a dabbing motion to mimic walkers brushing up against a plant. Seed of only one species were attached to each box per run. There

Table 1. Seed traits of the 33 species of weeds used in experiments to assess factors affecting seed retention potential on a range of fabrics.

	Seed			Number of seed used per experiment		Attachment structure(s)
Species	Length (mm)	Weight (mg)	Width (mm)	Total	Av. per replicate	
Acaena novae-zelandiae	9.68	2.64	1.18	871	58 ± 2	yes
Ageratum houstonianum[a]	3.30	0.12	0.54	1157	77 ± 3	yes
Avena barbata	60.96	14.45	1.66	525	35 ± 6	yes
Bidens pilosa[a,b]	10.78	1.19	0.74	1030	69 ± 3	yes
Bromus diandrus	49.46	23.09	1.5	423	28 ± 5	yes
Bromus hordeaceus	11.80	2.32	1.92	1007	67 ± 7	yes
Bromus tectorum[b]	21.90	2.94	1.26	904	60 ± 7	yes
Chloris gayana	7.42	0.48	1.58	1545	103 ± 5	yes
Conyza canadensis	4.08	0.06	0.3	1202	80 ± 3	yes
Cynodon dactylon[b]	2.04	0.29	1.1	1632	109 ± 9	no
Dactylis glomerata[b]	0.46	0.88	1.66	1157	77 ± 6	yes
Echinochloa polystachya[b]	2.72	2.70	1.58	1272	85 ± 6	yes
Enneapogon nigricans	6.50	1.62	1.4	763	51 ± 3	yes
Festuca rubra	6.02	1.56	1.02	1332	89 ± 4	yes
Hieracium caespitosum	14.8	0.32	0.48	774	52 ± 4	yes
Holcus lanatus[b]	4.42	0.27	1.62	1213	81 ± 4	yes
Hordeum glaucum	9.90	2.35	1.26	858	57 ± 4	yes
Megathyrsus maximus	3.08	0.32	1.12	12777	85 ± 6	no
Melinis minutiflora[a,b]	13.92	0.21	0.58	1497	100 ± 8	yes
Melinis repens	4.76	0.30	1.22	1162	77 ± 4	yes
Myosotis sylvatica[b]	1.58	0.24	1.28	940	63 ± 5	yes
Paspalum urvillei	2.14	0.45	1.46	1688	113 ± 9	yes
Plantago lanceolata[b]	2.44	1.62	1.24	695	46 ± 5	no
Poa petrophila	3.00	0.46	0.78	1574	105 ± 6	no
Poa pratensis[b]	2.56	0.21	0.68	1186	79 ± 6	no
Rumex conglomeratus[a,b]	4.02	1.57	2.5	944	63 ± 6	yes
Rumex crispus[b]	4.28	2.41	3.86	569	38 ± 6	no
Sanguisorba minor	4.38	8.12	3.02	325	22 ± 5	no
Senecio quadridentatus	8.28	0.14	0.36	871	58 ± 2	yes
Setaria sphacelata[a]	2.56	0.32	1.38	1066	71 ± 6	no
Sporobolus africanus[b]	0.90	0.18	0.46	1464	98 ± 2	yes
Taraxacum officinale	16.1	0.46	0.94	853	57 ± 6	yes
Triumfetta rhomboidea	5.86	14.75	5.88	773	52 ± 1	yes

Attachment structures include hairs, awns and pappus that could aid in attachment; Seed length (mm) was measured as the longest axis of the seed including all appendages; width (mm) was the second longest axis, which was measured as perpendicular to length and includes all appendages; weight (mg) was measured by weighing 6 replicates of 50 seed per species and the mean calculated for one single seed.

[a] These five species were used in both experiments.

[b] International environmental weeds according to Weber (2003).

was variation in the initial number of seed attaching to the fabric due to the variability in seed size and their ability to attach to different types of fabric, with a range of 22–113 seed attached to fabric per replicate in each of the experiments (Table 1). The laboratory conditions were kept constant for all replicates in both experiments.

In the first experiment, we assessed the retention potential of seed from the 33 species of weeds using the shaking machine to simulate short walks (5 min of shaking) and longer walks (50 min of shaking). Retention potential was assessed for three common types of fabrics worn by walkers: Drill cotton (commonly used for trousers), Ribbed cotton/nylon blend (for socks), and Fleece (commonly used for outdoor jumpers/jackets). There were five replicates per fabric and species assessed; resulting in 99 combinations of seed and fabrics and 495 replicates in total. For each replicate run, the shaking machine was stopped after 5 min (short walk) and then run for another 45 min to simulate the longer walk.

The effect of a wide range of fabrics on seed retention was assessed in the second experiment, where seed retention was compared among 10 types of fabric using seed from five weed species: *Ageratum houstonianum*, *B. pilosa*, *Melinis minutiflora*, *Rumex conglomeratus*, and *Setaria sphacelata*. The fabrics selected are those often used in outdoor clothing including for trousers (canvas, denim, drill cotton and fine nylon weave), socks (ribbed cotton/nylon blend and double weave wool nylon blend) and jumpers/shirts (fleece, knitted wool, pure cotton; polyester mesh fabric) (Appendix A: Table A3). They include woven and knitted fabrics, natural and 'man-made' fibres, and differed in fibre arrangement and surface textures (Appendix A: Table A3). There were 10 replicates per species and clothing combination (e.g., 50 combinations and a total of 500 replicates) with seed retention assessed for simulated relatively short walks (5 min of shaking, ~300 m), medium walks (20 min of shaking, ~1200 m) and longer walks (50 min of shaking, ~3000 m). For each replicate run, the machine was stopped after 5 min (short walk), run for another 15 min for the medium walk and then run for an additional 30 min to simulate the longer walk.

When seed retention on fabric using the machine was compared to that from walkers, for a subsample of the fabrics (drill cotton and ribbed nylon/cotton blend) and weed seed (e.g., *B. pilosa*, *Chloris gayana*, *Conyza canadensis*, *C. dactylon* and *Paspalum urvillei)*, out of the 20 combinations tested, the 95% confidence intervals for the walk and shaking machine overlapped for nine, indicating that the shaking machine can provide similar results to walkers. The machine, however, underestimated seed retention for another nine combinations, and overestimated it for two combinations (Appendix A: Fig. A3). The results from the shaking machine, therefore, do not always match those for the same species/fabrics from walking. The shaking machine, however, allowed a large number of species and fabrics to be compared under standardized conditions as had previously been done for fur, allowing statistical comparisons of the effects of seed traits on retention (Bläß et al., 2010; Römermann et al., 2005; Tackenberg et al., 2006; Will et al., 2007).

Statistical analysis

Differences in the proportion of seed retained for different seed species, types of fabric and shaking times, were examined using linear mixed models (LMM) methods in SPSS version 22. A range of models were investigated, with the best model selected by comparing the Akaike information criterion (AIC). We used the ‘unstructured’ covariance function to model the random error structure in all the models presented. The dependent variable, proportion of seed retained, was arcsine square root transformed. The best model was comprised of the fixed factors ‘fabrics’ ‘species’ and ‘time’, and included a variance component structure for the random effects: replicates nested within species by fabrics.

To determine which seed traits influenced retention potential on the different fabrics, data from the first experiment assessing 33 species was analysed using LMM. Prior to the LMM we had compared seed traits to determine which traits were highly correlated, using Pearson product-moment correlation coefficients. Based on these results, we used the traits: seed length, weight and a dummy variable called appendage (presence/absence of attachment structure). In the LMM the independent variables were log transformed seed length, log transformed seed weight, and appendage, which were all entered as covariates, while time was entered as subjects. The dependent variable was the arcsine square root of the proportion of seed retained. Separate models were fitted to each of the three types of fabric (cotton drill, ribbed cotton/nylon blend and fleece) assessed. The final model from the LMM was comprised of a random intercept and random slopes of the covariates seed length and weight. The random intercept and slope values of both seed weight and length were very small, and in some cases, negligible for the three types of fabric. There was no significant difference between models with, or without, random intercept, random slope or both. We retained the current model because it had a slightly lower AIC compared to the alternate models (but the AIC difference between the models was never >2).

Table 2. Results from the Linear Mixed Model showing the effects of fabric, species and time on the proportion of seed retained (arcsine square root transformed data).

Fixed effects	Numerator df	*F*	*p*
Fabric	2	393.7	**<0.001**
Species	32	32.2	**<0.001**
Time	1	310.5	**<0.001**
Time × Fabric	2	12.0	**<0.001**
Species × Fabric	64	6.0	**<0.001**
Species × Time	32	2.6	**<0.001**
Species × Time × Fabric	64	1.1	0.266
Random effects	**Estimate**	**Wald Z**	***p***
Subject (Fabric × Species)	0.027 ± 0.002	13.282	**<0.001**

Time was treated as a repeated factor. Bold *p* values are significant at $p < 0.05$, and the denominator df = 396.

Results

What is the retention potential of different types of weed seed on common types of fabric?

The retention potential differed significantly between the 33 species ($p < 0.001$) (Table 2) both after short (5 min) and longer shaking times (50 min). Values ranged from 2.4% of seed retained for *C. dactylon* to 67.7% of seed retained for *C. canadensis* after 5 min of shaking (Fig. 1). After 50 min of shaking, values ranged from 1.5% seed retained for *C. dactylon* to 63.3% for *Myosotis sylvatica* (Fig. 1). There was an interaction between species and time ($F_{(32,\ 396)} = 2.55$, $p < 0.001$), reflecting some differences in the ranking of species retention potential between 5 and 50 min shaking (Fig. 1).

Based on the retention potential, it was possible to group species into those with a high retention potential (>50% seed still retained), moderate (20–50% seed retained), or low retention potential (<20%) after shaking for 5 min (Fig. 1). Using this categorization, there were only five species with high retention potential: *A. novae-zelandiae*, *B. pilosa*, *C. canadensis*, *M. sylvatica*, and *Triumfetta rhomboidea*. Four of these species still had more than 50% of their seed attached after another 45 min of shaking. There were ten species with

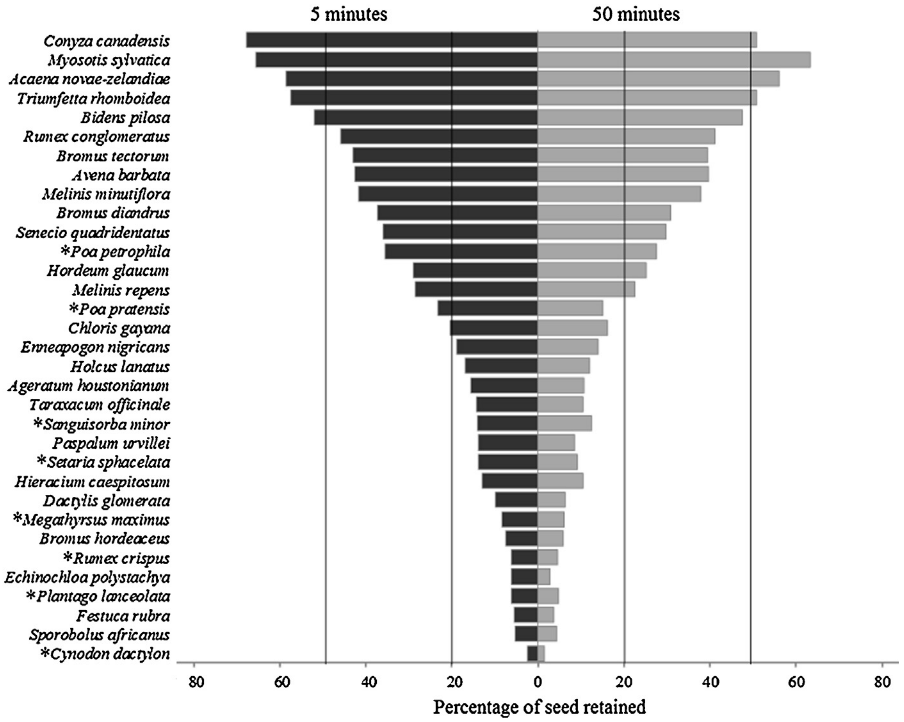

Fig. 1. Seed retention potential (percentage seed still attached) for 33 species of weeds after shaking for 5 and 50 min. Species with >50% of seed retained were classified as having high retention potential, those with 20–50% seed retained were considered as having moderate retention potential while those with <20% seed retained were categorized as having low retention potential. Species without appendages are marked with asterisks (*).

moderate retention potential at 5 min, and 17 species with low retention potential (Fig. 1).

The retention potential of the species varied depending on the type of fabric (interaction effect: $F_{(64,\ 396)} = 6.02$, $p < 0.001$), with some species with a high retention potential on one fabric and lower values on others. For example, *Sanguisorba minor* with small and burred seed (achenes), had a moderate retention potential of 41% on fleece, a very low potential on ribbed cotton/nylon blend (0.7% retained) and no seed retained on drill cotton after 5 min of shaking (Fig. 2). For *Bromus tectorum* with long awns, retention potential was high on fleece (81%), moderate on ribbed cotton/nylon blend (47%), but very low on drill cotton (2%).

Overall, species tended to have moderate retention potential on fleece (40%, average for 33 species and both times), slightly lower on ribbed cotton/nylon blend (27%), but very low on drill cotton (5%). Similarly, all 33 species had some seed left attached after 5 min of shaking on fleece, with 11 species with <20% of seed retained, 11 species with 20–50% of seed retained, and 11 species with >50% of seed retained. Although, all 33 species had some seed left attached after 5 min of shaking on ribbed cotton/nylon blend, only six species had more than 50% of seed retained, with 13 species retaining between 20% and 50% of seed, and 14 species retaining <20% of seed. On drill cotton, 26 species still had seed retained after 5 min of shaking, with only three species with between 20% and 50% and the rest with <20% seed retained (Fig. 2).

What seed traits influence the proportion of seed retained?

Seed length significantly predicted seed retention potential on fleece ($F_{(1,\ 328)} = 16.62$, $p < 0.001$), ribbed cotton/nylon blend ($F_{(1,\ 328)} = 9.03$, $p = 0.003$) and drill cotton ($F_{(3,\ 328)} = 7.70$, $p = 0.006$), with an increase in seed length resulting in a corresponding increase in seed retention potential on all three fabrics (Table 3). Seed weight significantly predicted seed retention potential on fleece ($F_{(1,\ 328)} = 10.66$, $p = 0.001$) and drill cotton ($F_{(1,\ 328)} = 54.34$, $p < 0.001$), but not on ribbed cotton/nylon blend ($F_{(1,\ 328)} = 1.50$, $p = 0.221$). Heavier seed tend to stay longer on fleece but had lower retention potential on drill cotton compared to lighter seed. On ribbed cotton/nylon blend, however, the weight of the seed was not important. The presence of attachment structure also significantly predicted seed retention potential on fleece ($F_{(1,\ 328)} = 15.63$, $p < 0.001$), socks ($F_{(1,\ 328)} = 11.29$, $p = 0.001$), but not on drill cotton ($F_{(1,\ 328)} = 0.056$, $p = 0.813$). Seed with attachment structures had higher retention potential on fleece and on ribbed cotton/nylon blend, but this effect was not significant on drill cotton (Table 3).

How does the retention potential of seed vary among different types of fabrics?

Seed retention potential varied among the 10 types of fabric tested (Table 4). Fleece had the highest seed retention

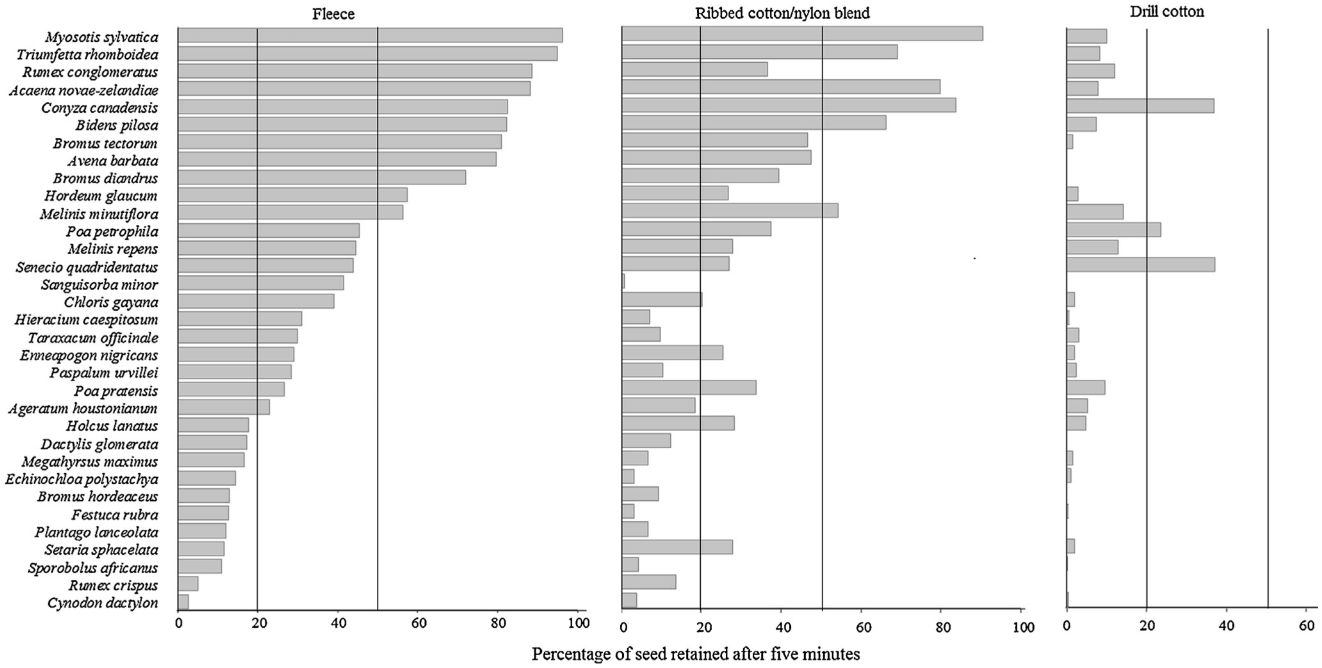

Fig. 2. Variation in seed retention potential among the 33 species after 5 min of shaking using fleece, ribbed cotton/nylon blend and drill cotton as an example. Species more than 50% of seed retained were classified as having high retention potential, those with 20–50% seed retained were considered as having moderate retention potential while those with <20% seed retained were categorized as having low retention potential.

Table 3. Results from the Linear Mixed Model with random intercept and slope (seed weight and length) showing the influence of seed length, weight, and presence of attachment structures on the proportion of seed retained (arcsine square root transformed) on fleece, socks and drill cotton.

Fixed effect	Fleece			Ribbed cotton/nylon blend			Drill cotton		
	$b \pm$ SE	t	p	$b \pm$ SE	t	p	$b \pm$ SE	t	p
Intercept	0.164 ± 0.082			0.127 ± 0.081			0.089 ± 0.045		
Length	0.225 ± 0.055	4.077	**<0.001**	0.148 ± 0.050	2.992	**0.003**	0.078 ± 0.282	2.762	**0.006**
Weight	0.113 ± 0.035	3.264	**0.001**	−0.038 ± 0.031	−1.219	0.224	−0.131 ± 0.018	−7.268	**0.028**
Appendage	0.193 ± 0.049	3.954	**<0.001**	0.146 ± 0.044	3.344	**0.001**	0.059 ± 0.025	0.236	0.814
Random	**Estimate** ± SE	**Wald Z**	***p***	**Estimate** ± SE	**Wald Z**	***p***	**Estimate** ± SE	**Wald Z**	***p***
Intercept	0.002 ± 0.003	0.464	0.643	0.003 ± 0.005	0.571	0.568	0.0006 ± 0.001	0.518	0.605
Weight	–	–	–	–	–	–	0.0001 ± 0.001	0.018	0.986
Length	–	–	–	–	–	–	–	–	–

Note: The upper part shows the estimate for the fixed variables on the three different fabrics. Seed length, Seed weight, and the presence of attachment structures influenced the proportion of seed retained on fleece; only seed weight did not influence the proportion of seed retained on ribbed cotton/nylon blend while on drill cotton the presence of appendence had no influence on the proportion of seed retained. The lower table shows the estimates for the random intercept and random slope of seed weight and length, The result indicates the estimates where not significant and for the random slope the estimates were mostly negligible except on drill cotton; indicating that there was no variation in the intercept and slope of seed weight and seed length on each of the fabric.
Time was treated as a repeated factor. Bold p values are significant at $p < 0.05$.

potential (54% after 5 min of shaking, 48% after 50 min, average 5 species) (Fig. 3). Fabrics with moderate retention potential were knitted wool (43%, 5 min of shaking), double weave wool nylon blend (41%), ribbed cotton/nylon blend (38%) and polyester mesh (23%). Pure cotton (17%) canvas (15%), fine nylon weave (12%), denim (10%) and drill cotton (9%) had low retention potential (Fig. 3). The interaction effect of species and fabric was again significant, indicating that some seed traits may benefit species more on one type of fabric than another (Table 4).

Discussion

This study demonstrates how the seed of common weeds have the potential to remain attached to clothing made of

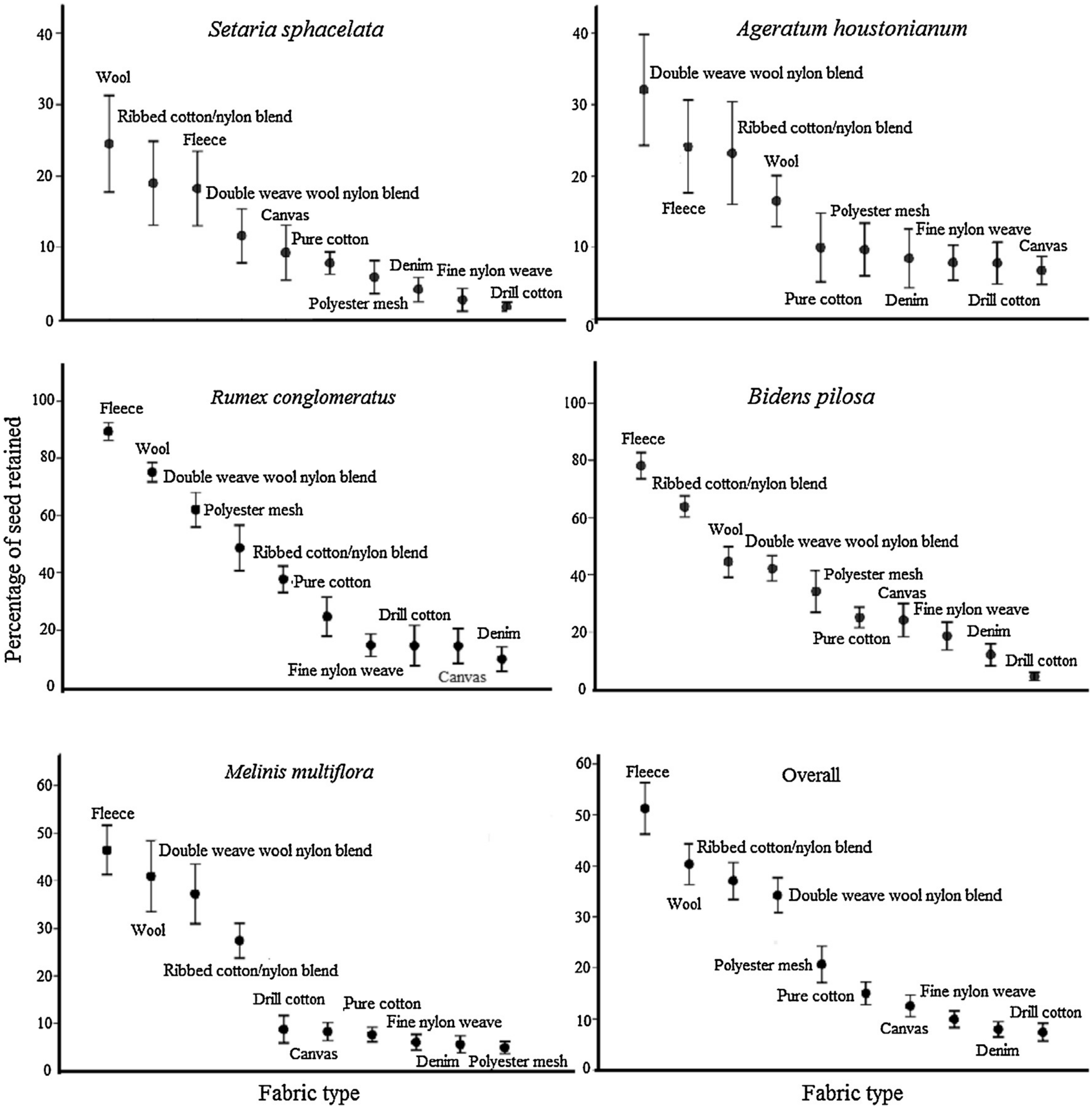

Fig. 3. Mean retention potential of seed from five different weed species on 10 different fabrics commonly used in outdoor clothing, and for all five species combined. Error bars represent the standard error of the mean.

Table 4. Results from the Linear Mixed Model showing the effect of time, fabric, species, and their interaction on the proportion of seed retained (arcsine square root transformed) on ten different types of fabric.

Source	Num. df	Denom. df	*F*	*p*
Species	4	450	90.046	**<0.001**
Fabric	9	450	73.730	**<0.001**
Time	2	866	257.744	**<0.001**
Species × Fabric	36	450	5.882	**<0.001**
Species × Time	8	866	0.411	0.914
Fabric × Time	18	866	1.340	0.158
Species × Fabric × Time	72	866	1.246	0.097

Num. df = Numerator degree of freedom; Denom. df = Denominator degree of freedom. Time was treated as a repeated factor. Bold *p* values are significant at $p < 0.05$.

different fabrics for long times/distances. Some seed from each of the 33 species tested, for instance, remained attached to fleece and ribbed cotton/nylon after 50 min of shaking, and even on drill cotton there were still seed from 26 species attached after prolonged shaking. This indicates that fabrics often used in outdoor clothing may facilitate seed dispersal of important weeds over relatively long distances. The study further shows that seed morphology affects seed dispersal via clothing in similar ways to the effects of seed morphology on dispersal from different types of animal fur.

Seed retention potential varies among weeds

Seed dispersal on clothing appears to benefit some weeds more than others. Weeds such as *A. novae-zelandiae* and *B. pilosa* appear more likely to have their seed dispersed over longer distances than others such as *C. dactylon, F. rubra* and *Plantago lanceolata*, once seed becomes attached to clothing. This corroborates results of other studies experimentally assessing seed detaching from clothing (Ansong et al., 2015; Pickering et al., 2011). Those species that benefit from seed dispersal from clothing could be dispersed into new environments including pristine and remote areas (Chown et al., 2012; Ware et al., 2012) and, if able to adapt to these new habitats, may spread and damage many ecosystems.

A range of additional factors to those assessed here need to be taken into consideration when assessing which species may benefit from long-distance dispersal via clothing. These include the number of seed available for dispersal, where the seed are located on the plants, the number and behaviour of people that come in contact with the species, and the way the seed attach to fabrics (Cousens et al., 2008). These factors can influence the frequency and quantity of the seed attached to clothing and hence the number of seed dispersed (Cousens et al., 2008).

Seed traits affect seed retention potential

Seed traits such as weight, length and the presence of attachment structures affect how long seed remain attached to clothing depending on the interaction between seed traits and the fabric types (Ansong & Pickering, 2014b). In our study, seed with attachment structures such as *R. conglomeratus*, *Avena barbata*, and *Bromus diandrus* had higher retention potential on fabrics with “woolly” or “fleecy” characteristics, but not on fabrics with smoother surfaces such as drill cotton. A similar pattern has been observed for seed retention on fur where there was also an interaction between seed traits and types of fur (Couvreur et al., 2004; Couvreur et al., 2005; Kiviniemi & Telenius, 1998; Römermann et al., 2005; Shmida & Ellner, 1983; Tackenberg et al., 2006; Will & Tackenberg, 2008). *P. lanceolata*, for example, with no distinct attachment structures had a higher retention potential on the less dense fur of cattle (40%) than that of sheep (33%) (Couvreur et al., 2004).

Generally, seed with attachment structures are more likely to remain attached to dense, thin fur than on thick, less-dense fur, while the reverse is common for seed without appendages (Couvreur et al., 2004; Couvreur et al., 2005; Römermann et al., 2005). Also, smaller seed remained attached to fur for longer than larger ones; for example *Holcus lanatus* seed with attachment structures had a high retention potential on the fur of sheep (79%) and cattle (38%) than *S. minor* seed (37% on sheep, 1% on cattle) which do not have distinct attachment structures (Römermann et al., 2005). If large seed (<100 mg) had attachment structures; however, they remained attached to fur for longer (Couvreur et al., 2004; Kiviniemi & Telenius, 1998; Römermann et al., 2005).

Fabric type affects seed retention

What people wear affects seed retention, with seed on some fabrics much more likely to be carried over longer distances than others. Seed tended to be more tightly attached to “woolly” or “fleecy” fabrics than smoother fabrics in our experiments. The fluffy surface of the “fleecy” or “woolly” clothing may result in a greater penetration of attachment structures into the fabric, hence resulting in seed staying attached for longer. In contrast, clothing with smooth surfaces appears to provide relatively poor ‘grip’ for seed even for those seed with awns and hooks. Large and heavy seed, including those with attachment structures, fell off more easily from these fabrics than small and light seed as attachment structures do not appear to penetrate the fabric. Therefore, what people wear is likely to affect the types of seed they might unintentionally disperse. In general, people wearing clothing made of fleece, wool and ribbed cotton/nylon blend materials are more likely to disperse seed with attachment structures over longer distances than those wearing clothing made of pure cotton, canvas, fine nylon weave, denim and drill cotton.

Seed that are tightly attached to clothing may ultimately have to be deliberately pulled from some fabrics for dispersal to occur, as some seed did not fall off even after extensive shaking. When people deliberately remove seed from their clothing, they may dispose of the seed in ways that could enhance, rather than minimise weed invasions (Ansong & Pickering, 2015). For instance, when visitors to a protected area were surveyed, many reported finding seed on their clothing before entering, or after visiting parks (Ansong & Pickering, 2014a). A third of them removed and indiscriminately disposed of the seed (Ansong & Pickering, 2014a). This indicates that, in some circumstances, seed tightly attached to clothing could actually ‘benefit’ from such directed or targeted dispersal. As people, especially visitors to parks and other scenic natural areas, tend to congregate in the same places, it is possible that some of the seed actively dispersed by visitors may contribute to new weed populations. This may occur if the places where the seed are discarded are suitable for weed seed germination and establishment, such as highly disturbed areas on the verges of tracks, car parks and roads.

Context and further research

The current study focused on how seed traits and fabrics affect seed retention once seed was attached to clothing in a laboratory. Hence it did not assess other important factors that also affect the amount and location of seed on clothing, e.g., the spatial distribution and fruiting phenology of the plants (Cousens et al., 2008). It also did not examine the effect of variation in the behaviour of walkers including how fast they walk and where they go, or the effect of weather conditions, such as wet or windy conditions which can affect seed attachment and detachment (Cousens et al., 2008). As seed were manually attached to fabrics in these experiments and a shaking machine was used for the simulations, we cannot expect the retention potential values obtained here to accurately describe the values for each species under all circumstances. The results, however, help us to understand the process and the importance of two key factors affecting retention potential: seed traits and fabric type, by controlling/minimising variation in other factors that affect both attachment and seed retention. It also re-enforces the importance of simple strategies for reducing the risk of spreading weed seed from clothing including wearing clothing made of smooth fabrics. Further testing will, however, help establish the level to which the results provided by the shaking machine under controlled conditions apply more generally, including the risk that they may have underestimated retention potential for some species.

Conclusion

The results presented here highlight how seed from a range of weeds can remain attached to clothing despite shaking, and hence have the potential to be dispersed over long distances by walkers. As mammals, including humans, often move long distances, epizoochory, particularly when humans are involved, may be more important than is generally recognized in biological invasions. Epizoochory, for instance, may play an important role in meta-population dynamics as well as in the spatial distribution of seed at a small scale (Auffret & Cousins, 2013a) and hence could affect species success in a rapidly changing climate.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2016.03.002.

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