Unintentional human dispersal of weed seed

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STATEMENT OF ORIGINALITY

This work has not previously been submitted for a degree or diploma at any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

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ABSTRACT

Seed dispersal is an important biological process as propagule pressure affects the success of plant invasions. The role and importance of humans in this process is increasingly recognised, particularly in relation to long distance seed dispersal. There is still comparatively limited research on unintentional human-mediated seed dispersal, including for seed dispersed from clothing, compared to other dispersal mechanisms such as wind or seed attached to fur. With more people travelling globally, including to remote locations, humans can unintentionally transport seeds over long distances. This can facilitate biological invasions in urban, rural and remote natural areas when it involves the dispersal of weed seed.

Weeds, which are often defined as plants growing in sites where they are not wanted, are a major problem in both natural and agricultural systems. They can reduce biodiversity in natural ecosystems and productivity in agricultural regions, and once established, they are expensive to control or eradicate. Therefore, limiting weed seed dispersal, including over long distances, is important in controlling their spread globally. This thesis examines aspects of unintentional human-mediated weed seed dispersal, using data mining, experimental, modelling and social methods.

First, the thesis assessed the current state of knowledge of how cars, horses and clothing can acts as dispersal vectors, through a systematic quantitative literature review. Across the 49 original research studies that list species with seed dispersed from cars (13 studies), horse dung (15 studies) and clothing (21 studies); a total of 1,021 species were recorded representing 87 families. This includes seed collected from cars (626 species), seed germinating from horse dung (449 species) and/or seed from clothing (249 species), most of which were grasses (Poaceae, 24%, 254 species) or daisies (Asteraceae, 139 species). Nearly all the species (91%, 933 species) collected from these vectors are listed as weeds in some part of the world, with 397 species considered invasive and 121 species classified as important international environmental weeds.

Having highlighted the importance of these vectors, experiments were conducted to quantify important aspects of weed seed dispersal from clothing including the effects of seed traits, distance travelled and the type of fabric. Models showed that the rate of seed detachment decreased with time/distance since attachment for
experimental data on seed dispersal from clothing for eight species of weeds. The results demonstrate that most seeds loosely attached to clothing and hence dispersed over short distances (m), but a small proportion of seeds tightly attached, and can be carried much further (km).

When seed attachment to clothing was standardized to test how retention/detachment rates vary among 33 species and 10 types of fabrics, the majority of species had low retention potentials except on “woolly” or “fleecy” fabrics where some seed remained attached for much longer than on fabrics with a smooth surface. Seed traits such as weight, length and the presence of attachment structures affect how long seed remain attached to fabrics, but which traits are important varied depending on the type of fabric.

Finally a survey was conducted to assess knowledge and attitudes towards weeds of visitors to a popular peri-urban national park, including how they dispose of seeds attached to their clothing. Visitor’s knowledge of weeds and concerns about their impacts was high and they were willing to support spending money on weed management. Although most visitors also supported cleaning clothing before entering parks to reduce the risk of spreading weed seed, the majority had found seed on their clothing that they then disposed of in ways that could contribute to the introduction and spread of weeds in natural areas.

My research makes an original contribution and addresses important gaps in our understanding of how humans unintentionally contribute to the spread of a wide diversity of weed seed. It highlights how where we go, what we wear and what we do with seed on our clothing is important and can affect weed seed dispersal between different habitats on local, national, regional, and transcontinental scales. It also demonstrates that clothing is a highly selective dispersal mechanism that is likely to benefit some weeds over others. The results from this research have important practical implications for weed management, including identifying the risks involved in this type of seed dispersal and how these risks can be minimised.
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GLOSSARY

Terms used in the thesis are based on this glossary which was directly adopted from Richardson (2011) with no major modifications.

**Alien species** (synonyms: adventive, exotic, foreign, introduced, non-indigenous, non-native) – Those species whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (i.e. human–mediated extra-range dispersal).

**Biotic homogenization** – The addition to, and often the partial if not extensive replacement of, local biotas by alien species which can result in decreased compositional turnover of species between distant areas, both in terms of taxonomic and phylogenetic similarity.

**Casual species** – Alien species that do not form self-replacing populations in the invaded region and whose persistence depends on repeated introductions of propagules.

**Dispersal pathway** – The combination of processes and opportunities resulting in the movement of propagules from one area to another.

**Impact** – The description or quantification of how an alien species affects the physical, chemical and biological environment.

**Introduction** – Movement of a species, intentionally or accidentally, owing to human activity, from an area where it is native to a region outside that range (‘introduced’ is synonymous with alien).

**Introduction pathway** – Describes the processes that result in the introduction of alien species from one geographical location to another. It is a subset of dispersal pathways – those that are mediated by human activities.

**Invasion** – The multi-stage process whereby an alien organism negotiates a series of potential barriers in the naturalization – invasion continuum.

**Invasive species** – Alien species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances.
**Invasiveness** – The features of an alien organism, such as their life-history traits and modes of reproduction that define their capacity to invade.

**Long-distance dispersal** – Dispersal of propagules over a long distance, defined either by the absolute distance travelled, or by a set proportion of all propagules that disperse the farthest.

**Native species** (synonym: indigenous species) Species that have evolved in a given area or that arrived there by natural means (through range expansion), without the intentional or accidental intervention of humans from an area where they are native.

**Naturalized species** (synonym: established species) – Those alien species that sustain self-replacing populations for several life cycles or a given period of time (10 years is advocated for plants) without direct intervention by people, or despite human intervention. Invasive species are a subset of naturalized species; not all naturalized species become invasive.

**Propagule pressure** – A concept that encompasses variation in the quantity, quality, composition and rate of supply of alien organisms resulting from the transport conditions and pathways between source and recipient regions.

**Vectors** – A broadly defined phenomenon involving dispersal mechanisms that can be both non-human-mediated (wind, water, birds, mammals, amphibians, etc.) and human-mediated. It is synonymized with mode, transport mechanism, carrier, and bearer.

**Weeds** - Plants (not necessarily alien) that grow in sites where they are not wanted and that have detectable economic or environmental impacts.

**Reference**

PUBLISHED PAPERS INCLUDED IN THE THESIS

This thesis includes published papers in Chapters 2, 3, 4, 5, 6, and 7, which are peer-reviewed and co-authored with my supervisors. My contribution to each co-authored paper is outlined at the front of the relevant chapters. The bibliographic details for these papers including all authors are:


Appropriate acknowledgements of those who contributed to the research but did not qualify as authors are included in each paper.

Signed ........................................ Date: ...........................

Michael Ansong

Signed ........................................ Date: ...........................

Professor Catherine Pickering
1.1 Seed dispersal

Seed dispersal is a critical step in the life cycle of plants, involving the movement or transport of propagules/seeds away from parent plants (Janzen 1970, Connell 1971, Baker 1974, Howe and Smallwood 1982, Willson and Traveset 2000, Levin et al. 2003). It is an important filter in biological invasion; the process where dispersed/introduced plants spread outside their native range or from the first introduced site (Vitousek et al. 1997, Richardson et al. 2000, Hulme et al. 2008, Blackburn et al. 2011, Richardson 2011). Although the majority of plants dispersed/introduced into a region do not become invasive, those that do can have substantial impacts in their new environment (Vitousek et al. 1997, Richardson et al. 2000, Pimentel et al. 2001, Pyšek and Richardson 2010, Vilà et al. 2011).

There are several types of dispersal mechanisms for plants (Ridley 1930, Fosberg 1958, Benvenuti 2007, Vittoz and Engler 2007). The most common dispersal mechanisms are anemochory (dispersal by wind), hydrochory (dispersal by water) and zoochory (dispersal by animals) (Ridley 1930). Other mechanisms such as barachory (gravity) and autochory (self-dispersal) are less common, but also important (Fosberg 1958, Benvenuti 2007, Vittoz and Engler 2007). Most of the seed dispersal by these mechanisms occur over short distances (metres), but some can result in longer distance (>10 m) dispersal including some types of zoochory.

Zoochory consists of epizoochory where dispersal is by the adhesion of seed on the outside of animals and endozoochory, which involves animals ingesting seed (Fosberg 1958, Benvenuti 2007, Vittoz and Engler 2007). Epizoochory can involve seed adhering/attaching to fur, feathers or other parts of the animal and then being transported on the vector away from the site of attachment (Ridley 1930, Sorensen 1986, Benvenuti 2007, Vittoz and Engler 2007, Bullock et al. 2011). Although, seeds of diverse morphology and size from plants with different growth forms and life spans are dispersed by epizoochory, seed with structures such as hooks, spines, barbs, and sticky secretions that increase seed attachment and retention on animals are often favoured (Shmida and Ellner 1983, Sorensen 1986, Mouissie et al. 2005, Romermann et al. 2005, Tackenberg et al. 2006, Mount and Pickering 2009, Pickering et al. 2011). In contrast, endozoochory dispersal occurs when seed in fruits that are ingested by animals are viable after defecation by the animal (Janzen 1984, Pakeman et al. 2002,
Cavallero et al. 2012). Seed with small size and those with seed coats resistant to digestion are mostly favoured by this mechanism (Janzen 1984, Pakeman et al. 2002). Both epizoochory and endozoochory can be effective mechanisms for dispersing seed over long distances, particularly when humans are involved (Shmida and Ellner 1983, Sorensen 1986, Mount and Pickering 2009).

1.2 Human-mediated seed dispersal

Humans intentionally and unintentionally disperse seed from a wide diversity of plants over long distances and including into new regions (Vitousek et al. 1997, Mack and Lonsdale 2001, Randall 2007, Hulme et al. 2008, Pyšek and Richardson 2010, McNeill et al. 2011, Pysek et al. 2011, Richardson 2011, Chown et al. 2012, Ware et al. 2012). This special case of zoochory, called *anthropochory* (human-mediated dispersal), and has been cited as the main cause of biological invasions (Hulme et al. 2008, Blackburn et al. 2011, Richardson 2011). Anthropochory contributes to global weed floras with species that are easily spread by this mechanism and are well adapted to diverse environments, which subsequently start to dominate many ecosystems (Vitousek et al. 1997, Mack and Lonsdale 2001, Randall 2007, Pyšek and Richardson 2010).

Three broad mechanisms have been identified by which seed, as a direct or indirect result of human activity, arrive and invade a new region (Figure 1.1). These are: the importation of a commodity, human transportation, and facilitating natural spread from a neighbouring region (Hulme et al. 2008). These mechanisms have further been classified into six principal pathways: *release, escape, contaminant, stowaway, corridor* and *unaided* (Figure 1.1) (Hulme et al. 2008). Pathways involving the direct assistance of humans such as intentional pathways where seed is introduced for agriculture, forestry or gardening are more efficient in terms of delivering species that become naturalized or invasive (Pyšek et al. 2011). Plants introduced intentionally have, therefore, been observed to naturalize and become more invasive than plants with seed unintentionally introduced. The relative impact of an introduced species, however, does not depend on whether it was introduced intentionally or unintentionally (Pyšek et al. 2011).
Figure 1.1 Framework to categorize pathways of initial introduction of alien species by humans into a new region, adapted from Hulme et al. (2008).

This thesis focuses mainly on epianthropochory, which is a special case of epizoochory, where seeds are unintentionally dispersed by humans, including where seed attach to and disperse from clothing or vehicles (Clifford 1959, Hodkinson and Thompson 1997, Vibrans 1999, Benvenuti 2007, Vittoz and Engler 2007, Mount and Pickering 2009, Wichmann et al. 2009, Pickering et al. 2011, Taylor et al. 2012, Ansong and Pickering 2013). This mechanism, which falls under the stowaway pathway is particularly important as seed can be dispersed over very long distances (Lee and Chown 2009a, e, Wichmann et al. 2009, McNeill et al. 2011, Pickering et al. 2011, Chown et al. 2012).

Human-mediated long-distance seed dispersal is particularly important where it involves weed seed (Lee and Chown 2009a, b, Wichmann et al. 2009, McNeill et al. 2011, Pickering et al. 2011, Chown et al. 2012). With increasing numbers of people moving between different habitats on local, national, regional, and transcontinental scales, there is an increased risk that they will disperse the seed of many species, including invasive ones. Large numbers of weed seeds from a diverse range of plants, for instance, have been recorded on people visiting remote area such as the Arctic and Antarctic (Chown et al. 2012, Ware et al. 2012).
1.3 Weeds

Weeds are often defined as plants growing where they are not wanted, and include plants that have negative economic and/or environmental impacts (Richardson et al. 2000, Richardson 2011). Weeds are diverse: they include annual, biennial, and perennial plants and can be graminoids, herbs, shrubs, vines, trees and aquatic plants. Weeds are also highly adaptable and grow in diverse habitats. They include agricultural weeds, which are plants that invade areas used for agriculture and have negative economic and environmental impacts, as well as environmental weeds, which are plants that invade natural vegetation and adversely affect biodiversity (Baker 1991, Vitousek et al. 1997, Weber 2003, Groves et al. 2005, Pyšek and Richardson 2010).

There are several characteristics that contribute to the success of a plant as weeds (Baker 1974, 1991). These include:

1) the ability to germinate in many environments,
2) discontinuous germination,
3) long lived seed,
4) rapid growth rates,
5) high seed production,
6) production of seed over long periods, including in unfavourable environmental conditions, and
8) adaptations for both short and long distance seed dispersal.

1.3.1 Impact of weeds

Weeds, especially invasive weed species, have a range of ecological impacts (Csurhes and Edwards 1998, Williams and West 2000, Levine et al. 2003, Groves et al. 2005, Pyšek and Richardson 2010). They can compete with native plants for moisture, light, nutrients, pollinators, and other resources, reducing the population of native plants, and in some cases increasing the risk of native species extinction. For example, competition from environmental weeds such as Bridal Creeper (Asparagus asparagoides) threatens many populations of Rice Flowers (Pimelea spicata) in Australia (Groves et al. 2005). They can alter critical ecosystem processes, such as modifying fire regimes, by changing characteristics such as the quantity and distribution of fuel and hence, influence fire behaviour. Changes in the movement of
water in both soil and watercourses due to weeds can also influence geomorphological and hydrological process as found for many aquatic systems invaded by willows (Csurhes and Edwards 1998, Williams and West 2000, Groves et al. 2005).

Weeds have a range of economic impacts. These include reduced productivity in many agricultural areas, increased management costs and reduced ecosystem services (Groves et al. 2005, Australian Weeds Committee 2012). Weeds are also expensive to control (Williams and West 2000, Sinden et al. 2004, Pyšek and Richardson 2010). Paterson’s curse (*Echium plantagineum*), for example, has been estimated to cost agriculture ~$30 million per year, and Lippia (*Phyla canescens*) costs the grazing industry ~$38 million per year in Australia (Groves et al. 2005). The total expenditure on weed control in natural environments in Australia was estimated in 2001–02 as $19.6 million, of which 43% was used for weed control by protected area agencies (Sinden et al. 2004).

### 1.3.2 Weeds in protected areas

Protected areas are “geographical spaces, recognised, dedicated and managed through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Dudley 2008). Weeds, particularly environmental weeds, can adversely affect the conservation value of these protected areas (Csurhes and Edwards 1998, Williams and West 2000, Groves et al. 2005). This includes where weeds have been deliberately introduced into protected areas such as those used in landscaping and rehabilitation, or where they were already established in the protected area prior to its declaration (Csurhes and Edwards 1998, Williams and West 2000, Groves et al. 2005). A third way in which weeds can invade protected areas is where they are unintentionally introduced by people visiting protected areas (Lonsdale and Lane 1994, Pickering and Mount 2010, Pickering et al. 2011).

Visitation to protected areas is increasing due to many factors, including an increasing desire among many people to engage in outdoor activities in natural settings, such as those within protected areas (Chiesura 2004, Florgård and Florgård 2006, Arnberger and Brandenburg 2007, Tzoulas et al. 2007, Newsome et al. 2013, Ngugi et al. 2014). Unfortunately, there are often negative environmental impacts from visitation (Liddle 1997, Pickering and Hill 2007, Newsome et al. 2013). Visitors to protected areas can unintentionally act as vectors for the dispersal of weed seed, including seed attached to their clothing and vehicles. A review of 19 studies on seed dispersal found that people can disperse
a wide variety of seed over long distances from their clothing, vehicles and horses (Pickering and Mount 2010). For instance, seed of >500 species were found on vehicles and >200 species on footwear and clothing, with 15% of these major invasive weeds (Pickering and Mount 2010). In addition, seed from >200 species were found to germinate from horse and donkey dung, including seed from 45 international environmental weeds (Pickering and Mount 2010). The amount of seed unintentionally transported on visitors is of concern, with estimates of over 2.4 million weed seed dispersed from visitors clothing in a single national park during summer (Pickering et al. 2011). Visitors’ attitude and behaviour, including how they dispose of seed they find on their clothing and equipment, is important for the success of many weed management strategies in protected areas.

1.4 Conceptual model for human-mediated dispersal through epianthropochory

A conceptual model of factors affecting seed dispersal including attachment and detachment of seed from clothing was developed based on the existing literature (Figure 1.2). Important factors affecting seed dispersal from clothing include the characteristics of the plant/seed, the vector, and environmental conditions during attachment, transport and dispersal. Many of these factors also may apply to seed dispersal from other vectors such as vehicles. This next section summarises the effects of these factors.

1.4.1 The seed

Seed must, of course, be present at a site used by humans for attachment to occur, so characteristics of plants that make them more likely to be found close to people increase the likelihood of human-mediated dispersal (Mount and Pickering 2009, Scott 2009, Pickering et al. 2011). The number of seeds available for attachment is also important (Sorensen 1986, Hovstad et al. 2009). Plants with more seeds are more likely to succeed in attaching more seed than those with fewer seeds, all else being equal. Seeds must be located on plants in such a way that they could come in contact with clothing or vehicles (Bullock and Primack 1977, Sorensen 1986). The height of the seed on the plant in relation to the vector is also important and likely to influence where/on what the seed could attach (Hovstad et al. 2009). The morphology of seeds is well known to influence seed attachment rates (Shmida and Ellner 1983, Sorensen 1986) with, for example, seed with adhesive structures having higher attachment rates than those without these structures (Graae 2002, Couvreur et al. 2004a, Couvreur et al. 2004d, Mount and Pickering 2009, Scott 2009, Pickering et al. 2011).
Figure 1.2 A conceptual framework for aspect of seeds and attributes of vectors that influence seed attachment and detachment/dispersal in human-mediated dispersal (epianthropochory) from clothing.
The number of seeds that become attached to the vector, the position of the seeds on the vector, and seed morphology all influence seed detachment (Figure 1.2). As dispersal is often proportional to the number of seed attached, the more seed attached, the greater the potential for some seed to be transported over longer distances (Howe and Smallwood 1982, Sorensen 1986, Willson and Traveset 2000, Levin et al. 2003). Where the seed becomes attached to a vector also influences how far the seeds may be transported (Scott 2009, Taylor et al. 2012).

Long distance dispersal is also often dependent on seed traits such as weight, size and presence/absence of attachment structures (Kiviniemi and Telenius 1998, Graae 2002, Couvreur et al. 2004a, Couvreur et al. 2004b, Kulbaba et al. 2009, Mount and Pickering 2009, Pickering et al. 2011). For example, seed with attachment structures such as long awns, hairs and hooks are more likely to remain attached to clothing than those without these structures (Kulbaba et al. 2009, Mount and Pickering 2009, Pyšek and Richardson 2010, Pickering et al. 2011).

1.4.2 The vector

The type and behaviour of vectors influences seed dispersal including epianthropochory. On clothing, for example, the type of material and the combination of clothing worn can affect the amount and type of seeds collected and how far they are dispersed (Mount and Pickering 2009). For the same type of clothing, the surface area of the item and the adhesive quality of material it is made from are also important (Bullock and Primack 1977, Whinam et al. 2005, Mount and Pickering 2009, Pickering et al. 2011, Ansong and Pickering 2013).

Using a habitat that contains a diverse range of plants, including those with many seeds, increases the chance that seed may attach to a vector compared to a habitat with low weed diversity and few seeds. Where people go can also influence seed detachment from clothing, for example, brushing against vegetation or other surfaces can increase seed detachment (Whinam et al. 2005, Mount and Pickering 2009, McNeill et al. 2011, Ware et al. 2012). Cleaning obviously removes seed, subsequently affecting the amount and type of seed attached and remaining attached.
over long distances on the vector. This underlies management recommendations to limit weed spread by regularly cleaning clothing/shoes and vehicles before entering protected areas.

Once seed becomes attached, the distance the vector travels determines the potential distance the seed is likely to be dispersed (Taylor et al. 2012, Auffret et al. 2014). It is expected that the majority of the seed would be dispersed close to the source, with few seed carried over longer distances. As the amount of seed that detaches is not constant, but varies with distance, it is difficult to experimentally determine where a seed will fall (Wichmann et al. 2009, Pickering et al. 2011, Taylor et al. 2012, Auffret et al. 2014). Detachment models that use statistical methodologies to produce dispersal kernels help predict how far seed could be dispersed once attached to human vectors such as clothing (Bullock and Clarke 2000, Levin et al. 2003, Nathan et al. 2003, Bullock et al. 2006, Nathan et al. 2008).

Dispersal kernels are the probability distribution of seed as a function of distance from the parent/source (Bullock and Clarke 2000, Nathan and Muller-Landau 2000, Nathan et al. 2003). They describe the probability of a seed being deposited at a particular distance from the parent plant or source. Dispersal kernels are increasingly used to describe and predict dispersal processes and patterns that provide useful ecological information (Bullock and Clarke 2000, Levin et al. 2003, Nathan et al. 2003, Bullock et al. 2006, Nathan et al. 2008). Species having a kernel with ‘fat’ tail (decays with distance at a slower rate), for instance, are considered to have a greater potential for long distance seed dispersal (Bullock and Clarke 2000, Nathan and Muller-Landau 2000, Nathan et al. 2003).

The shape of the dispersal kernels for seed can be used to test and model how far seed is dispersed and what factors affect dispersal. To date, there are few studies quantifying in detail the dispersal kernels for seed attached to clothing or vehicles. There are studies that have quantified seed dispersal from trousers and socks of hikers (Bullock and Primack 1977, Pickering et al. 2011, Ansong and Pickering 2013), assessed the dispersal of seed in soil on the soles of walking boots (Wichmann et al. 2009) or looked at seed dispersal in soil on vehicles (Taylor et al. 2012). The results of these studies indicate that the probability of seed detachment is not constant over time/distance but is a function of time/distance since attachment, with the overall
probability of seed detachment increasing with time/distance since attachment (Wichmann et al. 2009, Pickering et al. 2011).

1.4.3 Environmental conditions

Climatic conditions such as rain and wind affect seed attachment and detachment but their effects depend on the context, including the characteristics of the seed and vector. Wet conditions can affect the amounts of seed attaching and detaching. This includes from the bottom and sides of vehicles and footwear by increasing/decreasing the adhesive quality of mud/soil (Wichmann et al. 2009, Taylor et al. 2012). Some seeds have structures, that when wet, become sticky or twist into clothing (Ansong and Pickering 2013). As a result, attachment of seeds with these structures, and their subsequent long distance dispersal is more likely in wetter conditions (Couvreur et al. 2004b). High winds can blow seed onto or away from vectors, influencing attachment and the rate of seed detachment, ultimately reducing or increasing the distance seed are transported on vectors.

1.5 Justification for the study and research aims

Dispersal of seed is an important barrier for plants in biological invasions (Vitousek et al. 1997, Hulme et al. 2008, Blackburn et al. 2011, Richardson 2011). One of the mechanisms for long distance dispersal is unintended human seed dispersal, where seed become attached to humans, their vehicles and equipment and are carried and dispersed in new habitats including remote and protected areas (Lee and Chown 2009a, b, Pickering et al. 2011, Chown et al. 2012, Auffret and Cousins 2013a, b).

To date the limited research on this topic includes observational studies, experimental research on seed attachment and retention, and studies modelling dispersal (Lee and Chown 2009a, Wichmann et al. 2009, McNeill et al. 2011, Pickering et al. 2011, Chown et al. 2012, Auffret and Cousins 2013a, b). Studies that have measured actual dispersal distances of seed found that most seed were dispersed within metres of attachment, but some remained attached for much longer (Wichmann et al. 2009, Pickering et al. 2011, Taylor et al. 2012).
This thesis examines aspects of unintentional human-mediated dispersal using data mining, modelling and social methods. The aims of the thesis are to:

1) Quantify how many and which species have seed dispersed from cars (Chapter 2), via the dung of horses (Chapter 3) and/or from clothing (Chapter 4) based on existing scientific literature using systematic quantitative literature reviews (Pickering et al. 2014).

2) Assess if species with particular traits appear to be favoured by these three vectors (Chapters 2, 3 and 4).

3) Identify the attributes of seed and vectors that affect seed dispersal from clothing (Chapter 4), and then, in the following results chapters, test the effect of key attributes. These include:

4) Assess the effect of distance on seed retention/detachment from clothing (Chapter 5).

5) Assess if retention/detachment varies among species and types of fabric/clothing (Chapters 5 and 6).

6) Quantify the importance of seed traits and fabrics on retention/detachment from clothing (Chapter 6).

7) Assess the knowledge, attitudes and behaviour of protected area visitors about weeds, their management, including determining how they dispose of any seed they find on their clothing (Chapter 7).

1.6 Structure of the thesis

The structure of this thesis is in accordance with Griffith University policy on PhD thesis as published and unpublished papers (Appendix 1). It consists of eight chapters (Figure 1.3): a general Introduction (Chapter 1) and Discussion (Chapter 8), three systematic quantitative review results chapters (Chapters 2-4), two experimental results chapters (Chapters 5-6) and a survey results chapter (Chapter 7). All the chapters, other than the general Introduction and Discussion, are in the form of manuscripts formatted to meet the requirements of the peer reviewed academic journals where they were submitted. As a result, each of these chapters has its own introduction, methods, results and discussions and reference list formatted to the journal guidelines. Consequently, there is some repetition and overlap among the individual results chapters, including in the introduction, methods and reference lists.
Figure 1.3 Schematic overview of the content and structure of the thesis.
Published papers included as results chapters


Other publications completed during candidature but not included in this thesis:

Conference abstracts


Ansong, M., and C. Pickering. 2014. Human-mediated seed dispersal (Conference and abstract). Environment Futures Research Institute Student Research Symposium, Gold Coast, Australia, 4 November.


Related publications


1.7 References


CHAPTER 2- SEED DISPERSED FROM CARS

The introduction chapter provided an overview of the importance of seed dispersal including the types of dispersal mechanisms by which seed is disseminated. It also summarised the different ways humans can contribute to seed dispersal, including of weed seed, and how this is important in protected areas. The chapter also included a conceptual model that examined factors that affect human-mediated dispersal including on clothing. The objectives and structure of the thesis were also outlined.

Chapter 2, which is the first results chapter of the thesis, consists of a systematic quantitative review of the academic literature on seed dispersal by cars. It determines how many and which species have seed dispersed from cars, how many of them are weeds and if these species have traits that may increase the risk that their seed is dispersed on cars.

This chapter consists of the published version of a paper co-authored with my principal supervisor. The bibliographic details of the paper, including all authors, are:


My contribution to the paper involved: the compilation of the systematic quantitative literature review database, data analyses, drafting of the manuscript, tables and figures and submission to the journal.
Are Weeds Hitchhiking a Ride on Your Car? A Systematic Review of Seed Dispersal on Cars

Michael Ansong, Catherine Pickering

Environmental Futures Centre, Griffith University, Gold Coast, Queensland, Australia

Abstract

When traveling in cars, we can unintentionally carry and disperse weed seed; but which species, and where are they a problem? To answer these questions, we systematically searched the scientific literature to identify all original research studies that assess seed transported by cars and listed the species with seed on/in cars. From the 13 studies that fit these criteria, we found 626 species from 75 families that have seed that can be dispersed by cars. Of these, 599 are listed as weeds in some part of the world, with 439 listed as invasive or naturalized alien species in one or more European countries, 248 are invasive/noxious weeds in North America, 370 are naturalized alien species in Australia, 167 are alien species in India, 77 are invasive species in China and 23 are declared weeds/invaders in South Africa. One hundred and one are classified as internationally important environmental weeds. Although most (487) were only recorded once, some species such as Chenopodium album, Poa pratensis and Trifolium repens were common among studies. Perennial graminoids seem to be favoured over annual graminoids while annual forbs are favoured over perennial forbs. Species characteristics including seed size and morphology and where the plants grew affected the probability that their seed was transported by cars. Seeds can be found in many different places on cars including under the chassis, front and rear bumpers, wheel wells and rims, front and back mudguards, wheel arches, tyres and on interior floor mats. With increasing numbers of cars and expanding road networks in many regions, these results highlight the importance of cars as a dispersal mechanism, and how it may favour invasions by some species over others. Strategies to reduce the risk of seed dispersal by cars include reducing seed on cars by mowing road verges and cleaning cars.


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A full copy of this paper is available at the publisher’s website via the following link:

http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0080275
CHAPTER 3- SEED DISPERSED VIA HORSE DUNG

The previous results chapter determined the number and diversity of species, including weeds that have been reported to have seed dispersed from cars. It showed that seed from a wide diversity of weeds can ‘hitchhike’ a ride on cars. Among the traits common to species with seed collected on cars is the ability to produce large amounts of seed and have persistent seed banks.

Chapter 3 follows on from this by analysing the potential for weed seed dispersal via the dung of horses used by humans for recreational activities including in protected areas. The study assessed the diversity of species that could be spread through this mechanism including how long seeds can remain viable in the gut of a horse and whether the seed can germinate, grow and reproduce from dung. This chapter is also based on a systematic quantitative literature review.

This chapter consists of the published version of a paper co-authored with my principal supervisor. The bibliographic details of the paper, including all authors, are:


My contribution to the paper involved: the compilation of the systematic quantitative literature review database, data analyses, drafting of the manuscript, tables and figures and submission to the journal.
A global review of weeds that can germinate from horse dung

By Michael Ansong and Catherine Pickering

Summary To assess the diversity of weed seeds dispersed via horse dung, we reviewed 15 studies on seed germination from horse dung – six from Europe, four from North America, three from Australia and one study each from Africa and Central America. Seed from 249 species from 43 families have been identified germinating from horse dung. Almost two-thirds of the species were forbs and 33% graminoids, with over half being perennials and 32% annuals. Nearly every species (totalling 99% of those reviewed) is considered a weed somewhere, with 47% recorded as invasive and 19% international environmental weeds. Of the 2739 non-native plants that are naturalized in Australia, 156 have been shown to germinate from horse dung. This includes 16 of the 429 listed noxious weeds in Australia and two weeds of national significance. Seed from 105 of the 1596 invasive/noxious plant species in North America have also been identified germinating from horse dung. Seed traits including seed size, length, width and mass affect dispersal via horse dung. Habitat disturbance from trampling facilitates germination of seedlings from dung in both natural and experimental studies. Some studies found that plants germinating from dung reach maturity and flower, while others found plants did not survive due to unfavourable growing conditions in the field. The diversity of species with seed that can germinate from horse dung highlights the potential of horses to disperse a range of seed over long distances. Whether such dispersal is beneficial or harmful depends on the plant and the context in which it germinates. To maintain the conservation value of protected areas, it is important to understand and manage the different potential weed dispersal vectors, including horses.

Key words: endochory, protected area, recreational activity, tourism impact, weed dispersal, zoochory.

A full copy of this paper is available at the publisher’s website via the following link:

CHAPTER 4- SEED DISPERSED FROM CLOTHING

The previous results chapter assessed the diversity of weed seed dispersed via horse dung and showed that seed from a wide diversity of species can germinate from horse dung including the seed of many different types of weeds. The study further showed that horse dung is more likely to contain species with smaller seed, predominantly forbs and graminoids, but rarely the seed of shrubs or trees.

Chapter 4 examines another type of human-mediated seed dispersal, by determining the diversity and characteristics of species with seed that can attach and be dispersed from clothing. It is the third results chapter using a systematic quantitative literature review to assess current research. It examines the characteristics of clothing and the effects of environmental conditions on seed attachment and detachment from clothing, highlighting important research gaps that are addressed in later results chapters.

This chapter consists of the published version of a paper co-authored with my principal supervisor. The bibliographic details of the paper, including all authors, are: Ansong, M., and C. Pickering. 2014. Weed seeds on clothing: a global review. *Journal of Environmental Management, 144*, 203-211.

My contribution to the paper involved: the compilation of the systematic quantitative literature review database, data analyses, drafting of the manuscript, tables and figures and submission to the journal.
Weed seeds on clothing: A global review

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ABSTRACT

Weeds are a major threat to biodiversity including in areas of high conservation value. Unfortunately, people may be unintentionally introducing and dispersing weed seeds on their clothing when they visit these areas. To inform the management of these areas, we conducted a systematic quantitative literature review to determine the diversity and characteristics of species with seeds that can attach and be dispersed from clothing. Across 21 studies identified from systematic literature searches on this topic, seeds from 449 species have been recorded on clothing, more than double the diversity found in a previous review. Nearly all of them, 391 species, are listed weeds in one or more countries, with 58 classified as internationally-recognised environmental weeds. When our database was compared with weed lists from different countries and continents we found that clothing can carry the seeds of important regional weeds. A total of 287 of the species are listed as species in one or more countries in Europe, 156 are invasive species/noxious weeds in North America, 211 are naturalized alien plants in Australia, 97 are alien species in India, 33 are invasive species in China and 5 are declared weeds/invasives in South Africa. Seeds on the clothing of hikers can be carried to an average distance of 13 km, and where people travel in cars, trains, planes and boats, the seeds on their clothing can be carried much further. Factors that affect this type of seed dispersal include the type of clothing, the type of material the clothing is made from, the number and location of the seeds on plants, and seed traits such as adhesive and attachment structures. With increasing use of protected areas by tourists, including in remote regions, popular protected areas may be at great risk of biological invasions by weeds with seeds carried on clothing.

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CHAPTER 5- MODELLING SEED DISPERSAL ON CLOTHING

The previous results chapter assessed the diversity and characteristics of species with seed that can attach and be dispersed from clothing based on the current literature. It revealed that seed from a diversity of plants, many of them weeds, can be unintentionally carried and dispersed from clothing with clothing more likely to carry the seed of perennial forbs and graminoids, rather than their annual counterparts or the seed of shrubs or trees. The literature review also demonstrated that clothing type, the surface area, morphology of seed, speed and distance travelled and climatic conditions (e.g. rain) affect attachment and detachment of seed from clothing. It highlighted important gaps in the current literature on seed dispersal from clothing that are addressed in the next two results chapters. This results chapter, Chapter 5, modelled the effect of distance since attachment on dispersal for different types of seed and clothing using a standard seed attachment experiment. The study then estimated the potential number of seed that could be dispersed at different distances along a hypothetical walk in a park, using estimates of attachment rates obtained in the field.

This chapter consists of the published version of a paper co-authored with my principle supervisor. The bibliographic details of the paper, including all authors, are:


My contribution to the paper involved: field-work, data collection, data analyses, drafting of the manuscript, creating tables and figures and submission to the journal.
Modelling seed retention curves for eight weed species on clothing

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Abstract  Humans can unintentionally disperse plant propagules (herein referred to as seeds) including weed seeds from clothing when hiking. There is limited experimental or observational information, however, about unintended human-mediated seed dispersal, particularly from different types of clothing. We experimentally assessed the probability of seed detaching from socks and trousers along a 5 km standardized route for eight common environmental weeds: Bidens pilosa L., Chloris gayana Kunth., Cyniza canadensis L., Cynodon dactylon L., Drymaria cordata (L.) Willd. ex Schult., Poa annua L., Pastinum urvillei Steud. and Sporobolus elongatus R.Br. Seed detachment varied among species on both types of clothing, but seeds more easily detached from trousers than socks. When different models were fitted to the data, a three-parameter generalized exponential model with curves provided the best fit. The curves were leptokurtic, with peak close to the seed source and a long flat tail, which indicates that most seeds dispersed from clothing fall close (within 5 m) to the point of attachment with only a small proportion of seeds dispersed over long distances. Combining attachment and detachment data for the same species, we estimated the actual numbers of seeds potentially dispersed over a hike of 5 km. The study indicates that most seeds are likely to be dispersed at the start of walks, although the actual number of seeds will vary depending on several factors such as the behaviour of the hiker and the amount of weed seeds present at the start of the walk. Those few seeds dispersed much further may, however, be more important in terms of plant invasions. Covering socks with gaiters and avoiding walking through weedy areas such as road edges and car parks before starting walks could minimize the risk of seeds attaching to clothing and hence being dispersed.

Key words: biological invasion, human-mediated seed dispersal, invasive species, recreational ecology, tourism impact.

A full copy of this paper is available at the publisher’s website via the following link:

CHAPTER 6- EFFECT OF CLOTHING TYPE AND SEED TRAITS ON SEED RETENTION POTENTIAL

The previous chapter experimentally tested the effect of different types of clothing and seed on seed detachment over varying distances. The study demonstrated that once attached to clothing, the seed of common international weeds can be spread over long distances, particularly from socks. Detachment probability decreases with distance since attachment, suggesting that seed dispersed from clothing will not be evenly distributed along tracks or paths, but mostly dispersed close to the beginning of a walk with few seeds dispersed further along the tracks or paths.

This chapter (6) follows on by quantifying the importance of seed traits (length, weight and attachment structures) and different types of fabric on seed retention potentials. This was done by experimentally assessing (i) seed retention among 33 species of weeds that differ in seed morphology using three fabrics and (ii) seed retention for 10 different fabrics using five weed species.

This chapter consists of manuscript in review co-authored with my principle supervisor. The bibliographic details of the paper, including all authors, are:


My contribution to the paper involved: field-work logistics, field-work, data collection, data analyses, drafting the manuscript, production of tables, maps and figures and submission to the journal.
The effects of seed traits and fabric type on the retention of seed on different types of clothing

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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.

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A full copy of this paper is available at the publisher’s website via the following link:

http://dx.doi.org/10.1016/j.baae.2016.03.002
CHAPTER 7- KNOWLEDGE, ATTITUDE AND BEHAVIOUR OF PARK VISITORS ABOUT WEEDS

The previous chapter quantified the effects of seed traits, types of fabric and distance on the retention potential of weed seed on clothing. Retention potentials were shown to vary among fabrics, with seed more tightly attaching to fabrics with “woolly” or “fleecy” characteristics, than to smoother fabrics. The weight, length and presence of attachment structures affected how long seed remain attached to clothing suggesting that people wearing clothing made of different fabrics are likely to disperse different combinations of weed seed.

This last result chapter focused on people’s attitudes and behaviour to better understand the human aspect of seed dispersal. A social survey was used to assess visitor’s knowledge, attitudes and behaviour regarding weeds in a large, high conservation value and popular national park. The study examined the effect of different socio-demographic characteristics on visitor responses to provide a better understanding of the social dimensions of weed management, particularly in parks.

This chapter consists of the published version of a paper co-authored with my principle supervisor. The bibliographic details of the paper, including all authors, are: Ansong, M., and Pickering, C. (2015). What’s a weed? Knowledge, attitude and behaviour of park visitors about weeds. Plos One 10, e0135026.

My contribution to the paper involved: field-work, data collection, data analyses, drafting of the manuscript, creating tables and figures and submission to the journal.
What’s a Weed? Knowledge, Attitude and Behaviour of Park Visitors about Weeds

Michael Ansong*, Catherine Pickering
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Abstract

Weeds are a major threat to biodiversity globally degrading natural areas of high conservation value. But what are our attitudes about weeds and their management including weeds in national parks? Do we know what a weed is? Do we consider weeds a problem? Do we support their management? Are we unintentionally spreading weeds in parks? To answer these questions, we surveyed visitors entering a large popular national park near the city of Brisbane, Australia. Park visitors were knowledgeable about weeds; with >75% correctly defining weeds as “plants that grow where they are not wanted”. About 10% of the visitors, however, provided their own sophisticated definitions. This capacity to define weeds did not vary with people’s age, sex or level of education. We constructed a scale measuring visitors’ overall concern about weeds in parks using the responses to ten Likert scale statements. Over 85% of visitors were concerned about weeds with older visitors, hikers, and those who could correctly define weeds more concerned than their counterparts. The majority think visitors unintentionally introduce seeds into parks, with many (63%) having found seeds on their own clothing. However, over a third disposed of these seeds in ways that could facilitate weed spread. Therefore, although most visitors were knowledgeable and concerned about weeds, and support their control, there is a clear need for more effective communication regarding the risk of visitors unintentionally dispersing weed seeds in parks.

A full copy of this paper is available at the publisher’s website via the following link:

http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0135026
CHAPTER 8- DISCUSSION

8.1 Introduction

Seed dispersal is a critical step in biological invasions as propagule pressure contributes to invasion success. With more people travelling, more materials being transported, and more ways in which seed can be transported, unintentional human-mediated seed dispersal is an important type of seed dispersal. This is of particular concern when it involves the dispersal of weed seed due to their ecological and economic impacts.

Despite the importance of this issue there have been relatively few studies on this topic, particularly on seed dispersal from clothing (Ansong and Pickering 2013a, 2014). This is in contrast to the larger body of research on seed dispersal via non-human vectors such as wind (Bullock and Clarke 2000, Kuparinen 2006, Nathan et al. 2011, Thomson et al. 2011, von der Lippe et al. 2013), fur and feathers (Kiviniemi and Telenius 1998, Graae 2002, Couvreur et al. 2004a, Couvreur et al. 2004b, Romermann et al. 2005, Will and Tackenberg 2008, Cousens et al. 2010, Bullock et al. 2011). By conducting systematic quantitative literature reviews to assess existing research, and then using experimental, modelling, and survey methods to investigate key aspects of seed dispersal from clothing, my research makes an original contribution to existing knowledge about unintentional human-mediated seed dispersal.

Specifically the aims of this thesis were to:

1. Quantify how many and which species have seed dispersed from cars (Chapter 2), via the dung of horses (Chapter 3) and/or from clothing (Chapter 4) based on the existing scientific literature using systematic quantitative literature reviews (Pickering et al. 2014).
2. Assess if species with particular traits appear to be favoured by these three vectors (Chapters 2, 3 and 4).
3. Identify the attributes of seed and vectors that affect seed dispersal from clothing (Chapter 4), and then, in the following results chapters, test the effect of key attributes. These include:
4. Assess the effect of distance on seed retention/detachment from clothing (Chapter 5).

5. Assess if retention/detachment varies among species and types of fabric/clothing (Chapters 5 and 6).

6. Quantify the importance of seed traits and fabrics on retention/detachment from clothing (Chapter 6).

7. Assess the knowledge, attitudes and behaviour of protected area visitors about weeds, their management, including determining how they dispose of any seed they find on their clothing (Chapter 7).

All the result chapters in the thesis are published papers with their own abstracts, introductions, methods, results, discussions, conclusions and reference lists. This final chapter discusses the results across the whole thesis in relation to the literature, including how this research has advanced theory and methods in the discipline, the practical implications of the research and future research directions. Detailed discussions of the implications of individual results chapters are provided within each of them. Figure 8.1 summarises the attributes of seed and vectors that influence human-mediated seed dispersal, including those factors directly assessed in this thesis.
Figure 8.1 Key factors affecting human-mediated seed dispersal, including on clothing (epianthropochory). Bolded factors were directly assessed in this thesis.
8.2 A diversity of seed are dispersed via cars, horse dung and clothing.

Several plants have seed that can be dispersed from cars, via the dung of horses and from clothing. Using systematic quantitative reviews, I identified 49 original research studies listing species that have seed dispersed from cars (13 studies), horse dung (15 studies) and clothing (21 studies) (Table 8.1).

Table 8.1 Number of species recorded across the 49 studies examining seed from cars, in horse dung and from clothing.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cars (Chapter 2)</th>
<th>Horse dung (Chapter 3)</th>
<th>Clothing (Chapter 4)</th>
<th>Total for the three vectors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of studies</td>
<td>13 (26%)</td>
<td>15 (31%)</td>
<td>21 (43%)</td>
<td>49 (100%)</td>
</tr>
<tr>
<td>Number of species</td>
<td>626 (61%)</td>
<td>249 (24%)</td>
<td>449 (44%)</td>
<td>1021</td>
</tr>
<tr>
<td>Weed status globally</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weed</td>
<td>599 (64%)</td>
<td>246 (26%)</td>
<td>391 (42%)</td>
<td>933</td>
</tr>
<tr>
<td>Environmental weed</td>
<td>101 (83%)</td>
<td>48 (40%)</td>
<td>58 (48%)</td>
<td>121</td>
</tr>
<tr>
<td>Life span</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual/biennial</td>
<td>281 (74%)</td>
<td>99 (26%)</td>
<td>130 (34%)</td>
<td>382</td>
</tr>
<tr>
<td>Mixed</td>
<td>56 (67%)</td>
<td>16 (19%)</td>
<td>34 (40%)</td>
<td>84</td>
</tr>
<tr>
<td>Perennial</td>
<td>289 (52%)</td>
<td>134 (24%)</td>
<td>285 (51%)</td>
<td>555</td>
</tr>
<tr>
<td>Growth form</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Graminoids</td>
<td>202 (61%)</td>
<td>82 (25%)</td>
<td>163 (49%)</td>
<td>331</td>
</tr>
<tr>
<td>Forbs</td>
<td>360 (61%)</td>
<td>157 (26%)</td>
<td>256 (43%)</td>
<td>594</td>
</tr>
<tr>
<td>Tree</td>
<td>31 (76%)</td>
<td>6 (15%)</td>
<td>9 (22%)</td>
<td>41</td>
</tr>
<tr>
<td>Shrubs</td>
<td>33 (60%)</td>
<td>4 (7%)</td>
<td>21 (38%)</td>
<td>55</td>
</tr>
</tbody>
</table>

Note: The term mixed was used for those species that are biennial/perennial or annual/perennial. International environmental weed listed by Weber (2003). Global weed status according to Randall (2012).

A total of 1,021 species representing 87 families have seed collected from cars (626 species), horse dung (449 species) and/or clothing (249 species). These were predominantly grasses (Poaceae), representing 24% (254 species) of the total diversity, and daisies (Asteraceae) with 139 species, reflecting the high diversity of these two families. There were 74 species common to the three vectors, although only 13 were common to three or more studies (Table 8.2) indicating that some species may often be dispersed by these vectors and in a range of locations. In contrast, there
Table 8.2 Characteristics of the most common species recorded across the 49 studies of seed on cars, horse dung and clothing including plant family, growth form, life form and weed status.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Growth form</th>
<th>Life span</th>
<th>Weed</th>
<th>Global weed status</th>
<th>Number of studies recorded in</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Stellaria media</em></td>
<td>Caryophyllaceae</td>
<td>Herb</td>
<td>Annual</td>
<td>Yes</td>
<td>Yes</td>
<td>6</td>
</tr>
<tr>
<td><em>Medicago polymorpha</em></td>
<td>Fabaceae</td>
<td>Herb</td>
<td>Annual</td>
<td>Yes</td>
<td>Yes</td>
<td>3</td>
</tr>
<tr>
<td><em>Trifolium repens</em></td>
<td>Fabaceae</td>
<td>Herb</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>7</td>
</tr>
<tr>
<td><em>Plantago lanceolata</em></td>
<td>Plantaginaceae</td>
<td>Herb</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>3</td>
</tr>
<tr>
<td><em>Plantago major</em></td>
<td>Plantaginaceae</td>
<td>Herb</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>6</td>
</tr>
<tr>
<td><em>Agrostis capillaris</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>3</td>
</tr>
<tr>
<td><em>Agrostis stolonifera</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>3</td>
</tr>
<tr>
<td><em>Holcus lanatus</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>4</td>
</tr>
<tr>
<td><em>Lolium perenne</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>4</td>
</tr>
<tr>
<td><em>Poa annua</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Annual</td>
<td>Yes</td>
<td>Yes</td>
<td>6</td>
</tr>
<tr>
<td><em>Poa pratensis</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>7</td>
</tr>
<tr>
<td><em>Poa trivialis</em></td>
<td>Poaceae</td>
<td>Graminoid</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>5</td>
</tr>
<tr>
<td><em>Acetosella vulgaris</em></td>
<td>Polygonaceae</td>
<td>Herb</td>
<td>Perennial</td>
<td>Yes</td>
<td>Yes</td>
<td>4</td>
</tr>
</tbody>
</table>

Note: International environmental weed listed by Weber (2003); Weed status according to Randall (2012).
were many species unique to each vector with 417 species only collected from cars, 103 only from horse dung and 271 species only from clothing indicating that: 1) not all species may benefit from more than one of these vectors, and 2) there is a need for more research to better characterise the diversity of seed with potential to be distributed by these vectors.

Vehicles, horse dung and clothing facilitate the transportation of seed of a diversity of weeds. Nearly all the species (91%, 933) collected from these vectors to date have been cited as weeds in some part of the world (Randall 2012) (Table 8.1). These three vectors can carry seed of globally invasive species, with 397 of the species invasive somewhere in the world (Randall 2012) and 121 classified as important international environmental weeds (Weber 2003) (Table 8.1). All 74 species common to the three vectors are weeds and 53 of them are considered invasive while 27 are important international environmental weeds (Weber 2003). The majority of the species were not native to the country or continent where the study was conducted (See Chapters 2, 3 and 4). Therefore, these three vectors are important seed dispersal vectors that may collect and transport large numbers of seed of a range of species within and between different habitats.

In addition to the diversity of seed dispersed by the three vectors, some studies report that large numbers of seed can be dispersed (see Chapters 2, 3 and 4). For example, dry sludge from car washes in Australia were estimated to contain around 67,500 ± 7,300 seeds per ton of sludge (Nguyen 2011), the dung of horses over one year was estimated to contain half a million seeds per horse (Mouissie et al. 2005), while about 25,000 seed representing 70 taxa were collected from different types of clothing worn in Kosciuszko National Park, Australia (Mount and Pickering 2009). When extrapolating results from some of these studies, we see that large number of seed could be dispersed by these vectors. For instance, potentially 1.9-2.4 million seed could be dispersed from hikers clothing in the alpine area around Australia’s highest mountain, Mt Kosciuszko, depending on what visitors wear, where they walk and how much seed is produced by plants growing on the edge of the road at the start of the walk (Pickering et al. 2011). Also, based on the average number seed per car from one study (Chapter 2) and the number of cars in Australia (in 2012, ~12.7 million), over 25.4-50.8 million seed could be moved around daily by cars in Australia (Chapter 2).
8.3 Unintentional human-mediated seed dispersal varies depending on plant traits

Based on the results from the systematic quantitative literature reviews, it appears the three vectors favour species with particular traits and hence cars, horses and clothing are selective dispersal vectors. For instance, there was far greater diversity of forbs (58%), than graminoids (32%) and shrubs/trees (1%) listed in the studies indicating that the seed of many species of shrubs and trees are unlikely to be dispersed by these vectors. Instead it appears that cars, horse and clothing are more likely to disperse seed from perennial than annual plants (Table 8.1). Combining both life history and growth form, it appears that these vectors are more likely to disperse the seed of perennial graminoids (220 species) than annual/biennial graminoids (91), but more annual/biennial forbs (291) than perennial forbs (241).

Although there was considerable variation in species among studies, the species that were common tend to benefit from disturbance and often produce large numbers of small seed that are persistent in seed banks (Table 8.1, Chapters 2, 3 and 4). Most of them favour open habitats with low tolerance for shade. For horse dung, the majority of the species germinating are associated with fertile rather than infertile soils and have hard seed coats (Chapter 3).

Seed dispersed by the three vectors were nearly always weeds (Table 8.1). As weeds benefit from disturbance they often dominate sites used by people, and hence may be more likely to occur in places where they could attach to the vectors such as road verges and car parks for cars, paddocks for horses, and the edge of hiking tracks for clothing. Weeds also tend to produce large numbers of seed and hence more of their seed may attach to the vectors, and could have also been favoured by most of the germination regime used in the studies reviewed. These factors may account, at least in part, for the high diversity of weed seed recorded across the different studies.

These results demonstrate that many species have seed that can be dispersed by one or more of these vectors, but also the limited nature of research on this topic. New studies add to the number of species known to be dispersed by one or more of these vectors. For example, these more recent reviews found 121 additional species with seed dispersed by cars, 33 species by horses, and 221 species by clothing than recorded in a previous review in 2010 (Pickering and Mount 2010).
Generalizations need to be interpreted in the light of the limitation of the current studies. For instance: 1) As new studies continue to add to the number of species transported by these vectors trends identified are far from fully representative of the diversity and types of species that could be dispersed by these vectors. 2) Making comparison across studies is very difficult as there are no comparative studies among the vectors and consistence in the methodologies used by the various studies. 3) There is often limited information about the vegetation where the original studies were conducted, so it is hard to compare seed composition with species composition in the source locations. 4) Germination studies are likely to benefit some species over others as species of plants vary in germination conditions.

Having highlighted the importance of the three vectors for seed dispersal, the rest of the results chapters of the thesis (Chapters 5-7) focused on seed dispersal from clothing. Specifically Chapters 5 and 6 assessed the effects of seed traits, distance travelled by the vector and types of fabric on seed retention on clothing, while the social survey chapter (Chapter 7) assessed vector behaviour, in including how visitors to national parks dispose of seed they find attached to their clothing. Recommendations regarding the other two seed vectors, cars and horses, including future research directions and ways to minimise the spread of seed by these vectors were included in Chapters 2 and 3.

8.4 Attributes of seed and people affect seed dispersal from clothing

The attributes of seed, types of clothing, the combination of clothing worn and the behaviour of those wearing them all affect the amount and type of seed dispersed from clothing (Chapter 4). The amount of seed dispersed from clothing depends on the number of seed attaching to clothing, where on the clothing seed attach, and seed morphology (Chapter 4). The more seeds that attach to clothing, the greater the potential for some of them to remain attached for longer and hence be dispersed over greater distances. Seed morphology is also important, with those seed with long awns, hairs and hooks tending to remain attached to clothing longer than seed without these structures (Chapters 4, 5 and 6).

Where the seed becomes attached and the type of clothing they attach to also influence how far the seed may be transported (Chapter 4). For instance, seed
attaching to the outside of clothes tend to be dispersed over shorter distances than seed lodged in pockets, cuffs and Velcro fastenings (Chapter 4). Seeds were also found to detach faster from drill cotton trousers than cotton/nylon blend socks (Chapter 5). Different numbers and types of seed can attach to shoes, socks and trousers (Mount and Pickering 2009, Wichmann et al. 2009).

The behaviour of people, including where they walk, how fast they walk, and how often they clean their clothing can affect seed dispersal from clothing (Chapter 4). People who walk where many plants are seeding and where plants produce large amounts of seed such as road verges, are more likely to have seed on their clothing, than those who avoid these types of sites. For instance, people walking off-track in a protected area end up with more native than weed seed on their clothing while people walking along roadsides had more weed than native seed on their clothing (Mount and Pickering 2009). Cleaning clothing, obviously removes seed, and hence affects where seed are dispersed. People can also deliberately remove seed from their clothing (Chapter 7), often disposing of them in ways that can increase the chance of weed spread, including in protected areas.

8.5 Distance affects seed retention on clothing

The probability of seed detachment is not constant over time but a function of time/distance since attachment (Figure 8.2). Most seed attach loosely to clothing and hence, are dispersed at short distances, with a small proportion of seed tightly attach and hence, are carried much longer distances (Chapter 5).
Figure 8.2 The proportion of seed retained on clothing of hikers as a function of the distance walked. The figure shows the different regions where high, moderate and low concentrations of seed could be expected as distance increases from the source of seed.

When seed attachment and detachment rates were combined, I found that most seed on the clothing falls to the ground in the first few metres of a walk, with few seed falling off beyond 5 m (Chapter 5). Therefore, seed dispersed from clothing will not be evenly distributed along trails used by hikers, with most seed dispersed close to where they attached and few seed dispersed further along trails (Pickering et al. 2011).

Models where the rate of detachment was not constant but a function of distance/time, particularly those where detachment probability decreased with time/distance since attachment, provided the best fit for experimental data on seed dispersal from clothing [Chapter 4, see also (Pickering et al. 2011)]. A three-
parameter generalised exponential model that combined a simple and a two-parameter power exponential model provided the best fit to the data (Chapter 5). The curves from the model were leptokurtic, with the peak close to the seed source and a long flat tail, which indicates that most seed dispersed from clothing fall close (within 5 m) to the point of attachment with only a small proportion of seed dispersed over long distances (Figure 8.2).

8.6 Retention/detachment varies among species and types of fabrics/clothing

8.6.1 Variation in retention/detachment rates among species

Seed retention/detachment rates vary among species. When seed attachment to clothing was standardized to test how retention/detachment rates vary among species, the majority of species had low retention potentials (Chapter 5). When data was compared for 14 species from studies using the same protocol (Pickering et al. 2011, Ansong and Pickering 2013b, Ansong et al. 2015), considerable variation occurs among species (Figure 8.3).

Seeds of the weeds *Heteropogon contortus* and *Bidens pilosa*, for instance, tightly attached to socks with few seed dispersed within the first 5 m of a hike compared to the seed of *Paspalum urvillei* and *Dramaria glomerata* which were loosely attached with most seed falling off within 5 m of the start of a walk (Figure 8.3). Seed dispersal by clothing, therefore, is likely to benefit some species more than others. Species such as *Acaena novae-zelandiae* are likely to be dispersed over much longer distances than *Cynodon dactylon* seed once attached to clothing. This, however, in part depends on the type of clothing/fabric, with some species having higher retention/detachment rates for some fabrics/clothing compared to others (Chapters 5 and 6). For instance, *Bromus tectorum* seed had a high retention potential on fleece, moderate on socks and but very low potential on drill cotton (Chapter 6), indicating the influence of different types of clothing/fabric on this type of seed dispersal.
Figure 8.3 Ranking of the dispersal potential of the seed of 14 species of weeds based on the percentage of seed dispersed from socks and trousers within the first 5 m of a hike and by the end of 5000 m hike.

8.6.2 Variation in retention/detachment rates among fabrics/clothing

There was variation in the retention/detachment rates of seed among different types of clothing/fabrics (Chapters 4, 5, 6). This is due, in part, to variation in the adhesive quality of the fabric. Generally, seeds have high retention potentials (more tightly...
attach) on “woolly” or “fleecy” clothing such as fleece, wool, hiking socks and nylon/cotton sport sock than smoother fabrics such as canvas, nylon pants, denim and drill cotton (Chapter 6). It appears that the “woolly” or “fleecy” characteristics of some fabrics enable a greater grip and penetration of seed than fabrics with smooth surfaces.

The type of clothing worn also affects the amount and type of seed dispersed (Chapters 4, 5, 6). Seed of eight species were retained for longer on socks than trousers (Chapter 5). Different numbers and diversity of seed were also found on shoes, socks and trousers in a field experiment with uncovered socks and laces collecting significantly more seeds than covered socks and laces (Mount and Pickering 2009). Variation in dispersal distances among different types of shoes has also been found, with seed retained for longer on walking boots made of leather than Wellington boots made of rubber (Wichmann et al. 2009). What people wear, therefore, affects both the distances over which seed can be dispersed and the type of seed dispersed.

8.7 Seed traits affect how long seed remain attached to clothing but this varies depending on the fabric

Seed traits such as weight, length and the presence of attachment structures affect how long seed remain attached to clothing, but which traits are important varies depending on the type of fabric (Chapter 6). Overall, increases in seed length and weight and the presence of attachment structures increased the retention potential of seeds on fleece (Table 8.3). On socks, longer seeds and those with attachment structures had higher seed retention potentials. In contrast, on drill cotton, the retention potential of seed with, or without, attachment structures were similar, but heavier seeds had lower seed retention potentials than lighter seeds. Longer seed, however, still had higher retention potentials than shorter seed (Chapter 6).

A similar pattern has been observed in studies assessing seed retention on fur where there was also an interaction between the effect of seed traits and types of fur (Kiviniemi and Telenius 1998, Couvreur et al. 2004b, Couvreur et al. 2005, Romermann et al. 2005, Tackenberg et al. 2006, Will et al. 2007, Will and Tackenberg 2008, Bläß et al. 2010, Bullock et al. 2011). It is important to note that
most of the heavy and longer seed possessed more attachment structures, which might have compensated for the effect of the weight. Seed with weight above a certain threshold (>100 mg) are, however, reported not to be dispersed by epizoochory on fur (Romermann et al. 2005).

**Table 8.3** Effect of seed traits on seed retention on different types of clothing/fabrics

<table>
<thead>
<tr>
<th>Surface texture of fabric</th>
<th>Retention potential</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High</td>
<td>Low</td>
<td></td>
</tr>
<tr>
<td>Fleecy/Woolly e.g. Fleece</td>
<td>Longer seeds</td>
<td>Shorter seeds</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Heavier seeds</td>
<td>Lighter seeds</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Presence of structures</td>
<td>Absent of structures</td>
<td></td>
</tr>
<tr>
<td>Moderate woolly/fleecy e.g. Sport socks</td>
<td>Longer seeds</td>
<td>Shorter seed</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Weight not important</td>
<td>Weight not important</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Presence of structures</td>
<td>Absent of structures</td>
<td></td>
</tr>
<tr>
<td>Smooth e.g. Drill cotton</td>
<td>Longer seeds</td>
<td>Shorter seed</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lighter seed</td>
<td>Heavier seeds</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Structure not important</td>
<td>Structure not important</td>
<td></td>
</tr>
</tbody>
</table>

8.8 **Park visitors tend to be knowledgeable and concerned about weeds, and support their control, but may actively disperse seed in parks**

Most of the park visitors surveyed in a popular protected area in Australia could define weeds, and are concerned about them (Chapter 7). As a result they supported actions that reduce the spread of weeds, including cleaning clothing before entering parks and financially supporting weed management. Concerns about weeds were not uniform, with older visitors, hikers, and those who know more about the impacts of weeds more concerned than their counterparts (Chapter 7). The majority of visitors also think people unintentionally introduce seed into parks, and many have found seed on their own clothing.

Unfortunately, the majority of visitors also actively disperse seed in parks by indiscriminately disposing of the seed they found on their clothing (Chapter 7). This
included “brushing and dusting their clothing before leaving the park”, “shaking shoes before entering car”, “brushing the seed off wherever they are”, “discarding the seed carelessly”, or “picking the seed and leaving it at the place where they checked their clothing”. Some visitors even stated they had not given much thought to how they disposed of seed. These results highlight the need for better community education regarding the risk of unintentionally dispersing weed seed including in parks (Sheley et al. 1996, Bardsley and Edwards-Jones 2006, Sharp et al. 2011).

8.9 Research contributions and implications

8.9.1 Contribution to knowledge

The current research makes an original contribution and addresses important gaps in our understanding of how humans unintentionally contribute to seed dispersal of different species within and between different habitats. My study demonstrates how unintentional human-mediated dispersal is a very selective dispersal mechanism favouring some species more than others. Seed of perennial graminoids and annual/biennial forbs tend to benefit more from unintentional human-mediated dispersal than others. Species of these growth forms and life spans that are able to adapt to new habitats may spread and hence could affect the dynamics and structure of many sites.

The results of my study further suggest that unintentional human-mediated dispersal is an important issue in biological invasions as most of the seed dispersed via this means are weeds (Ansong and Pickering 2013a, b, 2014). This has particular importance for weed dispersal in high conservation regions, such as protected areas, where people may be unintentionally introduce and spread weed seed on their vehicles and clothing when they enter and use the area for a range of recreational activities (Pickering and Mount 2010, Pickering et al. 2011). The study, therefore, highlights the need for more research on vehicles and clothing as dispersal mechanisms.

The current research adds further evidence highlighting the increasing risk of unintentional human-mediated seed dispersal as human movement between different habitats on local, national, regional, and transcontinental scales increases globally. I have shown that many viable weed seed can be transported long distances (Ansong
and Pickering 2013a, c, 2014, Ansong et al. 2015). The increasing movement of humans between different habitats means that weed seed can be dispersed between different landscapes, isolated habitats and even between continents (Ansong and Pickering 2013a, 2014). At the local scale, weeds can also benefit from directed or targeted dispersal as human tends to follow regular patterns of movement, visit and aggregate in the same habitat (Ansong and Pickering 2013a, 2014). Seed are, therefore, not randomly dispersed but often deposited in sites where there are higher chances that they will germinate, survive, and reproduce (Ansong and Pickering 2013h, Ansong et al. 2015). In many national parks, for example, weeds dominate disturbed sites that are used by visitors such as edges of roads, tracks and car parks (Mount and Pickering 2009).

Species that benefit from human-mediated dispersal could be at an advantage under the constraints posed by the changing climate as their seed could be dispersed over long distances (Cain et al. 2000, Bullock 2012). As climatic conditions change, species that cannot adapt to the new climatic conditions or disperse to suitable habitat are likely to decline (Engler et al. 2009). In contrast, plants with long distance dispersal mechanisms may be able to more rapidly colonising new sites (Pearson and Dawson 2005, Engler et al. 2009). Therefore, species that benefit from human-mediated dispersal, both intentional and unintentional, over long distances, including many of those species identified in this study, may increase in comparison to others, with climate change.

8.9.2 Implications for weed management

The results from this thesis have important practical implications for weed management. These include better communication of the risks involved in this type of seed dispersal both for biosecurity and protected areas management. Policies and best practices to assist people including park visitors, explorers, field researchers, and park managers in minimizing the risk of transferring invasive species while conducting field activities are therefore essential.

Communication

Greater appreciation by people, particularly those travelling to remote natural areas, of the risks of introducing seed, and their support can reduce the threat of unintentional human-mediated seed dispersal (Powell 1968, Sheley et al. 1996, Miller
and Hobbs 2002, Lee and Chown 2009, Eiswerth et al. 2011, McNeill et al. 2011). This could be done mainly through more effective communication to reduce the risk of human-mediated dispersal.

Communicating strategies that highlight the importance of weed hygiene, including the careful disposal of seed on clothing and equipment of international travellers, park visitors and staff could be done via different media. Preventive strategies, for instance, could be incorporated into education programmes for people using protected areas (Sheley et al. 1996, Whinam et al. 2005, Mount and Pickering 2009, Eiswerth et al. 2011, McNeill et al. 2011, Ware et al. 2012). The information could also be incorporated into minimum impact codes such as walking guides and educational materials for conservation areas (Whinam et al. 2005, Mount and Pickering 2009, McNeill et al. 2011, Ware et al. 2012) and disseminated through traditional methods such as posters, notices or brochures at visitor centres and park entry points. They could also be available on mobile applications and internet based platforms, including social media such as Facebook and Twitter (Mount and Pickering 2009, Scott 2009, Pickering et al. 2011).

Strategies for protected area management

Methods to reduce the risk of unintended human-mediated dispersal in protected areas include:

- If dominated by weeds, mowing road verges before seeding could help prevent weed seed attaching to vehicles (Chapter 2).
- People using protected areas could reduce their exposure to seeds by, for instance, avoiding walking through areas such as road verges and car parks, where weeds can occur, prior to the start of walks in protected areas (Mount and Pickering 2009, Pickering et al. 2011).
- Both park managers and visitors need to regularly clean vehicles and other machinery; particularly before and after driving on unpaved roads and/or in muddy conditions (Rew and Fleming 2011).
- Clothing should be checked regularly for weed seed. Selecting clothing such as gaiters, rubber knee boots, not using Velcro fastenings is advised, and keeping pockets closed/zipped reduces the risk of dispersing weed seed (Chapters 4, 5 and 6).
• Carefully disposing of seeds that become attached to clothing and vehicles including not removing and then leaving the seeds in parks (Chapter 7). Where seed are removed from clothing they could be disposed of, for example, in the trash.

• If riding still authorized then it is important limit access by horses to areas of high conservation value, at least in part, due to the risk of them introducing weed seed. However, it should be noted that such a recommendation is very context dependent, as in Europe, horses and other domesticated animals are deliberately introduced into areas of high conservation value because of their potential to disperse seed (Chapter 3).

8.9.3 Research context and further research directions

Estimating seed retention including on clothing/animals is complicated. This is why experiments on seed retention focus on specific aspects of the process to assess their relative effects. The results help us to understand the process and the importance of key factors affecting retention potentials, including seed traits and types of fabric, by controlling/minimising variation in other factors. Some limitations need to be considered when interpreting the results and the implications of this research as some of the results are context and time specific.

The results of the three systematic review chapters indicated that there are more species dispersed by vehicles, horse dung and clothing than previously thought, as new studies continue to add to the number of species transported by these vectors. Therefore, although important trends were identified from the reviews, they are far from fully representative of the diversity and types of species that could be dispersed by the three vectors. Further field research on seed dispersal via these vectors combined with regular updating of the existing database, will assist in providing a more comprehensive assessment of the propensity of species to be disperse via these vectors and risk involved. Correspondingly, research on seed dispersal from other means of transport such as mountain bikes, trail bikes (motorized bikes) and quad bikes is also required to better understand the risk associated with different types of recreational activities dispersing weed seed in protected areas.

There is also the need for more comparative studies to help compare the seed dispersed among different vectors. For instance, studies comparing seed attachment
between bikes and horses or bikers and hikers will have the same units of measurement, enabling easy comparison and quantifiable differences in the diversity of species and number of seeds capable of being dispersed by the different vectors. Such studies will provide important information that could underpin management decisions.

Studies assessing human mediated dispersal also need to have consistency in the methodologies and approaches used. The majority of the studies have been observational or opportunistic with no standardized experimental design and statistical analyses. This makes results context dependent and limit the capacity to make generalization.

The experimental Chapters 5 and 6, which assessed how seed traits and fabrics affected seed retention did not assess some of the other factors affecting seed dispersal such as the amount and location of seed attaching to clothing, and the spatial distribution and fruiting phenology of the plants. The experiments in these chapters also did not examine the effects of variation in the behaviour of walkers including how fast they walk and where they go, or the effect of weather conditions, which can affect seed attachment and detachment. Also, seeds were manually attached to fabric in these experiments. The retention potential values obtained in the experiments do not fully account for how each species might be dispersed under all circumstances. Further testing will help establish the extent to which the results provided by the shaking machine under controlled conditions apply more generally, including the risk that the results in Chapter 6 may have underestimated retention potentials for some species.

Although the results of the park survey in Chapter 7 provided important information about the knowledge, attitudes and behaviour of park visitors in regard to weeds and seed on clothing, the survey was only for one park and at a time of high usage. It is important that additional surveys be conducted in a greater range of parks and at different times to more comprehensively assess these issues for park visitors. Also, more general surveys of the attitudes of other sections of the community, in addition to that of park visitors, are required such as those undertaken by Bremner and Park (2007), Sheley et al. (1996) and Bardsley and Edwards-Jones (2006). This could include surveys of international visitors entering Australia or other countries, as well
as farmers, forestry works, explorers and scientists. This would help in dealing with issues regarding weed management more broadly.

More research on unintended human-mediated seed dispersal will improve our understanding of how many and which types of weeds have seed that can be transported by clothing and how far, and the success of different management actions to reduce their spread. To complement existing research, studies from the Americas, Asia and Africa are required as there are still surprisingly few papers on this topic in the academic literature from those regions. Research is needed to quantify the diversity and composition of seed and species that can attach to and be disperse from different types of clothing. Such studies will help determine how the type of material clothing is made from affects the number of seed that attach and are dispersed, and better quantify the effects of seed traits.

8.10 Conclusions

This thesis contributes to research on human-mediated seed dispersal by examining different aspects of this dispersal mechanism, mainly from clothing, with experimental, modelling and social methods. The research has shown that although people support weed management, they can unintentionally disperse a wide diversity of seed via their cars, animals (horses) and on their clothing. The types of seeds dispersed and the distance the seed is dispersed vary depending on plants traits, seed traits and the behaviour of people, including what they wear. Assessing the dispersal characteristics of weed species from clothing is a useful addition to the weed science literature and provides information for conservation managers to assist them in better managing popular areas of high conservation value. By characterising the risk of weed spread posed by walkers, the thesis starts to quantify this process and hence identifies were generalisations can be made to reduce the risk of the spread of weeds by these vectors.

8.11 References


APPENDICES


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A thesis may include published or unpublished papers where such papers have been produced under supervision and during the period of candidature, and where the quality of such papers is appropriate to Doctoral, or MPhil, level research. For the purpose of this requirement, papers are defined as a journal article, conference publication, book or book chapter. Papers which have been rejected by a publisher must not be included unless they have been substantially rewritten to address the reviewers’ comments, or have since been accepted for publication.

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A thesis may entirely or partly be composed of papers. Where a thesis is entirely composed of papers, there is no minimum requirement for the number of papers that must be included and is a matter of professional judgment for the supervisor and the student. The papers may be rewritten for the thesis (post-print or pre-print versions); or they can be inserted in their published format, subject to copyright approval as detailed above. A paper may form a single chapter, or several papers may form successive chapters. Passages from papers may be transferred directly or in modified form into one or more of the chapters of the thesis. Students may retype the papers to be consistent with the thesis. However, this is at the discretion of the student.

Linking chapters
The thesis must be more than a collection of papers in the following ways. The chapters must be in logical order and strongly linked together. Students who submit a thesis in this format may introduce each new chapter with a foreword which introduces the research and establishes its links to previous chapters. In general, the thesis should include a general introduction which sets out the context of the thesis. The thesis should also include a conclusion which draws together the main findings of the thesis and establishes the significance of the work.

Declarations
All theses that include papers must include declarations which specify the publication status of the paper(s), your contribution to the paper(s), and the copyright status of the paper(s). The declarations must be signed by the corresponding author (where applicable). If you are the sole author, this still needs to be specified. The declaration will need to be inserted at the beginning of the thesis, and for any co-authored papers, additional declarations will need to be inserted at the beginning of each relevant chapter. You may wish to consult the declaration requirements for inclusion of papers diagram to ensure that you insert the correct declaration(s) within the thesis. Please note that completion of the declaration(s) does not negate the need to comply with any other University requirement relating to co-authored works as outlined in the Griffith University Code for the Responsible Conduct of Research.

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