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Pollen- and Seed-Mediated Gene Flow in Kochia (*Kochia scoparia*)

Hugh J. Beckie, Robert E. Blackshaw, Linda M. Hall, and Eric N. Johnson*

Efficient natural dispersal of herbicide-resistance alleles via seed and pollen can markedly accelerate the incidence of herbicide-resistant weed populations across an agroecoregion. Studies were conducted in western Canada in 2014 and 2015 to investigate pollen- and seed-mediated gene flow in kochia. Pollen-mediated gene flow (PMGF) from glyphosate-resistant (GR) to non-GR kochia was quantified in a field trial (hub and spoke design) at Saskatoon, Saskatchewan. Seed-mediated gene flow of acetolactate synthase (ALS) inhibitor-resistant kochia as a function of tumbleweed speed and distance was estimated in cereal stubble fields at Lethbridge, Alberta and Scott, Saskatchewan. Regression analysis indicated that outcrossing from GR to adjacent non-GR kochia ranged from 5.3 to 7.5%, declining exponentially to 0.1 to 0.4% at 96 m distance. However, PMGF was significantly influenced by prevailing wind direction during pollination (maximum of 11 to 17% outcrossing down-wind). Seed dropped by tumbleweeds varied with distance and plant speed, approaching 90% or more (ca. 100,000 seeds or more) at distances of up to 1,000 m and plant speeds of up to 300 cm s^{-1}. This study highlights the efficient proximal (pollen) and distal (seed) gene movement of this important GR weed.

Nomenclature: Glyphosate; kochia, *Kochia scoparia* (L.) Schrad., KCHSC.

Key words: ALS-inhibitor resistance, glyphosate resistance, herbicide resistance, multiple resistance, pollen flow.

Kochia is the 10th most abundant weed across the Canadian prairies, but fourth most abundant weed in the southern semiarid Grassland region (Leeson et al. 2005). A competitive tumbleweed with early emergence (Schwinghamer and Van Acker 2008), abundant seed production, and stress tolerance, it occurs in agricultural land, ruderal areas, and rangelands (Friesen et al. 2009). Kochia resistant to ALS inhibitors was first reported in the Canadian prairies in 1988 (Heap 2016). Beckie et al. (2011b) found that 20 yr later, about 90% of prairie populations tested were ALS inhibitor-resistant. Today, all screened populations are found to be ALS inhibitor-resistant.

GR kochia was first identified in Kansas in 2007 (Waite 2008; Waite et al. 2013), and is now reported in 10 states (Heap 2016). In western Canada, kochia with multiple resistance to glyphosate and ALS inhibitors was first discovered in 2011 in three chemical fallow fields in southern Alberta (Beckie et al. 2013, 2014). The mechanism of glyphosate resistance in kochia populations in Canada and the United States is increased 5-enol-pyruvylshikimate-3-phosphate synthase (EPSPS) expression resulting from gene amplification (Wiersma et al. 2015). The EPSPS gene copy number in kochia is increased through tandem gene amplification on a single chromosome, and resistance is inherited following a Mendelian single locus (monogenic) model (Jugulam et al. 2014; Niehues 2014). Moreover, EPSPS copy number is correlated with level of glyphosate resistance, with seven or greater copy number conferring a high level of resistance (Godar et al. 2015). Canadian GR kochia populations have up to 27 EPSPS copies (S. Martin, personal communication). To date, there are over 100 sites across western Canada with this multiple-resistant biotype (Beckie et al. 2015, unpublished data; Hall et al. 2014).

Kochia is self-compatible and produces protogynous flowers where the stigmas emerge before anther development (Guttieri et al. 1995; Stallings et al. 1995). The stigmas usually emerge 1 wk before pollen is shed, are receptive to foreign pollen during that time, and deteriorate before anther dehiscence that prevents self-pollination within the same flower (Stallings et al. 1995).

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Pollen grains are spheroidal, 20 to 40 μm in diameter, and granular with 100 to 130 pores uniformly distributed over the grain surface (Stallings et al. 1995). Mulugeta et al. (1992) collected pollen from greenhouse- and field-grown kochia plants and measured viability during storage at three temperatures and five relative humidity levels. Pollen stored at 4 C and high relative humidity retained at least 10% viability after 9 d. Pollen stored under conditions more typical of late summer in the Great Plains (28 C and 33% relative humidity) retained 10% viability after about 2 d. In another study of field-collected kochia pollen, viability was 68, 27, and 9% at 0, 24, and 48 h after dehiscence, respectively, when stored at 23 C and 18% relative humidity (Stallings et al. 1995). Pollen counts from traps at 0.5- to 1.0-m height were highly correlated with prevailing wind direction; up to 23 pollen grains cm^{-2} were recovered 50 m from the pollen source (Mulugeta 1991). Mulugeta et al. (1994) estimated that 0.1% of shed pollen would be deposited more than 150 m from the source.

Wind is an important pollination vector, but bees (Colletidae and Halictidae) also contribute to cross-pollination in kochia (Blackwell and Powell 1981). Adult kochia plants produce copious amounts of pollen for extended periods (Mulugeta 1991), which generally is an indication that the plant species is naturally highly outcrossing. Kochia biotypes or ecotypes can exhibit large variability in days to flowering, which, in turn, may affect synchrony of pollination. In a field study in North Dakota, Bell et al. (1972) reported time from emergence to flowering among 13 kochia accessions collected from across the western United States varied from 57 to 100 d. Two kochia biotypes from North Dakota, which differed markedly in plant structure, also differed in time to flower initiation by as much as 24 d (Stallings et al. 1995). Guttieri and Eberlein (1998) inferred that field populations of kochia are effectively undergoing random mating based on inbreeding coefficients for nine Idaho populations, although PMGF was not directly measured.

Thus, it was generally believed that kochia was predominantly outcrossing (Thill et al. 1991). However, a high degree of self-pollination was evident by fecundity of kochia plants enclosed in plastic and nylon mesh bags in the greenhouse (Thompson et al. 1994a). Studies utilizing ALS-inhibitor resistance as a marker have concluded that kochia is primarily self-pollinated, aided by an extended period of pollen production of an individual plant. However, substantial outcrossing can occur. Outcrossing between ALS inhibitor-resistant and -susceptible plants occurred at a maximum rate of 13% at 1.5 m distance and declined to 1.4% at 29 m, the farthest distance sampled (Mallory-Smith et al. 1993; Stallings et al. 1995). Similarly, in a pollen flow study between a natural ALS inhibitor-resistant kochia population and transplanted susceptible plants, Mulugeta et al. (1992) reported that about 4% of progeny of the susceptible plants were resistant; distances between resistant and susceptible plants were not specified.

Kochia is a prolific seed producer. Seed production per plant depends upon stand density and the extent of intra- and interspecific competition (Becker 1978; Mulugeta 1991). Seed production of field-grown kochia ranges widely, from 2,000 to 30,000 seeds per plant (Stallings et al. 1995). Thill and Mallory-Smith (1996) concluded that kochia typically produces over 14,000 seeds per plant. In a summary of small-plot studies across western Canada, Watson et al. (2001) listed maximum seed production of kochia at 15,000 to 25,000 seeds per plant. In noncompetitive studies conducted in the greenhouse, ALS inhibitor-resistant or susceptible kochia produced about 12,000 seeds per plant (Thompson et al. 1994b).

In a field study in Montana of kochia seed dispersal, seedling populations of up to 30,000 plants m^{-2} were counted beneath individual mother plants (Fay et al. 1992). This seed represents the portion that is dropped prior to stem abscission. Seed dispersal decreased exponentially with increasing distance from the base of the stem. Progressive desiccation of the plant at maturity subsequently results in abscission at the base of the stem and tumbling of the shoot by wind (Becker 1978). Stem breakage during senescence and associated tumbling capability are accentuated in autumns with extremes of soil moisture conditions (Baker et al. 2008). As a consequence of the tumbleweed mode of seed dispersal, kochia had the highest rate of spread among alien weeds in the western United States from 1880 to 1980 as determined by the number of counties where it occurred each decade (Forcella 1985).

With the increasing occurrence of multiple-resistant (including GR) kochia across the Great Plains of North America and limited information on kochia gene flow, studies were conducted in 2014 and 2015 in western Canada to quantify pollen- and seed-mediated gene flow (SMGF) of this important weed species. PMGF from GR to non-GR kochia was quantified in a confined field trial (hub and spoke design) at Saskatoon, Saskatchewan. Seed dispersal of ALS inhibitor-resistant kochia as a function of tumbleweed speed and distance was estimated in cereal stubble fields at Lethbridge, Alberta and Scott, Saskatchewan.

Materials and Methods

Pollen-Mediated Gene Flow (PMGF). Pollen flow (i.e., outcrossing frequency as a function of distance) of GR (+ALS inhibitor-resistant) kochia was measured in a tilled fallow field at the Agriculture and Agri-Food Canada (AAFC) Research Farm in Saskatoon, SK in 2014 and 2015. The experiment was arranged in a radial (i.e., hub and spoke) design with eight spokes or rays of non-GR (but ALS inhibitor-resistant) kochia plants oriented in the four cardinal directions (N, S, E, W) and four ordinal directions (NE, NW, SE, SW) from a central block of GR kochia. GR kochia seed (100% GR) originated from plants grown the previous year that were sprayed with glyphosate at 900 g ae ha^{-1} in field plots at Lethbridge, Alberta (i.e., seed increase); the population originated in a field in southern Alberta (Beckie et al. 2013). Non-GR kochia seed originated in a field in southern Saskatchewan in 2013, and was confirmed as 100% susceptible to glyphosate. Kochia seed was planted in 25-cm diam pots and grown to preflowering stage in the greenhouse. At that time, pots (thinned to one plant per pot) were moved to the field with no naturally occurring kochia population and buried at ground level (July 5, 2014, and June 17, 2015). Pots of GR kochia were placed in the center of the field in a 10- by 10-m square area, with pots placed 1 m apart for a total of 121 pots (11 rows by 11 rows). Non-GR kochia pots were placed at intervals of 0, 1, 2, 4, 8, 16, 32, 64, and 96 m from the central GR kochia block in each of the eight directions. For each spoke, there were four pots (replicates) at distances of 0, 1, 2, and 4 m, eight pots at a distance of 8 m, and 16 pots at distances of 16, 32, 64, and 96 m (88 pots per spoke or 704 pots total). Pots were watered as needed, but not fertilized. Meteorological data were obtained from an on-site weather station.

After pollination, pots were returned to the greenhouse and seeds harvested by hand at maturity. Progeny of non-GR plants were screened with glyphosate to determine the frequency of outcrossing. The number of progeny screened (for each spoke) were determined by power analysis ($\alpha = 0.05$, power $= 0.80$; Jhala et al. 2011): 5,000 at each of 0, 1, and 2 m; 10,000 at 4 m; 20,000 at 8 m; and 40,000 at each of 16, 32, 64, and 96 m. For each sample (progeny of a parental plant), seeds were planted in 52- by 26- by 5-cm flats containing potting soil. Seedlings (3 to 5 cm tall) were sprayed with glyphosate (Roundup WeatherMax, 540 g ae L^{-1}) at 900 g ae ha^{-1} (2X label discriminating dose; Beckie et al. 2013). Glyphosate was applied using a moving-nozzle cabinet sprayer equipped with a flat-fan nozzle tip (TeeJet 8002VS, Spraying Systems Co., Wheaton, IL) calibrated to deliver 200 L ha^{-1} of spray solution at 275 kPa. Three weeks after treatment, plant response to herbicide application was visually scored as susceptible (dead or nearly dead) or resistant (some injury but new growth, or no injury). Assessments were made relative to herbicide-treated and -untreated susceptible and resistant check populations (as described in Beckie et al. 2013). For each sample, PMGF (%) was calculated as the number of GR seedlings divided by the total number of seedlings tested in a sample, multiplied by 100.

Seed-Mediated Gene Flow (SMGF). This study was conducted in cereal stubble (15- to 20-cm height) fields at the AAFC Research Farm at Scott, Saskatchewan and AAFC Research Centre at Lethbridge, Alberta in October 2014 and repeated in October 2015. In early October of each year, 24 mature non-GR (but ALS-inhibitor resistant) kochia tumbleweeds in nearby noncrop areas were harvested by cutting the stem at ground level. Each plant was placed in a preweighed cotton bag.

Underneath 12 of those plants, plant residue on the soil surface was vacuumed to determine the amount of seed dropped. Vacuumed residue from under a tumbleweed was placed in an aluminum tray and allowed to dry at room temperature. Kochia seed was separated from soil and plant material by repeated sieving and washing samples. The cleaned, air-dried seed was weighed and 1,000-seed weight determined from four subsamples. Each plant was hand-threshed by manually crushing the tumbleweed in the bag; seed was separated from plant residue and measured as described above. The harvest index (HI) for a plant was calculated as seed weight divided by total plant weight (seed + residue).

The remaining 12-collected plants were used to estimate seed dropped as a function of mean tumbleweed speed and distance. The experiment comprised four tumbleweeds (replicates) used in each of three consecutive experimental runs (repetitions). The experiment was conducted when wind speeds were generally 20 km h^{-1} (observed threshold for tumbleweed movement) or greater. A GPS mini-collar (Quantum 4000; Telemetry Solutions, Concord, CA), which weighed 7 g, was attached to the base of the stem of a tumbleweed to track movement at 5-s intervals. Tumbleweed plant weight ranged from 150 to 775 g. Maximum field distance of tumbleweed movement was set at 1,000 m (1 km), the limit of the study area. At the termination of a run, each plant was placed back in the same bag, re-weighed, then later hand-threshed to determine the amount of seed retained on the plant. Pretumble seed weight was calculated as pretumble plant weight multiplied by mean HI of nontumbled plants. Amount (weight) of seed dropped by tumbling plants was calculated as pretumble seed weight minus posttumble seed weight. Number of seeds dropped was calculated using 1,000-seed weight values. Percentage seed dropped was calculated as weight of seed dropped divided by pretumble seed weight, multiplied by 100.

Data Analysis. Data were tested for the assumptions of normality and homogeneity of variances using the Shapiro-Wilk and Levene's test (SAS Institute 2013). When required, data were arcsin- or log-transformed prior to ANOVA. Data (PMGF as affected by distance or direction; SMGF as affected by tumbleweed distance or speed) were subjected to ANOVA using PROC MIXED (SAS Institute 2013). PMGF (y) was regressed against distance (x) from the GR kochia pollen donor using the double-exponential decay model (Equation 1) (Beckie et al. 2011a):

$$y = ae^{-bx} + ce^{-dx} \quad [1]$$

where $a + c$ is the intercept and b, d quantify the slope. Data were fitted to the model using PROC NLMIXED (SAS Institute 2013). The coefficient of determination (R^2) that quantifies the goodness of fit was calculated as described by Kvalseth (1985) using the residual sum of squares value from the analysis output, and significance at $P = 0.05$ (denoted in figures as '*') and 0.01 (**) determined. In addition, root mean square error (RMSE) was calculated to verify the goodness of fit for nonlinear models (Sarangi et al. 2015). The maximum likelihood ratio test was used to determine if PMGF significantly varied among directional blocks (spokes); the effect of direction on the frequency of PMGF was displayed using box and whisker plots (SAS Institute 2013). Additionally, the distribution and frequency of wind speed and direction during pollination was illustrated using wind rose diagrams.

Regression analysis was conducted to determine the relationship between kochia seed dropped (percentage and number) per tumbleweed vs. distance or mean tumbleweed speed. Replicate rather than mean data were used in regression analysis, as speed or distance ('x' axis) varied by tumbleweed (replicate). Regression models that provided the best fit (as determined by R^2 or RMSE values) were linear (Equation 2), exponential reciprocal (Equation 3), or power (Equation 4) (SAS Institute 2013):

$$y = ax + b \quad [2]$$

where y is kochia seed dropped (percentage or number of seeds), x is distance (m) or mean tumbleweed speed (cm s^{-1}), a is the slope, and b is the y-intercept;

$$y = ae^{-b/x} \quad [3]$$

where a is the asymptote and b is a slope parameter (y and x as defined above);

$$y = e^{a}x^{b} \quad [4]$$

where a is the scaling factor and b is the power (y and x as defined above). Data were fitted to the linear model using PROC REG or nonlinear models (Equations 3 and 4) using PROC NLMIXED (SAS Institute 2013).

Results and Discussion

Pollen-Mediated Gene Flow (PMGF). In both years, good flowering synchrony was observed between pollen donor and receptor plants. In both years, PMGF significantly differed ($P < 0.05$) according to distance and direction as indicated by ANOVA. In 2014, PMGF (% outcrossing) from GR kochia pollen donor to non-GR receptor plants varied by direction, as determined from the maximum-likelihood ratio test ($P < 0.05$); maximum outcrossing (17%) occurred in receptor plants located in the west-oriented spoke (Figure 1). In 2014, pollination occurred over the period July 7 to August 15. During that period, winds were predominantly from the east (45% of the time) (Figure 2). Winds from the west and northwest accounted for 12 and 10% of the time, respectively.

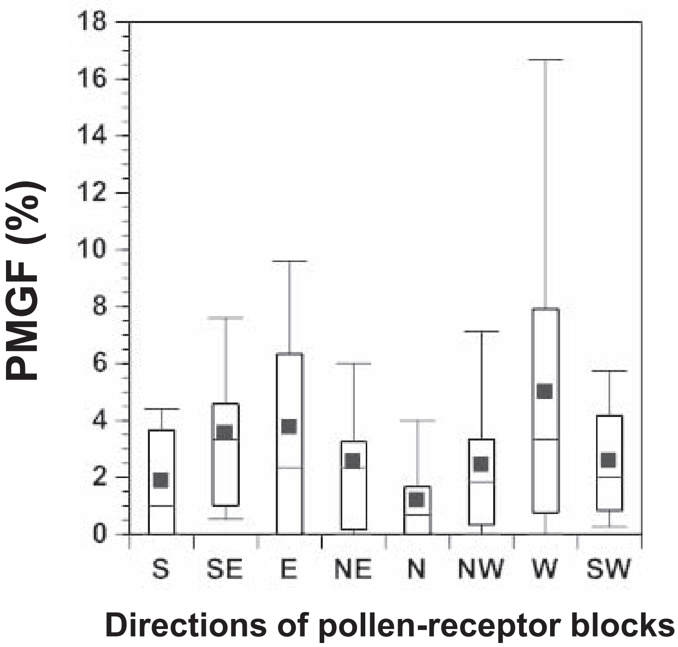

Figure 1. Pollen-mediated gene flow (PMGF) (% outcrossing) from glyphosate-resistant (GR) kochia pollen donor to varying directional orientation of non-GR receptor plants at a field site at Saskatoon, Saskatchewan in 2014. The top, bottom, and middle line of the box corresponds to the 75th percentile (top quartile), 25th percentile (bottom quartile), and 50th percentile (median), respectively. The whiskers extend from the 10th percentile (bottom decile) and the top 90th percentile (top decile). The symbol within the box represents the mean for the data range.

When averaged among the eight spokes, mean frequency of PMGF was 7.5% for receptor plants closest to the GR kochia pollen donor block, declining exponentially to 0.4% at 96 m (study limit) (Figure 3). The predicted distances where 50 and 90% reduction in PMGF occurred were 2.5 and 13.5 m, respectively.

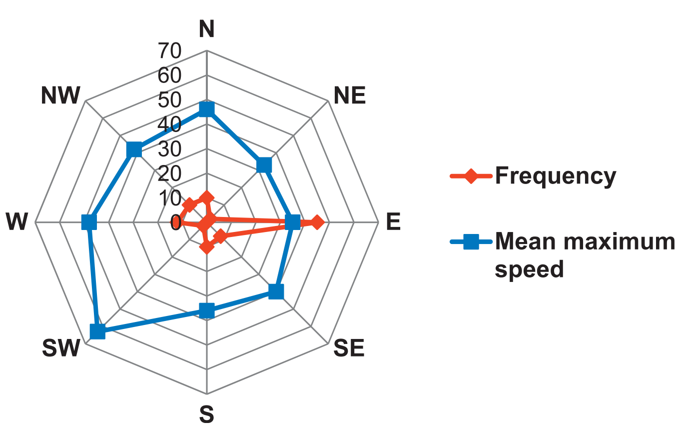

Figure 2. Distribution and frequency of maximum daily wind speed (km h^{-1}) and direction (blowing from) during pollination at a field site at Saskatoon, Saskatchewan in 2014. (Color for this figure is available in the online version of this article.)

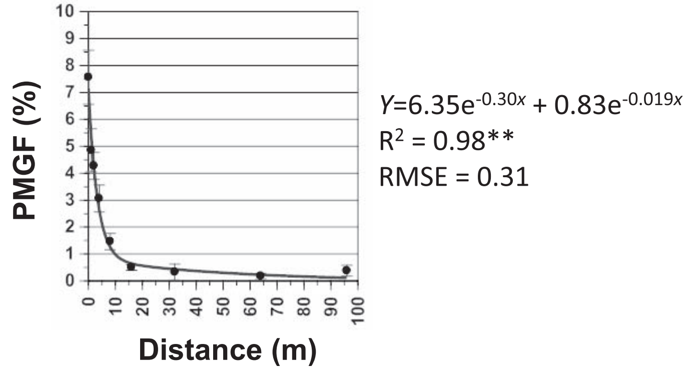

Figure 3. Pollen-mediated gene flow (PMGF) (% outcrossing ± SE) from glyphosate-resistant (GR) kochia pollen donor to varying distances of non-GR receptor plants at a field site at Saskatoon, Saskatchewan in 2014 (see text for model description). Abbreviation: RMSE, root mean square error.

In 2015, PMGF similarly varied by directional orientation of non-GR receptor plants (Figure 4). Maximum outcrossing (11%) occurred in the east-oriented spoke. In 2015, pollination occurred over the period June 22 to July 27. During that period, winds were predominantly from the west (44% of the time) (Figure 5). Therefore, the level of outcrossing observed in receptor plants in the eight spokes corresponded well with the prevailing winds during the pollination period in both years. When

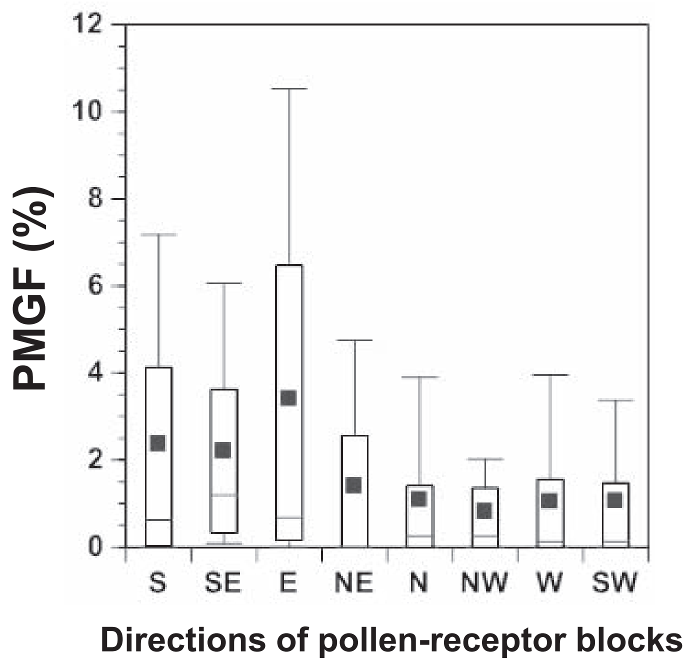

Figure 4. Pollen-mediated gene flow (PMGF) (% outcrossing) from glyphosate-resistant (GR) kochia pollen donor to varying directional orientation of non-GR receptor plants at a field site at Saskatoon, Saskatchewan in 2015.

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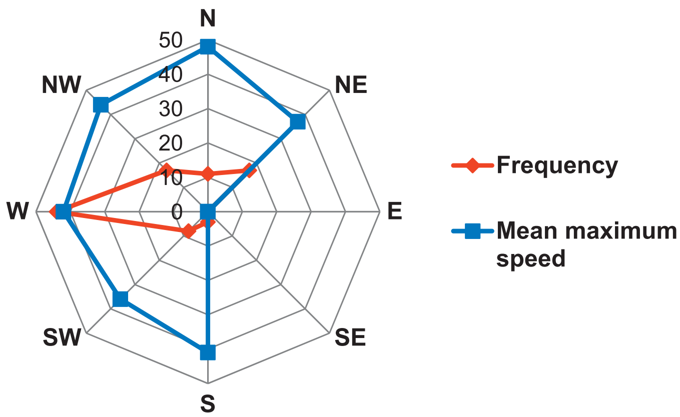

Figure 5. Distribution and frequency of maximum daily wind speed (km h^{-1}) and direction (blowing from) during pollination at a field site at Saskatoon, Saskatchewan in 2015. (Color for this figure is available in the online version of this article.)

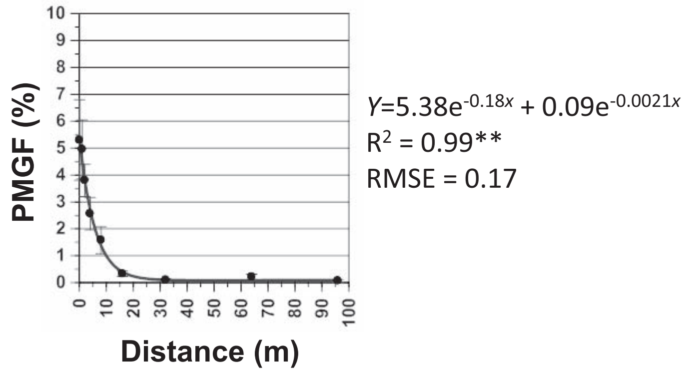

Figure 6. Pollen-mediated gene flow (PMGF) (% outcrossing ± SE) from glyphosate-resistant (GR) kochia pollen donor to varying distances of non-GR receptor plants at a field site at Saskatoon, Saskatchewan in 2015 (see text for model description). Abbreviation: RMSE, root mean square error.

averaged among the eight spokes, mean frequency of PMGF was 5.3% in plants closest to the GR kochia pollen donor block, declining exponentially to 0.1% at 96 m (Figure 6). The predicted distances where 50 and 90% reduction in PMGF occurred were similar to those in 2014, at 4.1 and 14.3 m, respectively.

In this study, the distance of kochia PMGF was over threefold greater than previously documented in the western United States (96 vs. 29 m) (Mallory-Smith et al. 1993; Stallings et al. 1995). In both studies, PMGF was documented to the maximum distance investigated between donor and receptor plants. However, Mulugeta et al. (1994) estimated that a small fraction of shed pollen could be deposited more than 150 m from the source. Overall, levels of outcrossing in the previous study were relatively similar to those found in this study. The maximum rate of outcrossing between ALS inhibitor-resistant and -susceptible kochia plants in close proximity was 13% (Mallory-Smith et al. 1993; Stallings et al. 1995), whereas the maximum rate of outcrossing between GR and non-GR kochia in close proximity was 17 and 11% in 2014 and 2015, respectively. Mean outcrossing at 32 m in this study was 0.1 (2015) to 0.3% (2014), compared with 1.4% at 29 m in the previous study. Kochia PMGF in the study in the United States was conducted in a spring barley (*Hordeum vulgare* L) field, whereas our study was conducted in a fallow field. The main reasons for excluding a crop were compliance of confined field trial protocols, but more importantly, to simulate a worst-case scenario that favored PMGF because of lack of potential crop pollen competition or the crop canopy acting as a wind break.

In summary, PMGF of GR kochia is likely to be an important vector for proximal GR allele dispersal, such as within fields; PMGF may contribute to an increase in EPSPS copy number and therefore, levels of resistance to glyphosate. Additionally, PMGF in this species can contribute to rapid accumulation of herbicide resistance alleles in an individual or population. This phenomenon can result in individuals possessing different mutations that confer resistance to herbicides of the same site of action, such as ALS-inhibitor resistance (Beckie et al. 2011b; Guttieri et al 1995). Of greater concern, however, is outcrossing leading to resistance to multiple site-of-action herbicides, such as reported in a kochia population resistant to ALS inhibitors, photosystem-II inhibitors, glyphosate, and synthetic auxins (Varanasi et al. 2015).

Seed-Mediated Gene Flow (SMGF). The ANOVA results indicated that SMGF varied with distance traveled and plant speed ($P < 0.05$). ANOVA further indicated that the amount of kochia seed dropped beneath a plant did not vary across site-years. On average, 2.9% of total plant seed was dropped underneath the mother plant, equivalent to 3,300 seeds. Even though a small percentage of seed was dropped from attached plants, it is still a sufficiently large amount to aid short-distance seed dispersal and recruitment from the soil seed bank the following year. Similarly, HI values of control (nontumbled) plants did not significantly differ among site-years. These values ranged from 0.29 at Lethbridge in 2014 to 0.33 at Scott in 2015.

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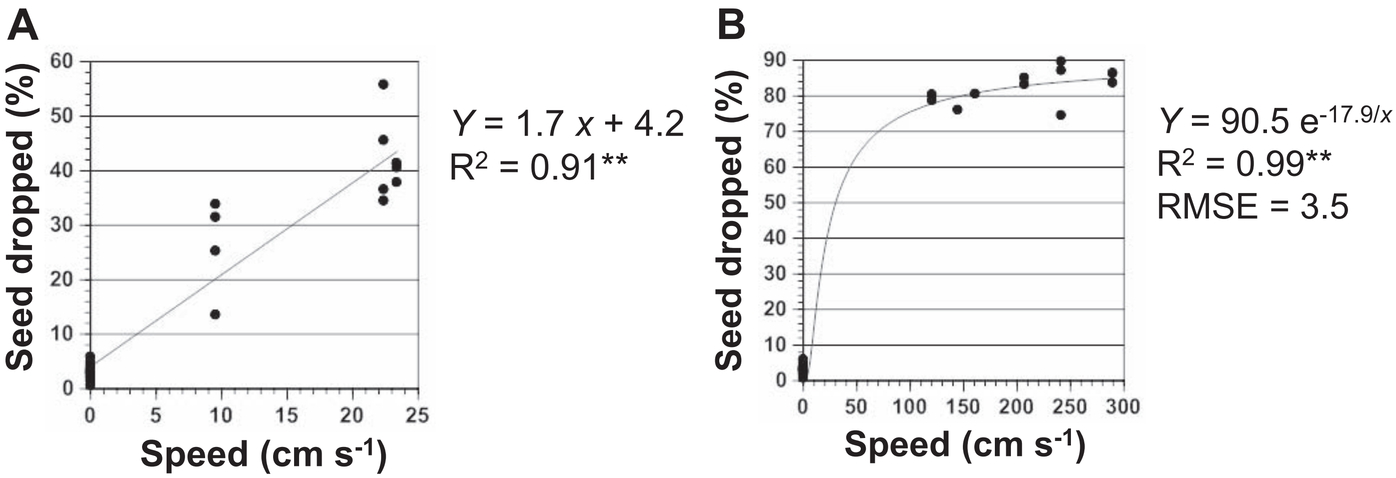

Figure 7. Kochia tumbleweed seed dropped (%) with increasing plant speed at a field site at Scott, Saskatchewan in 2014 (A) and 2015 (B) (see text for model description). Abbreviation: RMSE, root mean square error.

Because of varying wind speeds and field conditions (e.g., dimensions) among site-years, results are presented by site-year. In 2014 at Scott, SK, seed dropped by ALS inhibitor-resistant kochia tumbleweeds increased linearly with tumbleweed speed to a maximum of 40 to 50% per plant at 20 to 25 cm s^{-1} (Figure 7A). Therefore, maximum number of seeds dropped were about 40,000 per plant (figure not shown; regression equation, $y = 1570\ x + 3440$). In 2014, all tumbleweeds moved the same distance of 300 m (plants stopped at fence line). In 2015 at Scott, wind speeds were much greater than conditions in 2014, with plant speeds approaching 300 cm s^{-1} (Figure 7B). The amount of seed dropped vs. speed was best fit (as indicated by R^2 and RMSE values) using the exponential reciprocal regression model, which indicated 80 to 90% seed dropped at speeds of 125 cm s^{-1} or greater. Maximum amount of seed dropped exceeded 100,000 seeds per plant (figure not shown; regression equation, $y = 132100\ e^{-53.5/x}$). In 2015 at Scott, all tumbleweeds moved the same distance of 1,000 m or 1 km (plants stopped at fence line).

At Lethbridge, AB in 2014, kochia seed dropped increased linearly with increasing distance to 1,000 m maximum. Maximum seed dropped reached 90% (Figure 8A) or about 100,000 seeds (figure not shown; regression equation, $y = 95\ x + 12300$). For that trial, the exponential reciprocal function best described seed dropped as a function of plant speed. At speeds approaching 70 to 80 cm s^{-1}, seed dropped exceeded 80% (Figure 8B) or about 100,000 seeds per plant (figure not shown; regression equation, $y = 109000\ e^{-4.7/x}$). At Lethbridge in 2015, as in 2014, kochia seed dropped

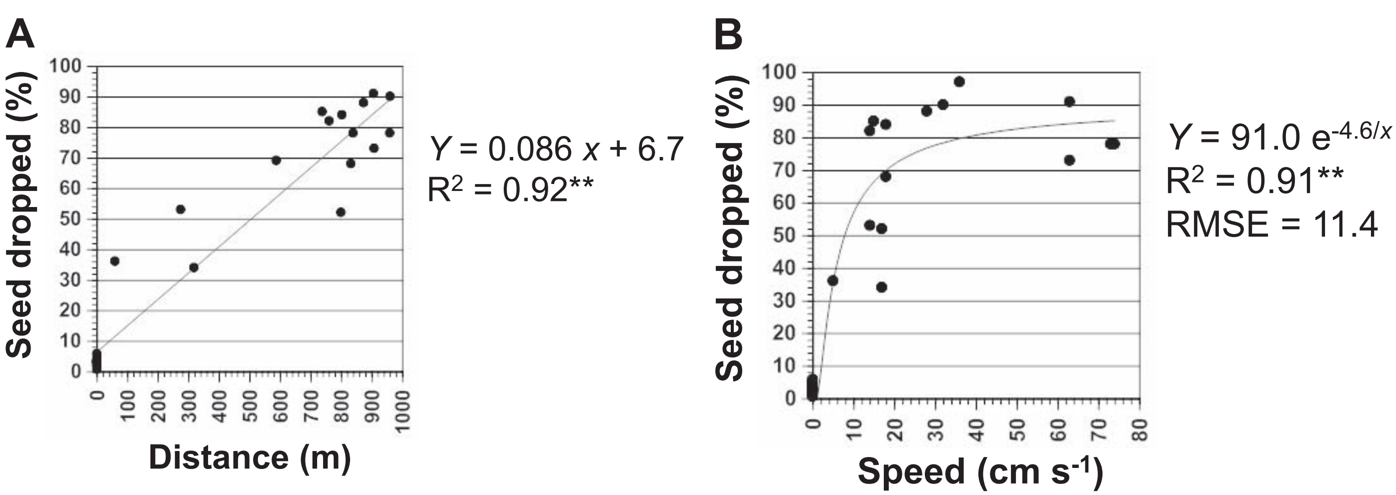

Figure 8. Kochia tumbleweed seed dropped at a field site at Lethbridge, Alberta in 2014, expressed as a percentage with increasing distance (A) and plant speed (B) (see text for model description). Abbreviation: RMSE, root mean square error.

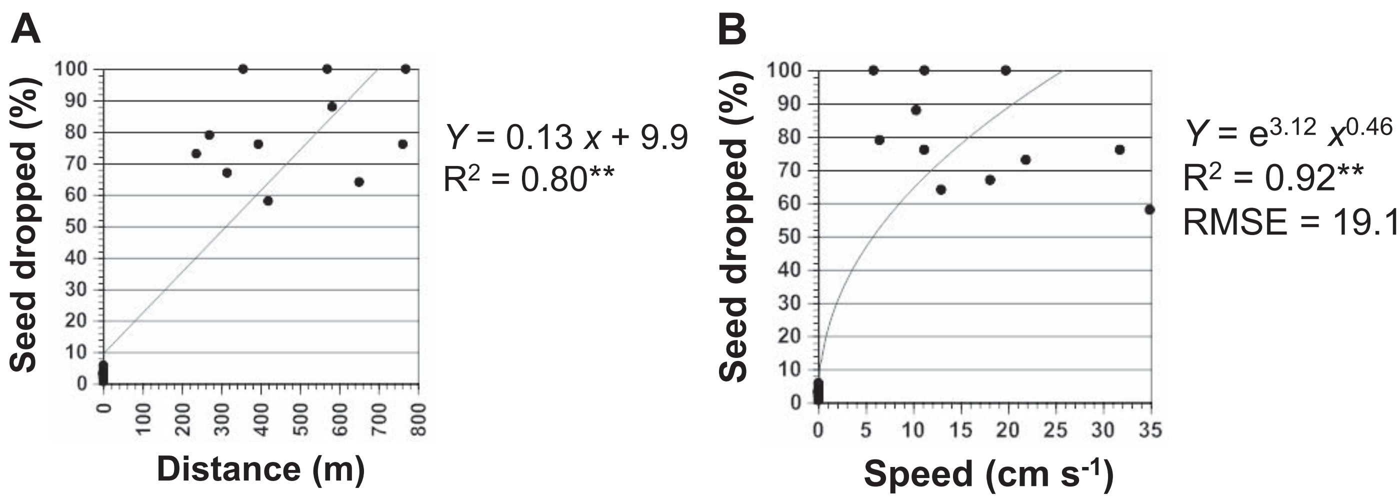

Figure 9. Kochia tumbleweed seed dropped at a field site at Lethbridge, Alberta in 2015, expressed as a percentage with increasing distance (A) and plant speed (B) (see text for model description). Abbreviation: RMSE, root mean square error.

increased linearly with increasing distance to 800 m maximum. Seed dropped approached 100% (Figure 9A) or 120,000 seeds per plant (figure not shown; regression equation, $y = 146\ x + 13100$) at the maximum distance. This extensive percentage (Figure 9B) and amount (figure not shown; regression equation, $y = e^{10.1}\ x^{0.49}$) of seed dropped by tumbling kochia plants occurred at relatively low plant speeds, as modeled by the power function (maximum of 35 cm s^{-1}). We observed that the plants used in this trial were very mature and dry, having had time to dry down in the cotton bags between the harvest and experiment run dates (latter dictated by sufficiently strong winds to conduct the trial). The high degree of senescence of the collected plants likely resulted in the high rate and extent of seed loss with increasing travel distance or speed.

Overall, the results of the study quantify, for the first time, the magnitude of seed dispersal in this important tumbleweed. For experimental purposes, tumbleweeds were stopped and we did not establish the maximum distance they could travel and continue to disperse seed. Harvested seeds from the tumbleweeds used in this study had uniformly high viability and germination (> 80%, data not shown). Kochia seed has little innate dormancy; freshly harvested seed readily germinates (Friesen et al. 2009). This study highlights the potential for long-distance SMGF within and among fields, and is considered an important factor in the rapid northern range expansion of this weed under a changing climate (Beckie et al. 2012).

Seed dispersal also is the predominant factor in incidence of ALS inhibitor-resistant kochia going from 0 to > 90% of populations across the Canadian prairies in less than 20 yr (Beckie et al. 2011b). Regular, periodic field surveys will be important in determining if the rate of increase in occurrence of GR kochia populations over time will be similar to that of ALS inhibitor-resistant kochia across western Canada. However, it is unknown if fitness (including fecundity) of GR kochia is similar to that of ALS inhibitor-resistant kochia (Légère et al. 2013). Results of this study emphasize the need for prevention of kochia seed production by managers of both agricultural and nonagricultural (e.g., roadsides/ditches, railway rights-of-way, oil well sites) land. Even a few surviving GR kochia plants have the potential to replenish the soil seed bank and disperse seed beyond field borders. This study reiterates the conclusion of previous research on GR kochia of the need for a collective regional response to significantly mitigate GR allele spread in this weed.

Acknowledgments

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