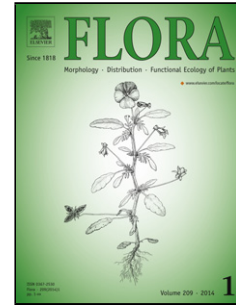


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**Diaspore heteromorphism in the invasive *Bromus tectorum* L.
(Poaceae): sterile florets increase dispersal propensity and distance**

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Highlights:

- *Bromus tectorum* is a troublesome invasive grass in North America.
- The sterility of terminal florets induces a diaspore heteromorphism.
- Dispersal of diaspores with and without sterile florets attached was investigated.
- Primary and secondary dispersal by biotic and abiotic agents were considered.
- Across the study, diaspores with sterile florets were better dispersers.

Abstract

Within a species, the distance travelled by a particular diaspore depends on its morphology. In Poaceae, the presence of terminal sterile florets can lead to diaspore heteromorphism, which may influence dispersal. We tested the hypothesis that the presence of sterile florets favored dispersal in *Bromus tectorum* L., an invasive grass in the Western US.

We used field and controlled experiments to study the dispersal of caryopses with and without sterile florets attached (respectively complex and simple diaspores), as well as pieces of inflorescence that detached from the mother plants. We considered both primary and secondary dispersal, as well as abiotic and biotic dispersal agents. The distance travelled by the diaspores and their attachment to animal fur were related to the presence and number of sterile florets. Abiotic agents moved diaspores over relatively short distances, both in terms of primary and secondary dispersal. A significant proportion of diaspores attached to fur, suggesting a potential for dispersal over long distances. Complex diaspores were better dispersers than simple ones (and pieces of inflorescence), and this pattern was consistent across the study. However, among complex diaspores, the number of sterile florets had little or no influence.

Considering primary and secondary dispersal by abiotic and biotic agents provided a general picture of the dispersal ecology of *B. tectorum*. For all the dispersal steps and dispersal agents we studied, the presence of sterile florets favored dispersal. These results highlight the functional significance of diaspore heteromorphism induced by floret sterility in the dispersal of Poaceae.

Keywords Anemochory; cheatgrass; dispersal ecology; downy brome; epizoochory; seed dimorphism

1. Introduction

Seed dispersal is an essential component of plant life history and fundamental in determining spatial patterns, population growth rates, and rates of species expansion (Clobert et al., 2001; Cousens et al., 2008). An enhanced understanding of dispersal mechanisms in troublesome invaders can therefore help to better understand colonization dynamics and prevent further spread (Davies and Sheley, 2007; Hastings et al., 2005; Kot et al., 1996; Monty and Mahy, 2010). Within a particular species, diaspore morphological variability can profoundly influence dispersal in both time and space (Cousens et al., 2008; Matlack, 1987; Monty et al., 2008). Such diaspore morphological variability can, on one hand, arise from continuous trait variation such as size, mass or length of a dispersal structure (Harper, 1977; Ortmans et al., 2016). On the other hand, variability can originate from the production of two or more types of diaspores by plant individuals, i.e. diaspore heteromorphism (Imbert, 2002; Mandak, 1997).

Diaspore heteromorphism in the broad sense, i.e. including heterospermy and heterocarpy, was defined by Venable (1985) as “the production by single individuals of seeds (or single-seeded fruits) of different form or behavior”. According to Imbert (2002), diaspore heteromorphism has been described in 18 plant families but is most common in the Asteraceae (138 species) Chenopodiaceae (18 species) and Brassicaceae (12 species). Diaspore heteromorphism is documented but less common in other plant families, such as Caryophyllaceae (Telenius, 1992) and Poaceae (Campbell et al., 1983; Dyer, 2004). Ecological strategies related to diaspore heteromorphism notably include differential competitive ability (Venable, 1985), dormancy (Mandak, 1997) and dispersal (Telenius, 1992).

The presence/absence of dispersal structures is a functionally significant case of diaspore heteromorphism (Cheptou et al., 2008; Imbert, 2002; Kucewicz and Gojło, 2014). Diaspore morphological variability is largely maternally controlled, and dispersal structures are generally formed from the maternal plant’s tissues such as outgrowths of the ovary wall, the receptacle or the achene (Donohue, 1999; Harper, 1977; Zhang et al., 2014). Diaspore variability can also

originate from ovule abortion (Ganeshaiah and Shaanker, 1988). In *Dalbergia sissoo* (Fabaceae) and *Cryptantha flava* (Boraginaceae), fruit morphology variation due to ovule abortion was shown to influence dispersal (Casper and Wiens, 1981; Ganeshaiah and Shaanker, 1988). Lack of pollination or insufficient resources are often implicated as causal factors for ovule abortion (Lee and Bazzaz, 1986), but it can also be genetically predetermined (Casper and Wiens, 1981; Wiens, 1984).

In grasses, dispersal structures can be formed during inflorescence development when, for example in Paniceae, the meristem produces a bristle in place of a spikelet or a branch (Doust and Kellogg, 2002). In other grasses, the presence of appendices on one diaspore can result from the abortion of terminal florets: the meristem continually produces lateral structures that shorten more and more as the number of meristematic cells becomes increasingly limited (Kellogg et al., 2013; McKone, 1985). Such terminal sterile florets, if they remain attached to the most distal fertile caryopsis, could play the role of dispersal structure and create a diaspore heteromorphism. This is notably likely when sterile florets carry awns, resulting in a dispersal unit with awns pointing in different directions. Awns were shown to play a key role in the dispersal and establishment of several grasses species (Ansong and Pickering, 2014; Cheplick, 1998; Peart, 1981).

Bromus tectorum L. (downy brome or cheatgrass, Poaceae) presents such inflorescence development. On a spikelet, the most distal florets often abort and remain attached to the most distal mature caryopsis (McKone, 1985; Monty et al., 2013). Caryopses and sterile florets bear pubescent awns. This species is one of the most widespread introduced annual grasses in North America and continues to spread (Bromberg et al., 2011). It is a highly problematic invasive plant in the western United States (US) that influences fire cycles and has profoundly altered some ecosystems of the North American West (D'Antonio and Vitousek, 1992; Knapp, 1996; Mack, 1981). Despite documentation of wind dispersal in this species in particular environments (Johnston, 2011; Monty et al., 2013), little is known about its dispersal ecology and the role in dispersal of diaspore heteromorphism caused by the presence or absence of sterile florets.

Understanding the determinants of dispersal in a spreading plant is of interest from both basic and applied perspectives, but the task is very challenging due to the many sources of complexity: (1) a particular plant species can disperse in various ways and have several dispersal agents (Van der Pijl, 1970); (2) dispersal is often a multi-stage process, i.e. diaspores are first transported from the plant to a surface (primary dispersal), then surface-lying diaspores can be redistributed until they germinate, are permanently trapped or dispersal structures deteriorate (secondary dispersal) (Matlack, 1989; Schurr et al., 2005; Vander Wall et al., 2005); (3) dispersal is affected by the environment, notably the presence of obstructions that can stop diaspore movements, the vegetation structure that can modulate wind speeds, and/or the animals that can play a significant role in redistributing diaspores over the landscape (Horvitz and Schemske, 1986; Nathan and Muller-Landau, 2000). Therefore, to describe the dispersal ecology of a plant species, both primary and secondary dispersal by its different dispersal agents should be investigated in different habitats.

In this study we investigated the dispersal ecology of *B. tectorum* and tested the hypothesis that sterile florets had a positive role on dispersal for both primary and secondary dispersal by abiotic and biotic agents. To do so, we conducted field and controlled experiments in different environments and tested 1) whether diaspores with sterile florets (henceforth referred to as *complex diaspores*) were better dispersers than those without (referred to as *simple diaspores*); and 2) among complex diaspores, whether the number of sterile florets attached was positively correlated to dispersal.

2. Material and methods

2.1. Study species – *B. tectorum* is native to Eurasia and Mediterranean region. It is a highly autogamous, cleistogamous winter annual. It germinates in the fall when precipitation is sufficient, achieves its maturity in late spring and dies in early summer (Klemmedson and Smith, 1964). Seeds lose dormancy through dry after-ripening over the summer, and then germinate when sufficient moisture is present (Klemmedson and Smith, 1964; Upadhyaya et al., 1986).

Caryopses can be disseminated within a few weeks after maturity by different agents including rain, wind, and animals (Klemmedson and Smith, 1964; Upadhyaya et al., 1986).

The inflorescence is a large, open, and drooping panicle from 5 to 20 cm long and is formed by spikelets on very slender branches. Spikelets from 2 to 4 cm long are composed of two to eight florets (Upadhyaya et al., 1986). An awn is attached to the surface of the outer membrane, the lemma, of these pubescent or villous florets. The most distal florets are often sterile, and remain attached to the most distal fertile caryopsis after fruit set. This results in two types of diaspores (Monty et al., 2013): the *simple* ones, consisting of a single filled caryopsis with an awned lemma and the *complex* ones including one filled caryopsis and one or several sterile florets, resulting in a diaspore with two or more awns (Fig. 1). Thus, the number of awns of a complex diaspore is equal to the number of sterile florets plus one. An illustration of sterile florets is given in appendix (Fig. A).

2.2. Study area and site selection – We conducted our field studies in Fort Collins and surrounding areas in Larimer County, Colorado, USA. Larimer County is part of the eastern plains and foothills region. This region, at an elevation around 1,500 m, is characterized by relatively flat terrain with gentle hills and bluffs. The vegetation is dominated by grasslands, especially short-grass prairie.

The study of abiotic primary dispersal and secondary dispersal of *B. tectorum* was conducted in six sites in three types of habitats (disturbed area, grassland and shrubland). In both sites classified as disturbed (Douglas reservoir, Nix Natural area), experimental work took place on ancient railway tracks and road margins with ruderal vegetation and a relatively high proportion of bare soil. The sites classified as grasslands were located on a sown mixed grassland (Wasson Reservoir) and a short-grass prairie rangeland (Clark Reservoir), both with a dense open vegetation dominated by grasses. The sites classified as shrubland were located on a east-facing slope recolonized by Pines (Horsetooth Reservoir) and on the banks of a small stream in a natural area (Running Deer Natural Area). In these two sites characterized by 10%

to 30% cover of shrubs and trees, experimental work was performed in areas dominated by shrubs or small trees, but not directly under the canopy. The collection of individuals used to study biotic primary dispersal (primary epizoochory) was done in five sites. Two of them were the same as used previously (Table 1).

2.3. Abiotic primary dispersal – Three individuals of *B. tectorum* (at least 30 m apart) were randomly selected in each of the six sites (Table 1). A geotextile square (DeWitt®, Sikeston, Missouri) of 1.5 x 1.5 m with a lip on outer edge of 0.15 m, was placed rough side up around these individuals, such that diaspores that fell onto it became stuck and would not move any farther. The geotextile square was pierced in its center to let the individual grow through it and was fixed with anchoring pins (DeWitt®, Sikeston, Missouri) and wooden stakes in the ground. All inflorescences of other *B. tectorum* plants in a buffer of ca 2 m around the geotextile squares were cut and removed to avoid dispersal from non-target plants. An illustration of the experimental design is given in appendix (Fig. B). The squares were installed during seed formation, before the first diaspore was dispersed (early June 2011) and were monitored until the end of the dispersal (early August 2011). Every three to five days, all diaspores that had fallen onto each square were collected. The number of visible awns of each diaspore was counted. When several diaspores remained attached together to a piece of inflorescence, we called it a *piece of inflorescence*. Examples of such pieces of inflorescence are illustrated in appendix (Fig. C). The distance from the fallen diaspores to the center of the square, which represents the primary dispersal distance, was measured with a meter tape.

2.4. Biotic primary dispersal (primary epizoochory) – Twenty individuals of *B. tectorum* were collected before seed formation (end of April and early May 2014) in each of the five sites (Table 1). The collected individuals were transplanted into pots of 1.08 liters filled with a homogeneous substrate (Growing Mix, Professional use, Fafard®, Agawam, Massachusetts), and transferred to a greenhouse at the Colorado State University (CSU), Fort Collins, CO, USA (average day

temperature=24°C, average night temperature=21°C, average day relative humidity=73% and average night relative humidity=82%). The individuals were watered daily. Pots were arranged in a completely randomized design and re-randomized weekly.

After the *B. tectorum* individuals had set seeds, from late May to early July 2014, a red fox tail (*Vulpes vulpes* L.) (Caro Furs ®, Namur, Belgium) was placed in contact with and moved across the first inflorescences reaching maturity to mimic epizoochory. Fur of red fox was used because this species has a wide geographical distribution (Northern hemisphere), large populations, high mobility and uses agricultural and ruderal habitats extensively (Hovstad et al., 2009). The fox tail was moved on each *B. tectorum* individual horizontally along the length of the tail one time in the direction of the hair and one time against the hair, twice a week, for two weeks. Each individual plant was put in a box during the movements of the fur to collect the diaspores that fell on the ground. The number of diaspores (and the corresponding number of awns) and pieces of inflorescence that fell in the box and that were attached to the fox tail were counted for each individual plant. After the last pass of fur, the number of diaspores (and their corresponding number of awns) that remained on the individual plant was also counted. The diaspores that remained on the individual and that fell to the ground were considered non-dispersed by epizoochory, according to Will et al. (2007). The proportions of dispersed diaspores for each type (number of diaspores of the considered type attached to fur divided by the total number of diaspores of the considered type) were calculated for each individual plant. All considered diaspores and pieces of inflorescence included at least one filled caryopsis.

2.6. Secondary dispersal – In June 2011, releases of sterilized diaspores marked with fluorescent powder (UV Gear ®, Reigate, Surrey, UK) were performed in each of the six sites (Table 1). The released diaspores were collected in Larimer County. A release consisted of 50 randomly-selected diaspores (25 simple diaspores and 25 complex diaspores) placed in a 5 cm diameter circle on the ground. Six releases were performed in each site at three different times. Each release was made at a different location within the site (at least 30 m apart). Different

colors were used to differentiate diaspores coming from various releases. A total of 1,800 diaspores were released (50 diaspores x 6 releases x 6 sites). The diaspores were sterilized by placing them on moist paper towels for 5 h, microwaving for 1 min on high power, and then oven-drying for 24 h at 70 °C.

After approximately 75 h, diaspores were recovered at night using a black light (UV Gear ®, Reigate, Surrey, UK). The number of awns was counted and the distance travelled by the diaspores from the release circle center was measured with a laser distance measuring device (Stanley, TRU LASER TLM100i, Stanley Black & Decker, New Britain, CT, USA). The diaspores recovered in the release circle were considered non-dispersed. The diaspores not recovered in a 20 m circle after a comprehensive search, were referred to as *exported* and assumed to have been dispersed by secondary epizoochory.

2.7. Data analysis – Abiotic primary dispersal distances were analyzed using generalized linear mixed models (GLMM) with the function `glmer` in the `lme4` package in R ver. 2.15.2 (R Development Core Team, 2011; Zuur et al., 2009). GLMM provides a flexible way to analyze data that do not satisfy the assumptions of a standard linear model (Zuur et al., 2009). Moreover, this type of model allows for a grouping structure in the data, i.e. several data for each replication (individuals, sites, etc.), by the use of one or several random grouping factor(s) (Bates, 2005; Cook et al., 2013; Hurlbert, 1984; Millar and Anderson, 2004; Sumasgutner et al., 2016; Zuur et al., 2009). *Site* (nested within *habitat*) and *individual* (nested within *site*) were included as random grouping factors to control for pseudo-replication (Bates, 2005; Hurlbert, 1984; Zuur et al., 2009). The Gamma distribution was chosen in the GLMMs because abiotic primary dispersal distance is a continuous and non-negative measure and did not follow a normal distribution (Zuur et al., 2009). Abiotic primary dispersal distances were log-transformed to achieve homoscedasticity of residuals. A first GLMM was performed with the two fixed factors *diaspore type* and *habitat* and the two random grouping factors *site* and *individual*. Then, a two-way ANOVA (*diaspore type* and *habitat* as crossed fixed factors) was performed on this GLMM,

followed by pairwise comparisons of means (t-test with Bonferroni's adjustment) in order to detect the general differences between the three types of diaspores (*simple* diaspore, *complex* diaspore and *piece of inflorescence*) in the three types of habitats. Thereafter, a second GLMM was performed on the complex diaspores with the two fixed factors *number of awns* and *habitat* and the two random grouping factors *site* and *individual*, in order to determine the influence of the number of awns on the abiotic primary dispersal distance.

Variations in primary epizoochory were also analyzed using GLMM with the function *glmer*. *Site* and *individual* (nested within *site*) were used included as random grouping factors to control for pseudo-replication (Bates, 2005; Hurlbert, 1984; Zuur et al., 2009). The binomial distribution was chosen because the data were binomial, i.e. dispersed or not (Zuur et al., 2009). A first GLMM was performed with the fixed factor *diaspore type* and the two random grouping factors *site* and *individual*. Then, a one-way ANOVA (*diaspore type* as fixed factor) was performed on this GLMM. A second GLMM was performed on the complex diaspores with the fixed factor *number of awns* and the two random grouping factors *site* and *individual*, in order to determine the influence of the number of awns on primary epizoochory.

Secondary dispersal distances were analyzed using GLMM with the function *glmer*. *Site* (nested within *habitat*) and *release* (nested within *site*) were included as random grouping factors to control for pseudo-replication (Bates, 2005; Hurlbert, 1984; Zuur et al., 2009). The Gamma distribution was chosen in the GLMMs because secondary dispersal distance is a continuous and non-negative measure and did not follow a normal distribution (Zuur et al., 2009). Secondary dispersal distances were log-transformed to achieve homoscedasticity of residuals. A first GLMM was performed with the two fixed factors *diaspore type* and *habitat* and the two random grouping factors *site* and *release*. Then, a two-way ANOVA (*diaspore type* and *habitat* as crossed fixed factors) was performed on this GLMM, followed by pairwise comparisons of means (t-test with Bonferroni's adjustment). Thereafter, a second GLMM was performed on the complex diaspores with the two fixed factors *number of awns* and *habitat* and the two random grouping factors *site* and *individual* in order to determine the influence of the number of awns on the

secondary dispersal distance. In order to compare the number of exported diaspores (i.e. dispersed by secondary epizoochory) for the two types of diaspores (*simple* and *complex* diaspores), a chi-square test was performed, with “exported or not” as columns and the type of diaspores as rows.

3. Results

3.1. Abiotic primary dispersal – 8,184 diaspores were collected: 704 were pieces of inflorescence, 2,104 were simple diaspores and 5,371 were complex diaspores. The two-way ANOVA of the GLMM revealed significant effects of *diaspore type* ($F_{2,8160}=8.109$, $P<0.001$), *habitat* ($F_{2,8160}=3.079$, $P=0.046$) and their interaction ($F_{4,8160}=3.201$, $P=0.012$) on abiotic primary dispersal distance.

Simple and complex diaspores were dispersed farther than pieces of inflorescence both in disturbed areas and in grasslands (Fig. 2, Table A). Complex diaspores were dispersed farther than simple diaspores in disturbed areas. In contrast, no difference between the three types of diaspores was found in shrublands. Abiotic primary dispersal distance of pieces of inflorescence did not differ among habitat types. Complex diaspores were dispersed farther in grasslands than in shrublands and even farther in disturbed areas. The simple diaspores were dispersed farther in disturbed areas and in grasslands than in shrublands.

Primary dispersal distance of complex diaspores increased slightly with the number of awns ($P=0.045$, $r=0.00127$).

3.2. Biotic primary dispersal (primary epizoochory) – Out of the 100 collected plants, 85 survived and set seeds. A total of 5,814 diaspores were counted: 1,113 were pieces of inflorescence (among which 520 attached to fur and 199 fell in the box), 2,927 were simple diaspores (among which 535 attached to fur and 274 fell in the box) and 1,774 were complex diaspores (among which 1,003 attached to fur and 442 fell in the box). The three-way ANOVA of the GLMM of the primary epizoochory revealed a significant effect of *diaspore type*

($F_{2,5727}=44.906$, $P<0.0001$). Complex diaspores attached more to fur than pieces of inflorescence, and pieces of inflorescence attached more than simple diaspores (Fig. 3). The primary epizoochory of the complex diaspores did not depend on the number of awns ($P=0.251$).

3.3. Secondary dispersal – Of the 1,800 diaspores studied, 532 were not dispersed and 35 were exported. The two-way ANOVA of the GLMM based on the 1,233 other diaspores revealed significant effects of *diaspore type* ($F_{1,1182}=44.906$, $P<0.001$) and *habitat* ($F_{2,1182}=5.870$, $P=0.003$) on secondary dispersal distances. Complex diaspores were dispersed farther than simple ones (Table A). Diaspores were dispersed farther in disturbed areas and in shrublands than in grasslands (Table A). The secondary dispersal distance of complex diaspores did not depend on the number of awns ($P=0.315$). More complex diaspores ($n=29$) were exported than simple diaspores ($n=6$) (Pearson Chi-Square=15.414, $P<0.001$).

4. Discussion

The dispersal of *B. tectorum* involves different steps and depends on various dispersal agents. Wind and rain disperse diaspores over relatively short distances, both from the mother plant to the ground (primary dispersal) and on the ground from place to place (secondary dispersal). Dispersal by abiotic agents is influenced by the surrounding vegetation that modulates local wind speeds and entraps ground-dispersing diaspores. In the presence of animals, a significant proportion of diaspores can attach to fur and potentially be dispersed over longer distances. Across all these dispersal steps and agents, we found that sterile florets attached to the most terminal fertile caryopsis had a positive effect on its dispersal.

4.1. Dispersal steps and agents – When *B. tectorum* plants reach maturity in early summer, diaspores are easily detached by abiotic or biotic agents. Most of them are dispersed in the form of caryopses, with or without sterile florets attached depending on their position on the spikelet. However, a small proportion is dispersed in the form of pieces of inflorescence, i.e. pieces of

spikelets or panicle, most likely because all the aboveground material is dry and easily broken. Generally, these pieces of inflorescence are not dispersed as far as caryopses by abiotic agents. This is not surprising because previous studies showed that an increase in diaspore size and weight reduced abiotic dispersal (Greene and Johnson, 1993; Monty et al., 2008).

Primary dispersal by abiotic agents represents a very short-scale process, with 95% of diaspores falling in the 33 cm around the mother plants. However, as *B. tectorum* seeds need after-ripening before they can germinate (Upadhyaya et al., 1986), secondary dispersal is likely to take place and redistribute diaspores in space. In our study, the main abiotic dispersal agent was the wind because rainfall events were scarce during early summer. This situation is representative of many regions invaded by *B. tectorum* (Bauer et al., 1998; Bromberg et al., 2011).

Primary dispersal distance decreased with the height and density of the surrounding vegetation, being highest in disturbed areas. This supports previous evidence that shrubs act as windbreaks and can reduce anemochory (McEvoy and Cox, 1987). Secondary dispersal was highest in disturbed areas and shrublands, i.e. in habitats where bare ground is common. In grasslands, where the vegetation cover is higher, seed entrapment strongly reduced average dispersal distances. These results confirm those of Johnston (2011) and Monty *et al.* (Monty et al., 2013), who found even more important rates of secondary dispersal of *B. tectorum* in areas with almost no vegetation (reclamation and burned areas, respectively). Research on other species also found an influence of vegetation on ground level dispersal through a decrease in wind speed, changes in wind turbulence and seed entrapment (Chambers, 2000; Marushia and Holt, 2006; McEvoy and Cox, 1987).

If mature *B. tectorum* plants are directly contacted by mammals, a significant proportion of diaspores can detach from the mother plant and attach to fur. This type of primary dispersal (i.e., epizoochory) can play an important role and enable seeds to travel over longer distances. This is particularly true for the red fox that we used as a model species because foxes can travel 10 to 100 km in one night (Zimen, 1984) and use a wide range of habitats. However, the patterns observed for the red fox fur are likely to be similar for other hairy animals, and even

for human clothes (A. Monty, personal observations). Our results suggest that animals can also play a role in secondary dispersal, i.e. when diaspores on the ground attach to them. Indeed two percent of the ground-lying diaspores in our secondary dispersal experiment were not recovered, even after a comprehensive search, suggesting an export by epizoochory from the release area.

Despite all this evidence, it is difficult to know the total distance travelled by *B. tectorum* diaspores because the different dispersal mechanisms are not exclusive; diaspores can be dispersed a number of times by different agents, and the distance travelled by epizoochory strongly depends on animal behavior.

4.2. Positive role of sterile florets –According to Volis (2014), “seed heteromorphism and its ecological consequences in Poaceae are poorly described”. The few well-documented examples include cases of amphicarp on one hand, and differences between seeds derived from cleistogamous vs chasmogamous flowers on the other hand (Campbell et al., 1983).

In the case of *B. tectorum*, we showed that the two forms of diaspores (excluding the pieces of inflorescence) resulting from the presence/absence of sterile florets to fertile ones showed different behavior in terms of dispersal ability. Throughout the study, we consistently found a higher dispersal capacity for complex diaspores as compared to simple ones (except in habitats where dispersal is lower). Complex diaspores result from the abscission of the most terminal fertile caryopsis without abscission of the sterile florets. As shown in Fig. 1, these diaspores have awns in several directions. Awns appear to play a key role in the different steps of *B. tectorum* dispersal. They increase air resistance, both from the plant to the ground and on the ground, and their roughness helps adhesion to fur (Mack, 1981). Complex diaspores may also remain attached to fur longer than simple diaspores because adhesive structures can have a positive effect on diaspore retention time (Tackenberg et al., 2006).

If the presence or absence of sterile caryopses had a significant effect on dispersal, it has to be noted that among complex diaspores the number of awns had little or no effect. In general, when

the number of awns of a species increases, the size and the weight of its diaspores increase too, which may thwart the positive effect of awns on plant dispersal (Tackenberg et al., 2006). Also, the incremental advantage of additional awns may decrease with the number of awns.

Diaspore heteromorphism has been described in many species found in frequently disturbed, habitats and relatively arid environments (Harper, 1977; Van der Pijl, 1970; Zohary and Pascher, 1937), such as those typically invaded by *B. tectorum*. Producing different diaspore types could represent a bet-hedging strategy, advantageous in unpredictable environments (Harper, 1977; Imbert, 2002). The differential dispersal of the diaspore types can maximize the spread in space and help both the expansion of existing populations and the colonization of new areas. As diaspore heteromorphism is known to affect other aspects of the life cycle, such as germination and survival (Baskin et al., 2014; Braza and García, 2010; e.g. Imbert, 1999), further research is needed to fully characterize the ecological consequences of diaspore dimorphism in *B. tectorum* invasion.

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Figure captions

Fig. 1. Two types of diaspores of *B. tectorum*. (A) complex diaspore, with sterile caryopses attached; (B) simple diaspore. Scale bar = 1cm.

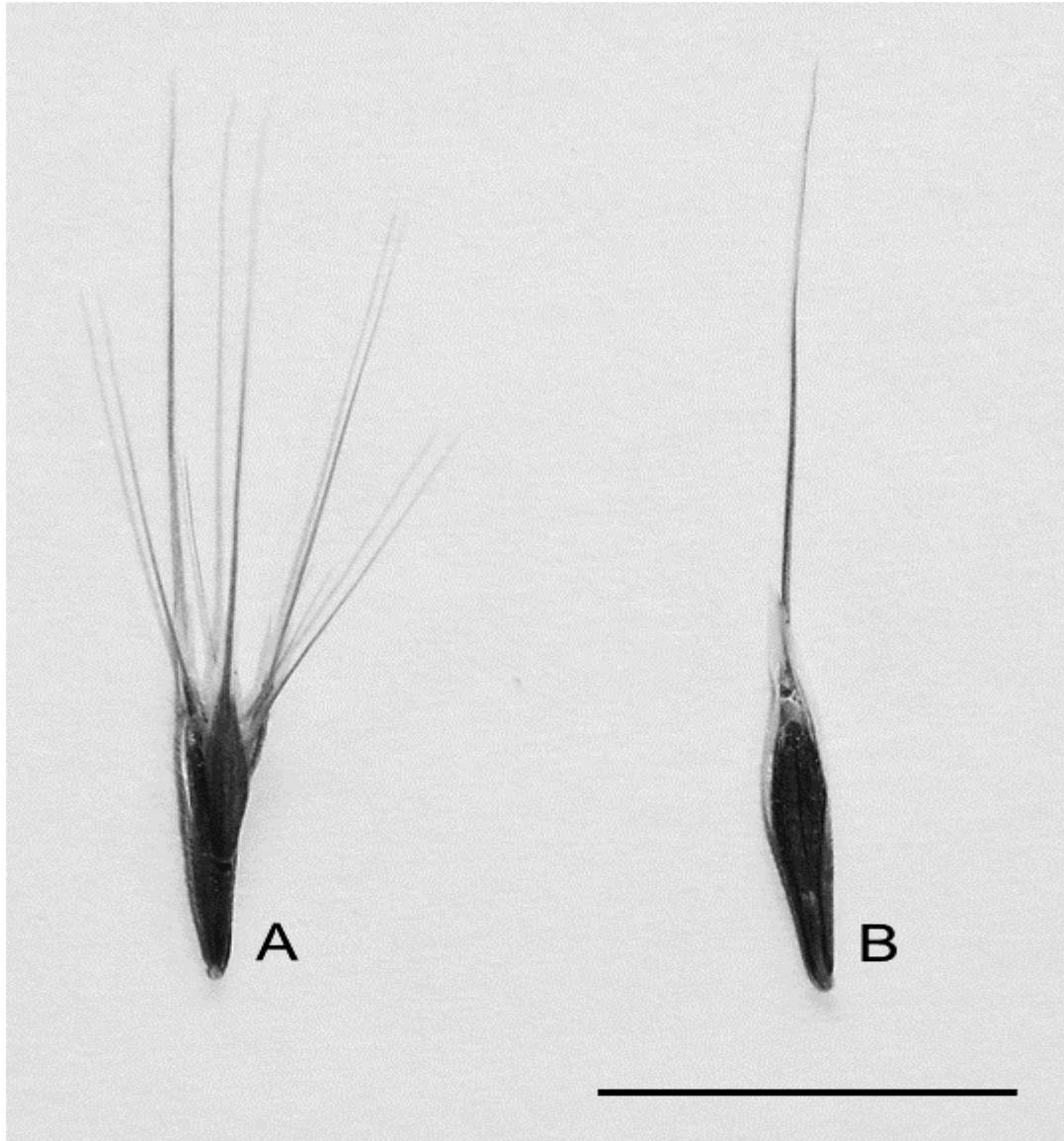


Fig. 2. Abiotic primary dispersal distance of *B. tectorum* for the three types of diaspores in the three types of habitats. Data are means with 95% confidence intervals. Different letters above bars indicate significant differences ($P < 0.05$).

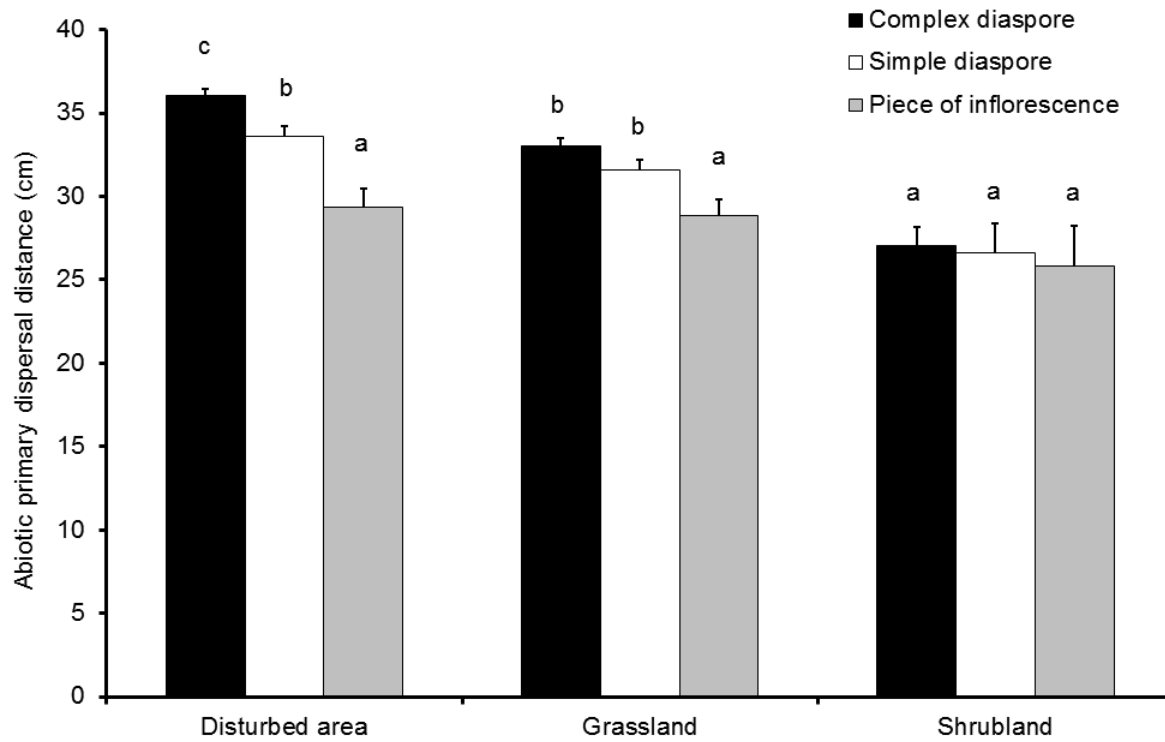
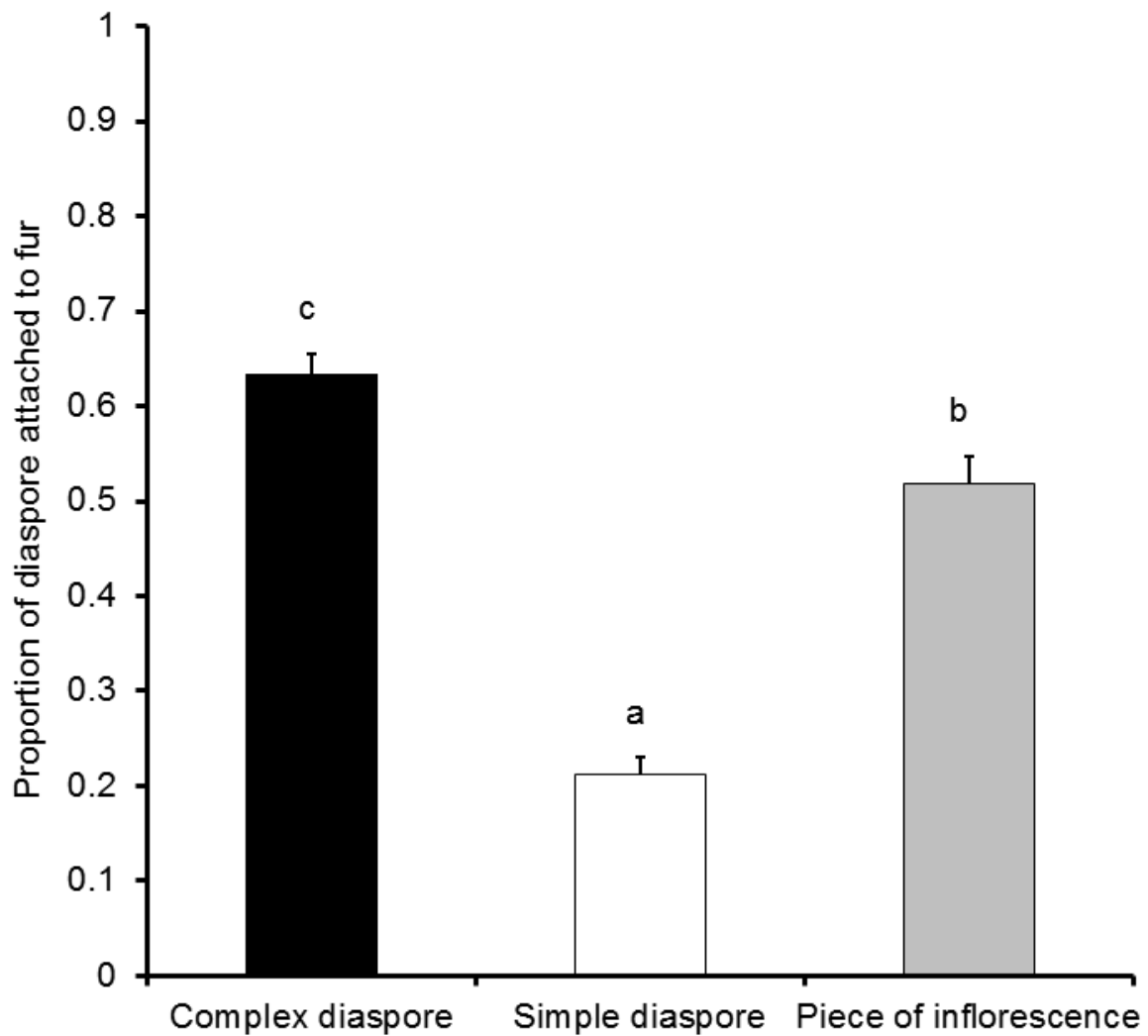


Fig. 3. Proportion of the three types of diaspores dispersed by primary epizoochory. The proportions (number of diaspores of the considered type attached to fur divided by the total number of diaspores of the considered type) were calculated for each plant then averaged. Intervals represent 95% confidence intervals. Different letters above bars indicate significant differences ($P < 0.05$).



Appendices captions

Fig. A. Illustration of the components of a complex diaspore: fertile caryopsis (A) and sterile florets (B1 to B7, from the most proximal to the most distal).

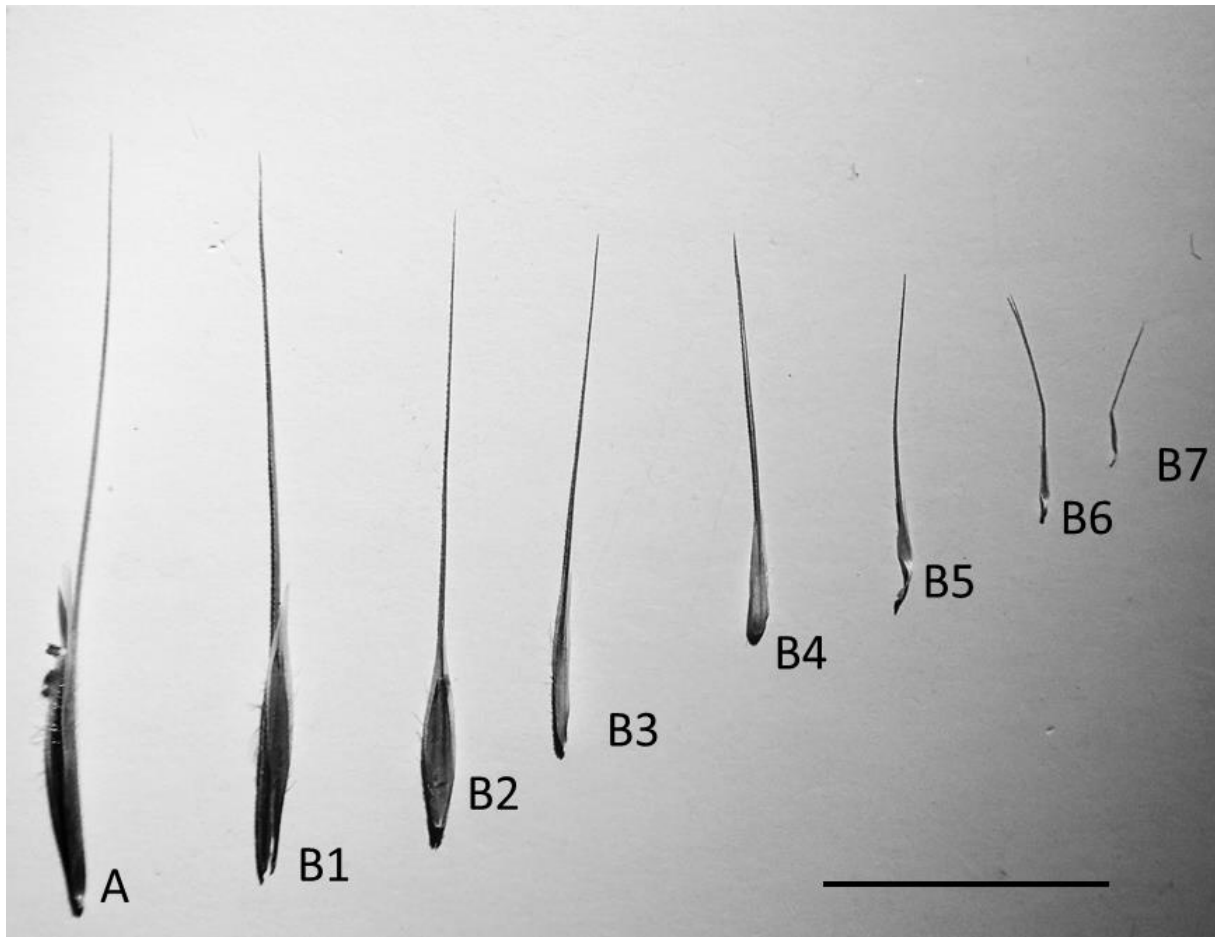


Fig. B. Illustration of a geotextile square used to study abiotic primary dispersal.



Fig. C. Illustration of pieces of inflorescence.



Table

Table 1. Sites used to study dispersal of *B. tectorum* with their geographical coordinates, elevation, habitat type and the number of diaspores studied.

Location	Geographical coordinates	Elevation (m)	Habitat type	Number of diaspores studied		
				Abiotic primary	Biotic primary	Secondary
Nix Natural Area	40°57'N - 105°05'W	1518	Disturbed area	1,177	1,853	300
Douglas Reservoir	40°71'N - 105°10'W	1601	Disturbed area	3,223	865	300
Wasson Reservoir	40°74'N - 105°06'W	1634	Grassland	1,397	0	300
Clark Reservoir	40°71'N - 104°95'W	1630	Grassland	1,755	0	300
Horsetooth Reservoir	40°52'N - 105°15'W	1616	Shrubland	136	0	300
Running Deer Natural Area	40°56'N - 105°01'W	1522	Shrubland	496	0	300
Bacon Elementary School	40°50'N - 105°04'W	1513	Disturbed area	0	1,138	0
Cattail Chorus Natural Area	40°57'N - 105°03'W	1495	Disturbed area	0	799	0
Mulberry Water	40°59'N - 105°07'W	1512	Disturbed area	0	1,159	0

Table A. Descriptive statistics of the primary and secondary dispersal distances (cm) of the different types of diaspores by abiotic agents, in the three types of habitats.

	Complex diaspore				Simple diaspore				Piece of inflorescence			
	Mean	± SD	Min	Max	Mean	± SD	Min	Max	Mean	± SD	Min	Max
Primary dispersal												
Disturbed area	36.0	± 22.3	2	99	33.6	± 20.0	3	95	29.3	± 19.8	2	90
Grassland	33.0	± 20.5	1	99	31.6	± 17.5	5	86	28.9	± 16.5	3	88
Shrubland	27.0	± 23.7	3	90	26.6	± 21.3	3	85	25.8	± 19.6	4	81
Secondary dispersal												
Disturbed area	16.4	± 30.2	3	208	8.2	± 10.3	3	60	-	-	-	-
Grassland	6.3	± 8.5	3	96	4.6	± 2.3	3	20	-	-	-	-
Shrubland	12.4	± 21.0	3	202	8.1	± 9.8	3	68	-	-	-	-