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Seed-shattering phenology at soybean harvest of economically important weeds in multiple regions of the United States. Part 3: Drivers of seed shatter

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Research Article

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Abstract

Seed retention, and ultimately seed shatter, are extremely important for the efficacy of harvest weed seed control (HWSC) and are likely influenced by various agroecological and environmental factors. Field studies investigated seed-shattering phenology of 22 weed species across three soybean [*Glycine max* (L.) Merr.]-producing regions in the United States. We further evaluated the potential drivers of seed shatter in terms of weather conditions, growing degree days, and plant biomass. Based on the results, weather conditions had no consistent impact on weed seed shatter. However, there was a positive correlation between individual weed plant biomass and delayed weed seed–shattering rates during harvest. This work demonstrates that HWSC can potentially reduce weed seedbank inputs of plants that have escaped early-season management practices and retained seed through harvest. However, smaller individuals of plants within the same population that shatter seed before harvest pose a risk of escaping early-season management and HWSC.

Introduction

Seed shattering from mature inflorescences is a key weediness trait that aids in seedbank replenishment and recruitment in subsequent seasons and favors species persistence (Maity et al. 2021). Seed shatter is primarily influenced by the phenological development of the plant (Marone et al. 1998); plant phenology is influenced by the environment (Taghizadeh et al.

2012). For example, the reproductive stage of plant growth can be triggered by the change in daylength (i.e., photoperiodism), temperature (i.e., vernalization), or age of the seedling. In addition to genetic factors, environmental conditions influence maternal plant phenology and can modify the timing of seed maturity, shatter, and dispersal (Maity et al. 2021; Taghizadeh et al. 2012). Various environmental (e.g., temperature, rainfall, growing season length) and agronomic (e.g., crop competition, weed population density) factors influence the inter- and intraspecific variation of seed shatter among weed species (Shirtliffe et al. 2000; Tidemann et al. 2017; Walsh and Powles 2014). Growing degree days (GDD), crop competition, and shattering habits of different species were shown to explain seed-shattering differences in wild oat (*Avena fatua* L.), false cleavers (*Galium spurium* L.), and volunteer canola (*Brassica napus* L.) (Tidemann et al. 2017). Accumulated heat units (i.e., GDD) were used by Shirtliffe et al. (2000) to predict the seed-shatter percentage of *A. fatua* before wheat harvest. Agronomic practices such as row spacing, cropping system, herbicide application timing (harvest aid or postharvest application), and harvest method (swathing vs. direct) have been shown to influence weed seed-shattering patterns (Beckie et al. 2017; Burton et al. 2016).

Many annual weed species retain a majority of seed before harvest, thus allowing the seeds to be collected by harvesting equipment that then spreads the seeds out of the rear of the combine, facilitating population dispersal and persistence and enabling weeds to persist in the seedbank (Forcella et al. 1996; Goplen et al. 2016; Schwartz et al. 2016; Schwartz-Lazaro et al. 2017, 2021a, 2021b; Soni et al. 2020; Walsh et al. 2013). The lack of weed seed shattering before harvest can be beneficial to newer integrated weed management (IWM) practices such as the use of harvest weed seed control (HWSC) tactics. HWSC can be achieved through a variety of techniques, such as chaff lining, chaff tramlining, chaff carts, direct baling, narrow-windrow burning, and seed impact mills, that intercept weed seeds contained within the harvested residue that would otherwise be spread by a combine harvester (Shergill et al. 2020; Walsh et al. 2018). HWSC targets the weed seeds retained by plants at the time of crop harvest, disrupting harvester-mediated seed dispersal and limiting additions to the soil seedbank. These methods have been shown to be widely successful in Australian cropping systems (Walsh et al. 2013, 2017, 2018), and more recently in U.S. cropping systems (Beam et al. 2019; Mirsky et al. 2019; Norsworthy et al. 2016, 2020; Schwartz-Lazaro et al. 2017; Shergill et al. 2020).

Plant growth simulation models incorporating phenological information can potentially be used in planning the timing of harvest and HWSC by predicting weed seed maturation date and total seed production (Weaver et al. 1993). Therefore, knowledge of the timing of seed shatter could potentially be used to plan the harvest timing of weed-affected crop fields. However, little research has been conducted to evaluate seed retention of various economically important weeds in three major U.S. grain-producing regions that currently face multiple herbicide resistant weed invasions: the north-central region, the south-central region, and the mid-Atlantic region. To help address this, studies were conducted to determine the seed-shattering phenology of 22 economically important weeds across these three regions (Schwartz-Lazaro et al. 2021a, 2021b). These studies aid in determining the potential for successful use of HWSC in grain production systems. In the current study, further investigation of the potential drivers of seed shatter in terms of weather conditions and plant biomass were evaluated.

Materials and Methods

A research protocol was outlined that included 14 states divided into three geographic areas: the north-central, mid-Atlantic, and south-central regions. Field experiments were conducted in 2016 and 2017. Each state collected data for both years, except for Pennsylvania and Tennessee, which only participated in 2016. Each location planted soybean [*Glycine max* (L.) Merr.] using local standard practices (see Schwartz-Lazaro et al. 2021a). In-season sampling protocols were the same for the broadleaf (Schwartz-Lazaro et al. 2021a) and grass (Schwartz-Lazaro et al. 2021b) weed data collection, in which the soybean crop was kept weed-free except for the desired weeds. At least three problematic grass or broadleaf weeds were chosen for each state. A total of 22 weed species were tested (Table 1). Once the weeds began to flower, four seed collection trays (F1721 Tray, T.O. Plastics, Clearwater, MN), measuring a total area of 0.2 m^2 each and 0.8 m^2 total with the four trays combined, were placed around the bottom of at least 10 randomly chosen individual plants per weed species to collect any seed shed from the plant. The trays, which were lined with weed-free fabric, were emptied weekly using a portable vacuum and placed into envelopes for counting. At the conclusion of the experiment, the plants were harvested to obtain a final seed count, determine the percentage of seed retention, and acquire final plant biomass. The actual frequency and duration of sampling varied by species and state. Additionally, environmental parameters such as hourly average wind speeds, minimum and maximum daily temperatures, hourly temperatures, and hourly precipitation were recorded beginning 2 wk before soybean planting through 2 wk past soybean harvest dates for each location either on-site or using nearby weather stations. The equipment used to collect this information was not standardized across locations.

Statistical Analysis

The analysis sought to identify covariates associated with weed seed–shatter phenology, focusing on individual plant biomass but also including environmental variables. Seed-shatter data processing is described in detail in Schwartz-Lazaro et al. (2021a, 2021b). The analysis of weed biomass used data from the sampling period centered 3 wk after soybean crop maturity, as this was the most likely time for cash crop harvest activity to begin. Biomass was normalized for each species during each year to range from 0 to 100 as 100*[biomass − min(biomass)]/max(biomass), where min and max biomass were the biomass of the smallest and largest plants of a species, respectively, during a given year. This allowed for model convergence and comparisons of slopes between species of different sizes. For each species, we applied a core pair of models using the proportion of total seed production shattered by 3 wk after crop maturity as the dependent variable and different fixed effects to be compared (either normalized plant biomass or an intercept only). The random effects structure was determined by the number of states and years in which the species was studied. In species with multiple years of data in multiple states, generalized linear mixed models were fit with binomial errors (i.e., mixed logistic regression) with random intercepts for each site by year combination. For species with replication across years but not states, random year effects only were fit. Likewise, for species with replication across states but not years, random state effects only were fit. Data for several species with a single site-year of data were fit to logistic regressions with no random effects. Models were then ranked with and without a fixed effect of relative biomass using the Akaike information criterion with bias correction

Table 1. Comprehensive list of the broadleaf and grass species evaluated by scientific name, common name, and EPPO code.

Scientific name	Common name	EPPO code
Abutilon theophrasti Medik.	Velvetleaf	ABUTH
Amaranthus hybridus L.	Smooth pigweed	AMACH
Amaranthus palmeri S. Watson	Palmer amaranth	AMAPA
Amaranthus retroflexus L.	Redroot pigweed	AMARE
Amaranthus tuberculatus (Moq.) Sauer	Common waterhemp	AMATA
Ambrosia artemisiifolia L.	Common ragweed	AMBEL
Ambrosia trifida L.	Giant ragweed	AMBTR
Senna obtusifolia (L.) Irwin & Barneby	Sicklepod	CASOB
Chenopodium album L.	Common lambsquarters	CHEAL
Datura stramonium L.	Jimsonweed	DATST
Digitaria sanguinalis (L.) Scop.	Large crabgrass	DIGSA
Echinochloa colona (L.) Link	Junglerice	ECHCG
Echinochloa crus-galli (L.) P. Beauv.	Barnyardgrass	ECHCO
Ipomoea lacunose L.	Pitted morningglory	IPOLA
Urochloa texana (Buckley) R. Webster	Texas millet	PANTE
Sesbania herbacea (Mill.) McVaugh	Hemp sesbania	SEBEX
Setaria faberi Herrm.	Giant foxtail	SETFA
Sida spinosa L.	Prickly sida	SIDSP
Sorghum halepense (L.) Pers.	Johnsongrass	SORHA
Urochloa platyphylla (Munro ex C. Wright) R.D. Webster	Broadleaf signalgrass	UROPL
Xanthium strumarium L.	Common cocklebur	XANST

Table 2. Results of modeling cumulative seed shatter as a function of weed biomass.[a]

Species[b]	Site-year	N[c]	Structure of best model	ΔAIC	Intercept	Intercept SE	Slope	Slope SE
ABUTH	7	76	Biomass + (1|State:Year)	529.22	−0.6816	0.5525	−1.3347	0.0581
AMACH	4	96	Biomass + (1|State:Year)	156,507.1	−2.3816	0.4013	−3.4199	0.0090
AMAPA	6	90	Biomass + (1|State:Year)	10,567.3	−4.0869	0.3695	−4.0571	0.0422
AMARE	3	53	Biomass + (1|State)	129,606.7	−0.3159	0.4390	−4.5669	0.0136
AMATA	7	68	Biomass + (1|State:Year)	7,674.8	−2.1447	0.6168	1.2202	0.0140
AMBEL	7	94	mass + (1|State:Year)	13,242.9	−0.6333	0.3798	−8.7523	0.0821
AMBTR	2	39	Biomass + (1|Year)	1,484.3	0.8878	0.2197	−1.2512	0.0326
CASOB	3	34	Biomass + (1|State:Year)	2,290.8	−0.5979	0.8869	−1.4643	0.0308
CHEAL	6	124	Biomass + (1|State:Year)	43,966.0	−1.5562	0.5762	−1.6947	0.0082
DATST	1	24	Biomass (no random effects)	2,506.0	−2.4681	0.0203	−3.3700	0.0794
DIGSA	1	24	Biomass (no random effects)	45,337.9	0.9359	0.0032	−1.0885	0.0052
ECHCG	5	50	Biomass + (1|State:Year)	83.6	−0.6821	1.1416	−0.4813	0.0513
ECHCO	1	8	Biomass (no random effects)	671.7	2.0617	0.0222	1.2323	0.0482
IPOLA	1	12	Biomass (no random effects)	780.8	0.9019	0.0311	−2.0216	0.0762
PANTE	2	9	intercept only	1.5	−0.4918	0.0069		
SEBEX	2	70	Biomass + (1|State:Year)	137.1	−17.4263	5.4807	−10.7463	0.9469
SETFA	5	77	Biomass + (1|State:Year)	8,975.4	−0.0051	0.5925	−0.9938	0.0106
SIDSP	2	22	Biomass + (1|Year)	1,685.1	0.5151	1.1635	−1.3933	0.0352
SORHA	2	13	Biomass + (1|Year)	417.4	−2.7234	0.1749	−2.3299	0.1228
UROPL	1	12	Biomass (no random effects)	10.2	−0.1658	0.0895	−0.5864	0.1618
XANST	6	62	Biomass + (1|State/Year)	233.4	−2.0961	0.3174	−1.3656	0.0889

[a]For each species, the proportion of total seed production that had shattered 3 wk after soybean maturity as a function of individual weed biomass was modeled and ranked against an alternative, intercept-only model. Random state and year effects were fit for species with data from multiple states and years. Akaike information criterion with bias correction (AICc) was used to select the fixed-effects model structure best supported by the data. Models were fit as generalized linear mixed models for species with random state or year effects or as generalized linear models for those with only fixed effects. Binomial errors were used in both cases. Parameter estimates of slope and intercept and their standard errors refer to the log odds of the marginal mean predicted values of the proportion of seed shattered for a given plant biomass.
[b]EPPO codes are used to denote species (see Table 1). XANST burs were counted, not the actual seeds.
[c]N is equivalent to the total number of plants for all sites and years.

(AICc) (Anderson 2008) to identify the predictors best supported by the data for each species.

The analysis of environmental drivers of shatter considered the correlations between weekly seed shatter (as a proportion of total season-long recorded shatter) and total precipitation (mm), cumulative growing degree days (GDD, base 10), and mean daily maximum wind speed during intervals between sample collections. For each state and year combination, a Pearson correlation was calculated for each species between percent shatter and each of the three environmental variables. These coefficients were examined individually on a site-year basis; additionally, calculations of the mean correlation coefficient for each species for each variable were made to assess the general strength of these relationships.

Results and Discussion

Final relative weed biomass was a negative predictor of cumulative seed shatter in all but three of the species studied (Table 1). While there was considerable variation in the strength of the relationships between states and years, the data overwhelmingly showed that larger individual weeds retained their seeds longer into the harvest season than smaller individuals in most species considered. Across

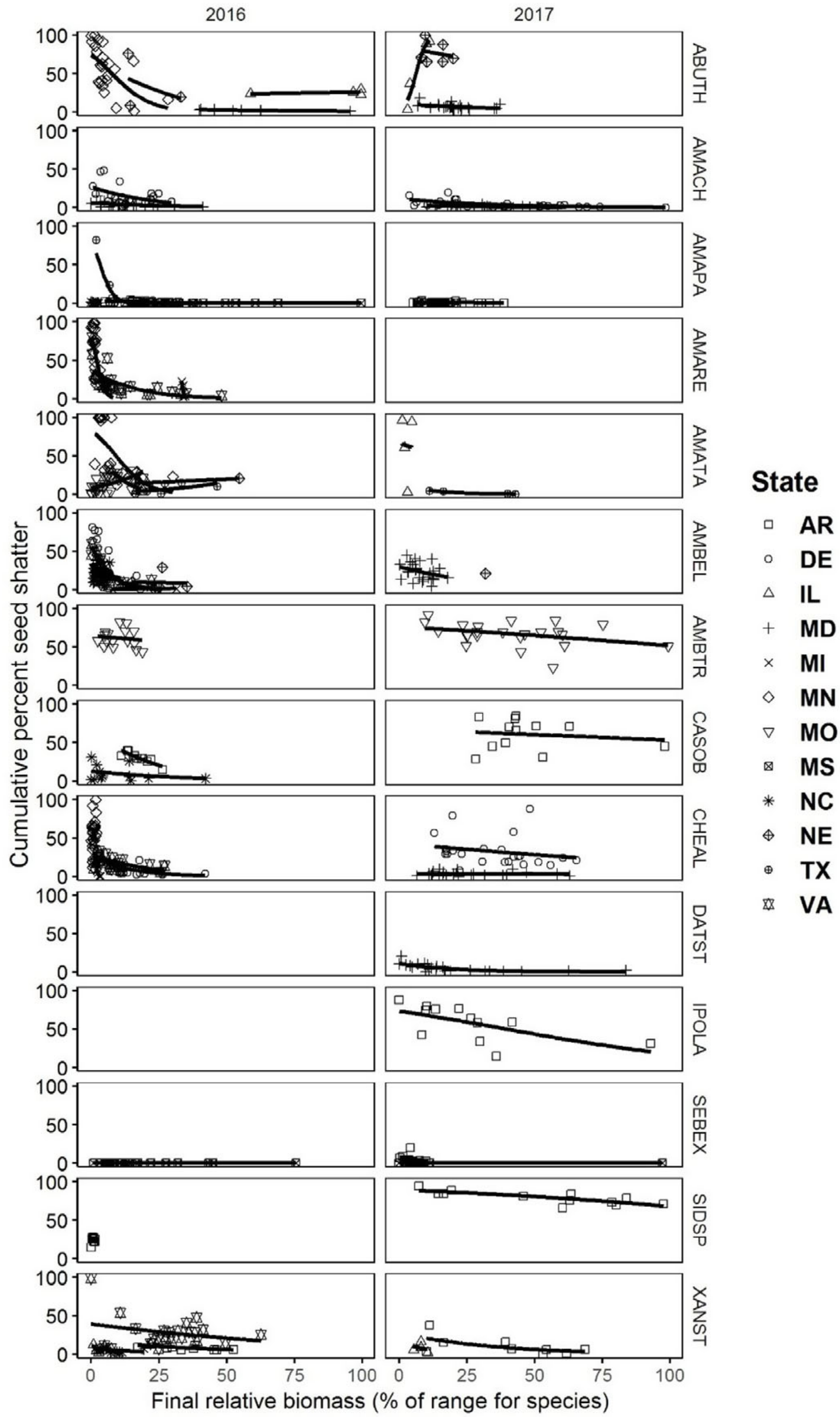

Figure 1. Cumulative percent seed shatter for all broadleaf species at 3 wk after soybean physiological maturity in relation to final relative biomass as a percent (%) of range for each state in 2016 and 2017. Species are denoted by their EPPO codes: ABUTH, *Abutilon theophrasti*; AMACH, *Amaranthus hybridus*; AMAPA, *Amaranthus palmeri*; AMARE, *Amaranthus retroflexus*; AMATA, *Amaranthus tuberculatus*; AMBEL, *Amaranthus tuberculatus*; AMBTR, *Ambrosia trifida*; CASOB, *Senna obtusifolia*; CHEAL, *Chenopodium album*; DATST, *Datura stramonium*; IPOLA, *Ipomoea lacunose*; SEBEX, *Sesbania herbacea*; SIDSP, *Sida spinosa*; XANST, *Xanthium strumarium*.

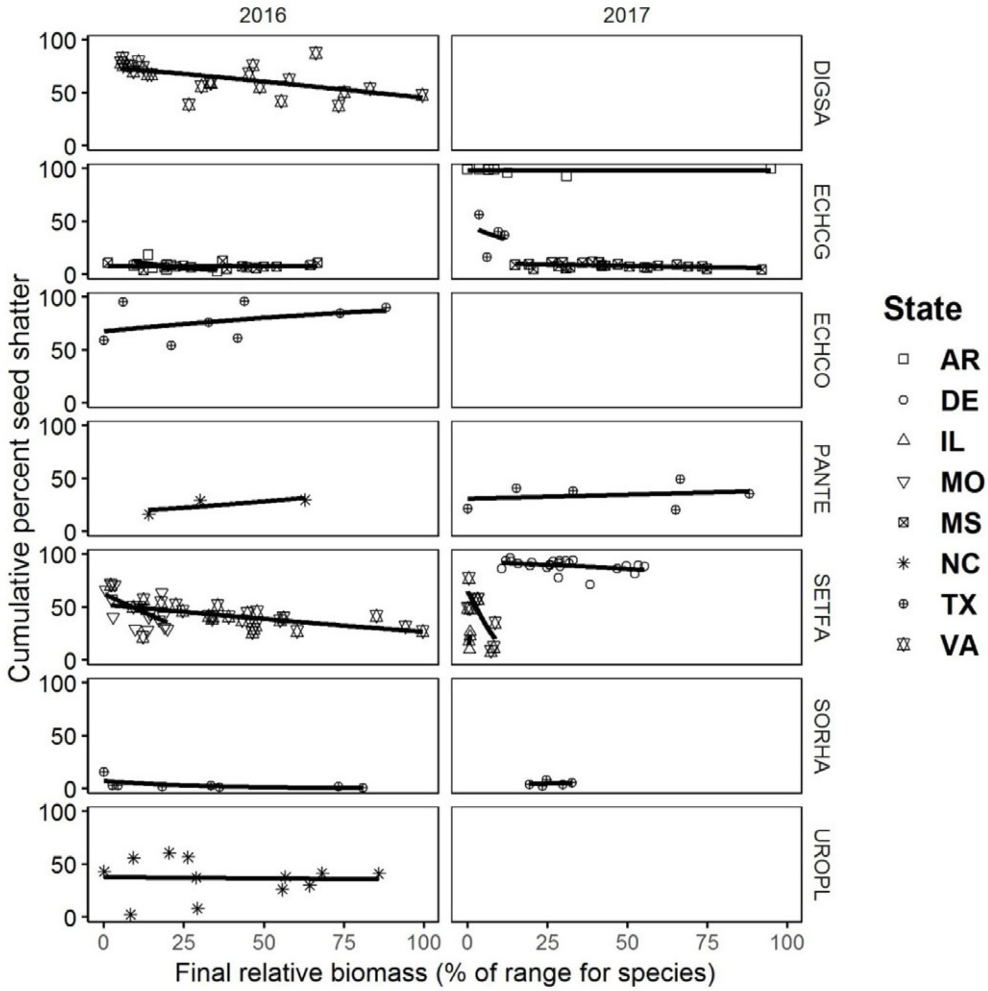

Figure 2. Cumulative percent seed shatter for all grass species 3 wk after soybean physiological maturity in relation to final relative biomass as a percent (%) of range for each state in 2016 and 2017. Species are denoted by EPPO codes: DIGSA, *Digitaria sanguinalis*; ECHCG, *Echinochloa colona*; ECHCO, barnyardgrass; PANTE, *Urochloa texana*; SEFTA, *Setaria faberi*; SORHA, *Sorghum halepense*; UROPL, *Urochloa platyphylla*.

multiple sites and years, broadleaf species like common ragweed (*Ambrosia artemisiifolia* L.) and common cocklebur (*Xanthium strumarium* L.) and grass species like giant foxtail (*Setaria faberi* Herrm.) showed consistently lower seed shatter as biomass of the plants increased. This was true of both broadleaf (Figure 1) and grass (Figure 2) species that had negative slopes and longer shatter time. In contrast the estimated slopes were positive for waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], junglerice [*Echinochloa colona* (L.) Link], and Texas millet [*Urochloa texana* (Buckley) R. Webster], indicating larger individuals shattered seeds earlier than smaller individuals (Table 2). This appears to be the case for *E. colona* (Supplementary Appendix 1m), but for *A. tuberculatus* (Supplementary Appendix 1e) this outcome may be an artifact of the method by which multiple states and years were combined in a mixed model for analysis. Examination of the data plotted as separate states and years shows that within many locations the relationship was, in fact, negative. *Urochloa texana* (Supplementary Appendix 1p) was the only species for which the model selection using AICc favored the intercept-only model, meaning that there was no relationship in the data between plant size and weed seed shatter.

The prolonged retention of seed by larger weed plants may be beneficial for HWSC strategies, as only retained seed can be collected and processed. However, smaller weeds, which could have emerged later in the season or may have been damaged and stunted from early-season control efforts, are more likely to shatter their seeds before harvest (Gage and Schwartz-Lazaro 2019). If these individuals are herbicide resistant, they may still contribute resistant seeds to the seedbank. It is unclear exactly which factors were the major drivers of weed size variation in our study. Weather conditions and other exogenous drivers can affect crop competition and weed growth as well, but we were unable to tease clear signals of these from the data. We suspect a combination of factors including individual plant variation, weather, and microclimate likely all contributed to variation in weed size within species.

Environmental drivers, such as seasonal temperatures, and weather events, such as wind, have been previously observed to have a large impact on the seed shattering of weed species (Forcella et al. 1996; Taghizadeh et al. 2012). The analysis of environmental drivers of seed shatter, however, revealed weak relationships at most (Table 3). Graphical analysis of time-series plots showing maximum wind speed, precipitation, and GDD (not shown) indicated weak and inconsistent relationships with seed shatter. In some species, there were occasional intervals of several weeks when one or more variables appeared correlated with seed

Table 3. Summary of average monthly planting to harvest (i.e., May [5] to November [11]) environmental conditions for maximum (wind max), mean daily maximum (wind max mean), and mean (wind mean) wind speed, maximum (T_{max}), minimum (T_{min}), and mean temperature (T_{mean}), cumulative precipitation, and growing degree days (GDD) for each state in 2016 and 2017.[a]

		Wind max		Wind max mean		Wind mean		T_{min}		T_{max}		T_{mean}		Cumulative precipitation		GDD[b]	
State	Month	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017
		m s^{-1}						C						mm			
AR	5	7.7		4.0		1.8		4.9	3.9	28.4	30.0	17.7	18.2	107.7	184.2	229.6	253.9
	6	4.6		2.9		1.2		13.8	11.7	34.8	31.7	25.2	22.8	45.0	46.2	455.0	382.8
	7	7.0		4.0		1.7		18.9	15.6	35.6	35.0	26.3	26.2	182.4	53.1	513.8	501.7
	8	5.5		3.4		1.4		12.9	14.4	35.1	33.9	25.1	23.3	74.8	188.7	477.9	411.9
	9	6.1		3.6		1.5		7.4	8.9	32.3	32.8	22.2	21.9	42.3	30.5	369.9	355.6
	10	7.0		4.0		2.0		4.0	−5.0	29.4	30.6	18.4	14.4	58.6	98.0	261.2	161.4
	11	9.6		3.8		1.8		−4.0	−3.3	27.6	26.7	11.7	11.1	18.9	41.9	94.8	70.8
DE	5					2.1	3.3	3.0	6.6	31.9	33.5	16.3	17.2	179.0	140.6	200.0	221.4
	6					2.2	3.1	10.3	8.8	34.1	34.5	22.3	23.2	103.0	52.8	368.5	391.7
	7					1.7	2.3	15.3	13.2	35.5	35.0	26.0	25.5	145.3	175.0	505.9	491.1
	8					1.6	2.1	14.0	13.0	35.2	32.6	25.3	23.0	74.4	134.5	479.8	408.8
	9					1.9	2.6	9.2	9.7	33.8	30.4	21.8	20.5	350.4	57.2	359.7	324.5
	10					2.4	2.6	−0.1	1.8	30.0	29.3	15.7	16.5	94.5	95.6	190.1	209.0
	11					2.9	2.9	−4.0	−5.4	28.2	25.3	9.4	8.9	9.0	57.9	40.7	41.4
IL	5	20.6	22.4	13.8	13.8	4.7	5.6	3.3	3.9	31.7	32.8	17.0	16.9	64.4	139.6	219.8	218.7
	6	16.5	20.1	10.5	12.7	3.8	4.6	10.0	8.3	34.4	36.1	23.5	23.1	131.9	39.8	405.2	393.9
	7	19.2	27.3	10.6	10.3	3.0	3.1	11.1	13.9	32.2	33.3	23.6	24.3	122.3	82.3	421.3	442.5
	8	18.3	12.5	9.2	8.5	2.8	2.8	12.2	10.6	32.2	32.8	24.0	21.4	101.4	30.1	433.2	352.7
	9	17.0	15.7	9.9	9.3	3.4	3.0	9.4	6.1	33.3	35.0	21.6	20.7	154.6	17.8	348.6	321.7
	10	19.2	21.5	11.3	11.8	4.5	4.7	0.6	−2.1	30.6	30.6	16.0	14.8	55.1	163.4	190.4	182.2
	11	20.1	19.7	11.1	11.8	4.7	5.2	−5.5	−7.1	27.2	21.7	8.5	6.1	72.4	61.5	42.5	14.8
MD	5	8.1	8.8	3.9	5.0	1.6	2.3	2.6	1.6	31.5	33.4	16.0	16.7	148.6	156.0	184.3	197.8
	6	10.2	7.3	5.3	4.9	2.1	2.2	7.4	8.2	34.7	34.9	22.5	23.2	109.7	27.7	365.1	376.1
	7	9.5	10.2	4.3	4.4	1.5	1.6	16.3	13.7	36.0	35.1	25.6	25.0	132.6	209.0	487.9	471.2
	8	8.3	6.5	3.6	3.5	1.4	1.3	14.1	11.9	36.1	32.3	25.3	22.3	120.4	169.9	475.6	382.9
	9	5.7	6.3	3.6	3.6	1.6	1.4	9.3	8.3	35.1	31.6	21.7	19.6	88.1	41.9	346.4	288.9
	10	9.1	9.7	4.5	4.2	1.8	1.7	−0.9	0.3	29.9	29.7	14.7	15.6	27.9	92.7	154.7	180.8
	11	11.8	11.1	5.1	4.6	2.0	1.9	−6.1	−5.8	25.6	24.8	8.2	7.5	38.1	54.9	26.7	25.8
MI	5							−1.7	−1.1	30.6	25.0	12.2	10.0	5.8	51.6	102.5	46.8
	6							6.1	3.3	32.2	32.2	17.4	17.1	24.8	30.4	222.7	213.5
	7							8.9	10.6	34.4	31.1	21.4	19.4	66.8	0.3	353.8	290.9
	8							10.6	8.3	33.9	31.7	21.4	19.3	16.8	5.1	354.6	288.8
	9							5.0	5.0	32.2	31.7	18.1	17.1	59.5	16.0	241.6	211.7
	10							−3.3	−1.1	26.7	26.7	10.5	12.2	64.5	104.9	74.2	105.4
	11							−6.7	−10.6	22.0	15.0	6.7	1.3	24.7	40.3	14.2	0.0
MN	5	9.2	8.3	5.1	5.0	2.7	2.7	−0.2	0.9	32.9	29.5	15.3	13.6	70.1	162.6	164.4	121.2
	6	9.5	8.9	5.6	4.9	3.0	2.5	10.0	6.2	34.6	33.9	20.6	20.3	85.7	90.9	317.8	299.8
	7	9.3	5.8	4.4	3.6	2.2	1.8	10.7	12.3	32.6	32.7	22.1	21.7	122.7	136.7	370.1	358.3
	8	5.6	6.6	3.3	3.2	1.6	1.6	10.3	10.1	30.2	28.2	20.9	17.9	187.0	121.8	337.3	251.4
	9	6.4	7.9	3.8	3.7	2.0	1.9	7.6	4.3	28.0	33.5	17.2	17.6	133.3	39.6	224.8	229.0
	10	9.1	8.0	4.7	4.9	2.5	2.7	−0.7	−4.0	24.3	24.2	10.6	9.4	100.3	100.4	67.1	59.3
	11	10.4	8.3	4.9	5.3	2.7	3.0	−6.4	−12.6	22.2	15.1	5.6	0.3	53.7	4.1	16.7	0.0
MO	5	16.5	18.5	8.7	10.5	10.0	3.0	4.4	3.9	30.6	29.3	16.9	17.4	80.8	113.8	208.7	231.3
	6	17.2	19.7	8.6	10.4			12.8	9.6	35.2	32.6	24.7	22.5	28.7	81.5	456.4	374.8
	7	15.9	16.5	8.5	7.4			14.9	13.4	34.7	36.2	24.9	25.0	274.0	116.3	447.5	466.1
	8	13.9	14.7	7.1	7.5			13.2	10.5	34.0	31.5	24.0	21.2	149.4	77.0	435.3	347.5
	9	12.2	10.4	7.5	7.3			8.6	7.0	33.5	32.5	21.4	20.6	142.5	19.8	352.6	318.0
	10	16.2	17.5	7.9	9.3			1.6	−5.2	31.7	29.6	16.3	14.2	24.9	97.8	185.2	169.8
	11		8.7		8.7				−0.8		22.4		9.8		0.0		68.3
MS	5						1.9	9.4	10.0	35.6	32.8	22.2	22.0	82.8	97.5	378.3	373.1
	6						1.8	18.3	13.9	36.7	34.4	27.7	25.2	128.5	135.6	531.1	456.4
	7						1.1	20.6	18.3	37.2	36.7	28.8	28.0	165.9	94.7	582.5	558.3
	8						1.2	21.1	17.8	37.2	36.1	28.0	26.6	139.2	259.6	558.1	516.1
	9						1.2	11.1	10.6	36.7	35.6	26.6	24.2	8.6	21.6	498.3	426.1
	10						1.7		−1.1		35.0		19.1		43.4		288.9
	11						1.9		−2.8		28.9		13.9		45.7		133.9
NC	5	10.1	12.4	6.0	7.5	2.0	2.6	6.9	6.4	32.4	32.9	19.8	20.7	93.5	125.2	303.4	330.9
	6	11.0	10.3	6.9	6.5	2.2	2.3	11.4	11.9	34.2	33.3	24.5	24.3	110.7	121.7	435.2	429.2
	7	15.2	10.1	6.5	6.1	1.9	2.2	19.9	14.5	35.7	37.0	27.4	27.1	490.5	150.9	539.4	528.4
	8	8.4	9.7	5.7	5.8	1.8	1.9	16.9	14.6	35.9	33.5	27.3	25.3	85.1	176.0	537.6	473.1
	9	11.6	8.5	6.1	6.0	2.1	2.1	14.7	11.5	35.3	33.3	24.1	22.3	246.4	75.7	422.5	369.0
	10	15.1	9.8	6.4	5.9	2.3	1.9	4.6	2.5	31.4	32.0	18.1	18.2	259.1	86.6	252.1	256.1
	11	9.9	11.2	5.4	5.5	1.6	1.7	−3.6	−3.1	29.0	27.6	11.3	10.4	19.8	29.0	74.9	59.6
NE	5					3.3	3.0	2.4	0.4	30.9	33.7	16.2	16.3	153.9	140.2	195.9	198.0
	6					2.7	3.0	9.4	8.3	36.8	36.1	24.3	23.0	91.4	75.2	428.4	391.4

(*Continued*)

Table 3. (*Continued*)

State	Month	Wind max		Wind max mean		Wind mean		T_{min}		T_{max}		T_{mean}		Cumulative precipitation		GDD[b]	
		2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017
	7					2.0	1.7	11.2	12.7	35.9	37.3	23.5	24.6	97.8	73.4	417.1	453.6
	8					1.9	1.7	8.6	9.3	35.2	29.9	22.0	20.3	130.3	104.9	373.1	320.8
	9					2.1	2.0	4.0	5.5	35.2	35.4	19.9	19.8	60.7	124.9	298.0	292.9
	10					2.3	2.9	−4.9	−7.4	28.2	28.5	13.2	12.0	38.6	114.3	116.0	108.9
	11					2.9	3.0	−6.6	−12.2	24.9	22.2	7.2	3.9	19.2	0.0	25.5	3.8
PA	5					3.1		0.5		30.8		13.6		87.1		120.2	
	6					2.7		4.9		30.3		19.5		79.0		275.7	
	7					2.7		9.9		35.1		22.4		85.1		385.7	
	8					1.8		10.7		31.9		22.9		111.3		386.0	
	9					1.9		4.2		31.7		18.5		132.1		264.2	
	10					1.6		−3.2		26.7		12.2		48.0		94.9	
	11					1.6		−4.0		22.0		6.4		70.9		11.4	
TN	8	0.9		0.6				16.1		35.0		26.6		29.0		515.8	
	9	1.8		0.8				7.8		35.0		24.3		55.6		428.1	
	10	0.6		0.5				10.6		28.3		18.2		0.0		255.5	
TX	5							11.7	10.6	31.7	34.0	23.1	23.6	304.5	115.3	406.7	421.1
	6	14.3		7.9				20.0	18.9	35.6	36.0	28.3	27.1	62.0	145.3	544.7	511.8
	7	15.6		8.9				23.3	22.0	37.2	40.0	30.5	30.3	6.1	20.1	631.7	628.8
	8	11.6		7.7	7.4			21.1	21.1	38.9	37.8	29.2	28.9	226.6	533.4	588.1	591.7
	9	12.5		6.9	5.9			12.8	16.1	36.1	33.9	27.9	26.5	48.5	24.9	531.4	502.5
	10	10.7		6.8	6.2			8.3	1.1	33.9	33.9	23.9	21.5	54.6	73.9	427.5	362.2
	11	13.0		7.8	6.1			1.1	2.8	30.6	30.6	18.7	18.5	69.3	16.8	255.8	256.7
VA	5	2.1		1.0	1.2	0.4	0.5	4.9	2.5	29.7	31.0	16.0	16.6	100.3	145.8	200.5	211.3
	6	1.8		0.9	0.9	0.3	0.3	5.9	6.7	31.9	30.5	20.8	20.0	88.1	37.8	333.7	303.8
	7	1.3		0.7	0.8	0.2	0.2	14.6	10.9	34.5	34.1	23.3	22.9	104.6	68.3	435.1	410.4
	8	1.0		0.7	2.9	0.2	1.1	11.8	10.5	33.2	31.2	22.8	20.8	97.5	50.5	426.5	346.8
	9	1.1		0.8	0.8	0.2	0.3	8.2	5.3	31.8	30.8	20.0	17.4	87.9	26.4	323.2	241.6
	10	1.8		0.9	0.8	0.3	0.3	−1.1	−0.6	29.7	30.4	13.8	13.3	41.1	136.9	155.0	160.2
	11	2.6		1.0	0.7	0.4	0.3	−8.9	−7.6	27.0	24.4	7.2	6.2	42.2	19.8	31.4	24.0

[a]Missing values are denoted by blank spaces and were not available from local weather stations.
[b]GDD values were scaled for 27 mo to reflect the entire month instead of being limited to the days of data collection.

shatter, but that relationship would then break down or would not appear in other states or subsequent years. Likewise, the calculated correlations showed that these relationships were variably positive or negative and most frequently not strong. The inconsistency of these relationships has led to the conclusion that, overall, weather events such as rain or windstorms are likely subordinate to the general seasonal progression of plant development in driving seed-shattering phenology. While environmental events certainly influence seed shatter, they did not appear to be major factors in the data considered here.

A strong correlation between seed shattering and GDD has historically been seen within specific cropping systems and locations, but not for an individual weed species within a region for a specific crop. For example, Bitarafan and Andreasen (2020) found that high and low precipitation were drivers of seed shatter, but the effect was species specific. Precipitation events are generally expected to increase seed shattering due to an increase in self-threshing on an individual plant. This same study also suggested that the differences in seed retention among 10 different species in Denmark were due to these species' responses to GDD and crop physiological maturity, which is impacted by environmental factors such as soil moisture. Further, wild mustard (*Sinapis arvensis* L.) retained no seeds at corn (*Zea mays* L.) harvest in a warm season but retained 33% of seeds in a cool season (Forcella et al. 1996). However, the present research examined individual weeds within soybean-producing regions and did not find GDD to be a strong predictor of weed seed shatter. Additionally, weeds with a larger biomass are likely to have some, if not all, inflorescences above header height, which may be exposed to wind events that could increase seed shatter (Burton et al. 2017; Shirtliffe et al. 2000; Tidemann et al. 2017; Zimdahl 2004). This hypothesis was also a weak and inconsistent predictor of weed seed shatter in this study.

For most species, the significant negative slope relationship, regardless of weed type, showed that plants with smaller relative biomass shattered more seeds than larger plants (Table 2). This was more apparent for the grass species, possibly because these species shatter their seeds earlier in the season than the broadleaf weeds (Schwartz-Lazaro et al. 2021b). Moreover, it has been reported that weed seed shatter varies across climatic conditions and agroecosystems, which was also apparent in this experiment (Taghizadeh et al. 2012).

These field studies investigated the potential for HWSC to be implemented across several major crop-producing regions in the US as an additional IWM tool (Schwartz-Lazaro et al. 2021a, 2021b). In general, annual broadleaf weeds are better suited to HWSC, based on the fact that these species retain their seeds for longer into the season in comparison to the annual grasses. Further investigation of the potential drivers of seed shatter in terms of weather conditions, GDD, and plant biomass is warranted. Based on these results, plant biomass was the strongest predictor of seed shatter in comparison to environmental factors. HWSC can potentially reduce weed seedbank inputs of plants that have escaped early-season IWM practices, likely due to being herbicide resistant. The added impact of HWSC practices can help to sustain existing IWM methods that are currently effective and prolong their use.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/wsc.2021.74

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