

Reconciling Seed Dispersal and Seed Bank Observations to Predict Smooth Brome (*Bromus inermis*) Invasions of a Northern Prairie

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The importance of dispersal in the establishment and proliferation of exotic populations make this life history stage critical in the prediction and management of biological invasions. We observed the dispersal of seeds by patches of smooth brome invading northern fescue prairies and applied an inverse power function model to explore its potential invasion patterns. Based on our observations of two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada, patterns of potential invasion were contingent upon the dispersal of seeds as individual florets or aggregated within spikelets and panicles. For example, although the majority of dispersed seeds were intercepted within one meter, inside and outside the margins of invading patches, slopes of the log–log plots of seed number against their dispersal distance were steeper for seeds dispersed as spikelets than individual florets. Despite the observed aggregation of seeds along the margins of invading patches, the number of dispersed seeds was poorly correlated with that germinated from the seed bank. The shallow dispersal gradient of individual florets and spikelets, combined with the steeper gradient of panicles suggest that smooth brome is capable of simultaneously invading along dense fronts and by establishing isolated foci. Although low correlations between the number of dispersed seeds and their recruitment from the seed bank might suggest postdispersal transport of seeds, other mechanisms, including seed predation and pathogens, remain unexplored. Conservation and restoration of northern fescue prairies must include efforts to control the dispersal of smooth brome seeds and reduce opportunities for their establishment.

Nomenclature: Smooth brome, *Bromus inermis* Leys.

Key words: Biological invasions, plant dispersal, inverse power function, spatial patterns, northern fescue prairie.

Impacts of exotic plants on natural habitats are contingent upon discrete stages in their life history (Kolar and Lodge 2001; Williamson and Fitter 1996). Each among these, including dispersal, establishment, and proliferation, illustrates the critical interplay between exotic plants and recipient environments (Dietz and Edwards 2006; Kolar and Lodge 2001; Puth and Post 2005; Richardson and Pyšek 2006; Williamson and Fitter 1996). Despite the large number of exotic species in most regional floras, the majority fail to become invaders, and many simply contribute to local species richness (Rosenzweig 2001). Consequently, the main

challenge in invasion biology rests in resolving the mechanisms that facilitate the invasiveness of a small number of exotic organisms (Richardson et al. 2000).

The contingent nature of biological invasions renders the initial dispersal of exotic organisms fundamental to all consecutive stages (Puth and Post 2005). By definition, all exotic species are initially dispersal-limited (Richardson et al. 2000) and depend on human activities, including cultivation, commerce, and recreation to overcome natural geographic barriers (Elton 1958; Lockwood et al. 2005; Lodge et al. 2006; Mack 2003). Once established, the invasiveness of exotic organisms often depends on their ability to spread away from sites of introduction (Richardson et al. 2000). The importance of dispersal in the initiation and proliferation of exotic populations (DiVittorio et al. 2007; Harper 1977; Higgins and Richardson 1999) also makes this stage key in the prediction and management of biological invasions (MacIssac et al. 2001; Tassin et al. 2007).

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Interpretive Summary

The importance of dispersal in the establishment and proliferation of exotic populations make this life history stage critical in the prediction and management of biological invasions. We observed seed dispersal from patches of smooth brome (*Bromus inermis* Leyss.) invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada, and applied an inverse power function model to explore its potential invasion patterns. Patterns of smooth brome invasion were contingent upon the dispersal of seeds as individual florets, or aggregated within spikelets and panicles. Although over 94% dispersed seeds were intercepted within 1 m, inside and outside the margins of invading patches, slopes of the log–log plots of seed number against their dispersal distance were steeper for seeds dispersed as spikelets than individual florets. As a result, the shallow dispersal gradient of individual florets combined with the steeper gradient of panicles and spikelets suggest that smooth brome is capable of simultaneously invading along dense invasion fronts as well as by establishing discrete foci. Although this invasion pattern could be facilitated by the postdispersal transport of propagules, the observed low correlations between the number of dispersed seeds and those germinated from the seed bank suggest other unexplored mechanisms, including seed predation and pathogens. Our observations illustrate that efforts to reduce seed dispersal among patches of smooth brome invading northern fescue prairies must constitute an important element in the management of this exotic invader and should be combined with programs to reduce opportunities for seed establishment.

Dispersal frequently determines the rate and extent of biological invasions (Buckling et al. 2000; Cassey et al. 2004; Higgins and Richardson 1999; Levine and D'Antonio 1999). For example, the proliferation of exotic populations is often directly proportional to the time since establishment and inversely related to the distance from the site of introduction (MacIassac et al. 2001). As a result, propagule pressure, or the frequency and intensity of introductions (Wilson et al. 2007), often determines the impact of biological invaders (Blackburn and Cassey 2007; Colautti et al. 2006; Lockwood et al. 2005; Williamson and Fitter 1996). Among plants, dispersal often combines primary mechanisms that move propagules away from parent plants and secondary mechanisms that move them away from subsequent locations (Nathan and Muller-Landau 2000). As a result, the distribution of dispersed propagules is often directly reflected in the spatial patterns of recruitment (Willson 1993). For example, Harper (1977), extending a model for the dispersal of pathogens (van der Plank 1960), proposed that plants limited to local dispersal tend to advance as a dense wave, whereas those dispersing across greater distances expand by establishing isolated populations (Willson 1993).

The objective of our study was to examine the dispersal dynamics of smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial threatening the structure and function of native prairie remnants throughout the Great Plains

(Otfinowski et al. 2007). Widely planted for hay, forage, and to revegetate disturbances, smooth brome often escapes to invade native prairies throughout the Great Plains (Frank and McNaughton 1992; Wilson and Belcher 1989). Although vegetative reproduction facilitates the encroachment of established patches (Otfinowski and Kenkel 2008), little is known about the contribution of seeds to the proliferation of this exotic invader. We directed our observations toward quantifying the production and dispersal of seeds by patches of smooth brome invading northern fescue prairies. Using a combination of field and greenhouse observations, we focused on resolving whether patterns of seed dispersal could predict future invasions. Given the perennial life cycle and prolonged seed dormancy of smooth brome (Otfinowski et al. 2007), our observations over a single growing season provide a short perspective of its dispersal dynamics; however, logistics prevented an extension of the period of measurement.

Materials and Methods

Study Area. Research was conducted in Riding Mountain National Park, Manitoba, Canada. The park occupies an area of 2,978 km² (1,148 mi²) in western Canada, 225 km northwest from Winnipeg (49°53'04"N, 97°08'47"W) and consists of large areas of rolling upland (550 to 640 m [1,804 to 2,099 ft]), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450 to 500 mm and a growing season of 168 to 173 d; mean temperatures range between –18 C (0 F) in January and 18 C (64 F) during July (Leeson et al. 2005). The park lies in the Mixedwood section of the Boreal Forest Region (Rowe 1972) and protects areas of northern fescue prairie (Cody 1988). In North America, fescue prairies form an arc around the northern and northwestern perimeter of the mixed prairie (Coupland 1961), occupying a transition between the warmer and drier grasslands and the cooler, moister aspen parkland (Coupland and Brayshaw 1953). Northern fescue prairies, dominated by rough fescue [*Festuca hallii* (Vasey) Piper], species of *Agropyron* and *Carex*, and a diversity of forbs, are threatened in western Canada by the impacts of grazing, cultivation, and exotic species invasions (Trottier 1986).

We focused our study on two fescue prairies representative of Riding Mountain National Park (Blood 1966). The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie (moisture [0 to 20 cm, July 2005] 7.5 ± 3.7% vs. 9.5 ± 4.2%, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen [0 to 15 cm; July 2005]: NH₄⁺, 5.3 ± 0.4 mg/kg vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; NO₃⁻, 0.60 ± 0.1 mg/kg vs. 2.1 ± 0.2 mg/

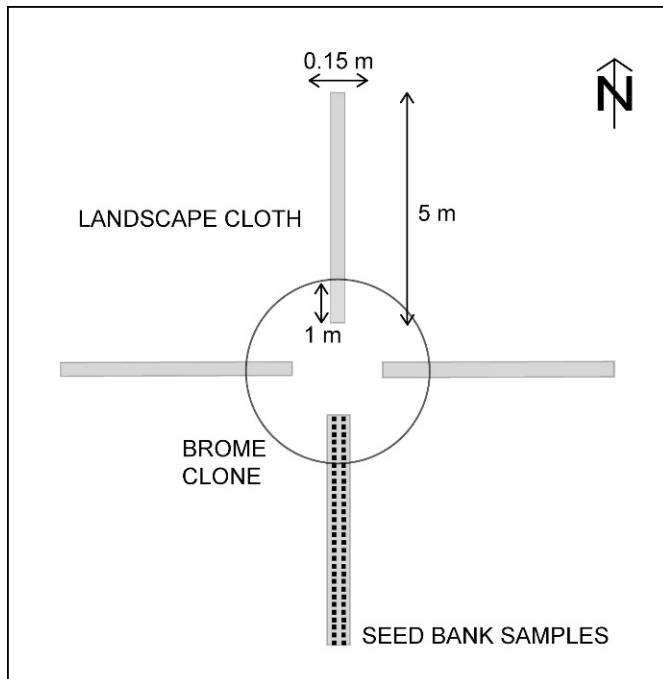


Figure 1. Measurement of seed dispersal away from smooth brome patches invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Strips of landscape cloth (0.15 by 5 m) were pinned 1 m inside each patch using lawn staples, extended 4 m into the adjacent prairie, and treated with Tanglefoot paste to capture dispersing seeds. For selected clones, seed bank samples were collected along the north and south dispersal transects.

kg, $F_{1,38} = 40.7$, $P < 0.0001$). Prairies in Riding Mountain National Park recently have been invaded by smooth brome, which continues to compromise their function and biodiversity (Otfinowski et al. 2007). Invading patches range between 50 and 900 m² in area and continuous fringes of smooth brome often line long sections of recreational trails inside the park.

Observations of Seed Dispersal. We examined the role of seed dispersal in smooth brome invasions using a combination of field and greenhouse observations. In the field, we used strips of landscape fabric to quantify seed dispersal away from patches and trail margins of smooth brome invading native prairies. During August 2003, strips of landscape fabric¹ (0.15 by 5 m) were installed in each of the two prairies. At each site, four strips were positioned in four cardinal directions around nine patches of smooth brome (Figure 1) and in four locations, perpendicular to the margins of recreational trails (52 strips/site = 39 m² sampling area). Selected clones and trail margins were located away from animal trails, forest margins, and neighboring smooth brome clones to reduce error and overlap among seed shadows. We further eliminated error

by clipping the inflorescences of any plants of smooth brome or the native fringed brome (*Bromus ciliatus* L.) in the vicinity of each strip of landscape fabric.

Each strip was pinned 1 m inside each invading patch or trail margin using aluminum fabric staples¹ and extended 4 m into the adjacent prairie (Figure 1). Strips were coated with Tanglefoot Paste² to intercept dispersing caryopses (seeds), and recoated as required. On three occasions between August and September 2003, we measured the distance of all smooth brome seeds adhered to the strips. Caryopses (seeds), the dry, indehiscent fruit of grasses (composed of a single seed and its seed coat, fused to the pericarp; Harris and Woolf Harris 1994), can disperse alone; as florets (subtended by a palea or lemma); or aggregated within parts of an inflorescence. Among these, we distinguished spikelets (clusters of several florets attached to a rachilla) and panicles (branches of several spikelets, attached to a rachis; Harris and Woolf Harris 1994). Only five individual caryopses were found adhered to the strips of landscape fabric, so we combined their numbers with those of florets. Fertility among populations of smooth brome ranges between 2.6 and 75.8% (Otfinowski et al. 2007). As a result, we also counted the number of mature seeds inside each dispersed floret, spikelet, and panicle. We terminated our observations in October, when dispersing seeds became scarce.

We compared the yield and viability of dispersing seeds at the start and end of our observations, and examined the viability of seeds overwintered on the prairie. Ten panicles, collected randomly from eight patches of smooth brome at each study site, were cleaned using a belt thresher and an air-screen separator³ and winnowed by hand. Collected panicles represented less than 1% of those produced by each patch of smooth brome and were harvested more than 4 m away from each strip of landscape cloth. Cleaned seeds were stored in the dark (5 C) for 7 mo prior to germination trials. To examine seed viability, 25 seeds from each patch of smooth brome were transferred into 9-cm-diam Petri dishes lined with filter paper, and placed inside a plant growth chamber⁴ (25/15 C, 12/12 h light/dark, 107 $\mu\text{mol}/\text{m}^2/\text{s}^1$ PPF). Deionized water was added to the plates as required. Germinated seeds, whose radicle penetrated the seed coat, were counted weekly and removed. After 1 mo, seed coats of ungerminated seeds were nicked at the embryo end using tweezers and returned to the growth chamber for an additional week. These, as well as any remaining seeds that contained a firm embryo, were considered dormant (Cavers et al. 1995). Stratification was not required for germination and seeds collected during October 2004 were 89% viable.

Soil Seed Bank Analysis. Measurements of seed dispersal by smooth brome were complimented with observations of its soil seed bank. At each study site, seed bank samples

were collected during October 2003, at the end of our dispersal observations. We randomly selected two patches from each site and collected two cores of soil (0 to 10 cm, 98 cm³) at 10-cm intervals along the S and N strips of landscape cloth (400 cores per study site; Figure 1). Cores were stored inside plastic Ziploc bags, air dried in the field, and placed in a cool room (4 C) for 6 wk to break seed dormancy (Bewley and Black 1982).

Samples were transferred to the greenhouse in November 2003, spread thinly (< 1 cm) inside 12 cm by 16 cm pots, over a base of moistened, sterilized, soil-less mix,⁵ and watered as required. We used artificial and natural lighting (21/15 C, 16/8 day/night). We did not observe any seed contamination of control pots filled with soil-less mix. All emerging seedlings of smooth brome were counted and removed, and several were transplanted into separate pots to verify our identification. The first phase of the experiment was terminated after no additional seedlings germinated for 2 wk, at which time all pots were returned to the cool room for an additional 6 wk. The experiment was terminated after 4 mo, when no additional seedlings emerged. Although prone to errors arising from specific germination requirements of individual species, germination offers a reliable estimate of the viability and composition of plant seed banks (Gross 1990) and has been successfully used to examine the persistence of smooth brome seeds in prairie seed banks (Grilz and Romo 1995). In separate trials, 91% of seeds collected from Riding Mountain National Park germinated under similar greenhouse conditions (R. Otfinowski, unpublished data).

Statistical Analysis. Data from all observed patches and trail margins at both study sites were pooled. We divided each dispersal transect into ten, 50-cm intervals and used the inverse power function to model seed dispersal as a function of distance from the margins of invading patches (Okubo and Levin 1989). We did not observe significant differences among the dispersal slopes of clones and trail margins ($t_8 = 1.13$, $P = 0.2916$) or among the four cardinal directions around each dispersing patch ($t_4 = 1.71$, $P = 0.1634$). The slope of the log-transformed inverse power function provides an estimate of the spatial pattern of population recruitment (Willson 1993); slopes steeper than that of the inverse square law (-2 on a log-log scale) characterize populations recruiting along a sharply defined front, whereas those with shallower slopes characterize populations establishing as isolated foci (van der Plank 1960). Due to their large surface area (50 to 900 m²), patches of smooth brome resembled long invasion fronts, perpendicular to the strips of landscape cloth (Greene and Johnson 1996). As a result, we did not convert the number of dispersed seeds to their expected number, as required for point source distributions (Willson 1993).

We used a linear regression model to explore the correlation between the number of smooth brome seeds dispersed and those germinated from the seed bank. The frequencies of dispersed and recruited seeds were log-transformed to improve the homogeneity of variance among observations (Zar 1999). Linear regression analyses were implemented using Data Desk 6.2,⁶ and we calculated a Student's t to compare the dispersal slopes among patches and trail margins of smooth brome and among florets and spikelets (Zar 1999).

Results and Discussion

Patterns of Seed Dispersal. Over 90% of seeds dispersed by patches of smooth brome invading northern fescue prairies were intercepted within 1 m, inside and outside their margin (Table 1). Over 94% (3,842 of 4,082) of seeds were dispersed as spikelets and panicles, accounting for the steep dispersal gradient of smooth brome (Table 1). Among seeds captured outside the invading patches, slopes of the log-log plots of seed number against their distance from patch margins were steeper for spikelets than individual florets ($t_7 = 11.80$, $P = 0.0001$; Figure 2). The viability of dispersing seeds increased between the initiation of their dispersal in August 2003 (78%) and its termination in October (84%; $F_{1,29} = 5.54$, $P = 0.0255$); however, neither the mass nor the number of seeds per panicle changed significantly (Table 2). Among the 4,082 seeds of smooth brome examined, fewer than 15% (599) contained a mature caryopsis. Seed viability remained high (84%) for overwintered seeds collected in May 2004.

The observed aggregation of smooth brome seeds in the vicinity of parents is characteristic of most plants, independent of their dispersal mode (Cook 1980; Czarnecka 2004; Willson 1993). Our observations confirm that this pattern is even more pronounced where seeds aggregate inside dispersing inflorescences, whose greater weight likely contributes to their short dispersal distance (Czarnecka 2004; Kjellsson 1992; Thompson 1986). Although potentially supporting dense "invasion fronts" (Harper 1977) and intensifying interactions with immediately adjacent communities (Kjellsson 1992), short distance dispersal can also contribute to a lag between the regional and local dominance of exotic invaders (MacDougall and Turkington 2006). As a result, the establishment of small, isolated foci, facilitated by longer-distance dispersal, could pose a more serious threat to the biodiversity of natural areas (Moody and Mack 1988). In addition to evading early detection, the greater edge of a large number of smaller foci increases their dispersal pressure on adjacent native communities, and can facilitate their rapid consolidation into larger infestations (Moody and Mack 1988). Our observations illustrate that the shallow dispersal gradient of smooth brome florets, characteristic of species

Table 1. Cumulative percentage of seeds dispersed by patches of smooth brome invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada (absolute seed numbers in parentheses). Each column represents the cumulative percentage of seeds dispersed as individual florets (subtended by a palea and lemma) or aggregated within parts of the inflorescences, including spikelets (clusters of several florets attached to a rachilla) and panicles (branches of several spikelets, attached to a rachis). Seeds were captured along 5 m strips of landscape cloth, pinned 1 m inside the fringe the invading patches (indicated by a dash). Mean number of seeds \pm 1 SE.

| | Distance | Panicles | Spikelets | Florets | Mean (m^{-2}) |
|---------------|----------|--------------|------------|------------|-------------------|
| Inside clone | 0–50 | 57.5 (1,099) | 45.2 (872) | 23.8 (57) | 260 \pm 47 |
| | 51–100 | 63.8 (120) | 74.4 (565) | 75.8 (125) | 104 \pm 19 |
| Outside clone | 101–150 | 95.4 (605) | 90.8 (316) | 89.2 (32) | 122 \pm 39 |
| | 151–200 | 100 (87) | 96.3 (106) | 92.9 (9) | 26 \pm 12 |
| | 201–250 | — | 98.1 (35) | 95.8 (7) | 5 \pm 2 |
| | 251–300 | — | 98.7 (11) | 97.9 (5) | 2 \pm 1 |
| | 301–350 | — | 99.6 (19) | 97.9 (0) | 2 \pm 1 |
| | 351–400 | — | 99.6 (0) | 97.9 (0) | 0 \pm 0 |
| | 401–450 | — | 100 (7) | 97.9 (0) | 1 \pm 1 |
| | 451–500 | — | — | 100 (5) | 1 \pm 1 |
| Sum | | 1,911 | 1,931 | 240 | 52 \pm 27 |

adapted to longer distance dispersal (Harper 1977), can contribute to this pattern of invasion within fescue prairies.

Persistence in the Seed Bank. Despite the observed aggregation of seeds around the margins of invading patches of smooth brome, the number of dispersed seeds was poorly correlated with the number germinated from the seed bank. Only 48% (16 of 33) of seeds germinated within 1 m of the patch margin (Table 3), and the number

of germinated seedlings was independent of the number of seeds dispersed ($F_{1,3} = 1.96$, $P = 0.2563$, $R^2 = 0.395$).

The abundance of dispersed seeds in the soil seed bank is a function of many factors. Previous correlations between the number of dispersed and recruited seeds have been attributed to short-distance dispersal (Jakobsson et al. 2006; Czarnecka 2004), the persistence of seeds in the soil (Dessaint et al. 1991; Kjellsson 1992), and plant density (Dessaint et al. 1991). Although characteristic of many plant populations (Czarnecka 2004; Kjellsson 1992; Matlack and Good 1990; Thompson 1986), postdispersal transport and predation often account for discrepancies between patterns of seed dispersal and deposition (Blaney and Kotanen 2001; Derksen and Watson 1998; Jakobsson et al. 2006; Schupp and Fuentes 1995). Our own observations suggest that winter dispersal of viable “aerial

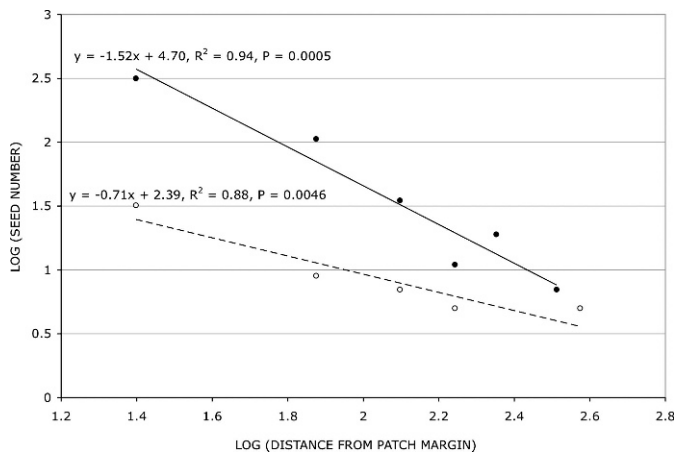


Figure 2. Relationship between the number of dispersed seeds and distance from the margins of smooth brome patches invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Open circles (dashed line) represent seeds dispersed as individual florets, subtended by a palea and lemma ($n = 58$); closed circles (solid line) represent seeds aggregated within spikelets ($n = 494$). Distances from the patch margin represent the mid-points of 50 cm intervals.

Table 2. Comparisons of the yield and viability of seeds collected from patches of smooth brome invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Data were collected at the beginning and end of seed dispersal and represent the pooled results from 16 invading patches, randomly selected from two prairies. Cleaned seeds from 10 panicles, randomly selected from each patch, were germinated in a growth chamber. Seed data were blocked by site to reduce between site variability within the ANOVA test. Mean number of seeds \pm 1 SE.

| | August | October | <i>F</i> | <i>df</i> | <i>P</i> |
|-------------------|----------------|----------------|----------|-----------|----------|
| Seeds per panicle | 23.9 \pm 4.2 | 15.6 \pm 3.5 | 1.33 | 1,29 | 0.2569 |
| Seed mass (mg) | 3.0 \pm 0.08 | 3.2 \pm 0.12 | 1.38 | 1,29 | 0.2501 |
| Germination (%) | 78.8 \pm 2.4 | 84.8 \pm 2.3 | 5.54 | 1,29 | 0.0255 |

Table 3. Comparisons between the numbers of smooth brome seeds dispersed and germinated from the seed bank surrounding four patches of smooth brome invading two northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Seeds were captured along 5 m strips of landscape cloth, pinned 1 m inside the fringe of invading patches (indicated by a dash). Germinable seeds account for the mean viability (84%) and proportion of dispersed seeds containing a mature caryopsis (15%). Means \pm 1 SE.

| | Distance | Seed rain | | | Seed bank | |
|---------------|----------|-----------|------------|-------------------|-----------|-------------------|
| | | Total | Germinable | Mean (m^{-2}) | Total | Mean (m^{-2}) |
| Inside clone | 0–50 | 263 | 33 | 55 \pm 21 | 8 | 13 \pm 5 |
| | 51–100 | 154 | 19 | 32 \pm 20 | 3 | 5 \pm 4 |
| Outside clone | 101–150 | 253 | 32 | 53 \pm 44 | 2 | 3 \pm 2 |
| | 151–200 | 16 | 2 | 3 \pm 3 | 3 | 5 \pm 4 |
| | 201–250 | 6 | 1 | 1 \pm 1 | 1 | 2 \pm 2 |
| | 251–300 | — | — | — | 2 | 3 \pm 2 |
| | 301–350 | — | — | — | 3 | 5 \pm 2 |
| | 351–400 | — | — | — | 2 | 3 \pm 2 |
| | 401–450 | — | — | — | 5 | 8 \pm 8 |
| | 451–500 | — | — | — | 4 | 7 \pm 4 |
| Sum | | 692 | 87 | 15 \pm 7 | 33 | 6 \pm 1 |

seed banks,” consisting of mature panicles (Csontos 2007), could also contribute to the low correlations between the seed rain and seed bank of invading clones. In other areas of the Great Plains, postdispersal transport of seeds by water, from smooth brome populations established along riparian areas (Potyondi 1995), could further contribute to discrepancies between local seed dispersal and recruitment, and facilitate invasions of new areas of native prairie. However, other mechanisms, including the impacts of seed predators and pathogens, remain unexplored.

Implementing Dispersal Models to Predict Invasion Patterns. Although biological invasions are contingent upon the dispersal of propagules, their arrival does not guarantee establishment (Nathan and Muller-Landau 2000). As a result, the availability of suitable recruitment sites, seedling mortality, and the demographic viability of established populations can restrict the ability of dispersal models to predict invasions patterns (Defossé et al. 1997; Eriksson and Kiviniemi 1999; Higgins and Richardson 1999; Schupp and Fuentes 1995; Vander Wall and Joyner 1998). For example, Bergelson et al. (1993) emphasized that “realized dispersal” and seedling establishment are constrained by landscape fragmentation and the spatial distribution of recruitment sites. Consequently, the potential of smooth brome seeds to generate dense invasion fronts remains highly contingent on local disturbances, facilitating their establishment. In native prairies, small, scattered animal-generated disturbances could provide ideal recruitment areas; however, their dense, competition-induced edges could restrict the proliferation of potential invaders (Reichman et al. 1993). As a result, the invasiveness of exotics such as smooth brome might depend on their ability to optimize sexual and vegetative

forms of reproduction during their colonization of perennial plant communities (Huenneke and Vitousek 1990). Consequently, tradeoffs between the dispersibility and competitiveness of propagules could help elucidate important differences among the potential impacts of exotic species (Duyck et al. 2007; Jakobsson et al. 2006). Such context dependence among different stages in an invader’s life history deserves further research and could account for important discrepancies in the ability of dispersal models to predict patterns of biological invasions (Dietz and Edwards 2006).

Sources of Materials

¹ Landscape fabric and fabric staples, Easy Gardener Inc., Waco, TX 76710.

² Tanglefoot Paste, The Tanglefoot Company, Grand Rapids, MI 49504–6485.

³ Clipper Seed Cleaner, Blount/Ferrell-Ross, Bluffton, IN 46714.

⁴ Plant growth chamber, Conviron Controlled Environments Limited, Winnipeg, Manitoba, Canada R3H 0R9.

⁵ Soil mix, Metro-Mix 220, Scotts Co., Maryville, OH 43041.

⁶ Data Desk, Data Description, Inc., Ithaca, NY 14852–4555.

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