

Fire promotes downy brome (*Bromus tectorum* L.) seed dispersal

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Abstract Particularly well-known among the many impacts of the invasive annual grass downy brome (*Bromus tectorum*, Poaceae) is its ability to alter fire cycles and increase in abundance after fire. However, little is known about how fire influences *B. tectorum* dispersal. We quantified fire effects on *B. tectorum* dispersal using three recently burned areas in the western region of the Colorado Rocky Mountains by marking diaspores (seeds) with fluorescent powder, and then recovering them at night using ultraviolet lights. Diaspores were of two types: with and without sterile florets attached. We also characterized

vegetation cover and near-surface wind speed in burned and unburned areas. Diaspores travelled much farther in burned areas than in nearby unburned areas (mean \pm standard error at the end of the experiment: 209 ± 16 cm and 38 ± 1 cm, respectively; maximal distance at the end of the experiment: 2,274 cm and 150 cm, respectively), indicating an increase in dispersal distance after fire. Diaspores with sterile florets attached dispersed longer distances than those without sterile florets (mean \pm standard error at the end of the experiment: 141 ± 14 cm and 88 ± 7 cm, respectively). Vegetation cover was lower and wind speeds were higher in the burned areas. Our results indicate that at least one of the mechanisms by which the spread of *B. tectorum* is promoted by fire is through increased seed dispersal distance. Preventing movement of seeds from nearby infestations into burned areas may help avoid the rapid population expansion often observed.

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Introduction

Disturbances have long been recognized as important in facilitating plant species invasions (Mack et al. 2000; Elton 1958; Bradford and Lauenroth 2006; Hobbs and Atkins 1988). The mechanism commonly reported involves resource availability; when disturbances

reduce or eliminate existing vegetation, resource availability increases, lowering the biotic resistance of the plant community and providing an opportunity for invading plants to become established (Burke and Grime 1996). The role of disturbances in altering seed dispersal is a less-studied mechanism that may also affect plant species invasions. Disturbances often change the structure of plant canopies, the microtopography of the soil surface, and/or the presence of a litter layer. Recent research has shown that such changes may affect how seeds are captured as they move across the landscape (Chambers 2000; Johnston 2011). If a disturbance alters the landscape in a way that facilitates dispersal, then the propagule supply of invasive plants could increase within the disturbed area, exacerbating the effect of the disturbance on promoting invasion (DiVittorio et al. 2007; Eschtruth and Battles 2009; Thomsen et al. 2006).

In the western United States, disturbance caused by fire and the expansion of the non-native annual grass *Bromus tectorum* (downy brome or cheatgrass, Poaceae) are strongly associated. As a winter annual grass, *B. tectorum* responds readily to the increased light and nutrients available following fire and takes advantage of newly available resources (Melgoza et al. 1990). The fine fuels produced as *B. tectorum* senesces then causes an increase in fire frequency, promoting expansion of the grass (D'Antonio and Vitousek 1992). This has resulted in a dramatic, extensive, and costly decline in the productivity and diversity of rangelands of the western United States (DiTomaso 2000). Despite the strong association between *B. tectorum* invasion and fire, the effect of fire on *B. tectorum* dispersal has not been studied.

Disturbances such as fire may have different effects on the dispersal of dissimilar propagule types. Propagule morphology has been shown to have a large effect on wind-mediated dispersal (Chambers 2000). If a disturbance such as fire alters near-surface wind speeds, then propagules with different appendages may respond differently to this change. Wind is an important dispersal agent after severe disturbance (Chambers and MacMahon 1994).

Here, we examine the effect of fire on wind-mediated dispersal of *B. tectorum*. Although animal-mediated dispersal of *B. tectorum* is likely most important for very long-distance dispersal, wind is important over smaller scales (Johnston 2011). Understanding the movement of the majority of seeds at

local scales is important for predicting the outcome of disturbances, as local seed movements determine the propagule pressure experienced at a given location. Prior work has shown that annual grass propagule pressure is directly related to the probability of establishment (Davies et al. 2008).

In this study, we compared dispersal distances of *B. tectorum* diaspores in recently burned areas and in paired, undisturbed areas. We focused on plant communities dominated by *Pinus edulis* Engelm. (two-needle pinyon) and *Juniperus osteosperma* (Torr.) Little (Utah juniper), as *B. tectorum* expansion into this plant community type has recently become a concern (Shinneman and Baker 2009) and as fires are frequent in this vegetation type. We also quantified the effect of diaspore dimorphism on *B. tectorum* dispersal. The two most common types of diaspores, single seeds and seeds attached to sterile, unfilled florets, were included. To aid our understanding of potential mechanisms for fire effects on dispersal, we also characterized the wind conditions and vegetation in burned and unburned study areas. Our research questions are (1) does fire promote diaspore dispersal at the scale of the site; (2) do the two diaspore types disperse differently in burned and/or unburned conditions, and (3) what is the general impact of fire on factors which may influence dispersal?

Methods

Study area and site selection

Field research was conducted in Moffat and Rio Blanco Counties, Colorado, USA (Fig. 1). The region is characterized by rolling hills and ridges and varies from 2,100 to 3,300 m in elevation. Elevations of 2,000–2,300 m, dominated by two-needle pinyon and Utah juniper, were the focus of this study. Criteria for study site selection included: (1) burned in either 2009 or 2010; (2) a control area matching the burned area in topography, slope, aspect, and soil type was available in the immediate area; and (3) the area was accessible by road. Three such sites were located, and all three were used in this study (Fig. 1).

The Pinyon Ridge burn (40°15'N; 108°22'W; elev. 2,030 m) happened in August 2010 on a 15 ha area and was considered to be moderate to high in severity (Ron Simpson, US Bureau of Land Management, pers. comm.). Only large branches remained on trees, and

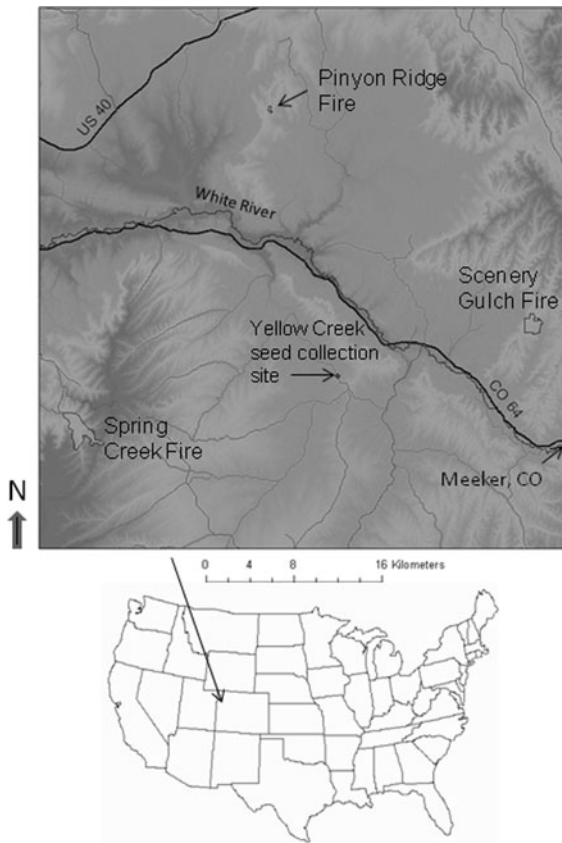


Fig. 1 Study area map indicating the three study burns and the diaspore collection site

no trees survived within the perimeter of the burn. Pinyon Ridge soils are within the Rentsac-Moyerson complex (Natural Resources Conservation Service Soil Survey Geographic; *hereafter* SSURGO). At the study site, soils appeared similar to the Moyerson portion of the complex, which lacks channers, rather than the very channery Rentsac formation. The soils were a silty clay with a strong, fine granular structure. Understory vegetation at Pinyon Ridge was dominated by *Artemisia tridentata* ssp. *wyomingensis* Nutt., *Ericameria nauseosa* (Pall. Ex Pursh), *Pascopyrum smithii* Rydb., *Achnatherum hymenoides* Roem. & Schult., *Pseudoroegneria spicata* (Pursh) Á. Löve, and *Koeleria macrantha* (Ledeb.) Schult.

The Scenery Gulch burn (40°06'N; 108°07'W; elev. 2,010 m) happened in early July 2009 on a 150 ha area and was considered of moderate severity (Garner Harris, US Bureau of Land Management, pers. comm.). Needles and fine branches were still evident on dead trees, and some trees survived within the perimeter of

the burn. Scenery Gulch soils were within the Forelle loam map unit (SSURGO), a fine, sandy loam with a strong, fine granular structure and 5 % fine gravel. Dominant understory vegetation at Scenery Gulch included *A. tridentata*, *A. hymenoides*, *K. macrantha*, *P. smithii*, *Machaeranthera canescens* (Pursh) A. Gray, and *Hesperostipa comata* (Trin. & Rupr.).

The Spring Creek burn (39°58'N; 108°40'W; elev. 2,290 m) happened in late July 2009 on a 540 ha area and was considered of high severity (Garner Harris, pers. comm.). Only large branches remained on trees, and no trees survived within the perimeter of the burn. Spring Creek soils were within the Moyerson stony clay loam map unit (SSURGO), a clay loam with a strong, fine granular structure. Understory vegetation included *A. tridentata*, *Amelanchier alnifolia* (Nutt.) Nutt. Ex M. Roem., *Symphoricarpos rotundifolius* A. Gray, *Purshia tridentata* (Pursh) DC., *P. smithii*, *Balsamorhiza sagittata* (Pursh) Nutt., *Eriogonum umbellatum* Torr., and *Poa fendleriana* (Steud.) Vasey.

Diaspore collection, preparation and weighing

Bulk *B. tectorum* plant material was collected using a lawnmower with a bag attachment from a near-monoculture in the Yellow Creek drainage (40°84'N; 108°19'W; elev. 1,870 m; Fig. 1) in July 2009, after plants had lost green color but before most seed had fallen from the inflorescences. Bulk material was allowed to dry and after-ripen in large shallow tubs over the winter of 2009–2010, during which time diaspores naturally separated. The majority of diaspores were of one of two types: (A) “simple” diaspores, consisting of a single seed with an awned lemma (Fig. 2a); or (B) “complex” diaspores, in which a single filled seed adhered to one or more unfilled sterile florets, resulting in a diaspore with two or more awned lemmas (Fig. 2b). Occasionally, two filled seeds adhered to one another; this diaspore type was not included in this study. Twelve groups of 100 diaspores, in which the two main diaspore types were represented in their naturally occurring proportion, were randomly drawn from the bulk material and sterilized. To sterilize seeds, we placed diaspores on moist paper towels for 5 h, microwaved them for 1 min on high power, and then oven-dried them for 24 h at 70 °C. Diaspores were then coated with yellow or orange fluorescent powder (DayGlo® Color Corporation, Cleveland, OH, USA) by gently swirling them in a small tin containing



Fig. 2 The two types of *B. tectorum* diaspores considered in this study, differing in the presence or absence of sterile florets. **a** simple diaspore, i.e. without sterile florets; **b** complex diaspore, i.e. with sterile florets

powder (for more details on the method, see Johnston 2011). In addition, 300 simple diaspores and 300 complex diaspores were weighed to the nearest 10^{-4} g, using a Sartorius BP 210 S microbalance.

Experimental design

In each of the three sites, two replicates were randomly selected, separated by at least 40 m. Replicates consisted of paired release points, one in the burned area and one in the control area, situated at similar elevation, slope and aspect. Release points consisted of a 40 cm-high pedestal on which colored diaspores were placed for release. Releases of 100 diaspores were made simultaneously in burn and control areas within a replicate. Different replicates in a site had release times separated by 18 h or more. Different replicates were assigned different colors of fluorescent powder (yellow or orange) to ensure that the origin of diaspores could be determined accurately.

Two to three days after release, at night, diaspores were tracked around each release point with a black light (68 LED Scorpion Hunter Hand Flashlight,

Blacklights, USA). A radius of 25 m from the release point was searched. Dispersal time was similar for both releases within a replicate. Distance to the pedestal was recorded using a laser distance measuring device (Stanley TRU LASER TLM100i, Stanley Black & Decker, New Britain, CT, USA). A second measurement round, 6–7 days after release, was performed in a similar way. We will refer to the distance travelled by diaspores on the ground between the first and second measurements as *additional dispersal*.

Characterization of site conditions in burned and unburned areas

Site conditions were characterized at the two release points and at two additional randomly-selected points (resulting in 4 *sampling points*) within burned and unburned areas at each site. This resulted in a total of 24 sampling points (3 sites \times 2 burn status \times 4 sampling points). At each sampling point, four 5 m transects originating at the point and extending in the cardinal directions were established. Point-intercept hits were recorded every 5 cm for a total of 400 hits for each sampling point. The following were measured at each hit: aerial cover of trees (live and dead), referred to as *tree cover*; aerial cover of understory plants by functional group (annual grass, perennial grass, forb, shrub and tree), referred to as *understory cover*; and cover at the ground level of plants by functional group and litter, referred to as *basal cover*. Assessing overhead tree cover was aided by the use of a strong laser mounted to a bubble level (Synergy Resource Solutions, Bozeman, MT, USA).

Soil roughness was assessed using a 0.1 m² Plexiglas plane held parallel to the soil surface by supporting legs. A laser distance measuring device (Stanley TRU LASER TLM100i) was held against the Plexiglas plane in 10 randomly chosen locations, and the distance between the plane and the soil surface was recorded. Locations above plants were ignored, and additional measurements were substituted. Locations above litter were included. The standard deviation of the 10 measurements was used as an estimate of soil roughness. The device was placed at the 1 and 3 m marks of each transect to result in eight measurements of soil roughness at each sampling point.

Average wind speed (ms^{-1}) and wind gust speed (ms^{-1}) were recorded at 2 min intervals using a WindSmart speed sensor and Microstation (Onset[®]

Computer Corporation, Bourne, MA, USA). The time over which wind data were recorded varied from 2 to 8 days depending on the site. Wind data were recorded at the same period dispersal experiments were performed (mid to late July). Sensors were mounted approximately 40 cm from the ground surface. Wind sensors were placed in both control and burned areas, equidistant between release points. One rain sensor (RainSmart rain sensor, Onset Computer Corporation) was installed at each study site, mounted 25 cm from the ground surface within a burned area.

Data analysis

The mass of the two diaspore types (300 of each type) was compared using a *t* test. Variation in dispersal distance in the field was analyzed using linear mixed-effects models with the function *lme* in the *nlme* package in R ver. 2.12.0 (R Development Core Team 2010; Bates 2005; Pinheiro et al. 2010). This type of model allows for a grouping structure in the data, i.e. several data for each replication (individuals, releases, etc.), by the use of one or several grouping factor(s) (Pinheiro et al. 2010; Monty and Mahy 2010). *Burn status*, *diaspore type* and *site* were considered fixed factors and were fully crossed. *Release* was used as a grouping factor. The analyses were conducted separately for dispersal distances at the first and second measurement. Dispersal distance data were log-transformed to meet the assumptions of statistical analyses. Backward selection was used to keep the minimal significant model.

Soil roughness was analyzed using the function *lme* in the *nlme* package in R ver. 2.12.0. *Burn status* and *site* were crossed fixed factors, and the grouping factor was *sampling point*. Backward selection was used to keep the minimal significant model.

Percent basal cover of the different functional groups (annual grass, perennial grass, forbs, shrub and tree) and litter were analyzed using MANOVA with *burn status* and *site* as crossed fixed factors, in order to detect general differences between burned and unburned areas. Similar analyses were performed for understory cover (including annual grass, perennial grass, forb and shrub), as well as for tree cover (including living and dead trees). Principle component analysis was performed to visualize the differences in vegetation cover between burned and unburned areas.

In order to characterize the movement of seeds closer to the tail of the distribution, we also compared

95 % quantile distances between burned and unburned areas. To do this, we fit a lognormal distribution to each release, as previous work has shown that the lognormal greatly outperforms the Wald, negative exponential, Laplace, 2DT, Gaussian, and inverse power distributions for wind-mediated dispersal of *B. tectorum* seeds over a scale of tens of meters (Johnston 2011). We did not fit separate curves for simple and complex diaspores, as this would have led to insufficient data for curve-fitting. We elected not to perform a censored tail reconstruction on our data (Hirsch et al. 2012) prior to fitting the curves. Censored tail reconstruction leads to overestimates of 95 % quantile distance when seeds are overlooked within the search radius (Hirsch et al. 2012), and the burned areas had loose, ashy soil, which caused seeds to become buried and led to lower recovery rates within burned areas. By fitting the distribution without reconstructing the tail, our estimates of 95 % quantile distance are likely conservative (Hirsch et al. 2012). Lognormal curves were fit with a location parameter of 0 and maximum-likelihood estimates for shape and scale parameters using the UNIVARIATE procedure in SAS 9.3 (Cary, NC, USA; see Online Resource Figs. S1–S3 for fit curves). The UNIVARIATE procedure also provided estimated 95 % quantile distances. The effect of *burn status*, *site*, and interaction were analyzed using ANOVA in the MIXED procedure in SAS 9.3, with all factors fixed.

Wind data (2-min-averaged wind speeds; and highest speed over the 2-min, i.e. wind gust speeds) were averaged by day. A two-way ANOVA was performed with *burn status* and *site* as crossed fixed factors. In all analyses *site* was considered a fixed factor because we were interested in differences among sites. Moreover, the sites were not chosen randomly (Bennington and Thayne 1994) but correspond to all available and reachable burns in the study area at the time the study was performed. Diaspore mass, vegetation cover, and wind data were analyzed using Minitab software version 15.1.0 (Minitab Inc., State College, PA, USA).

Results

Seed dispersal

The two diaspore types differed in mass ($t = 11.62$; $P < 0.001$), with 2.974 ± 0.0467 mg and 2.297 ± 0.0347 mg (mean \pm standard error of the mean) for

complex and simple diaspores, respectively. Recovery rates in the field experiments averaged 85.3 %, with 75.8 % in burned areas and 94.8 % in unburned areas. Recovery rates were slightly higher at the second measurement (80 additional diaspores, for a total of 1,024 diaspores recovered out of the 1,200 released) because we were able to extract the diaspores from the soil to recover them at that time; at the first measurement, we did not wish to influence the experiment by altering the ground surface.

Linear mixed-effects models of dispersal distance revealed significant effects of *diaspore type*, *burn status*, and the interaction between *burn status* and *site* at both measurements (Table 1; Fig. 3). The factor *site* was only significant at the second measurement. Diaspores dispersed farther in burned than in unburned areas at all sites (mean \pm standard error at second measurement: 209 \pm 16 cm and 38 \pm 1 cm, respectively) (Figs. 3, 4). Complex diaspores dispersed farther than simple diaspores in both burn statuses (mean \pm standard error at second measurement: 141 \pm 14 cm and 88 \pm 7 cm, respectively) (Fig. 3, 4). Additional dispersal (i.e. difference in average dispersal distance between the first and second measurements) was close to zero in the unburned control

Table 1 Backward-selected linear mixed effect models for the effect of burn status, diaspore type and site on dispersal distance of *B. tectorum* diaspores at the first (2–3 days after release) and second (6–7 days after release) measurements

Source of variation	numDF	denDF	F	P
First measurement				
Intercept	1	920	3,839.8	<0.001
Burn status	1	17	73.03	<0.001
Diaspore type	1	17	6.96	0.0173
Site	2	17	2.44	0.1175
Burn status \times site	2	17	14.09	<0.001
Second measurement				
Intercept	1	1,000	3,243.10	<0.001
Burn status	1	17	80.23	<0.001
Diaspore type	1	17	5.48	0.0317
Site	2	17	6.49	0.0081
Burn status \times site	2	17	21.51	<0.001

The datasets included 944 and 1,024 distance measurements for the first and second measurements, respectively, from 12 releases in 3 sites. The two diaspore types occurred in their naturally occurring proportion. Significant results are in bold ($\alpha = 0.05$)

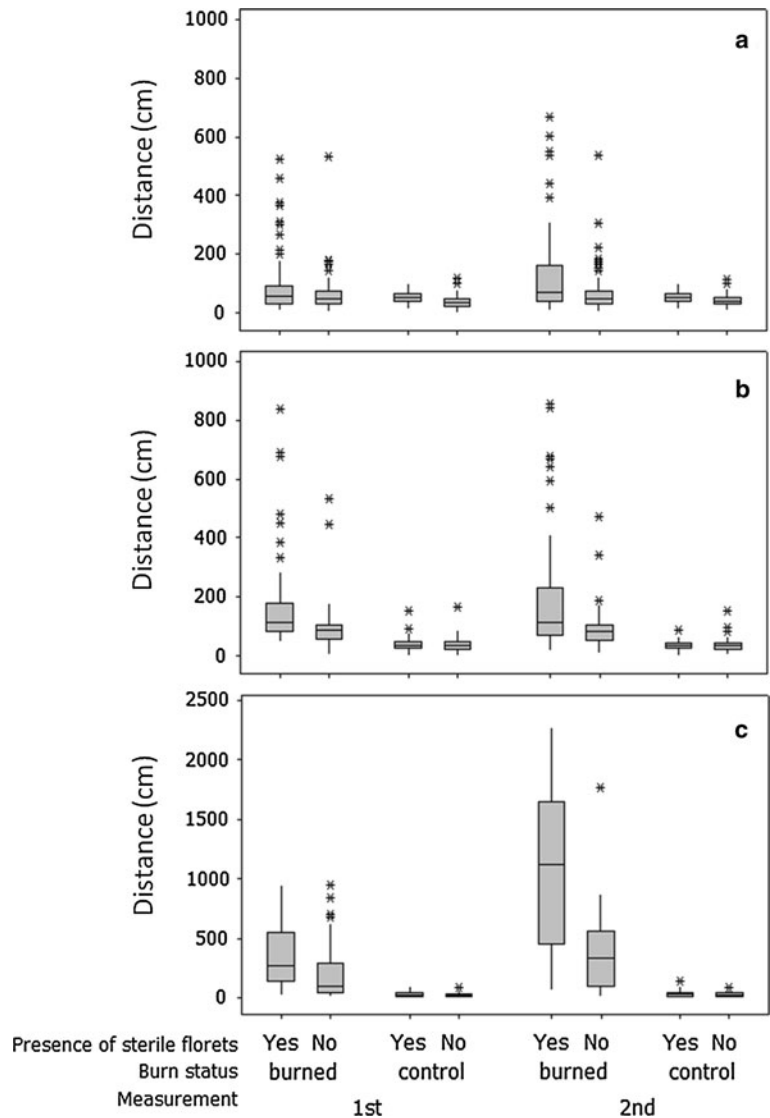
areas but occurred in the burned areas, especially at Pinyon Ridge (Fig. 3). Analysis of the lognormal modeled 95th percentiles at the second measurement revealed significant effects of *burn status*, *site*, and the interaction between *burn status* and *site* (Table 2). On average, 95 % quantile distance was 1,009 cm in burned areas and 96 cm in control areas. At Pinyon Ridge, 95 % quantile distance was 2,370 cm in burned areas and 102 cm in unburned areas. At Scenery Gulch and Spring Creek, significant effects on 95 % quantile distance were not detected at the site level. Maximal dispersal distance reached 2,274 and 1,770 cm in the burned areas for complex and simple diaspores, respectively, but only 166 cm and 150 m, respectively, in the control areas (Fig. 4).

Site characterization

MANOVA analyses revealed strong differences in cover between burned and unburned areas, and these differences varied among sites for basal cover and understory cover, but not for tree cover (Table 3). PCA analysis, i.e. the scores of each sampling point on the two first PCA axes, as well as the correlations with the loadings of each environmental variable, revealed the sources of these effects (Fig. 5). The first PCA axis roughly corresponds to cover (Fig. 5); negative values indicate low cover and positive values high cover. Understory forb and perennial grass cover, as well as basal litter cover, appeared to have had the strongest effects. The second PCA axis approximates a gradient from high herbaceous cover at negative values to high tree and shrub cover at positive values. Tree cover was lower in burned than unburned areas regardless of site. This can be seen by the strong association of the variables dead tree and basal dead tree with most of the burned study plots in Fig. 5. Although cover was lower in burned than unburned areas at all sites, the difference was most dramatic at Spring Creek, where shrub and tree cover in unburned areas was much higher than at other sites. Scenery Gulch had relatively high cover of herbaceous species at ground level after being burned compared to other sites.

In burned areas, litter cover on the ground (mean \pm standard error) ranged from 10.1 \pm 4.7 to 29.8 \pm 6.3 % at Spring Creek and Pinyon Ridge, respectively. In unburned areas, litter cover ranged from 59.6 \pm 8.3 to 81.0 \pm 4.3 % at Pinyon Ridge and Spring Creek, respectively. We did not find significant

Fig. 3 Boxplots of the dispersal distances of *B. tectorum* diaspores at the two measurements, according to burn status and diaspore type (with and without sterile florets attached), in the three sites. The bottom of the box is the first quartile (Q1) and the top of the box is the third quartile (Q3). The line inside the box is the median. The lower whisker extends to the lowest value within the lower limit [lower limit = $Q1 - 1.5(Q3 - Q1)$], and the upper whisker extends to the highest data value within the upper limit [upper limit = $Q3 + 1.5(Q3 - Q1)$]. Stars are data outside the limits. **a** Scenery Gulch; **b** Spring Creek; **c** Pinyon Ridge



effects of the factors *burn status* ($F_{1,18} = 2.46$; $P = 0.134$), *site* ($F_{2,18} = 0.78$; $P = 0.475$), or the interaction thereof ($F_{2,18} = 2.01$; $P = 0.162$) on soil roughness.

Overall, daily average wind speeds were significantly higher in burned areas ($1.04 \pm 0.08 \text{ ms}^{-1}$) than in unburned areas ($0.75 \pm 0.07 \text{ ms}^{-1}$) ($F_{1,34} = 18.00$; $P < 0.001$), but this varied among sites. Means (\pm standard error) in burned and unburned areas, respectively, were: 0.80 ± 0.09 and $0.92 \pm 0.10 \text{ ms}^{-1}$ at Scenery Gulch; 0.99 ± 0.12 and $0.19 \pm 0.08 \text{ ms}^{-1}$ at Spring Creek; and 1.29 ± 0.09 and $0.70 \pm 0.05 \text{ ms}^{-1}$ at Pinyon Ridge. The difference was significant in the

recent Pinyon Ridge burn (Tukey Simultaneous Tests; $P < 0.001$) and the most severe Spring Creek burn (Tukey Simultaneous Tests; $P = 0.030$), but not in the more moderate Scenery Gulch burn (Tukey Simultaneous Tests; $P = 0.893$). Daily average wind gust speeds were also higher in burned areas than in control areas ($F_{1,34} = 9.86$; $P = 0.003$) and the difference varied among sites (*burn status* \times *site* $F_{2,34} = 6.43$; $P = 0.004$) with a significant difference at Pinyon Ridge (Tukey Simultaneous Tests; $P = 0.004$) but not at Spring Creek (Tukey Simultaneous Tests; $P = 0.270$) and Scenery Gulch (Tukey Simultaneous Tests; $P = 0.984$). Means (\pm standard error) in burned

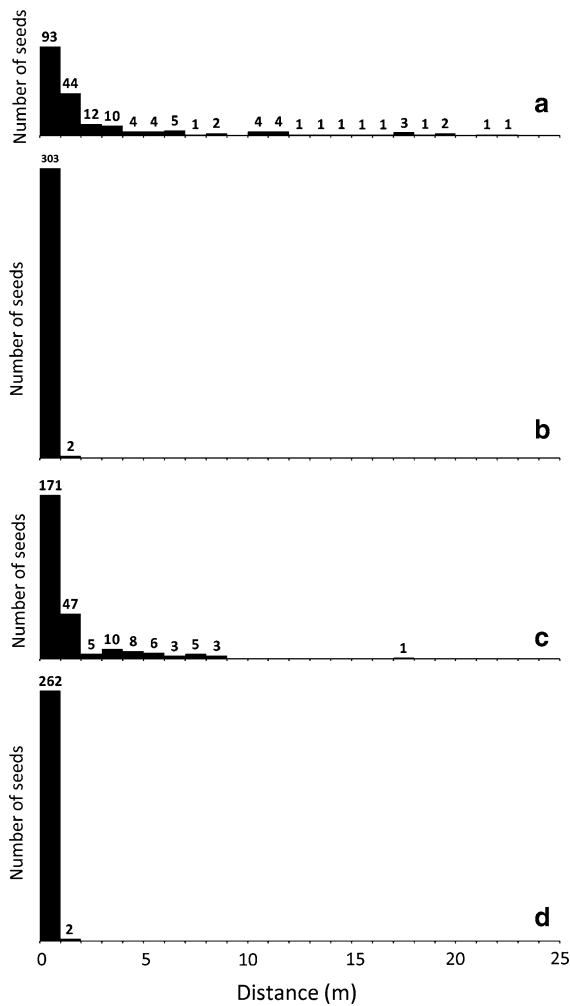


Fig. 4 Distribution of dispersal distances (step: 1 m) at the second measurement for both diaspore types in burned and unburned areas. Data from the different sites were pooled. A total of 1,200 diaspores were released, 600 in burned and 600 in unburned areas. The two diaspore types released were represented in their naturally occurring proportion. A total of 1,024 seeds (501 with and 523 without sterile florets) were recovered. **a, b** diaspores with sterile florets; **c, d** diaspores without sterile florets; **a, c** burned areas; **b, d** unburned areas

Table 2 Results of the two-way ANOVA performed on log-normal modeled dispersal distance 95 % quantile distances for the second measurement

Source of variation	numDF	denDF	F	P
Burn status	1	6	15.00	0.008
Site	2	6	8.45	0.018
Burn status × site	2	6	8.30	0.019

Significant results are in bold ($\alpha = 0.05$)

and control areas, respectively, were 1.48 ± 0.16 and $1.64 \pm 0.17 \text{ ms}^{-1}$ at Scenery Gulch; 1.50 ± 0.24 and $0.44 \pm 0.15 \text{ ms}^{-1}$ at Spring Creek; and 2.42 ± 0.18 and $1.50 \pm 0.15 \text{ ms}^{-1}$ at Pinyon Ridge.

Precipitation in the sites was extremely low during the measurement period with a maximum of 2.53 mm over the 8 days of measurement at Pinyon Ridge.

Discussion

Our study revealed that dispersal distance of *B. tectorum* diaspores by wind was farther in burned than in unburned areas. Mean distance increased over fivefold, and 95 % quantile distance increased up to 20-fold, depending on site conditions. Within-site seed movement was notably due to additional dispersal, as revealed by the increase in dispersal distance over time (Fig. 3). Spread rate (average distance travelled by the 100 released diaspores at a point between two measurements divided by the number of hours between the two measurements) reached 8.18 cm h^{-1} in the most recently burned site (Pinyon Ridge). In contrast, in unburned areas, additional dispersal was almost non-existent. At the end of the experiment, average dispersal distances in burned areas represented 194.7, 418.3 and 1,808.7 % of average dispersal distances in unburned areas, and maximal dispersal distances in burned areas represented 602.7, 1,160.0 and 1,590.2 % of maximal dispersal distances in unburned areas, in Scenery Gulch, Spring Creek and Pinyon Ridge, respectively.

Bromus tectorum invasion is known to have resulted in increased fire frequency, size, and intensity in parts of the western US (D’Antonio and Vitousek 1992). In the present study we showed that fire can enhance *B. tectorum* invasion due to an increase in dispersal distance. Enhanced dispersal in burned areas may profoundly affect the spread rate and colonization patterns of this invasive plant. *B. tectorum* is capable of seed productivity rates as high as 20,000 seeds per square meter (Hempy-Mayer and Pyke 2008). High seed productivity at the edges of the burn coupled with rapid spread rates may cause burned areas to quickly become dominated by *B. tectorum*. The importance of invasion from the edge would depend on the size and shape of the burn.

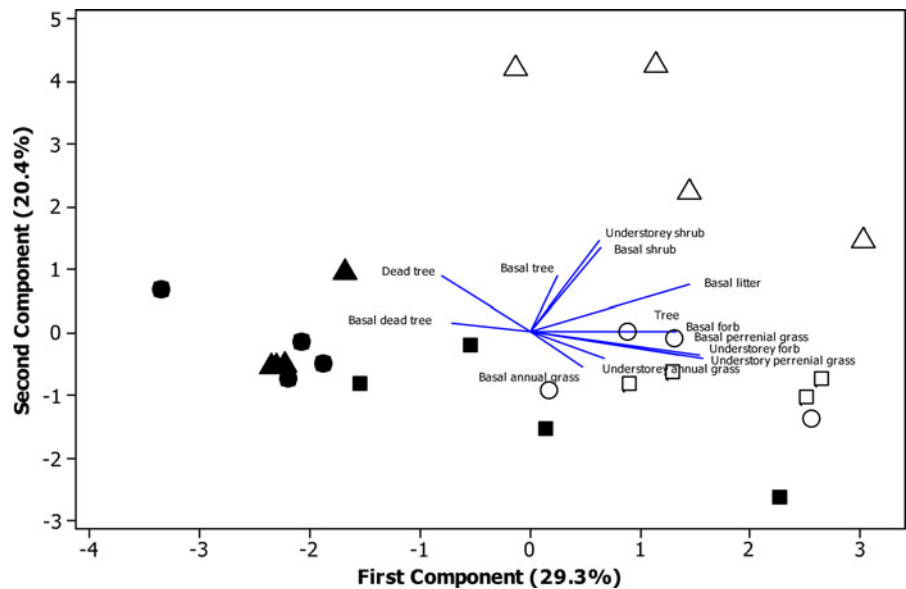
The fires drastically changed biotic and abiotic conditions and these changes corresponded to altered diaspore dispersal distances. Burned areas in the

Table 3 MANOVA results depicting the effects of burn status and site on the ground, understory and tree cover

	Wilks' statistic	F	Num DF	Denom DF	P
Ground cover (s = 2, m = 2.0, n = 5.0)					
Burn status	0.075	16.95	7	12	<0.001
Site	0.025	7.32	14	24	<0.001
Burn status × site	0.080	3.48	14	24	0.001
Understory cover (s = 1, m = 1.0, n = 6.5)					
Burn status	0.095	35.91	4	15	<0.001
Site	0.045	13.98	8	30	<0.001
Burn status × site	0.045	13.92	8	30	<0.001
Tree cover (s = 1, m = 0.0, n = 7.5)					
Burn status	0.470	9.60	2	17	0.002
Site	0.849	0.73	4	34	0.58
Burn status × Site	0.866	0.64	4	34	0.641

Ground cover includes percent cover of perennial grasses, annual grasses, shrubs, forbs, living and dead trees, and litter at the ground level. Understory cover includes percent aerial cover of perennial grasses, annual grasses, shrubs and forbs. Tree cover includes percent aerial cover of live and dead trees. Significant results are in bold

Fig. 5 Scores for each sampling point on the first two PCA axes generated from vegetation cover data, as well as the correlations with the loadings of each cover variable. *Black* symbols correspond to sampling points in burned areas; *open* symbols correspond to points in unburned controls. *Circles* Pinyon Ridge; *squares* Scenery Gulch; *triangles* Spring Creek



present study were characterized by lower cover of all types of vegetation (except dead trees). Figure 5 indicates that forbs and perennial grass cover in the understory were particularly variable among sites and differed drastically between burned and unburned areas. The decrease in the cover of these species after fire likely played an important role in the observed higher wind speeds and gusts near the ground surface.

Despite finding no significant differences in soil roughness between burned and unburned areas, litter cover on the ground varied greatly among sites and was lower in burned areas (significant difference between burn status for the litter cover, data not shown). This suggests that a noticeable proportion of litter burned, potentially reducing the possibility for seed entrapment. It should be noted that the way we

measured it, soil roughness refers to both microtopography and litter cover. Obstructions such as vegetation and litter are known to entrap seeds (Chambers 2000), and the removal of these obstructions may increase additional dispersal distance (Johnston 2011). Faster wind speeds and gusts would provide a greater energetic force to lift the seeds from the ground. We found no difference between average wind speeds in burned and unburned areas at Scenery Gulch, the site with the highest cover of herbaceous species (notably the highest perennial grass and forbs covers) after fire. Vegetation, litter and wind changes may have accelerated additional dispersal in burned areas. While we cannot definitively disentangle the biotic and abiotic influences on dispersal enhancement in this study, it is reasonable to conclude that wind speed increase was due to vegetation reduction (Allen and Hipps 1984), and therefore, that vegetation reduction was an important driving force behind the changes in dispersal. The decrease in litter cover most likely encouraged longer dispersal in burned areas. The interaction between fire and *B. tectorum* seed dispersal demonstrated by our study indicates that rapid invasion is promoted at the same time that plant cover, and presumably plant community resistance to invasion, is very low (Fig. 5) (Prevéy et al. 2010). Several recent studies have documented that disturbance and propagule pressure interact non-linearly to determine the likelihood of species invasions (Clark and Johnston 2009; Eschstruth and Battles 2009; Thomsen et al. 2006). Here, the greater than five-fold increase in average diaspore dispersal distance after fire shows that increased dispersal of propagules within disturbances is one mechanism that may explain these nonlinear effects.

The presence of sterile florets attached to seeds promoted dispersal (Figs. 3, 4). Although complex diaspores were heavier, they dispersed farther, and this effect was more pronounced in burned areas and with increasing time since release (Fig. 3). In complex diaspores, the awns of sterile florets are spread in all directions, thus there is always at least one awn “standing” that can be pushed forward by the wind (Fig. 2b). This is not the case for simple diaspores, the awn of which typically lies on the ground (Fig. 2a). The determinants of dimorphism in *B. tectorum* diaspores, as well as the consequences on the species ecology, are poorly documented. It is interesting to note that the dimorphism is actually related to the abortion of some florets, so increased dispersal

distances for seeds with sterile florets is likely an indirect effect of floret abortion rather than an adaptation for increasing dispersal distance.

The present study focused on within-site dispersal of *B. tectorum* propagules, which can profoundly impact the spatial and demographic dynamics of invasion (Matlack 2005). Indeed, the vast majority of seeds do not move far beyond the borders of the population (Willson 1993). However, animals can also be involved in *B. tectorum* dispersal (e.g. Young and Allen 1997), and they can be agents of long distance dispersal (Nathan et al. 2008).

Our study demonstrates synergies between disturbance and dispersal of an invasive plant that may facilitate its spread. Our results are important for applied ecologists and managers faced with decision-making concerning fires and *B. tectorum* invasion. Fire is natural and enhances growth of perennial grasses and re-sprouting shrubs when it occurs at appropriate frequencies and intensities, improving ecosystem quality for livestock and wildlife. As such, it can be used for management. On the other hand, when fires occur or are used for landscape management, attention should be paid to the presence of *B. tectorum* in surrounding vegetation due to the interaction between disturbance and propagule dispersal demonstrated in our study. In these situations, it may be possible to prevent spread of *B. tectorum* by using techniques such as wind breaks, seed barriers, or herbicide application in the area immediately surrounding the burn, but these approaches have yet to be tested.

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References

- Allen MF, Hipps LE (1984) Comparative microclimates of some mycorrhizal fungi: requirements for long-range dispersal of spores. *Mycol Soc Am Newslett* 35:17
- Bates D (2005) Fitting linear mixed models in R. *R News* 5(1):27–30
- Bennington CC, Thayne WV (1994) Use and misuse of mixed model analysis of variance in ecological studies. *Ecology* 75(3):717–722

- Bradford JB, Lauenroth WK (2006) Controls over invasion of *Bromus tectorum*: the importance of climate, soil, disturbance and seed availability. *J Veg Sci* 17(6):693–704
- Burke MJW, Grime JP (1996) An experimental study of plant community invisibility. *Ecology* 77(3):776–790
- Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecol Appl* 10(5):1400–1413
- Chambers JC, MacMahon JA (1994) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annu Rev Ecol Syst* 25:263–292
- Clark GF, Johnston EL (2009) Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. *Oikos* 118(11):1679–1686
- D'Antonio C, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Davies KW, Sheley RL, Bates JD (2008) Does fall prescribed burning *Artemisia tridentata* steppe promote invasion or resistance to invasion after a recovery period? *J Arid Env* 72(6):1076–1085
- DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Sci* 48(2):255–265
- DiVittorio CT, Corbin JD, D'Antonio CM (2007) Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. *Ecol Appl* 17(2):311–316
- Elton CS (1958) *The ecology of invasions by animals and plants*. Methuen, London
- Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecol Monogr* 79(2):265–280
- Hempy-Mayer K, Pyke DA (2008) Defoliation effects on *Bromus tectorum* seed production: implications for grazing. *Rangel Ecol Manag* 61(1):116–123
- Hirsch BT, Visser MD, Kays R, Jansen PA (2012) Quantifying seed dispersal kernels from truncated seed-tracking data. *Methods Ecol Evol* 3(3):595–602
- Hobbs RJ, Atkins L (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Aust J Ecol* 13(2):171–179
- Johnston DB (2011) Movement of weed seeds in reclamation areas. *Restor Ecol* 19(4):446–449
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10:689–710
- Matlack GR (2005) Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *J Ecol* 93(1):50–59
- Melgoza G, Nowak RS, Tausch RJ (1990) Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83(1):7–13
- Monty A, Mahy G (2010) Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). *Oikos* 119:1563–1570
- Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol Evol* 23(11):638–647
- Pinheiro J, Bates D, Debroy S, Sarkar D, R Development Core Team (2010) nlme: linear and nonlinear mixed effects models. R package Ver. 3.1
- Prevéy J, Germino M, Huntly N, Inouye R (2010) Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. *Plant Ecol* 207(1):39–51
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Shinneman DJ, Baker WL (2009) Environmental and climatic variables as potential drivers of post-fire cover of cheatgrass (*Bromus tectorum*) in seeded and unseeded semiarid ecosystems. *Int J Wildland Fire* 18:191–202
- Thomsen MA, D'Antonio CM, Suttle KB, Sousa WP (2006) Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecol Lett* 9(2):160–170
- Willson MF (1993) Dispersal mode, seed shadows, and colonization patterns. *Plant Ecol* 107–108(1):261–280
- Young JA, Allen FL (1997) Cheatgrass and range science: 1930–1950. *J Range Manag* 50(5):530–535