1-1-2021

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Abstract

Potential effectiveness of harvest weed seed control (HWSC) systems depends upon seed shatter of the target weed species at crop maturity, enabling its collection and processing at crop harvest. However, seed retention likely is influenced by agroecological and environmental factors. In 2016 and 2017, we assessed seed-shatter phenology in 13 economically important broadleaf weed species in soybean [*Glycine max* (L.) Merr.] from crop physiological maturity to 4 wk after physiological maturity at multiple sites spread across 14 states in the southern, northern, and mid-Atlantic United States. Greater proportions of seeds were retained by weeds in southern latitudes and shatter rate increased at northern latitudes. *Amaranthus* spp. seed shatter was low (0% to 2%), whereas shatter varied widely in common ragweed (*Ambrosia artemisiifolia* L.) (2% to 90%) over the weeks following soybean physiological maturity. Overall, the broadleaf species studied shattered less than 10% of their seeds by soybean harvest. Our results suggest that some of the broadleaf species with greater seed retention rates in the weeks following soybean physiological maturity may be good candidates for HWSC.

Research Article

Cite this article: Schwartz-Lazaro LM, Shergill LS, Evans JA, Bagavathiannan MV, Beam SC, Bish MD, Bond JA, Bradley KW, Curran WS, Davis AS, Everman WJ, Flessner ML, Haring SC, Jordan NR, Korres NE, Lindquist JL, Norsworthy JK, Sanders TL, Steckel LE, VanGessel MJ, Young B, Mirsky SB (2021) Seed-shattering phenology at soybean harvest of economically important weeds in multiple regions of the United States. Part 1: Broadleaf species. Weed Sci. **69**: 95–103. doi: 10.1017/wsc.2020.80

Received: 5 June 2020
Revised: 7 October 2020
Accepted: 26 October 2020
First published online: 4 November 2020

Associate Editor:
Prashant Jha, Iowa State University

Keywords:
Harvest weed seed control; herbicide-resistance management; integrated weed management; seed rain; seed shatter; soil seedbank; weed ecology and biology.

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Introduction

Farmers have relied on chemical weed control in row-crop production for decades, but the ongoing success of chemical tactics has been hindered by the evolution of resistance to a broad range of herbicide chemistries in many weed species (Heap 2019). The only certain way to break

this evolutionary process is to ensure that no individual weeds contribute seeds to future generations (Palumbi 2001). Weeds that escape management and do retain seeds at harvest are at a potential risk of evolving in ways that can impact how and when weed seeds enter into the soil seedbank, such as earlier shattering potential or more prostrate growth habit. Although herbicides remain the most cost-effective tools to manage weeds, new management practices are urgently needed as weeds continue to develop herbicide resistance (Heap 2019), and herbicide-resistance evolution has outpaced new herbicide commercialization for decades.

Weed seedbanks act as a primary source of annual weed infestations (Buhler et al. 1997; Gill and Holmes 1997). Therefore, reduction in seedbank replenishment is critical for effective weed management (Gallandt 2006; Haring and Flessner 2018; Schwartz-Lazaro and Copes 2019). Weeds that survive chemical and other control tactics or emerge after treatment are likely to disperse seed into the soil seedbank. Harvest weed seed control (HWSC) captures and processes the unshattered seed retained by weeds at harvest time to minimize the number of viable seeds dispersed to the soil. HWSC tactics were first developed and adopted in Australia and include practices such as narrow windrow burning, bale direct, chaff tramlining or lining, and seed impact mills, such as the vertical integrated Harrington Seed Destructor™ (vertical iHSD, de Bruin Engineering, Mount Gambier, SA, Australia), Seed Terminator™ (Seed Terminator, Tonsley, SA, Australia), or Redekop™ (Redekop Manufacturing, West Saskatoon, SK, Canada) system (Walsh et al. 2012, 2018; Walsh and Powles 2007). An additional HWSC tactic is the chaff cart, which was first developed in Canada and later refined and adopted in Australia. HWSC has the potential to prevent large proportions of viable seeds that remain on the weed plants at the time of harvest from entering the seedbank, substantially reducing the total seed rain of weeds, including herbicide-resistant weeds. Therefore, HWSC can negatively impact weed population dynamics by limiting seed addition and preventing the buildup of resistant subpopulations in the soil seedbank over time. Reducing viable weed seed additions to the soil seedbank by greater than 40% can reduce weed population growth and increase net returns to weed management (Liebman and Davis 2009). However, Tidemann et al. (2016) showed that 80% HWSC efficacy is required to reduce wild oat (*Avena fatua* L.) seedbank size.

Different HWSC systems aid in effectively managing 60% to 99% seed of various weed species in Australian production systems (Walsh et al. 2013), but the efficacy of these systems depends upon the proportion of weed seed retained on the weed plant at crop harvest, because only those seeds will be captured and thus removed or processed by the harvest machinery (Gill and Holmes 1997; Walsh et al. 2018). During crop harvest in the U.S. Corn Belt, seeds produced by many annual weed species remain undispersed on the mother plant and therefore have the potential to be harvested along with the grain crop (Davis 2008; Norsworthy et al. 2014).

Palmer amaranth (*Amaranthus palmeri* S. Watson), common waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], giant ragweed (*Ambrosia trifida* L.), common lambsquarters (*Chenopodium album* L.), and morningglory species (*Ipomoea* spp.) are the most problematic broadleaf weeds in corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] production systems in the United States (Van Wychen 2015, 2016). A large proportion (>50%) of seeds are retained in these weed species concurrent with the crop harvest window (Davis 2008; Goplen et al. 2016; Schwartz-Lazaro et al. 2016, 2017a). Goplen et al. (2016) observed that *A. trifida* retained on average 80% of total seeds produced by the time 75% of soybean were already harvested in Minnesota. High seed retention ranging from 95% to 100% in *A. palmeri* and *A. tuberculatus* at soybean maturity was reported in a survey across Arkansas, Tennessee, Illinois, Missouri, and Nebraska (Schwartz-Lazaro et al. 2016). Davis (2008) reported that ivyleaf morningglory (*Ipomoea hederacea* Jacq.) retained 75% and 85% of its seed in corn and soybean fields, respectively, in east-central Illinois. Studies examining weed seed retention at crop harvest in Australia and Canada have also reported a high proportion (>70 %) of seed retention at crop harvest in broadleaf weeds such as wild radish (*Raphanus raphanistrum* L.), common sowthistle (*Sonchus oleraceus* L.), flaxleaf fleabane [*Conyza bonariensis* (L.) Cronquist], African turnip weed (*Sisymbrium thellungii* O.E. Schulz), cleavers (*Galium* spp.), and wild mustard (*Sinapis arvensis* L.) (Burton et al. 2016; Walsh and Powles 2014; Widderick et al. 2014). Furthermore, Bitarafan and Andreasen (2020) showed that, on average, 260, 195, 411, and 316 seeds plant^{-1} were produced by black bindweed [*Fallopia convolvulus* (L.) Á. Löve], wild mustard (*Sinapis arvensis* L.), corn spurry (*Spergula arvensis* L.), and chickweed [*Stellaria media* (L.) Vill.], respectively, of which an average 44%, 67%, 45%, and 56% of the seeds were retained on the plants at spring oat (*Avena sativa* L.) harvest. However, the level of seed retention in a species is likely to be influenced by agroecological and environmental factors (Shirtliffe et al. 2000; Taghizadeh et al. 2012). Little research has been conducted to evaluate seed retention of various economically important weeds in major U.S. grain-producing regions that currently face multiple herbicide-resistant weed infestations. To address this, we conducted studies to determine the proportion of weed seeds shattered versus retained relative to the date of soybean physiological maturity of 13 economically important broadleaf weeds across the United States. These studies aid in determining the potential for successful use of HWSC in these three major U.S. grain-producing regions.

Materials and Methods

Study Sites

We outlined a common research protocol that included 14 states spread across the southern, northern, and mid-Atlantic United States. Field experiments were conducted in 2016 and 2017, except for Pennsylvania and Tennessee, which only participated in 2016. Each location planted soybeans 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

Within each location, at least three locally problematic broadleaf or grass weed species were chosen for study, and a total of 16 broadleaf species were investigated across locations. Grass species are presented separately in a sister paper (Schwartz-Lazaro et at. 2021). Shortly after soybean emergence, individual plants were marked with flags for study. At least 10 individuals of each species were selected at each location, but the number ranged from 10 to 25. 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 similar germination dates. The soybean was kept free of other weeds throughout the growing season by covering the target weeds with buckets and then applying a herbicide POST broadcast. Non-target

https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press

Table 1. Soybean planting, physiological maturity, and harvest dates for each region and state 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	MN	May 24	September 13	October 10	June 6	September 27	October 23
NC	MO	May 5	September 23	November 7	May 15	October 7	November 2
NC	NE	May 19	September 15	October 21	Mat 8	September 15	October 30
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	PA	May 26	October 14	November 9	NA	NA	NA
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), Minnesota (MN), Missouri (MO), and Nebraska (NE); and Mid-Atlantic (MA): Delaware (DE), Maryland (MD), North Carolina (NC), Pennsylvania (PA), and Virginia (VA).
[b]NA, unavailable data.

weeds that were not controlled by this application were removed by hand throughout the growing season. The target weeds used in the study were allowed to compete with the soybean crop until they began to flower. Once the target weeds began to flower, all soybean plants within 2 m were removed to ensure that any shattered seed would fall into the seed trays. Four seed-collection trays (F1721 Tray, T.O. Plastics, Clearwater, MN) measuring 0.2 m^2 each were placed around the bottom of each target plant to collect any seed shed from the plant. If a plant spread over the outer edges of the trays during the course of the study, it was trained using twine and stakes to keep the entire plant over the trays to ensure trays captured shattered seed. No apparent seed predation was observed, but it is noted that this likely occurred in some areas. The trays were lined with mesh fabric using all-purpose silicone caulk so that rainwater could pass through the trays, but the seeds would be contained within the seed-collection trays. The seed-collection trays were emptied weekly using a portable vacuum, and collected seeds were placed into paper envelopes for counting. The experiments were concluded when the soybean crop reached a harvestable maturity, defined by grain moisture ranging from 13% to 15%. Target weed plants were harvested to obtain a final seed count and determine the percentage of seed retention.

Data Processing and Statistical Analysis

HWSC efficacy for a given species is dependent on the fraction of its total seed production that can be captured by the combine. The amount of seed captured is a function of the timing of crop harvest relative to crop and weed maturity, as well as weed management tactics. We anchored our analysis to the physiological maturity date of soybean at each study site because of this, and because it is a time point that growers can identify easily and use to project potential future weed maturation based on the results of this study. We focused on metrics of cumulative seed-shatter progression over the weeks following crop physiological maturity.

We calculated cumulative seed shatter as the percentage of total seed production that had dropped by a given date:

$$S_{cum} = 100 \times \frac{\sum_{w=1}^{t} S_w}{\sum_{w=1}^{t\,max} S_w + S_{ret}} \quad [1]$$

where s_{cum} is the cumulative percent seed shatter, w is the sampling week, t is the week through which s_{cum} is calculated, s_w is the recorded seed shatter in a given sampling week, t_{max} is the end of the sampling season, and s_{ret} is the unshattered seed retained at t_{max}. We conducted three analyses based on this general calculation.

In the first analysis, we wanted to characterize broad spatial trends in seed-shatter progression of the overall weed community. Because each site chose locally dominant weeds for study, pooling the seeds at each site across species gives a generalized overview of seed-shatter phenology of common weeds at a large scale. To do this, we first calculated the cumulative percent seed shatter within each state for 2016 and 2017 by pooling the weekly seed production across species within 1 wk of soybean physiological maturity (maturity ±3 d, a 1-wk sampling window), and 2, 3, and 4 wk after soybean physiological maturity. We then plotted spatial heat maps of these values to visualize regional to continental patterns in the rates of combined broadleaf weed seed shatter during the weeks following soybean physiological 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.

Similar calculations allowed us to identify variation in seed rain timing within and among species in our second analysis. Cumulative seed shatter was calculated for graphical analysis of each species as the percentage of seed shattered at soybean physiological maturity, and 2, 3, and 4 wk after physiological maturity by pooling across individual sampled plants at each time point within each state in 2016 and 2017. This approach gave us one value per species, per state, and per year at each weekly time interval as data allowed. These species-specific shatter rates were reclassified as categorical values corresponding with 0%< = shatter <10%, 10%< = shatter <20%, and so forth. We then calculated the percent of site-years of data that fell into each categorical bin and plotted them as heat maps to visualize the frequency distribution of seed-shatter progression week by week for each species and to compare between species.

Finally, we estimated mean per capita daily seed rain rates (i.e., seeds $plant^{-1}$ day^{-1}) and mean per capita cumulative percent seed

https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press

shatter for each species during the first 1 to 4 wk following maturity, accounting for site and year differences. These metrics quantify the rate of HWSC opportunity loss for each species—an indicator of how soon growers should harvest the crop if they are hoping to control weed seeds with HWSC. To do this, we first calculated seed rain rate during the first week after physiological maturity for each sample plant as the cumulative number of seeds dropped per week after maturity minus the cumulative number of seeds dropped at physiological maturity (a week earlier) divided by the number of days elapsed between samples. We did the same for the second, third, and fourth weeks after physiological maturity by subtracting cumulative seed rain at maturity from cumulative seed rain 2, 3, or 4 wk after physiological maturity, respectively, on a per-sample basis and divided the number of days elapsed. For each species, we then fit a linear model with normally distributed errors using individual plants as the unit of replication to generate estimated marginal mean seed rain rates for each species that account for variation due to differences between sites or years. Estimates of cumulative percent seed shatter were generated by fitting generalized linear models with binomial errors (logistic regression models) to the cumulative seed-shatter data for each individual plant. Cumulative seed shatter for an individual plant at a given time point was calculated from the onset of seed shatter. These models used the same fixed-effects structures as the seed rain rate models for a given species. Estimated marginal mean values were calculated from the fitted models in the same way as the daily seed rain rate estimates. While the first two analyses quantified total seed rain pooled across individuals, these analyses included variation between individual plants, the implications of which will be explored elsewhere. Because not all species were sampled at the same sites during both 2016 and 2017, the model structures were tailored to the data available for each species. For example, species sampled in the same group of sites for both years had a balanced sampling design, so we could fit a model with site, year, and site by year interaction terms. Other species were sampled in multiple sites, but not all sites were sampled in both years. In this case, we fit an additive model with site and year effects. Still other species only allowed us to account for differences between sites or between years. These were evaluated with *F*-tests for seed rain rate models or χ^2 likelihood ratio tests for percent seed-shatter models. For species sampled only during a single site-year, we used an intercept-only fixed-effects structure evaluated with either a *t*-test or χ^2 test for seed rain rate or percent seed-shatter models, respectively. One species, *I. hederacea*, was not sampled the week of physiological maturity and could not be analyzed. All data processing and analyses were conducted in R (R Core Team 2018).

Results and Discussion

Amaranthus palmeri, *A. tuberculatus*, *A. trifida*, *C. album*, and *Ipomoea* spp. are the most common and problematic broadleaf weeds in soybean production systems in the United States (Van Wychen 2015, 2016). Within the different regions, the dominant species that co-occurred shifted with latitude. For example, *A. palmeri* in the South is a dominant weed that retains 95% to 100% of its seed at soybean physiological maturity (Schwartz et al. 2016). Furthermore, in this geographic area, target weeds examined retained a greater proportion of seeds from the beginning of crop physiological maturity window to 4 wk after physiological maturity compared with other areas (Figure 1). As we moved from the southern United States further north, the shatter rate increased. This result could be a function of temperature (a killing frost occurs sooner in the northern United States than in the South), weed species, and/or a cultural management strategy, such as planting date. A similar trend was seen in both 2016 and 2017.

Seed shatter progressed at different rates for different species, and some species had greater variation in shatter progression over space and time than others (Figures 2 and 3). Our ability to resolve this variation was limited for some species by the number of site-years sampled (Figure 2). Overall, the broadleaf species shattered less than 10% of their seeds by soybean harvest maturity at most of the sites. As time advanced, seed shatter increased for each species with the range of percent seed shatter increasing each week for all species, making timely harvest of the crop critical for success of HWSC (Table 2). *Amaranthus* spp. shattered a large number of seeds (17.5 to 945.7 seeds plant^{-1} day^{-1}), but retained 98% to 100% of their seeds, indicating that although a large number of seeds were added to the soil seedbank, the majority of the seeds remained on the plant. Several non-amaranths also had low seed shatter: jimsonweed (*Datura stramonium* L.) shattered only 3.5% of its seeds at 3 wk after crop maturity and 4.5% at 4 wk, while hemp sesbania [*Sesbania herbacea* (Mill.) McVaugh] still retained 100% of its seeds at 4 wk after maturity (Table 2). These results mirror those that showed that many weed species at physiological maturity retain a high proportion of weed seeds (Davis 2008; Goplen et al. 2016; Schwartz-Lazaro et al. 2016, 2017a). For example, Davis (2008) reported in east-central Illinois that *I. hederacea* retained 85% of its seed in soybean fields. In Minnesota, 80% seed retention was recorded for *A. trifida* at the time 75% of soybeans were already harvested in the region (Goplen et al. 2016), though we documented less than 40% retention in *A. trifida* at 4 wk (Table 2). High seed retention of >95% at soybean harvest maturity in *A. palmeri* and *A. tuberculatus* were observed in a survey conducted by Schwartz et al. (2016) across five states.

Further results show the variation in the progression of seed rain for each species as well as among species (Figure 3). The most important summary of the data set is contained in the recorded cumulative seed rain values for each species in each site during the weeks following soybean physiological maturity (Table 3). Further, the specific weeds studied were grouped geographically into one of the three regions with minimal overlap. One species that varied between states from 2016 to 2017 and ranged across all regions was *A. artemisiifolia*. *Ambrosia artemisiifolia* had a large range of percent seed shatter (2% to 90%) within a given year at 30 d past soybean maturity that appeared uncorrelated with state or region. It is unknown why there was such a large span of seed retention for the species. Overall, these results indicate that some of the broadleaf species with higher rates of seed retention in the weeks following soybean physiological maturity may be good candidates for HWSC.

Determining the amount of seed retention of a weed species at soybean physiological maturity through harvest is important to understand the potential inputs to the soil seedbank and to also determine which weeds would be appropriate candidates for

https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press

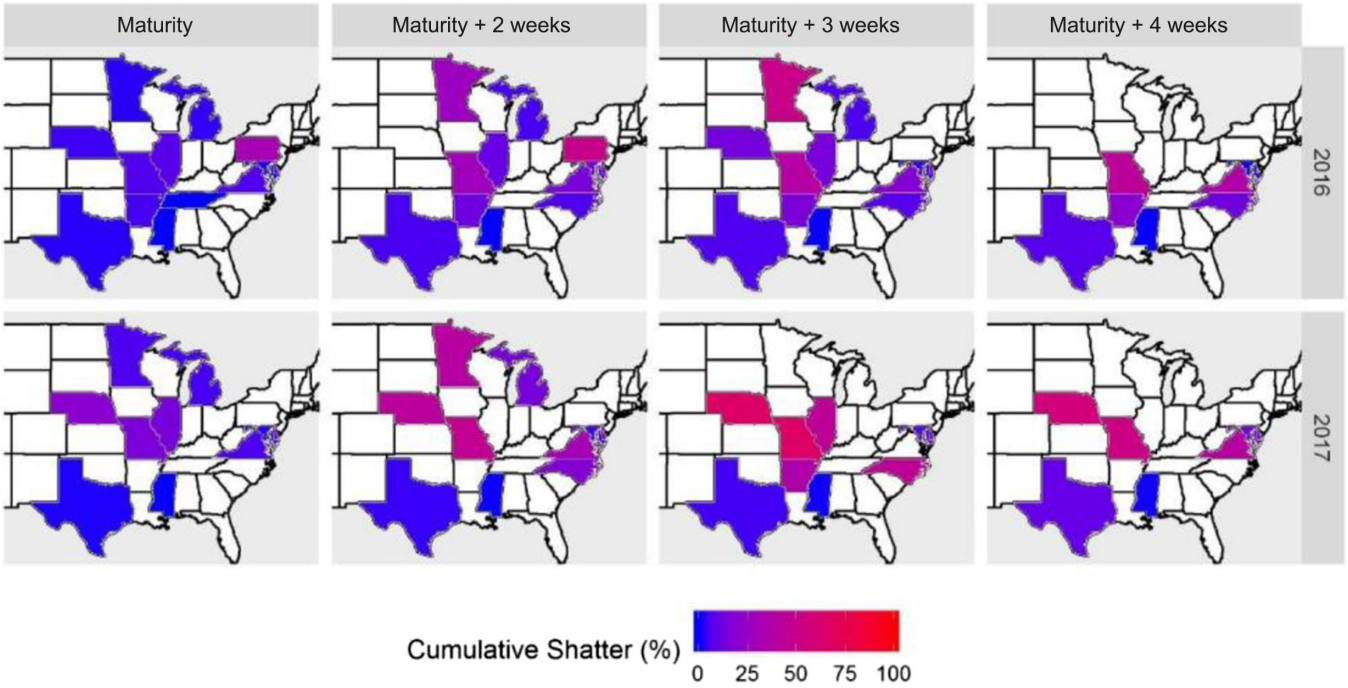

Figure 1. Heat map indicating the cumulative percent seed shatter across the participating states for a window starting from soybean physiological maturity to 4 wk past maturity in 2016 and 2017. States were included in these maps only if they conducted sampling during the week indicated (e.g., In 2017, 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.)

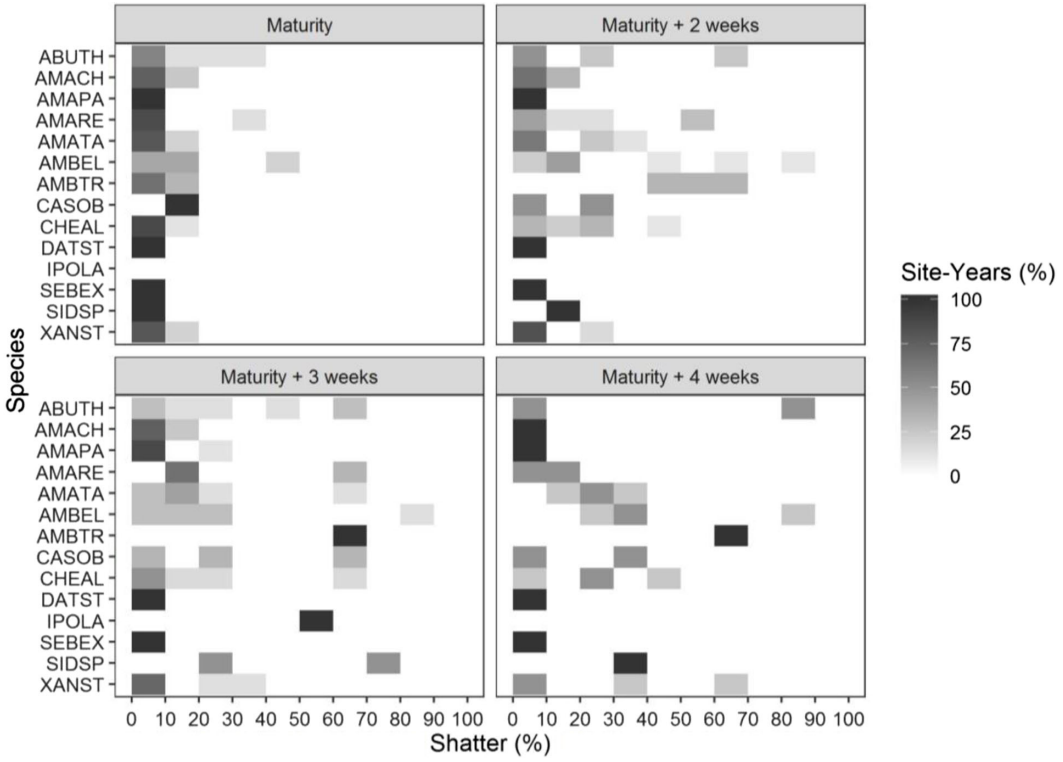

Figure 2. Cumulative percent shatter over four time periods (soybean physiological maturity, maturity + 2 wk, maturity + 3 wk, maturity + 4 wk) for each species. The darker the bar, the greater percent of sampled site-years that corresponded to the percent shatter value. This normalizes across species 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.

https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press

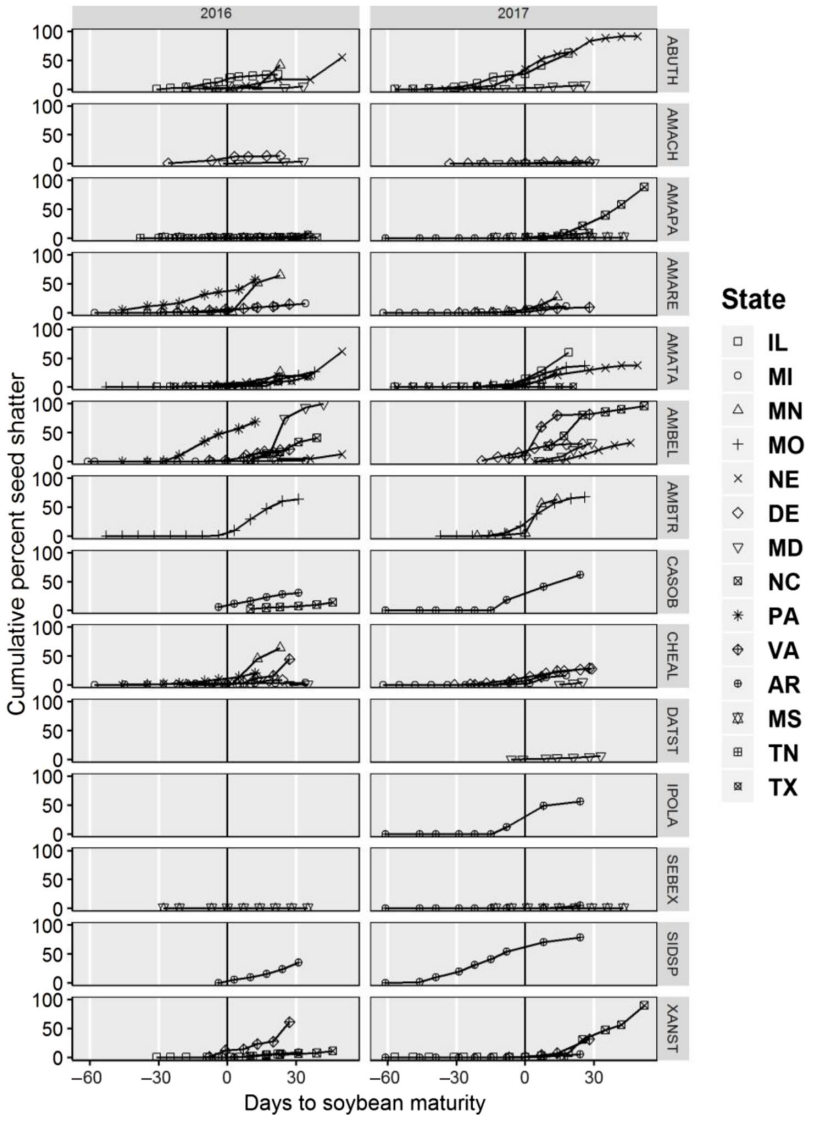

Figure 3. Cumulative percent seed shatter for all species from planting date to soybean physiological maturity (black vertical line) for each state in 2016 and 2017. Species are denoted by their EPPO codes.

HWSC. HWSC is a relatively new practice in the United States. While there has been research conducted on narrow windrow burning (Green 2019) and seed impact mills (both the Harrington Seed Destructor and the iHSD) (Schwartz-Lazaro et al. 2017b; Shergill et al. 2020), little research into other HWSC tactics or on large-scale use has been documented. Although this study examined a large geographic range of seed-shatter potential, it was also limited in several ways. These include: incomplete quantification of seeds lost to seed predation or seeds shattering outside the collection apparatus; unknown relevance of results to other broadleaf weeds, such as weeds with wind-dispersed seeds (e.g., Canadian horseweed [*Conyza canadensis* (L.) Cronquist]) that will likely escape HWSC; and weeds only growing in competition with soybean until weed inflorescenc. Additionally, how much seed reduction per species is necessary for HWSC to suppress weed populations to an economically meaningful level is unknown. Utilizing an additional integrated weed management tactic will only help preserve the effectiveness of ones that we currently have and use most often. Conversely, it is likely that HWSC use will be of most durable value when embedded within broader programs of integrated weed management, rather than used as a mainstay. In the latter scenario, HWSC may select strongly for early seed shed in weeds, and evolutionary changes in timing of seed shed are likely, given the well-established ability of weeds to rapidly evolve adaptive responses to weed management methods that become predominant selective forces in an agroecosystem (Clements et al. 2004).

Acknowledgments. We would like to thank the staff and students at each university for helping conduct this research, specifically Kreshnik Bejleri, Sheri Heard, John Sanders, Barbara Scott, Annie Klodd, Zach Schaefer, Russ Garetson, Vitor Damiao, Matheus Martins, Camille Werner, Bruno Flaibam, and Camila Grassmann, and each institute's research and experimental stations.

https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press

Table 2. Predicted per capita seed shatter (%) with standard error (SE) values at one to 4 wk after soybean physiological maturity.[a]

	Maturity + 1 wk								Maturity + 2 wk							
Species[b]	Site-year	*N*[c]	Seed rain (SE)	Test[d]	P	% Seed shatter (SE)	Test[d]	P	Site-Year	*N*[c]	Seed rain (SE)	Test[d]	P	% Seed shatter (SE)	Test[d]	P
Abutilon theophrasti	6	54	27.6 (3.6)	$F_{5,48} = 27.6$	0.0003	12.5 (0.1)	$\chi^2_5 = 47854.4$	<0.0001	4	65	17.7 (1.7)	$F_{3,61} = 28.5$	<0.0001	16.2 (0.1)	$\chi^2_3 = 40{,}917.9$	<0.0001
Amaranthus hybridus	4	96	159.9 (15.9)	$F_{3,92} = 159.9$	<0.0001	2.0 (0.0)	$\chi^2_3 = 666603.6$	<0.0001	3	72	64.1 (16.5)	$F_{2,69} = 27.1$	<0.0001	3.1 (0.0)	$\chi^2_2 = 637{,}211.5$	<0.0001
Amaranthus palmeri	6	95	6.9 (1.3)	$F_{4,90} = 6.9$	0.0006	0.6 (0.0)	$\chi^2_4 = 9046.0$	<0.0001	5	72	17.5 (3.9)	$F_{3,68} = 11.7$	<0.0001	1.3 (0.0)	$\chi^2_3 = 15{,}571$	<0.0001
Amaranthus retroflexus	5	96	151.7 (53.5)	$F_{4,91} = 151.7$	0.0025	14.7 (0.1)	$\chi^2_4 = 94017.6$	<0.0001	7	125	250.6 (45.9)	$F_{4,120} = 3.4$	0.0119	21.0 (0.1)	$\chi^2_4 = 38{,}4884.9$	<0.0001
Amaranthus tuberculatus	9	102	399.9 (291.6)	$F_{5,96} = 399.9$	<0.0001	7.5 (0.0)	$\chi^2_5 = 1070870.0$	<0.0001	8	122	945.7 (222.9)	$F_{5,11} = 13.8$	<0.0001	9.5 (0.0)	$\chi^2_5 = 15{,}52366.9$	<0.0001
Ambrosia artemisiifolia	4	82	73.4 (10.9)	$F_{3,78} = 73.4$	<0.0001	34.1 (0.1)	$\chi^2_3 = 53689.8$	<0.0001	4	62	96.9 (15.8)	$F_{3,58} = 15.1$	<0.0001	45.8 (0.6)	$\chi^2_3 = 75{,}755.5$	<0.0001
Ambrosia trifida	3	63	97.8 (24.2)	$F_{2,60} = 97.8$	0.2717	41.9 (0.2)	$\chi^2_2 = 6\ 216.8$	<0.0001	3	63	68.8 (13.2)	$F_{2,60} = 2.5$	0.0936	56.0 (0.2)	$\chi^2_2 = 2{,}043.2$	<0.0001
Senna obtusifolia	1	10	2.4 (0.3)	$t_9 = 2.4$	<0.0001	17.1 (0.7)	NA	NA	1	10	2.6 (0.2)	$t_9 = 13.0$	<0.0001	23.6 (0.8)	NA	NA
Chenopodium album	6	140	418.6 (46.9)	$F_{4,135} = 418.6$	<0.0001	10.4 (0.0)	$\chi^2_4 = 527{,}293.9$	<0.0001	8	169	482.5 (40.3)	$F_{5,16} = 26.0$	<0.0001	23.1 (0.0)	$\chi^2_5 = 453{,}485.1$	<0.0001
Datura stramonium	1	24	10.0 (1.7)	$t_{10} = 10.0$	<0.0001	1.7 (0.0)	NA	NA	1	24	11.0 (1.9)	$t_{23} = 5.9$	<0.0001	2.6 (0.0)	NA	NA
Sesbania herbacea	3	58	0 (0)	$F_{2,55} = 0.0$	<0.0001	0.0	NA	NA	3	58	0.0	$F_{2,55} = 0.0$	<0.0001	0.0	NA	NA
Sida spinosa	1	10	1.5 (0.3)	$t_9 = 1.5$	0.0003	10.0 (0.6)	NA	NA	1	10	1.8 (0.2)	$t_9 = 9.2$	<0.0001	15.9 (0.8)	NA	NA
Xanthium strumarium	5	65	3.9 (0.8)	$F_{3,61} = 3.9$	0.0001	6.1 (0.4)	$\chi^2_3 = 3{,}548.1$	<0.0001	4	61	4.4 (1.6)	$F_{3,57} = 5.8$	0.0016	12.8 (0.6)	$\chi^2_3 = 5{,}115.0$	<0.0001
	Maturity + 3 wk								Maturity + 4 wk							
Species[b]	Site-year	*N*[c]	Seed rain (SE)	Test[d]	P	% Seed shatter (SE)	Test[d]	P	Site-Year	*N*[c]	Seed rain (SE)	Test[d]	P	% Seed shatter (SE)	Test[d]	P
Abutilon theophrasti	7	73	27.6 (3.6)	$F_{4,68} = 4.2$	0.0044	30.3 (0.2)	$\chi^2_4 = 54{,}086.7$	<0.0001	2	36	24.3 (1.6)	$F_{1,34} = 1.0$	0.335	38.7 (0.3)	$\chi^2_1 = 54{,}147.1$	<0.0001
Amaranthus hybridus	4	96	159.9 (15.9)	$F_{3,92} = 5.0$	0.0028	3.5 (0.0)	$\chi^2_3 = 587{,}088.5$	<0.0001	2	48	142 (13.6)	$F_{1,46} = 6.4$	0.0146	2.2 (0.0)	$\chi^2_1 = 36{,}772.7$	<0.0001
Amaranthus palmeri	5	72	6.9 (1.3)	$F_{3,68} = 6.0$	0.0011	1.7 (0.0)	$\chi^2_3 = 31{,}192.8$	<0.0001	5	72	24.5 (8.1)	$F_{3,68} = 6.3$	0.0007	2.1 (0.0)	$\chi^2_3 = 41{,}753.7$	<0.0001
Amaranthus retroflexus	3	53	151.7 (53.5)	$F_{2,50} = 2.6$	0.0858	23.6 (0.1)	$\chi^2_2 = 279{,}064.1$	<0.0001	2	45	383.2 (34.5)	$F_{1,43} = 7.1$	0.0106	11.8 (0.0)	$\chi^2_1 = 40{,}059.8$	<0.0001
Amaranthus tuberculatus	7	69	399.9 (291.6)	$F_{5,63} = 1.0$	0.441	14.4 (0.0)	$\chi^2_5 = 481{,}463.4$	<0.0001	4	65	1,229.8 (237.8)	$F_{3,61} = 15.4$	<0.0001	23.5 (0.0)	$\chi^2_3 = 406{,}021.8$	<0.0001
Ambrosia artemisiifolia	2	28	73.4 (10.9)	$F_{1,26} = 8.9$	0.006	5.1 (0.2)	$\chi^2_1 = 3{,}819.2$	<0.0001	2	34	52.3 (8.4)	$F_{1,32} = 19.8$	0.0001	52.8 (0.2)	$\chi^2_1 = 33{,}617.1$	<0.0001
Ambrosia trifida	2	39	97.8 (24.2)	$F_{1,37} = 14.3$	0.0006	63.1 (0.2)	$\chi^2_1 = 246.7$	<0.0001	2	39	59.8 (4.2)	$F_{1,37} = 16.9$	0.0002	65.8 (0.2)	$\chi^2_1 = 155.4$	<0.0001
Senna obtusifolia	1	10	2.4 (0.3)	$t_9 = 16.1$	<0.0001	28.5 (0.8)	NA	NA	1	10	2.1 (0.1)	$t_9 = 15.7$	<0.0001	30.7 (0.8)	NA	NA
Chenopodium album	5	125	418.6 (46.9)	$F_{4,120} = 11.9$	<0.0001	26.4 (0.2)	$\chi^2_4 = 546{,}552.0$	<0.0001	3	66	708.8 (84.4)	$F_{2,63} = 3.7$	0.0304	36.2 (0.0)	$\chi^2_2 = 126{,}340.9$	<0.0001
Datura stramonium	1	24	10.0 (1.7)	$t_{23} = 7.4$	<0.0001	3.5 (0.0)	NA	NA	1	24	10.3 (1.4)	$t_{23} = 7.2$	<0.0001	4.5 (0.0)	NA	NA
Sesbania herbacea	3	58	0 (0)	$F_{2,55} = 0.0$	<0.0001	0.0	NA	NA	3	58	0.0	$F_{2,55} = 0$	<0.0001	0.0	NA	NA
Sida spinosa	1	10	2.1 (0.2)	$t_9 = 9.6$	<0.0001	24.2 (0.9)	NA	NA	1	10	2.5 (0.3)	$t_9 = 10.1$	<0.0001	35.6 (1.0)	NA	NA
Xanthium strumarium	4	41	4.2 (1.4)	$F_{3,37} = 10.7$	<0.0001	36.3 (1.7)	$\chi^2_3 = 1{,}339.8$	<0.0001	3	56	13.8 (5.5)	$F_{2,53} = 2.8$	0.0701	100.0 (2.3)	$\chi^2_2 = 8{,}295$	<0.0001

[a]Values are predicted across from fitted logistic regressions for each species after accounting for differences between states and years. IPOLA is not included, because it did not shatter any seeds in 2016 and was not sampled at maturity in 2017. SEBEX did not produce any seeds in 2016 in AR, and it retained 100% of its seeds during the sampling period in MS in 2016 or 2017. 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]XANST burs were counted, not the actual seed.

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

[d]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 site (i.e., 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.

			2016				2017			
Species	Region[a]	State	Maturity	Maturity + 2 wk	Maturity + 3 wk	Maturity + 4 wk	Maturity	Maturity + 2 wk	Maturity + 3 wk	Maturity + 4 wk
Abutilon theophrasti	NC	IL	19.7	24.9	25.6	—	27.2	—	62.5	—
Abutilon theophrasti	NC	MN	3.0	4.8	42.2	—	—	—	—	—
Abutilon theophrasti	NC	NE	1.7	—	16.7	—	34.6	61.4	65.5	83.3
Abutilon theophrasti	MA	MD	0.9	—	2.3	—	1.8	5.0	6.5	7.4
Amaranthus hybridus	MA	DE	12.2	13.6	14.1	—	1.4	2.7	2.9	3.1
Amaranthus hybridus	MA	MD	0.3	—	3.1	—	0.4	0.6	1.1	1.6
Amaranthus palmeri	MA	NC	—	0.3	0.3	0.6	—	8.1	21.2	—
Amaranthus palmeri	SC	AR	1.0	1.6	2.1	2.8	—	—	0.6	—
Amaranthus palmeri	SC	MS	0.2	0.3	0.4	0.4	0.4	0.6	0.7	0.8
Amaranthus palmeri	SC	TN	0.1	—	—	—	—	—	—	—
Amaranthus palmeri	SC	TX	0.8	1.6	2.6	3.2	1.7	5.0	6.8	9.5
Amaranthus retroflexus	NC	MI	3.6	9.5	11.3	—	6.2	11.6	—	—
Amaranthus retroflexus	NC	MN	1.8	52.0	64.9	—	5.6	27.2	—	—
Amaranthus retroflexus	MA	PA	35.9	57.0	—	—	—	—	—	—
Amaranthus retroflexus	MA	VA	6.0	9.3	11.1	14.9	1.6	7.6	—	9.3
Amaranthus rudis	NC	IL	1.2	2.5	11.7	—	14.3	—	60.2	—
Amaranthus rudis	NC	MN	0.1	3.6	26.2	—	6.3	26.5	—	—
Amaranthus rudis	NC	MO	2.4	8.0	15.3	20.7	14.0	34.6	—	37.1
Amaranthus rudis	NC	NE	5.5	—	19.2	—	3.9	21.3	—	29.6
Amaranthus rudis	SC	TX	2.1	8.2	9.2	11.3	0.0	0.6	1.0	—
Ambrosia artemisiifolia	NC	MI	1.0	1.3	1.4	—	—	—	—	—
Ambrosia artemisiifolia	NC	NE	—	—	5.0	—	—	—	—	—
Ambrosia artemisiifolia	MA	DE	—	17.4	20.1	—	15.0	—	—	—
Ambrosia artemisiifolia	MA	MD	—	11.1	—	—	—	9.0	20.3	32.7
Ambrosia artemisiifolia	MA	NC	—	13.7	16.5	33.7	—	44.6	80.8	—
Ambrosia artemisiifolia	MA	PA	47.9	69.1	—	—	—	—	—	—
Ambrosia artemisiifolia	MA	VA	2.3	14.2	16.7	21.3	10.7	80.4	—	82.2
Ambrosia trifida	NC	MN	—	—	—	—	5.3	63.8	—	—
Ambrosia trifida	NC	MO	9.7	47.9	60.8	64.0	17.0	57.7	65.5	67.6
Senna obtusifolia	MA	NC	—	5.0	6.2	7.8	—	—	—	—
Senna obtusifolia	SC	AR	11.7	23.6	28.5	30.7	—	—	62.1	—
Chenopodium album	NC	MI	2.9	3.4	3.4	—	3.1	16.3	—	—
Chenopodium album	NC	MN	1.6	45.4	64.5	—	—	—	—	—
Chenopodium album	MA	DE	1.1	8.0	9.1	—	14.9	24.1	26.9	28.3
Chenopodium album	MA	MD	—	—	—	0.5	—	0.7	2.9	—
Chenopodium album	MA	PA	9.9	20.4	—	—	—	—	—	—
Chenopodium album	MA	VA	2.8	12.5	15.7	44.8	7.6	24.2	—	29.1
Datura stramonium	MA	MD	—	—	—	—	0.3	2.6	3.5	4.5
Ipomoea lacunosa	SC	AR	—	—	—	—	—	—	56.1	—
Sesbania herbacea	SC	AR	—	—	—	—	—	—	5.5	—
Sesbania herbacea	SC	MS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sida spinosa	SC	AR	5.4	15.9	24.2	35.6	—	—	79.1	—
Xanthium strumarium	NC	IL	0.3	4.2	5.8	—	0.3	—	7.9	—
Xanthium strumarium	MA	NC	—	4.3	4.9	6.6	—	0.2	30.9	—
Xanthium strumarium	MA	VA	12.4	23.1	27.5	61.1	1.2	7.3	—	31.4
Xanthium strumarium	SC	AR	0.0	5.7	7.3	8.8	—	—	5.6	—

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

The authors would also like to thank the U.S. Department of Agriculture, Agricultural Research Service Areawide program for funding and the HATCH Program of the National Institute of Food and Agriculture and the U.S. Department of Agriculture for providing partial funding. No conflicts of interest have been declared.

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https://doi.org/10.1017/wsc.2020.80 Published online by Cambridge University Press