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Seed-shattering phenology at soybean harvest of economically important weeds in multiple regions of the United States. Part 2: Grass species

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Abstract

Seed shatter is an important weediness trait on which the efficacy of harvest weed seed control (HWSC) depends. The level of seed shatter in a species is likely influenced by agroecological and environmental factors. In 2016 and 2017, we assessed seed shatter of eight economically important grass weed species in soybean [*Glycine max* (L.) Merr.] from crop physiological maturity to 4 wk after maturity at multiple sites spread across 11 states in the southern, northern, and mid-Atlantic United States. From soybean maturity to 4 wk after maturity, cumulative percent seed shatter was lowest in the southern U.S. regions and increased moving north through the states. At soybean maturity, the percent of seed shatter ranged from 1% to 70%. That range had shifted to 5% to 100% (mean: 42%) by 25 d after soybean maturity. There were considerable differences in seed-shatter onset and rate of progression between sites and years in some species that could impact their susceptibility to HWSC. Our results suggest that many summer annual grass species are likely not ideal candidates for HWSC, although HWSC could substantially reduce their seed output during certain years.

Introduction

Grasses such as giant foxtail (*Setaria faberi* Herrm.), yellow foxtail [*Setaria pumila* (Poir.) Roem. & Schult.], and large crabgrass [*Digitaria sanguinalis* (L.) Scop.], each resistant to several herbicide sites of action (Heap 2019), are among the most common and problematic grass weeds in

Table 1. Information pertaining to soybean planting, physiological maturity, and harvest dates across the different study sites in 2016 and 2017.

		2016[b]			2017[b]		
Region[a]	State	Planting	Physiological maturity	Harvest	Planting	Physiological maturity	Harvest
SC	AR	May 15	September 2	October 3	June 8	October 10	November 17
SC	MS	May 5	August 30	October 5	April 25	August 28	October 4
SC	TN	May 5	October 6	October 15	NA	NA	NA
SC	TX	May 10	September 14	October 19	June 19	October 6	November 10
NC	IL	May 20	September 11	October 16	May 15	September 21	October 9
NC	MI	May 26	October 7	November 11	May 21	October 1	October 9
NC	MO	May 5	September 23	November 7	May 15	October 7	November 2
MA	DE	June 14	October 10	November 3	May 18	October 23	November 22
MA	MD	May 27	September 9	October 24	May 18	September 20	October 23
MA	NC	May 25	October 11	Did not harvest	May 10	October 6	Did not harvest
MA	VA	June 22	October 13	October 20	May 18	October 23	November 22

[a]Regions include South-Central (SC): Arkansas (AR), Mississippi (MS), Tennessee (TN), and Texas (TX); North-Central (NC): Illinois (IL), Michigan (MI), and Missouri (MO); and Mid-Atlantic (MA): Delaware (DE), Maryland (MD), North Carolina (NC), and Virginia (VA).
[b]NA, data unavailable.

soybean [*Glycine max* (L.) Merr.] crop production systems in the United States (Van Wychen 2015, 2016). Barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] and jungle rice [*Echinochloa colona* (L.) Link] are two other troublesome monocot weeds in the midsouthern United States that have evolved resistance to seven and three herbicide mechanisms of action, respectively (Heap 2019; Rouse et al. 2018; Schwartz-Lazaro et al. 2017). Because herbicide options to control these weeds are limited, new management practices are urgently needed as weeds throughout the United States continue to develop herbicide resistance (Heap 2019; Norsworthy et al. 2014; Walsh et al. 2018).

Harvest weed seed control (HWSC), a nonchemical weed control approach that targets the collection and destruction of weed seeds during grain harvest, has helped Australian growers manage herbicide-resistant weed populations (Walsh et al. 2013). Potential effectiveness of HWSC systems depends upon seed retention of the target weed species at crop maturity, enabling its collection and processing at crop harvest and the effectiveness of the specific HWSC tactics employed (Walsh et al. 2018). Plants of many annual weed species shatter seeds at crop maturity in the United States (Davis 2008; Norsworthy et al. 2014; Schwartz-Lazaro et al. 2017; Walsh et al. 2018). The efficacy of seed destruction necessary to reduce the soil seedbank using HWSC varies from 40% to 80% (Liebman and Davis 2009; Tidemann et al. 2016). Davis (2008) reported that *S. faberi* shattered 35% of seed in corn (*Zea mays* L.) and 45% of seed in soybean fields by harvest in east-central Illinois. Grass weeds such as jointed goatgrass (*Aegilops cylindrica* Host) and downy brome (*Bromus tectorum* L.) have been found to shatter a low proportion (<25%) of seed at crop maturity in eastern Colorado (Walsh et al. 2018). Preliminary field surveys of winter wheat (*Triticum aestivum* L.) fields near Pullman, WA, in 2013 found that 42% of Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot] seeds were shattered 15 cm (header height) above the soil surface at harvest (Walsh et al. 2018). However, lower seed retention (41% at harvest, and 32% at 1 mo later) of *E. crus-galli* in soybean was reported from Arkansas (Schwartz-Lazaro et al. 2017).

In studies conducted in Alberta and Saskatchewan, Canada, green foxtail [*Setaria viridis* (L.) P. Beauv.], a common weed in the northern Great Plains, had high seed retention rates (≥80%) making it a suitable candidate for HWSC (Beckie et al. 2017; Burton et al. 2016). However, the lower seed retention (20%) for *S. viridis* observed in Minnesota cornfields at harvest (Forcella et al. 1996) limits the benefit of using HWSC for *S. viridis* in the region. The amount of weed seed retention at crop harvest varies among weed species and is influenced by agronomic factors and environmental conditions (Shirtliffe et al. 2000; Taghizadeh et al. 2012). However, little research has been conducted to quantify the seed retention rates of various economically important monocot weeds in the United States, leaving the potential for HWSC systems to manage problematic grass weeds in U.S. cropping systems largely unknown. Here we present studies conducted to determine the seed retention of eight economically important grass weeds across the three major U.S. grain-producing regions.

Materials and Methods

Study Sites

We outlined a research protocol that included 11 states that were divided into three geographical regions: South-Central, Mid-Atlantic, and the North-Central regions. Field experiments were conducted in 2016 and 2017. Each state collected data both years, except for Tennessee, which only participated in 2016. Each location planted soybean using local standard practices described in local extension bulletins, including variety, seeding rate, row spacing, fertility, and other practices, and collected information on planting date, physiological maturity progression, and harvest date (Table 1).

Data Collection

Sampling protocols were the same as the broadleaf species data collection in Schwartz-Lazaro et al. (2021). Locally (within-state) problematic weeds were chosen for study for each state. Weeds that did not emerge from the soil seedbank were either seeded or transplanted into the crop. Transplanted weeds were of the same growth stage as those in the study field to mimic having germinated with the soybean crop. Weeds were transplanted in-row if the soil seedbank was not high enough to support a specific weed. A total of eight grass species were examined. Other than the individual weeds used in the studies, the soybean crop was kept weed-free throughout the growing season. Once the weeds began to flower, four seed-collection trays (F1721 Tray, T.O. Plastics, Clearwater, MN) were placed around the bottom of at least 10 randomly chosen plants to collect any seed shed from the plant. Trays were placed so that there was not a gap between the trays or the tray and the base of the plant. To help ensure trays captured shattered seed, if a plant spread over the outer edges of the trays during the course of the

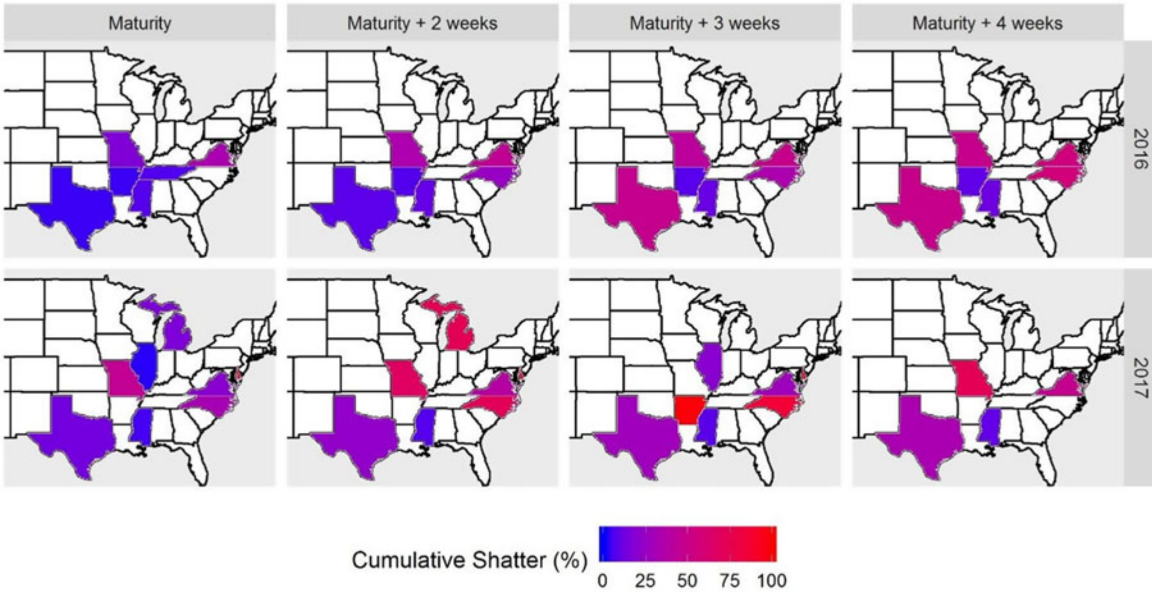

Figure 1. Heat map indicating the cumulative percent seed shatter across the participating states for a window starting from soybean physiological maturity to 4 wk past physiological maturity in 2016 and 2017. States were included in these maps only if they conducted sampling during the week indicated. (e.g., In 2017, Arkansas sampled on October 2, October 18, and November 3, none of which are within ±3 d of the October 10 maturity date or maturity +2 wk on October 24 in the state that year. Hence only data from maturity +3 wk are for Arkansas for 2017.)

study, it was trained using twine and stakes to keep the entire plant over the trays. The greenhouse trays were emptied weekly using a portable vacuum and placed into envelopes for counting (see Schwartz-Lazaro et al. 2021). At the conclusion of the experiment, the plants were harvested to obtain a final seed count and determine the percentage of seed retention.

Data Processing and Statistical Analysis

Our analysis of grass species was conducted using the same methods as our broadleaf analysis. For details, readers should refer to the statistical methods in "Part 1: Broadleaf Species" (Schwartz-Lazaro et al. 2021). The emphasis of the analysis was to quantitatively and qualitatively describe the phenology of seed shatter at the site, species, and individual plant level in relation to soybean maturity. We will very briefly summarize the analysis here. All analyses were based on calculations of percent cumulative seed shatter over time, either at the site, species, or individual plant level. Seed shatter was calculated as the number of seeds that had shattered at a particular time point divided by the total seasonal seed production, including unshattered seed that was retained.

We plotted spatial heat maps to visualize regional to continental patterns in the rates of combined grass weed seed shatter during the weeks following soybean maturity. These were created using calculations of total cumulative seed shatter of all grass species studied within each state during the week of soybean maturity and at 2, 3, and 4 wk following maturity. States were only plotted on the map if they sampled during a given time interval. For example, if a state sampled within ±3 d of maturity (a 7-d window centered on the maturity date), we plotted it on the "week of maturity" map. To visualize how the distribution of seed shatter progressed at the species level, looking across states, the cumulative seed-shatter percentage values were converted to categorical groups and binned by increments of 10% (i.e., 0%<= shatter <10%, 10%<= shatter <20%, etc.), and the number of site-years in each bin was tallied for each species. These were then plotted as heat maps showing the percent of site-years for each species in each bin for each time interval. Finally, we calculated mean per capita daily seed rain rates (i.e., seeds plant^{-1} d^{-1}) and mean per capita cumulative percent seed shatter for each species during the first 1 to 4 wk following maturity, accounting for site and year differences. The models used individual sample plants as the unit of replication with site, year, and their interaction as fixed effects. For analyses of seed rain rate, we used linear models with normally distributed errors. For analyses of percent seed shatter, we used generalized linear models with binomial errors for the proper fitting of proportion data. Because not all species were sampled in the same sites during both 2016 and 2017, the model structure had to be tailored to the data available for each species. The model structure and selection process are detailed in Schwartz-Lazaro et al. (2021). We ran these tests with different model structures depending on data availability, because some species were not sampled in multiple sites, and others were only sampled in a single year. Although some species were studied in multiple sites and for multiple years, most were not studied in the same set of sites for both years. Thus, we were only able to fit site by year interactions in *S. faberi* (Schwartz-Lazaro et al. 2021). For one species, goosegrass [*Eleusine indica* (L.) Gaertn.], sampling was ended before the second week postmaturity and was only assessed at week 1. For two others, broadleaf signalgrass [*Urochloa platyphylla* (Munro ex C. Wright) R.D. Webster], and Texas millet [*Urochloa texana* (Buckley) R. Webster], sampling began after soybean maturity in 2016. All others were sampled at soybean maturity and at both 1 and 2 wk after maturity. All data processing and analyses were conducted in R (R Core Team 2018).

Results and Discussion

As in our study of broadleaf weed phenology (Schwartz-Lazaro et al. 2021), cumulative percent seed shatter was lowest in the southern U.S. regions and increased moving north through the states (Figure 1). This trend remained from soybean physiological maturity through maturity plus 4 wk. This result is consistent with

Table 2. Predicted daily per capita seed rain rate (seeds plant^{-1} day^{-1}) and per capita cumulative seed shatter (%) with their standard error (SE) values.[a]

	Maturity + 1 wk								Maturity + 2 wk							
Species	Site-year	N[b]	Seed rain (SE)	Test[c]	P	% Seed shatter (SE)	Test[c]	P	Site-year	N[b]	Seed rain (SE)	Test[c]	P	% Seed shatter (SE)	Test[c]	P
Digitaria sanguinalis	2	39	417.8 (76.1)	$F_{1,37} = 417.8$	0.0442	46.1 (0.1)	$\chi^2_1 = 7.2$	0.0075	2	39	528.1 (90.3)	$F_{1,37} = 14.9$	0.0004	53.4 (0.1)	$\chi^2_1 = 1{,}151$	0.0001
Echinochloa crus-galli	4	64	30.9 (3.9)	$F_{3,60} = 30.9$	<0.0001	9.7 (0.1)	$\chi^2_3 = 11{,}155.6$	0.0001	4	64	30.5 (3.1)	$F_{3,60} = 30.9$	<0.0001	12.2 (0.1)	$\chi^2_3 = 15{,}468.7$	0.0001
Echinochloa colona	1	8	228.5 (56.4)	$t_7 = 228.5$	0.0049	8.3 (0.0)	NA	NA	1	8	316.9 (99.2)	$t_7 = 3.2$	0.0152	14.0 (0.1)	NA	NA
Eleusine indica	1	24	12.2 (1.9)	$t_{23} = 12.2$	<0.0001	7.7 (0.1)	NA	NA	0	0	NA	NA	NA	NA	NA	NA
Urochloa texana	2	16	75.4 (19.2)	$F_{1,14} = 75.4$	0.0547	32.1 (0.2)	$\chi^2_1 = 1{,}787.3$	0.0001	2	16	82.9 (19.1)	$F_{1,14} = 3.2$	0.0957	47.5 (0.2)	$\chi^2_1 = 8{,}558.7$	0.0001
Setaria faberi	7	105	55.8 (24.9)	$F_{5,99} = 55.8$	<0.0001	36.9 (0.3)	$\chi^2_5 = 297{,}863.4$	0.0001	6	101	102.4 (16.0)	$F_{4,96} = 7.1$	0.0001	61.5 (0.2)	$\chi^2_4 = 230{,}677$	0.0001
Sorghum halepense	2	13	1.7 (0.4)	$F_{1,11} = 1.7$	0.4521	2.1 (0.1)	$\chi^2_1 = 29.2$	0.0001	2	13	1.7 (0.3)	$F_{1,11} = 7.3$	0.0207	2.7 (0.1)	$\chi^2_1 = 129.3$	0.0001
Urochloa platyphylla	1	16	68.1 (10.3)	$t_{15} = 68.1$	<0.0001	50.0 (0.2)	$\chi^2_1 = 7.2$	0.0075	1	16	78.4 (10.3)	$t_{15} = 7.6$	<0.0001	76.8 (0.2)	NA	NA

	Maturity + 3 wk								Maturity + 4 wk							
Species	Site-year	N[b]	Seed rain (SE)	Test[c]	P	% Seed shatter (SE)	Test[c]	P	Site-year	N[b]	Seed rain (SE)	Test[c]	P	% Seed shatter (SE)	Test[c]	P
Digitaria sanguinalis	1	24	714.3 (97.0)	$t_{23} = 7.4$	<0.0001	58.6 (0.0)	NA	NA	2	39	357.6 (54.3)	$t_{37} = 16.7$	0.0002	60.6 (0.1)	$\chi^2_1 = 93.1$	<0.0001
Echinochloa crus-galli	4	64	31.4 (4.0)	$F_{3,60} = 21.2$	<0.0001	14.5 (0.1)	$\chi^2_3 = 22{,}402.7$	0.0001	4	64	30.9 (3.9)	$F_{3,60} = 21.4$	<0.0001	17.3 (0.1)	$\chi^2_3 = 26{,}600.6$	<0.0001
Echinochloa colona	1	8	1,980.5 (1,749.6)	$t_7 = 1.1$	0.2949	93.2 (0.0)	NA	NA	1	8	1,583.4 (1,374.5)	$t_7 = 1.2$	0.2871	94.7 (0.0)	NA	NA
Eleusine indica	0	0	NA	NA	NA	NA	NA	NA	0	0	NA	NA	NA	NA	NA	NA
Urochloa texana	2	15	89.7 (21.6)	$F_{1,13} = 2.5$	0.1346	62.7 (0.2)	$\chi^2_1 = 15{,}587.8$	0.0001	1	6	130.1 (49.3)	$F_{1,5} = 2.6$	0.0459	46.3 (0.2)	NA	NA
Setaria faberi	5	77	75.6 (9.2)	$F_{4,72} = 34.9$	<0.0001	49.4 (0.3)	$\chi^2_4 = 160{,}563.9$	0.0001	4	73	119.4 (11.4)	$F_{3,69} = 20.1$	<0.0001	51.4 (0.1)	$\chi^2_3 = 44{,}094.9$	<0.0001
Sorghum halepense	2	13	1.7 (0.3)	$F_{1,11} = 0.1$	0.7078	3.1 (0.1)	$\chi^2_1 = 102.7$	0.0001	2	13	1.9 (0.5)	$F_{1,11} = 0.0$	0.8964	3.7 (0.1)	$\chi^2_1 = 128.1$	<0.0001
Urochloa platyphylla	1	16	69.6 (8.7)	$t_{15} = 8.0$	<0.0001	87.4 (0.1)	NA	NA	0	0	NA	NA	NA	60.6 (0.1)	$\chi^2_1 = 93.1$	<0.0001

[a]Seed rain rates were calculated from soybean physiological maturity to 1, 2, 3, or 4 wk after maturity. Cumulative seed shatter was calculated from the beginning of seed shatter through 1, 2, 3, or 4 wk after soybean physiological maturity. Cumulative shatter values are predicted from fitted logistic regressions for each species after accounting for differences due to states and years. χ^2 values are from likelihood ratio tests comparing the fitted model with a null model. No test was performed for species with just a single site-year of data (indicated as "NA"), because we had already fit intercept-only null models to these.

[b]N is equivalent to the total number of plants for all sites and years.

[c]Model structures were dependent on the number of sites and years for each species. The model test used in seed rain rate analyses is determined by the model structure that was fit to each species: F-tests were used for seed rain rate models with state and/or year fixed effects; t-tests were used for intercept-only seed rain rate models; χ^2 tests were used for likelihood ratio tests of binomial generalized linear models of seed shatter (%). No likelihood ratio tests were conducted for species with only 1 site-year of data.

Table 3. Cumulative percent seed shatter of the pooled individual plants at each time interval, separated by species, state, and region.

Species	Region[a]	State	2016 Maturity	2016 Maturity + 2 wk	2016 Maturity + 3 wk	2016 Maturity + 4 wk	2017 Maturity	2017 Maturity + 2 wk	2017 Maturity + 3 wk	2017 Maturity + 4 wk
Digitaria sanguinalis	MA	VA	40.9	55.3	58.6	60.0	32.1	51.4	—	61.1
Echinochloa crus-galli	SC	AR	3.3	6.4	7.2	9.0	—	—	98.4	—
Echinochloa crus-galli	SC	MS	6.8	9.5	10.4	11.4	4.2	6.7	7.7	9.0
Echinochloa crus-galli	SC	TX	—	—	—	—	17.7	30.9	39.0	45.3
Echinochloa colona	SC	TX	5.0	14.0	93.2	94.7	—	—	—	—
Eleusine indica	SC	TN	6.2	—	—	—	—	—	—	—
Urochloa texana	MA	NC	—	20.0	28.8	53.1	29.6	65.7	83.1	—
Urochloa texana	SC	TX	—	—	—	—	19.6	31.6	38.7	46.3
Setaria faberi	NC	IL	—	—	—	—	1.6	—	19.3	—
Setaria faberi	NC	MI	—	—	—	—	16.0	72.8	—	—
Setaria faberi	NC	MO	16.5	33.9	42.2	48.2	45.4	67.4	—	71.9
Setaria faberi	MA	DE	—	—	—	—	86.1	88.7	89.0	—
Setaria faberi	MA	VA	23.6	34.0	39.0	50.2	6.7	26.8	27.6	34.4
Sorghum halepense	SC	TX	1.5	1.8	2.2	2.6	1.7	4.1	4.4	5.3
Urochloa platyphylla	MA	NC	—	29.0	38.7	60.2	32.8	76.8	87.4	—

[a]Regions include South-Central (SC): Arkansas (AR), Mississippi (MS), Tennessee (TN), and Texas (TX); North-Central (NC): Illinois (IL), Michigan (MI), and Missouri (MO); and the Mid-Atlantic (MA): Delaware (DE), Maryland (MD), North Carolina (NC), and Virginia (VA). A dashed line (—) indicates that there are no data for that time period.

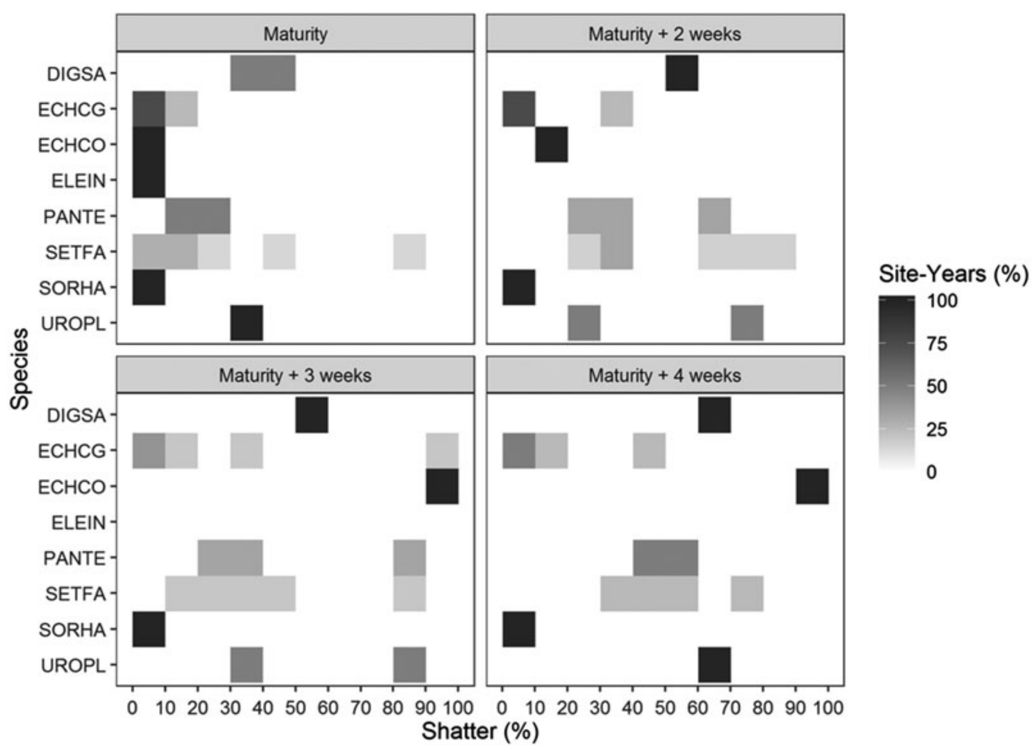

Figure 2. Cumulative percent shatter over four time periods (maturity, maturity + 2 wk, maturity + 3 wk, maturity + 4 wk) for each species. The darker the bar, the greater percent of sampled site-years that corresponded to the percent shatter value. This normalizes across species with different sampling efforts. Species sampled in just a single site-year are indicated by a single black square, which represents 100% of the sampling effort. Species are denoted by their EPPO codes

previous studies that showed low seed retention (<40%) for *S. faberi*, *E. crus-galli*, *A. fatua*, spiny annual sow thistle [*Sonchus asper* (L.) Hill], and *S. viridis* in North American regions (Beckie et al. 2017; Burton et al. 2016; Forcella et al. 1996; Schwartz-Lazaro et al. 2017; Shirtliffe et al. 2000; Tidemann et al. 2017). Further, the eight grass weed species' percent shatter continually increased from soybean physiological maturity to harvest maturity (Tables 2 and 3; Figure 2). While the annual grass weeds have low seed retention, Johnsongrass [*Sorghum halepense* (L.) Pers.], a perennial grass weed, had high seed retention of >96% in Texas (Tables 2 and 3), which is similar to results reported by Walsh et al. 2018. This finding potentially indicates that the life cycle of the weed influences seed retention of a species.

The two most frequently examined grass species in the present study were *E. crus-galli* and *S. faberi*. *Echinochloa crus-galli* was examined by most of the South-Central region states and *S. faberi* by the North-Central and Mid-Atlantic regions (Figure 3). As for the broadleaf weeds (Schwartz-Lazaro et al. 2021), one of the more

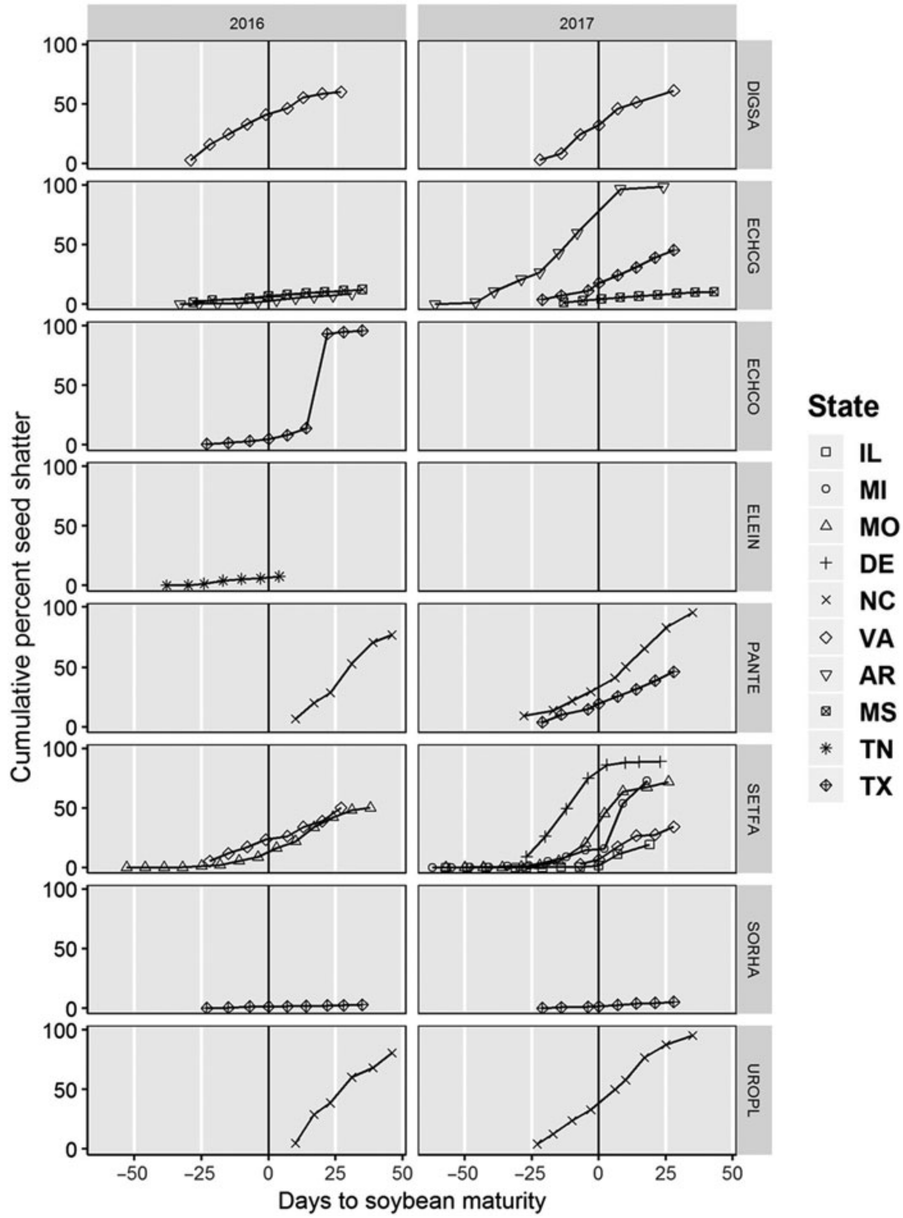

Figure 3. Cumulative percent seed shatter for all species from planting date to soybean physiological maturity (black vertical line) across the participating states in 2016 and 2017.

striking outcomes was the difference in variation across sites from year to year. In both species, there was little variation in seed-shatter progression between sites in 2016, while seed shatter was highly varied across sites in 2017. Both species were studied in more sites in 2017, but the pattern is noteworthy. Of the differences that were seen, more seed shatter occurred in 2017 overall than in 2016. The large range of percent seed shattered in these species could be due in part to annual differences in weather or regional differences. At soybean maturity the percent of seeds shattered ranged from 1% to 70% across species (Table 2). However, at 3 to 4 wk after soybean maturity, that range shifted to 5% to 100% (mean: 42%) seeds shattered. After accounting for site and year differences, *E. crus-galli* still retained over 80% of its seeds at 4 wk after soybean physiological maturity (Table 2) and considerably more during some sites and years (Table 3; Figure 3).

These results indicate that many summer annual grass species are likely not to be controlled consistently or adequately with HWSC, but *S. halepense*, a perennial, could be. While seed spread can be contained through HWSC, it will not manage rhizomes and other belowground perennial structures, so these must be managed by other means. Seed shatter in the annual grasses began before soybean maturity; thus, some additions to the soil seedbank had already been made by harvest. Soybean harvest can vary dramatically across regions, being earlier in the year in the southern United States and later (1 to 3 mo) in the northern United States. However, in some annual species (e.g., *E. crus-galli*), it may be possible to capture a significant amount (60% to 90%) of seed production with HWSC within 2 to 4 wk of soybean maturity during certain years, Variation within species across sites might indicate that the outcome will be variable between years and locations. While this would not result in eradication, it could lead to meaningful reductions in weed populations. Furthermore, header height, seed that is below the header, seed that is shattered at the header and not brought into the combine, and delayed harvest are all factors that could result in a limited amount of weed seed entering the combine to go through a HWSC tactic. More research is needed on what can be done to reduce inputs from grassy weeds to the soil seedbank as well as the amount of time that these weeds could begin to select for earlier shattering potential with the selection pressures of HWSC. Additionally, other economically important summer and cool-season annual grass weeds need to be evaluated for seed retention at harvest.

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