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Weed seed shatter in spring wheat in Alberta

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Abstract: The efficacy of harvest weed seed control depends on the extent of seed shatter of targeted weeds. Seed shatter of nine weed species, namely wild oat (*Avena fatua* L.), green foxtail [*Setaria viridis* (L.) P. Beauv.], wild mustard (*Sinapis arvensis* L.), cleavers (*Galium spurium* L. and *G. aparine* L.), spiny annual sow thistle [*Sonchus asper* (L.) Hill], lambsquarters (*Chenopodium album* L.), redroot pigweed (*Amaranthus retroflexus* L.), round-leaved mallow (*Malva pusilla* Sm.), and kochia [*Kochia scoparia* (L.) Schrad.] was measured in spring wheat (small-plot trials or producer fields) from 2014 to 2016 near Lacombe and Lethbridge, Alberta. Seed shatter was assessed using shatter trays collected periodically during crop ripening, as well as at swathing and direct-harvest (direct-combining) stages. If $\leq 20\%$ and $\geq 80\%$ seed shatter by direct-harvest stage is considered low and high, respectively, then green foxtail, lambsquarters, kochia and round-leaved mallow are classified as low, wild oat and annual sow thistle as high, with the other investigated species classed as intermediate. Seed retention of most species was improved by swathing compared with direct-combining. Study results indicate that harvest weed seed control practices have good potential for several weed species in western Canada.

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Abbreviations: GDD, growing degree-days; HWSC, harvest weed seed control; RMSE, root mean square error.

Key words: harvest weed seed control, herbicide resistance, integrated weed management, weed seed retention, weed seed shatter.

Introduction

Abundance rankings of weed species in a 2010 pre-harvest Alberta survey of cereal, oilseed and pulse crops (those pertinent to this study) were as follows: wild oat (*Avena fatua* L.), 2nd; cleavers (*Galium spurium* L. and *G. aparine* L.), 3rd; lambsquarters (*Chenopodium album* L.), 8th; spiny annual sow thistle [*Sonchus asper* (L.) Hill], 9th; green foxtail [*Setaria viridis* (L.) P. Beauv.], 18th; kochia [*Kochia scoparia* (L.) Schrad.], 19th; redroot pigweed (*Amaranthus retroflexus* L.), 21st; round-leaved mallow ((*Malva pusilla* Sm.), 37th; and wild mustard (*Sinapis arvensis* L.), 43rd (Leeson et al. 2012). In spring wheat (*Triticum aestivum* L.), however, three of these weeds were ranked higher: spiny annual sow thistle, 6th; green foxtail, 10th; and redroot pigweed, 18th. Because this survey was conducted after completion of in-crop herbicide applications, a high relative abundance ranking signifies species that are not being adequately controlled. Therefore, these populations can potentially reach physiological maturity, set viable seed, and replenish the soil seed bank.

Seed shatter is an important weediness trait that aids weed seed dispersal and increases weed fitness by allowing seeds to enter the seed bank for future recruitment (Shirtliffe et al. 2000). Weed seed shatter occurs when the plant's seeds ripen, detach, and fall to the ground. The shattering of seeds before harvest enables weed seeds to avoid collection by harvesting equipment and thereby persist within the field (Shivrain et al. 2010). The amount of weed seed shatter before harvest varies among weed species, and is influenced by environmental conditions and agronomic factors (Shirtliffe et al. 2000; Walsh and Powles 2014).

In Manitoba, Shirtliffe et al. (2000) found 50 and 10% of wild oat seed remained on the plant at 1,575 and 1,800 growing degree-days (GDD) (base 0 °C), respectively, after weed emergence. Another study conducted in western Canada found that 50% of wild oat seeds were retained on the plant at wheat maturity (Feldman and Reed 1974). A recent study in central Saskatchewan found over 70% wild oat seed retention (i.e., up to 30% shattering) in spring wheat and field pea (*Pisum sativum* L.) at direct-harvest (direct-combining) stage (Burton et al. 2016, 2017). In contrast, Tidemann et al. (2017) found only about 30% retention in direct-harvested spring wheat and fababean (*Vicia faba* L.) in Alberta or Saskatchewan.

Seeds readily fall from green foxtail panicles at maturity (Douglas et al. 1985). In Minnesota, Forcella et al. (1996) found that only 20% of green foxtail seeds were retained on the plant at harvest time of corn (*Zea mays* L.), a late-maturing crop. In contrast, green foxtail seed retention averaged over 90% in direct-harvested field pea and wheat in Saskatchewan (Burton et al. 2016, 2017).

Seed shatter has also been investigated in a number of broadleaf weed species. In small-grain cereals in western Canada, wild mustard pods typically remain intact until crop harvest (Mulligan and Bailey 1975). Forcella et al. (1996) determined that one-third of wild mustard seeds were retained at corn harvest in a cool growing season, but had completely shattered in a warm growing season. In Saskatchewan, wild mustard seed retention at field pea and wheat direct-harvest stage was 90% or more (Burton et al. 2016, 2017). Those studies noted similar results for cleavers, although Tidemann et al. (2017) found only 62 and 50% retention in direct-harvested wheat and fababean, respectively. Kochia is often cut at the stem by crop harvesters before the seeds become mature (Mickelson et al. 2004). In the southern Canadian prairies, kochia seed is often immature and non-viable at normal cereal crop harvest time (Friesen et al.

2009). In direct-harvested spring wheat in Saskatchewan, kochia seed shed was almost nil (Burton et al. 2017).

One non-herbicidal weed control strategy that has helped Australian producers manage their herbicide-resistant weed populations is harvest weed seed control (HWSC) (Walsh et al. 2013). The HWSC practices include chaff carts, direct-harvest crop residue baling, narrow-windrow burning, and seed pulverization via the Harrington Seed Destructor™. These practices can be one part of an integrated weed management system to reduce the seed bank, reduce reliance on herbicides, and thereby slow the selection of herbicide-resistant weeds. As quantified in studies in western Canada, weed seed retention to enable HWSC is favoured in early-maturing or competitive crops, and those that are swathed versus direct-harvested (Burton et al. 2016, 2017; Tidemann et al. 2017). For example, seed shatter of wild oat in swathed canola (*Brassica napus* L.) (at 50% seed color change on the main stem) in Saskatchewan was less than 5% (Burton et al. 2017).

Evaluating seed shatter of major weed species is a critical first step in assessing the potential of HWSC in western Canada for sustainable weed management. Recent studies by Burton et al. (2016, 2017) and Tidemann et al. (2017) have found significant differences and variation in seed shatter/retention both among and within weed species. Such variation may be associated with weed genotype or ecotype, crop or cultivar, agronomic practices, edaphic or environmental conditions, or their interactions. To further investigate this issue, seed shatter of nine weed species was determined in spring wheat (small-plot trials or producer fields) from 2014 to 2016 near Lacombe and Lethbridge, AB.

Materials and Methods

Small-plot experiment

Field trials were conducted in 2014, 2015, and 2016 at the Agriculture and Agri-Food Canada (AAFC) Research Centre at Lethbridge, AB (49.6°N; 112.8°W). The soil is an Orthic Dark Brown Chernozem loam with 3.2% organic matter content and pH 7.8. Meteorological data were provided by an on-site weather station.

The study was conducted in spring wheat. Experimental procedures followed that of Burton et al. (2016) and Tidemann et al. (2017). The experiment was arranged in a randomized complete block design with four treatments replicated four times. The treatments consisted of four weed species: wild oat, green foxtail, wild mustard, and kochia. Plot size was 4.25 m wide by 5 m long. Experiments were established on barley (*Hordeum vulgare* L.) stubble. Glyphosate at 900 g ae ha⁻¹ was applied before seeding as a burndown treatment. The trial was seeded on May 23, 2014, May 22, 2015, and May 18, 2016. Weed seeds were broadcast prior to seeding and pressed into the soil with drill packer wheels. Wild oat and wild mustard were seeded at 200 viable seeds m⁻², green foxtail at 300 viable seeds m⁻², and kochia at 150 viable seeds m⁻². Seedlots originated from local populations collected the previous year. Spring wheat was seeded using an air seeder with knife openers at 30-cm row spacing. The wheat cultivar 'AC Lillian' was seeded at a rate of 300 seeds m⁻². Granular fertilizer was side-banded or seed-placed at the time of crop planting, with N and P rates based on soil test recommendations. Crop seeding depth was 4 to 5 cm.

Three weeks before expected crop swathing stage, four 1-m² quadrats per plot (two quadrats per harvest date: swathing and direct-harvest stages) were randomly placed with corners flagged. Rectangular seed catch trays (15 by 60 cm) were placed in the middle of two quadrats. A wire screen was mounted above the bottom of each tray, allowing the capture of shattered seeds above the screen. Holes on the bottom of the tray allowed rainwater drainage. Weed seeds were

collected weekly from trays until trial termination. Collected seeds were identified, counted, and weighed to quantify seed shattering of each weed species.

The first harvest date (swathing stage) occurred when the crop reached seed moisture content between 30 and 40%, a ripening stage of phenological development scale (BBCH) 85-87. The second harvest date (direct-harvest/combine) occurred when the crop reached grain moisture content < 14%, a fully-ripe stage of BBCH 89. The crop and weeds were separated by species, samples placed in paper bags, then oven-dried for 3 days at 60 °C. Samples were threshed by hand, and seed weights were measured. Thousand-seed weights were determined by counting 250 seeds and multiplying the resulting weight by a factor of four.

Total seed shatter for each weed species at each crop maturation date was expressed as a percentage of total seeds produced (y), calculated using the following equation:

$$y = (\text{No. seeds shattered} / (\text{No. seeds shattered} + \text{no. seeds retained})) \times 100 \quad [1]$$

Producer wheat fields

This study was also conducted in spring wheat. Experimental procedures followed that of Burton et al. (2017). The experiment was conducted from 2014 to 2016 in six producer fields (64 ha each) within a 100-km radius of Lacombe (52.4°N; 113.8°W) in the Black soil climatic zone and from 2014 to 2016 in eight producer fields within a 100-km radius of Lethbridge in the Dark Brown soil climatic zone. Respective meteorological data were provided by the on-site weather stations at Lacombe and Lethbridge Research Centres. Fields (considered replications) were chosen based on presence of target weed populations (principally wild oat, cleavers, wild mustard, and kochia). Near Lacombe, two fields were selected each year; near Lethbridge, three

fields were selected in each of 2014 and 2015 and two fields in 2016. All crops were seeded in early to mid-May of each year, using recommended cultivars and agronomic practices.

Three weeks before expected crop swathing stage, 12, 1-m² quadrats per field were flagged. Rectangular seed catch trays (15 by 60 cm) were placed in the middle of the quadrats as described previously. Remaining experimental procedures are the same as described above.

Over the winter period following seed collection, germination tests were conducted to determine the viability of the weed seeds collected from the Lethbridge small-plot trial and Lacombe producer field sites. Seeds collected from the seed catch trays each week were combined into a composite sample. Seeds retained on the plant at crop swathing and direct-harvest stages were tested separately. One hundred seeds per replicate were counted and placed in Petri dishes (25 seeds replicated four times). Dishes measured 100 mm diameter by 15 mm deep, and were lined with blue blotting paper (Anchor Paper Co., St. Paul, MN, USA). Six ml distilled water was added to each plate, and seeds were separated from each other on the plates to mitigate mold growth. Plates were covered and placed in the dark at 22 °C. Plates were checked daily, germinated seeds counted and removed, and plates were moistened when needed. Once germination ceased, a squash test was performed to determine viability. All ungerminated seeds were squeezed with forceps and classified as viable if the endosperm was white and firm. Seeds were considered non-viable if they appeared powdery, black, or brown when crushed (Sawma and Mohler 2002).

Statistical analyses

Analyses were conducted separately on the three datasets: Lethbridge small-plot experiment, Lethbridge producer field experiment (Dark Brown soil climatic zone), and Lacombe producer

field experiment (Black soil climatic zone). Except for wild oat, weed species composition varied by climatic zone. 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 analysis of variance, but back-transformed values are presented. Data were subjected to analysis of variance using PROC MIXED (SAS Institute 2013). Treatment (weed species) was considered a fixed effect, whereas year and replicate were considered random effects in the statistical model. The COVTEST option in PROC MIXED was used to determine if years could be combined; years were combined due to no significant ($\alpha = 0.05$) year main effect or year by treatment (weed) interaction. Using appropriate error terms, treatment means were compared using Fisher's protected least significant difference (LSD) test ($\alpha = 0.05$) (Yang 2010).

Regression analysis was conducted in DeltaGraph Version 6 to analyze cumulative seed shatter (% of total production; equation 1) as a function of GDD (base 5 °C). The GDD were calculated from weed emergence to crop harvest using the following equation:

$$GDD = \sum \left[\left(\frac{T_{max} + T_{min}}{2} \right) \right] - T_{base} \quad [2]$$

where T_{max} is the daily maximum air temperature, T_{min} is the daily minimum air temperature, and T_{base} is the base temperature (5 °C). Regression analyses were performed on treatment means averaged over replications. A logistic regression model (equation 3) was found to best fit the data for each species in both small-plot and producer field experiments (Pollard 1971):

$$y = a / (1 + be^{-cx}) \quad [3]$$

where y is cumulative seed shatter, x is GDD, a is the upper asymptote, b is a lower asymptote parameter and c is a slope parameter. 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 $\alpha = 0.05$ (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 lack-of-fit F test was used to compare response curves at $\alpha = 0.05$, as outlined by Seefeldt et al. (1995).

Results and Discussion

In the small-plot experiment at Lethbridge, seed shatter of wild oat at swathing and direct-harvest stages of wheat was greater than that of wild mustard, green foxtail, or kochia when averaged across years (Table 1). Wild oat shatter at the two harvest dates averaged 72 and 90%, respectively. In contrast, seed shatter of wild mustard was 17 and 65%, green foxtail 7 and 11%, and kochia nil and 0.3%, respectively. In addition, wild oat shattering began earlier than wild mustard or green foxtail (Figure 1). As indicated by R^2 and RMSE values, the relationship between seed shatter of all three species and GDD was described well by the logistic regression model.

Viability of shattered seeds was high for wild mustard and green foxtail (> 80%), lower for wild oat (68%), and least for kochia (only 27%) (Table 1). Any shattered kochia seed was not fully ripened. For retained seeds at either harvest stage, viability of wild mustard was greatest (> 85%), followed by wild oat and green foxtail (60-75%), then kochia (23-30%).

In the eight producer wheat fields near Lethbridge, seed shatter of wild oat, wild mustard, and kochia was similar to that measured in the small-plot experiment, although the level of wild mustard shattering at direct-harvest in the producer fields tended to be lower (40%; Table 2). This is the first report of seed shatter of four broadleaf weeds in western Canada – spiny annual

sow thistle, redroot pigweed, lambsquarters, and round-leaved mallow. No seed shatter was recorded for round-leaved mallow. Seed shatter of spiny annual sow thistle ranged from 59 to 92% at swathing and direct-harvest stages, respectively. At direct-harvest, order of decreasing shattering among species was as follows: wild oat and spiny annual sow thistle > wild mustard and redroot pigweed > lambsquarters > kochia and round-leaved mallow (Table 2). However, cumulative seed shatter as a function of GDD indicated that the response curve for wild oat differed from that of spiny annual sow thistle (Figure 2). The response curves for wild mustard and redroot pigweed were not statistically different ($P > 0.05$). Viability of shattered and retained seeds was not measured in this study.

In the six producer wheat fields near Lacombe, sufficient multi-year data were only available for two weed species – wild oat and cleavers. Similar to results in southern Alberta sites, wild oat seed shatter was extensive – 80 and 97% at swathing and direct-harvest stages, respectively (Table 3 and Figure 3). Cleavers shed less seed by these two dates – 23 and 55%, respectively. Viability of both shattered and retained seeds of both species was high, although that of shattered wild oat was < 80% (Table 3).

When results of recent weed seed shatter/retention studies in western Canada are summarized (Table 4), it is apparent that there is significant variation both within and among investigated weed species. For example, at wheat direct-harvest stage, wild oat seed shatter ranges from 28 to 96%, cleavers' shattering ranges from 5 to 55%, and wild mustard shattering ranges from 2 to 65%. For wild oat, required GDD for 50% seed shatter are lower at Lacombe (ca. 950; Figure 3) vs. Lethbridge (> 1400; Figures 1 and 2), indicating climatic adaptation over time. That is, wild oat growth and development have adapted over generations to the cooler, shorter growing season at Lacombe vs. Lethbridge. A myriad of interacting factors, whether genotypic, ecotypic,

agronomic, edaphic, or environmental, are likely responsible for such variation in seed shatter within or among weed species. However, some weeds, such as kochia, consistently shatter little by harvest time.

Potential to manage these or other weed species with HWSC practices is inversely related to level of seed shatter. If $\leq 20\%$ and $\geq 80\%$ seed shatter by direct-harvest time is considered low and high, respectively, then results of this study indicate that green foxtail, lambsquarters, kochia and round-leaved mallow are classified as low, wild oat and annual sow thistle as high, with the other investigated species classed as intermediate. Seed retention of most species was improved by swathing compared with direct-combining. Overall, results of this study and of previous studies indicate that HWSC practices have good potential for several weed species in western Canada – particularly green foxtail, lambsquarters, kochia and round-leaved mallow. Those species with fair to good potential for HWSC include cleavers, wild mustard, and redroot pigweed. These basic weed biology studies lay the necessary groundwork for on-farm evaluation of the Harrington Seed Destructor in swathed or direct-harvested spring wheat, canola, and field pea in western Canada beginning in 2017.

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Table 1. Shattering, as a percentage of total seeds produced, and viability of seeds of wild oat, green foxtail, wild mustard, and kochia in a small-plot experiment at Lethbridge, Alberta (data combined across years 2014–2016; SE in parentheses).

	Shattering (%)		Viability (%)		
	Swathing	Direct-harvest	Shattered	Retained	
				Swathing	Direct-harvest
Wild oat	72.3a (2.9)	89.7a (1.4)	67.8b (4.8)	73.8b (3.8)	68.7b (2.4)
Wild mustard	17.0b (6.6)	65.3b (5.0)	94.3a (1.0)	90.3a (2.5)	86.0a (2.6)
Green foxtail	7.0c (2.1)	10.7c (2.2)	84.4a (4.0)	61.2b (4.2)	60.9b (7.3)
Kochia	0d (0)	0.3d (0.1)	26.6c (11.2)	22.7c (7.3)	30.5c (6.1)

Note: Numbers followed by the same letters within a column are not significantly different according to the LSD test ($\alpha = 0.05$).

Table 2. Shattering, as a percentage of total seeds produced, of wild oat and various broadleaf weeds in eight producer spring wheat fields near Lethbridge, Alberta (data combined across years 2014–2016; SE in parentheses).

	Swathing	Direct-harvest
Wild oat	72.2a (3.7)	95.3a (4.1)
Spiny annual sow thistle	58.6b (7.2)	92.3a (5.3)
Wild mustard	24.3c (1.2)	40.4b (4.2)
Redroot pigweed	10.8d (1.1)	34.1b (5.2)
Lambsquarters	1.0e (0.1)	9.9c (1.1)
Kochia	0.1e (0.1)	0.2d (0.1)
Round-leaved mallow	0e (0)	0d (0)

Note: Numbers followed by the same letters within a column are not significantly different according to the LSD test ($\alpha = 0.05$). Number of fields where present: wild oat, 5; wild mustard, 3; kochia, 3; sow thistle, 3; lambsquarters, 4; redroot pigweed, 3; round-leaved mallow, 2.

Table 3. Shattering, as a percentage of total seeds produced, and viability of seeds of wild oat and cleavers in six producer spring wheat fields near Lacombe Alberta (data combined across years 2014–2016; SE in parentheses).

	Shattering (%)		Viability (%)			
	Swathing	Direct-harvest	Shattered	Retained		
				Swathing	Direct-harvest	
Wild oat	80.1a (9.9)	96.6a (1.4)	76.6 (9.2)	93.7 (2.0)	86.8 (5.9)	
Cleavers	23.0b (7.4)	55.0b (5.8)	97.1 (1.4)	93.8 (4.2)	97.6 (1.3)	

Note: Numbers followed by the same letters (or no letters) within a column are not significantly different according to the *t* test ($\alpha = 0.05$). Number of fields where present: wild oat, 6; cleavers, 5.

Table 4. Results of weed seed shatter/retention studies in western Canada (at time of swathing or direct-harvest (DH), expressed as a percentage of total seeds produced).^a

Weed species	Crop ^a	Shatter (%)		Retention (%)		Reference
		Swathing	DH	Swathing	DH	
Green foxtail	Field pea-sp	0.1	0.5	99.9	99.5	Burton et al. 2016
	Field pea-pf	6.0	8.5	94.0	91.5	Burton et al. 2017
	Wheat-sp	0.6	0.8	99.4	99.2	Burton et al. 2016
	Wheat-sp	7.0	10.7	93.0	89.3	Present study
	Wheat-pf	4.3	5.7	95.7	94.3	Burton et al. 2017
	Canola-pf	0.6	-	99.4	-	Burton et al. 2017
Wild oat	Field pea-sp	12.9	28.9	87.1	71.1	Burton et al. 2016
	Field pea-pf	19.5	21.6	80.5	78.4	Burton et al. 2017
	Wheat-sp	19.3	28.0	80.7	72.0	Burton et al. 2016
	Wheat-sp	44.0	67.0	56.0	33.0	Tidemmann et al. 2017
	Wheat-sp	72.3	89.7	27.7	10.3	Present study
	Wheat-pf	17.0	26.0	83.0	74.0	Burton et al. 2017
	Wheat-pf	76.2	96.0	23.8	4.0	Present study
	Fababean-sp	-	70.0	-	30.0	Tidemmann et al. 2017
	Canola-pf	3.7	-	96.3	-	Burton et al. 2017
Spiny annual sow thistle	Wheat-pf	58.6	92.3	41.4	7.7	Present study
Cleavers	Field pea-sp	1.9	3.5	98.1	96.5	Burton et al. 2016
	Field pea-pf	1.1	2.0	98.9	98.0	Burton et al. 2017
	Wheat-sp	3.7	5.2	96.3	94.8	Burton et al. 2016
	Wheat-sp	16.0	38.0	84.0	62.0	Tidemmann et al. 2017
	Wheat-pf	2.5	5.9	97.5	94.1	Burton et al. 2017
	Wheat-pf	23.0	55.0	77.0	45.0	Present study
	Fababean-sp	-	50.0	-	50.0	Tidemmann et al. 2017
Kochia	Canola-pf	0.3	-	99.7	-	Burton et al. 2017
	Wheat-sp	0	0.3	100	99.7	Present study
	Wheat-pf	<0.1	0.1	>99.9	99.9	Burton et al. 2017
	Wheat-pf	0.1	0.2	99.9	99.8	Present study
Lambsquarters	Wheat-pf	1.0	9.9	99.0	90.1	Present study
Redroot pigweed	Wheat-pf	10.8	34.1	89.2	65.9	Present study
Round-leaved mallow	Wheat-pf	0	0	100.0	100.0	Present study
Volunteer canola	Wheat-sp	0.8	1.8	99.2	98.2	Tidemmann et al. 2017
	Fababean-sp	-	5.7	-	94.3	Tidemmann et al. 2017
Wild buckwheat	Field pea-pf	0.3	2.4	99.7	97.6	Burton et al. 2017
	Wheat-pf	1.8	18.0	98.2	82.0	Burton et al. 2017
Wild mustard	Field pea-sp	0.2	0.4	99.8	99.6	Burton et al. 2016
	Field pea-pf	0.1	2.4	99.9	97.6	Burton et al. 2017
	Wheat-sp	1.7	1.8	98.3	98.2	Burton et al. 2016
	Wheat-sp	17.0	65.3	83.0	34.7	Present study
	Wheat-pf	0.3	10.6	99.7	89.4	Burton et al. 2017
	Wheat-pf	24.3	40.4	75.7	59.6	Present study
	Canola-pf	0.9	-	99.1	-	Burton et al. 2017

^a sp = small-plot trial; pf = producer field, '-' = not measured; wild buckwheat, *Polygonum convolvulus* L.

FIGURE CAPTIONS

Fig. 1. Cumulative seed shatter, as a percentage of total seeds produced ($\pm$ SE), of wild oat, wild mustard, and green foxtail as a function of growing degree-days in a small-plot experiment at Lethbridge, Alberta (data combined across years 2014-2016); see logistic equation 3 in text (**, significant at $\alpha = 0.01$; RMSE, root mean square error).

Fig. 2. Cumulative seed shatter, as a percentage of total seeds produced ($\pm$ SE), of wild oat and various broadleaf weeds as a function of growing degree-days in eight producer spring wheat fields near Lethbridge, Alberta (data combined across years 2014-2016); see logistic equation 3 in text (**, significant at $\alpha = 0.01$; RMSE, root mean square error).

Fig. 3. Cumulative seed shatter, as a percentage of total seeds produced ($\pm$ SE), of wild oat and cleavers as a function of growing degree-days in six producer spring wheat fields near Lacombe, Alberta (data combined across years 2014-2016); see logistic equation 3 in text (**, significant at $\alpha = 0.01$; RMSE, root mean square error).

Wild oat $Y = 96.8 / (1 + 4.15 \times 10^5 e^{-0.0090x})$
 $R^2 = 0.99^{**}$ RMSE = 0.2

Wild mustard $Y = 153.1 / (1 + 4.33 \times 10^6 e^{-0.0087x})$
 $R^2 = 0.98^{**}$ RMSE = 0.7

Green foxtail $Y = 19.7 / (1 + 8.99 \times 10^3 e^{-0.0054x})$
 $R^2 = 0.93^{**}$ RMSE = 1.4

Wild oat	$Y = 100.4 / (1 + 2.56 \times 10^5 e^{-0.0088x})$ $R^2 = 0.98^{**}$ RMSE = 1.1
Sow thistle	$Y = 116.7 / (1 + 2.01 \times 10^6 e^{-0.0094x})$ $R^2 = 0.98^{**}$ RMSE = 0.9
Wild mustard	$Y = 167.8 / (1 + 3.75 \times 10^3 e^{-0.0041x})$ $R^2 = 0.94^{**}$ RMSE = 1.4
Redroot pigweed	$Y = 156.2 / (1 + 6.30 \times 10^3 e^{-0.0042x})$ $R^2 = 0.94^{**}$ RMSE = 1.3
Lambsquarters	$Y = 54.5 / (1 + 3.09 \times 10^4 e^{-0.0049x})$ $R^2 = 0.87^{**}$ RMSE = 5.8