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Seed retention of grass weeds at wheat harvest in the Pacific Northwest

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Abstract

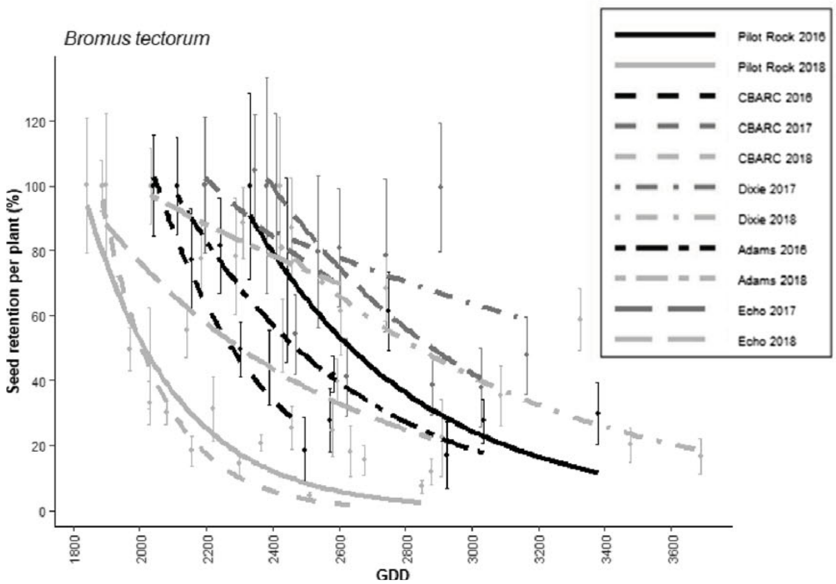
Harvest weed seed control (HWSC) may control problematic weeds by decreasing contributions to the weed seedbank. However, HWSC practices will not be effective if plants have shed a great part of their seeds before harvest or if a low proportion of seed production is retained at a height that enables collection during harvest. The seed-shattering pattern of several weed species was evaluated over three growing seasons to determine their potential to be controlled with HWSC in the Pacific Northwest (PNW). The studied weed species were downy brome (*Bromus tectorum* L.), feral rye (*Secale cereale* L.), Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot], and rattail fescue [*Vulpia myuros* (L.) C.C. Gmel.]. Seed retention at harvest, seed production, and plant height differed among species, locations, and years. Environmental conditions influenced seed-shattering patterns, particularly the time plants started to shatter seeds and the rate of the shattering. Agronomic factors such as herbicide use, interrow space, or crop height/vigor also seemed to affect shattering patterns and seed production, but more specific studies must be conducted to determine their individual effects. *Bromus tectorum*, *L. perenne* ssp. *multiflorum*, and *V. myuros* had an average seed retention at harvest of less than 50%. In addition, the low seed retention height of *V. myuros* makes this species a poor candidate for HWSC. *Secale cereale* had average seed retention at harvest greater than 50%, and seed retention height was greater than 30 cm. The variability of seed retention in different species will make the efficacy of HWSC practices species and environment dependent in PNW winter wheat (*Triticum aestivum* L.) cropping systems. Harvesting the wheat crop as early as possible will be crucial to the success of HWSC.

Introduction

Among other strategies, annual weed species guarantee their populations' persistence in crops with the replenishment of their seedbanks by shattering mature seed before crop harvest (Shirtliffe et al. 2000) or retaining seeds on the plant and creating the potential for weed seed dispersal by harvesters (Barroso et al. 2006). Weed infestations present at harvest are usually a consequence of an earlier ineffective weed control practice. The reliance on the same or similar herbicides as the only form of weed control in cropping systems has led to herbicide-resistance problems worldwide (Heap 2020; Norsworthy et al. 2012). In the Pacific Northwest (PNW), some prevalent weeds such as downy brome (*Bromus tectorum* L.) or Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot] have evolved resistance to different herbicide mechanisms of action (Barroso 2019; Heap 2020; Rodriguez et al. 2018). Other species, such as rattail fescue [*Vulpia myuros* (L.) C.C. Gmel.], present problems for chemical control, not due to herbicide resistance but to the lack of efficacious herbicides (Ball et al. 2007).

Harvest weed seed control (HWSC) is a way of preventing weed seedbank replenishment (Walsh et al. 2013, 2018b; Walsh and Powles 2014). HWSC practices include chaff collection with chaff carts, collection of chaff plus straw using bale-direct systems, processing the chaff with impact mills (e.g., the iHSD® Harrington Seed Destructor, the Seed Control Unit [REDEKOP™], or the Seed Terminator™), concentration of straw plus chaff in narrow windrows to burn (narrow-windrow burning), and concentration of chaff in narrow rows (chaff lining and chaff tramlining) (Lyon et al. 2016; Walsh and Newman 2007; Walsh et al. 2012, 2018b; Walsh and Powles 2007). Thus, most HWSC practices decrease weed seed return to the soil seedbank in the chaff or concentrate the weed seed in narrow rows, as opposed to chaff-spreading systems in traditional combines, which contribute to the spread and persistence of weed populations (Barroso et al. 2006; Blanco-Moreno et al. 2004).

The efficacy of different HWSC practices will largely depend on the percentage of weed seeds retained on the plant at harvest as well as the height of those seeds on the plant (Walsh and



Population (Location+Year)	Seed retention	Rate of reduction	Beginning of shattering
Pilot Rock 2016	27.9	0.173	9 June
CBARC 2016	20.0	0.309	16 June
Adams 2016	34.8	0.189	17 June
CBARC 2017	86.6	0.096	7 July
Echo 2017	59.0	0.143	30 June
Dixie 2017	81.0	0.052	11 July
Pilot Rock 2018	3.74	0.364	1 June
CBARC 2018	5.03	0.538	18 June
Adams 2018	78.1	0.059	27 June
Echo 2018	25.3	0.140	1 June
Dixie 2018	49.3	0.114	27 June
Average	42.8	0.198	

Figure 1. Seed retention per *Bromus tectorum* plant (%) in relation to accumulated growing degree days (GDD) in sampled locations. Dots with vertical lines (standard errors) indicate experimental data, and curves represent the fitted models. The table presents the parameter *c* (rate of reduction) of the fitted model per location, the parameter Y_o for the accumulated GDD by July 15 (seed retention), and the sampling date with the greatest seed number per plant, which was considered the beginning of shattering.

Powles 2014). If the percentage of seed retention is not great enough at harvest, HWSC might not be an effective weed management option for that species. The boundary condition, in which the percentage of seed retention is reasonable in terms of HWSC success, is difficult to determine. Walsh and Powles (2014) indicated the potential of HWSC with seed retention percentages >75% in wheat (*Triticum aestivum* L.) fields in Australia, whereas Beckie et al. (2018) considered >80% seed retention for potential HWSC practices in Canada. Although lower values of seed retention may impede control with these practices in the short term, HWSC may still be important to reduce inputs into the seedbank as part of an integrated weed management strategy. For instance, lower values of seed retention may be acceptable if weed infestations in fields are large, the weed species is highly competitive and reduces crop yield (e.g., *B. tectorum* in winter wheat; Daugovish et al. 1999; Rydrych 1974; Stahlman and Miller 1990), or the weed species releases allelopathic substances that can cause wheat growth inhibition (e.g., tumble mustard [*Sisymbrium altissimum* L.]; Tian et al. 2016). Seed retention is likely to be influenced by weed species biology, climate, and agronomic variables (Barroso et al. 2006; Shirtliffe et al. 2000), with the potential for significant variation across regions. In addition to the percentage of seed retention, the efficacy of HWSC will also depend on the height of seeds on the plant (Walsh et al. 2018b). Species with a significant proportion of their seeds under the crop cutting height will be more difficult to control with HWSC practices, especially when practical limitations (rocks, uneven ground, etc.) prevent lowering the cutting bar during harvest.

Although HWSC practices have successfully reduced reliance on herbicides in several crops in Australia (Walsh and Newman 2007; Walsh et al. 2012, 2018a), they have not been generally adopted in other parts of the world. In the inland PNW, where winter wheat is the predominant crop totaling 291,000 ha (USDA NASS 2018), only one HWSC system, the effect of narrow-windrow burning on *L. perenne* ssp. *multiflorum* control was investigated (Lyon et al. 2016). Studies of seed retention exist in other parts of the world for winter wheat (Soni et al. 2020; Widderick et al. 2014) or spring wheat (Beckie et al. 2018; Burton et al. 2016, 2017; Tidemann et al. 2017). However, due to the specifics of the wheat production system and the climate in the PNW, seed retention studies of main weeds in the region are necessary to determine the suitability of HWSC in this region.

The primary objective of this investigation was to study the seed shattering of important annual grass weed species in winter wheat fields of the PNW, including *B. tectorum*, feral rye (*Secale cereale* L.), *L. perenne* ssp. *multiflorum*, and *V. myuros*. The second objective was to relate the seed-shattering pattern per species to the most common harvest date in the region to evaluate the potential of HWSC in wheat production systems of the PNW.

Materials and Methods

Study Area and Collection of Weed Populations

Weed populations used in this experiment were naturally occurring in winter wheat crops located on five commercial farms in northeastern Oregon (Umatilla County) and southeastern Washington (Walla Walla and Whitman counties) (Figure 1) during 2016, 2017, and 2018. Farms were named according to locations: Pilot Rock (45.52°N, 118.76°W), Adams (45.76°N, 118.56°W), and Echo (45.72°N, 119.05°W) in Umatilla County; Dixie (46.13°N, 118.17°W) in Walla Walla County; and Albion (46.82°N, 117.19°W) in Whitman County. In addition to the on-farm experiments, we conducted supplemental plant collections at the Oregon State University Columbia Basin Agricultural Research Center (CBARC; 45.72°N, 118.63°W), located in Adams, OR (Umatilla County), and the Washington State University Cook Agronomy Farm (WSUCAF; 46.78°N, 117.10°W), located in Pullman, WA (Whitman County). Locations were not sampled all years because of crop rotations (only winter wheat fields were sampled), and studied species were not sampled in each location. Locations sampled by year, the species sampled by location, the herbicide treatments applied at the sampled fields for weed control, and some agronomic and environmental information for those

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Table 1. Wheat field characteristics (seeding date, harvest date, and herbicide application), climatic characteristics (accumulated growing degree days [GDD] by harvest [July 15 or August 1] and accumulated precipitation during growing season from seeding to harvest date), and weed species collected.

Farm[a]	Sampling year	Wheat seeding date	Wheat harvest date	Herbicide application	Accumulated GDD by harvest	Accumulated precipitation by harvest	Sampled species[b]
						—mm—	
Pilot Rock	2016	1 Oct 2015	10 Aug 2016	None	3,005	312	BRTE, SECE, VUMY
	2018	15 Oct 2017	23 Jul 2018	None	2,726	318	BRTE, SECE, VUMY
CBARC	2016	16 Oct 2015	14 Jul 2016	None	2,575	356	BRTE
	2017	12 Oct 2016	27 Jul 2017	None	2,373	437	BRTE
	2018	10 Oct 2017	24 Jul 2018	None	2,434	362	BRTE, VUMY
Albion	2017	1 Oct 2016	1 Aug 2017	Pyroxasulfone (PRE, 3 Oct 2016)	2,046	622	LOPEM
	2018	1 Oct 2017	1 Aug 2018	Pyroxasulfone + carfentrazone (PRE, 3 Oct 2017)	2,058	572	LOPEM
WSUCAF	2017	16 Oct 2016	14 Aug 2017	Clopyralid + fluroxypyr + pyroxsulam and thifesulfuron + tribenuron (POST, 26 Apr 2017)	2,046	564	LOPEM
	2018	10 Oct 2017	6 Aug 2018	Metribuzin + flufenacet (PRE, 16 Oct 2017)	2,058	567	LOPEM
Dixie	2017	10 Oct 2016	28 Aug 2017	Imazamox (POST, April 2017)	2,769	500	BRTE, SECE, VUMY, LOPEM
	2018	20 Oct 2017	20 Aug 2018	Pyroxasulfone (PRE, 20 Oct 2017) Mesosulfuron (POST, Apr 2018)	2,848	424	BRTE, SECE, LOPEM
Adams	2016	10 Oct 2015	3 Aug 2016	Pyroxsulam (POST, early Mar 2016)	2,661	356	BRTE
	2018	13 Oct 2017	2 Aug 2018	Pyroxasulfone + carfentrazone (PRE, 15 Oct 2017) Imazamox (POST, early Mar 2018)	2,405	352	BRTE
Echo	2017	6 Oct 2016	17 Jul 2017	Bromoxynil + pyrasulfotole and mesosulfuron (POST, 31 Mar 2017)	2,767	310	BRTE, SECE
	2018	6 Oct 2017	24 Jul 2018	Bromoxynil + pyrasulfotole and mesosulfuron (POST, 9 Apr 2018)	2,794	224	BRTE, SECE

[a]CBARC, Oregon State University Columbia Basin Agricultural Research Center; WSUCAF, Washington State University Cook Agronomy Farm.
[b]BRTE, *Bromus tectorum*; SECE, *Secale cereale*; VUMY, *Vulpia myuros*; LOPEM, *Lolium perenne* ssp. *multiflorum*.

sampled fields/locations are provided in Table 1. Temperature data for each site were obtained from the nearest available weather station (NOAA 2019). Daily minimum and maximum temperatures were used to calculate the accumulated growing degree days (GDD) throughout the growing season from crop seeding until harvest according to the following equation:

$$\mathrm{GDD} = \sum\left[\left(\frac{T_{\max} - T_{\min}}{2}\right)\right] - T_{\mathrm{base}} \qquad [1]$$

where $T_{\max}$ and $T_{\min}$ are the maximum and minimum daily temperatures, and T_{base} is the base temperature (0 C) below which plant growth is zero.

Plant sampling consisted of random collections of 10 plants per species in each location (sampled field) at each sampling date. Plant collection was conducted in winter wheat fields during the preharvest period approximately once per week until crop harvest in 2016, 2017, and 2018 (crop harvest dates are given in Table 1). Plant collection started before total maturation of crop and weed seed to determine the sampling date of maximum weed seed production per species before seed shattering. Once the sampling date with the maximum number of mature seeds per species was identified (referred as "initial date" hereafter), the previous sampling dates were dismissed, and 100% of seed retention was assigned to the initial date. The percentage of seed retention per plant for the remaining sampling dates was calculated in relation to the initial date. If results from two consecutive weeks around the initial date were very similar, data were reduced to regular plant sizes (stem number), ignoring very big or small plants (keeping a minimum of 6 data/plants per sampling date), to reduce variability and ensure correct selection. For all species, plant collection consisted of cutting (as close to the ground as possible) the aerial biomass (destructive sampling) of 10 plants per species at each sampling time and location. Each plant was bagged independently in a paper bag for later processing. The bagging process was conducted carefully to avoid losing seeds. In addition to plant collections, the maximum height and the distance from the lowermost portion of the inflorescence to the ground were measured on 10 random plants at the first and last sampling dates.

Sample Processing

A tailored protocol per weed species based on inflorescence type was followed to estimate the number of seeds per plant as precisely as possible at each collection time and to subsequently determine the shattering pattern.

Bromus Tectorum

Panicles per plant were counted and then threshed by hand, making friction with a swinging paddle (2.5 by 20 cm deck board wrapped with rubber) against a coarse mat. Seeds, including the affixed lemma and palea, were weighed. A subsample of the threshed mix was weighed and the seeds in it counted. Seeds per plant were estimated from seeds in each subsample.

Vulpia Myuros

The entire plant was weighed and threshed by hand, following the same technique as for *B. tectorum*. Before seeds were weighed, the affixed lemma and palea and stems were removed from the threshed mix. A subsample of the threshed mix was weighed and the seeds in it counted. Seeds per plant were estimated from seeds in each subsample.

Lolium Perenne Spp. Multiflorum

Spikes per plant were counted and weighed. One spike was selected randomly and weighed, and the seeds were counted to estimate seeds per plant.

Secale Cereale

Spikes (referred to as "heads" hereafter) were counted per plant, and the number of seeds in a randomly selected head were counted, with this count used to estimate seeds per plant.

Data Analysis

Linear and nonlinear models were fit per weed species, site (location), and year to study seed-shattering patterns of each weed species before wheat harvest. Locations were considered by year, because the sampling of each species was not conducted in all locations and years. The most appropriate model to describe the data per species was identified using the Akaike information criterion (AIC) (Symonds and Moussalli 2011). Seed-shattering patterns responded better to a negative exponential model (Equation 2). Only the seed-shattering pattern of *L. perenne* ssp. *multiflorum* (at one location and year) responded better to a linear model. However, for the aforementioned *L. perenne* case, the difference in the AIC between models was very low ($\Delta AIC = 0.7$), and therefore, exponential models were fit for all locations to perform comparisons.

$$Y = Y_o e^{-cX} \quad [2]$$

where Y is the percentage of seeds retained per plant, Y_o (intercept) is the predicted highest percentage of seeds retained per plant (in the initial date), X is the accumulated GDD, and c is the predicted rates of reduction of percentage of seeds retained per plant over time in the model.

Fitted models were used to determine the number of weed seeds retained per species at the beginning of harvest time for winter wheat crops in the PNW. Although the date when the fields were ready for harvesting (crop is at physiological maturity and grain has adequate low moisture) was not estimated in each particular field, July 15 was considered as the common date for the beginning of harvest as reported for Oregon and Washington (USDA-NASS 1997). However, August 1 was used as a more appropriate beginning of harvest for Whitman County farms (Albion and WSUCAF), where harvest is delayed due to its higher latitude and elevation.

To study whether significant differences existed in relation to the rate of seed shattering (parameter c in Equation 2) among fit models per species in relation to location and year, mixed model analyses were conducted. The location within year was included as a fixed effect, whereas the sampling date nested in the location and year was included as a random effect. To accomplish the comparison among locations and years, the negative exponential model (Equation 2) was used for all species. Analyses were implemented using the NLME package in the R program v. 3.3.2 (R Core Team 2016).

ANOVA was used to look for differences in the percentage of seed retention at harvest time among locations and years. Robust ANOVAs (Mair and Wilcox 2020) were used for all species but *V. myuros*, for which a ($\log + 1$) transformation allowed for the use of regular ANOVA (data distributed normally and with homogeneous variances). Post hoc tests were used to compare pairs. Tukey's test was used for the ANOVA, and the *lincon* function on trimmed means (WRS2 package in R) was used for the robust ANOVA.

Results and Discussion

Weed species differed in plant height, inflorescence base height, sampling date at which plants reached the greatest number of seeds, and seed production (Table 2). The exponential response of seed shattering indicated that seed shattering is more rapid shortly after seed maturity than later (Figures 1–4). *Bromus tectorum* and *L. perenne* ssp. *multiflorum* were the species with a higher shattering rate ($c = 0.193$ on average), followed closely by *V. myuros* ($c = 0.181$ on average). *Secale cereale* was the species with the slowest shattering rate ($c = 0.091$ on average).

However, these average values should be interpreted with care, because significant differences were found within species among locations/years in relation to seed-shattering rate (Table 3), except for *L. perenne* ssp. *multiflorum*. The differences in seed-shattering rates together with different moments in which seed shattering began (Table 2; Figures 1–4) led to different percentages of seed retention per locations/years at the beginning of harvest for *B. tectorum* and *V. myuros*. The descriptions of responses by species are given in the following sections.

Bromus Tectorum

Bromus tectorum, the most ubiquitous weed species in small grain crops of the PNW (Young and Thorne 2004), was collected at three farms in 2016 and 2017 and five farms in 2018 (Table 1). The seed-shattering rate in this species differed significantly among years and among locations in 2018 (Table 3). The beginning of seed shattering was also different among locations and years, with the populations collected at Pilot Rock, CBARC, and Echo farms in 2018 being the earliest, with less than 2,000 accumulated GDD (Figure 1). The populations collected at Dixie and Echo farms in 2017 were the latest, with seed shattering beginning around 2,400 accumulated GDD. Consequently, the percentage of seed retention by the beginning of winter wheat harvest (July 15) differed for many populations (Table 3).

Bromus tectorum had different seed retention percentages (differences between 4% and 87%) that were dependent on the environmental conditions of the year, the location, and certain agronomic aspects (Figure 1; Table 1). Higher percentages of retention were found in 2017, a year that was generally colder and wetter than 2016 and 2018. An anomalous cold winter in 2017 resulted in

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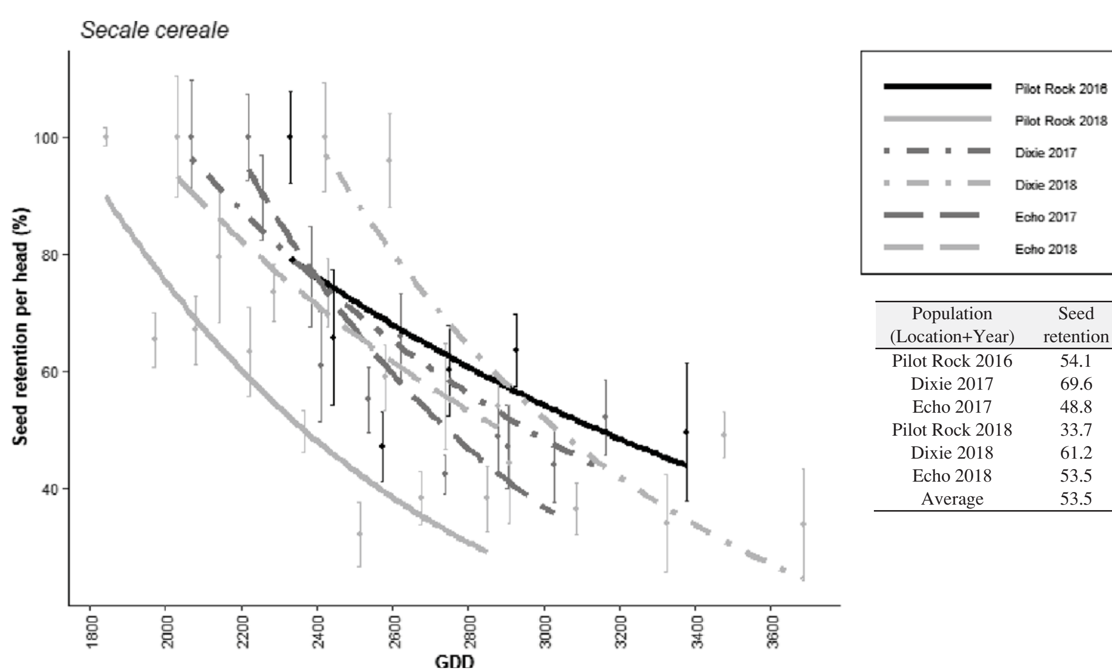
Table 2. Average plant height ±SD, average inflorescence base height ±SD, accumulated precipitation at seed shattering beginning (Precip), rainfall during seed shattering ($Precip_h$), and average seed production predicted per plant on the date with the greatest number of seeds ("initial date") ±SD.[a]

Species	Year	Farm[b]	Plant height	Inflorescence base height	Precip/$Precip_h$	Seed production
			———cm———		—mm/mm—	——no. plant^{-1}——
Bromus tectorum	2016	Pilot Rock	43 ± 11	34 ± 9	296/16	303 ± 229
		CBARC	105 ± 7	93 ± 7	330/26	516 ± 243
		Adams	93 ± 11	84 ± 9	330/26	430 ± 195
	2017	CBARC	102 ± 10	87 ± 12	437/0	199 ± 131
		Dixie	63 ± 19	34 ± 15	500/0	300 ± 213
		Echo	41 ± 13	16 ± 10	310/0	465 ± 488
	2018	Pilot Rock	64 ± 19	50 ± 23	297/21	361 ± 225
		CBARC	93 ± 12	81 ± 11	376/6	428 ± 102
		Dixie	56 ± 16	39 ± 15	424/0	147 ± 93
		Adams	96 ± 7	87 ± 6	381/0	188 ± 70
		Echo	66 ± 12	34 ± 23	224/0	1,350 ± 949
Secale cereale[c]	2016	Pilot Rock	75 ± 9	69 ± 10	296/16	252 ± 99 (41 ± 10)
	2017	Dixie	120 ± 14	94 ± 22	500/0	171 ± 202 (35 ± 10)
		Echo	120 ± 12	81 ± 18	305/5	935 ± 798 (49 ± 11)
	2018	Pilot Rock	127 ± 13	109 ± 18	297/21	111 ± 102 (47 ± 13)
		Dixie	115 ± 8	90 ± 22	424/0	252 ± 188 (45 ± 12)
		Echo	114 ± 14	86 ± 14	224/0	454 ± 394 (47 ± 14)
Lolium perenne ssp. *multiflorum*	2017	Albion	135 ± 22	67 ± 15	622/0	1,016 ± 777
		WSUCAF	137 ± 18	46 ± 10	563/1	632 ± 424
		Dixie	111 ± 10	78 ± 17	500/0	886 ± 824
	2018	Albion	—	—	572/0	1,108 ± 885
		WSUCAF	—	—	567/0	597 ± 208
		Dixie	105 ± 12	77 ± 18	424/0	378 ± 230
Vulpia myuros	2016	Pilot Rock	27 ± 7	20 ± 6	296/16	695 ± 666
	2017	Dixie	32 ± 13	6 ± 7	500/0	514 ± 302
	2018	Pilot Rock	38 ± 15	21 ± 9	297/21	1,344 ± 618
		CBARC	46 ± 23	28 ± 25	376/6	1,252 ± 1,027

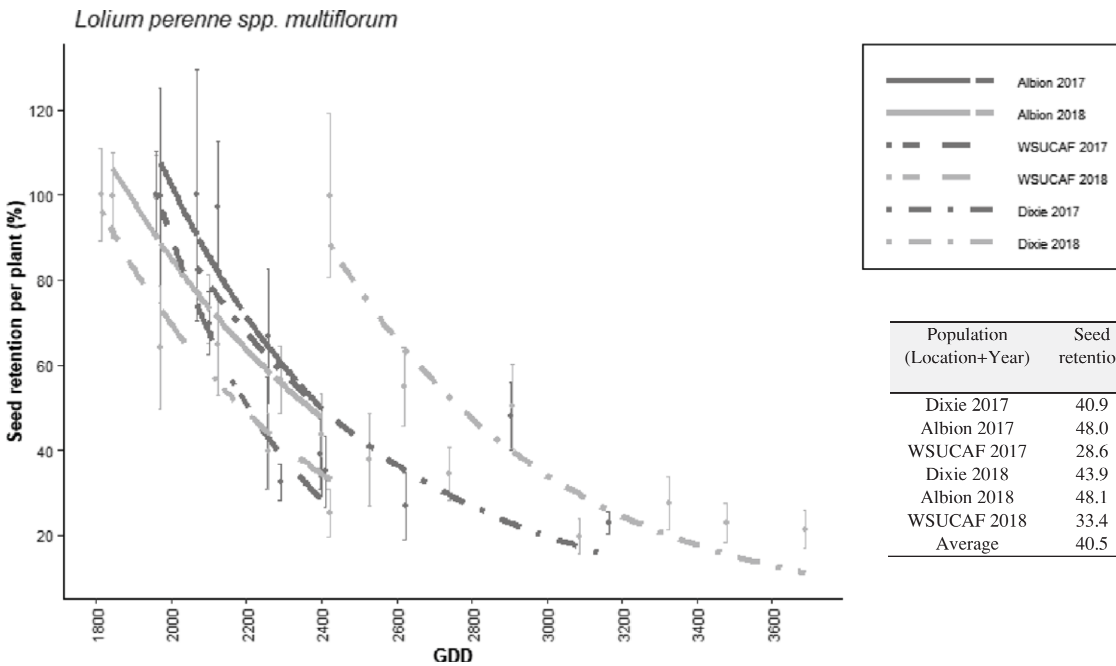
[a]Data are indicated per species, year, and location.
[b]CBARC, Oregon State University Columbia Basin Agricultural Research Center; WSUCAF, Washington State University Cook Agronomy Farm.
[c]The information indicated in parenthesis for *S. cereale* is the number of seeds per head (spike).



Population (Location+Year)	Seed retention	Rate of reduction	Beginning of shattering
Pilot Rock 2016	54.1	0.056	9 June
Dixie 2017	69.6	0.074	27 June
Echo 2017	48.8	0.121	23 June
Pilot Rock 2018	33.7	0.111	1 June
Dixie 2018	61.2	0.109	27 June
Echo 2018	53.5	0.072	8 June
Average	53.5	0.091	

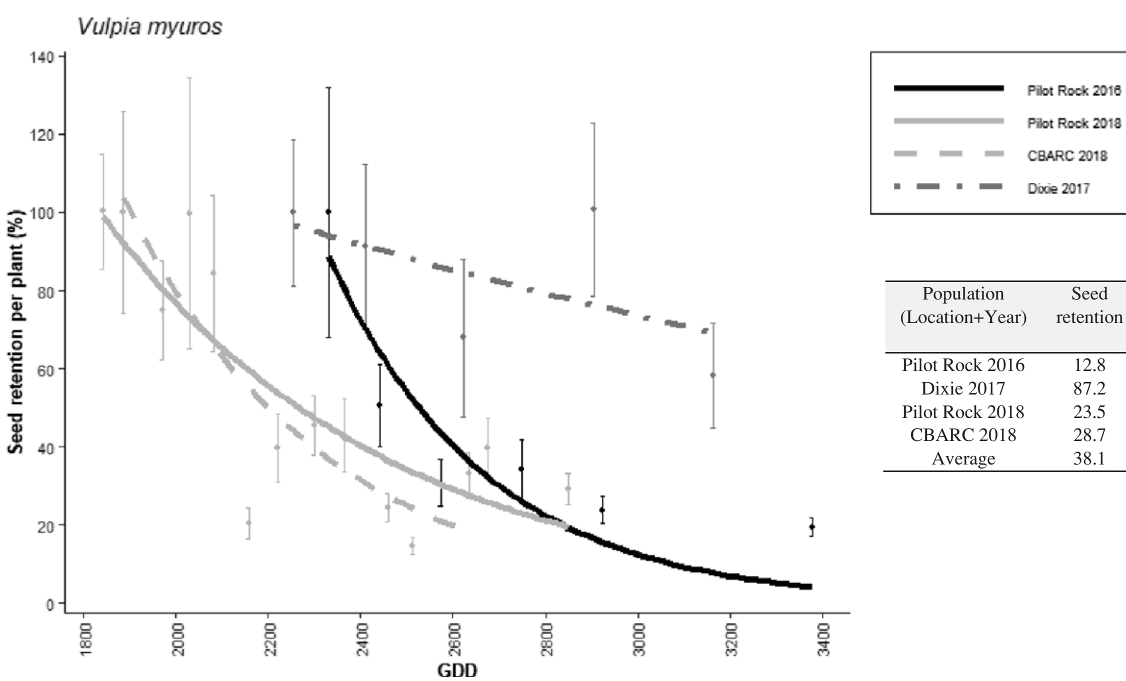
Figure 2. Seed retention per *Secale cereale* head (%) in relation to accumulated growing degree days (GDD) in sampled locations. Dots with vertical lines (standard errors) indicate experimental data, and curves represent the fitted models. The table presents the parameter *c* (rate of reduction) of the fitted model per location, the parameter Y_o for the accumulated GDD by July 15 (seed retention), and the sampling date with the greatest seed number per plant, which was considered the beginning of shattering.

almost 3 mo of snow-covered ground. This could have delayed plant development and seed shattering. Seed shattering did not start until early to mid-July in 2017, whereas it started in mid-June in 2016 and from early to late June in 2018 (Figure 1). The accumulated GDD needed to start shattering also varied depending on the year and site, but in general for this species, shattering started beyond 1,800 accumulated GDD and no later than 2,425 accumulated GDD. The southernmost locations consistently



Population (Location+Year)	Seed retention	Rate of reduction	Beginning of shattering
Dixie 2017	40.9	0.161	27 June
Albion 2017	48.0	0.144	11 July
WSUCAF 2017	28.6	0.286	11 July
Dixie 2018	43.9	0.165	27 June
Albion 2018	48.1	0.188	11 July
WSUCAF 2018	33.4	0.175	2 July
Average	40.5	0.187	

Figure 3. Seed retention per *Lolium perenne* ssp. *multiflorum* plant (%) in relation to accumulated growing degree days (GDD) in sampled locations. Dots with vertical lines (standard errors) indicate experimental data, and curves represent the fitted models. The table presents the parameter *c* (rate of reduction) of the fitted model per location, the parameter Y_o for the accumulated GDD by July 15 for Dixie and by August 1 for Albion and WSUCAF (seed retention by beginning of harvest), and the sampling date with the greatest seed number per plant, which was considered the beginning of shattering.



Population (Location+Year)	Seed retention	Rate of reduction	Beginning of shattering
Pilot Rock 2016	12.8	0.285	9 June
Dixie 2017	87.2	0.042	5 July
Pilot Rock 2018	23.5	0.163	1 June
CBARC 2018	28.7	0.234	18 June
Average	38.1	0.181	

Figure 4. Seed retention per *Vulpia myuros* plant (%) in relation to accumulated growing degree days (GDD) in sampled locations. Dots with vertical lines (standard errors) indicate experimental data, and curves represent the fitted models. The table presents the parameter *c* (rate of reduction) of the fitted model per location/year, the parameter Y_o for the accumulated GDD by July 15 (seed retention), and the sampling date with the greatest seed number per plant, which was considered the beginning of shattering.

had the earliest *B. tectorum* seed shattering. Taghizadeh et al. (2012) found that the dispersion of fruits of wild radish (*Raphanus raphanistrum* L.) began before wheat maturity when drought was severe and more slowly or later for plants with plentiful water supply. In line with these previous authors, based on the results from this research, HWSC practices in the PNW will be more effective in wet years than in drier years.

Previous studies found narrower ranges of seed retention rates for other *Bromus* species that fell within the range observed in this study (4% to 87%). Glasner et al. (2019) reported a 41% seed retention rate for soft brome (*Bromus hordeaceus* L.) in Denmark, whereas Walsh and Powles (2014) reported for several brome species (*Bromus* spp.) in Australia that 77% of seeds were retained at crop maturity (which would decrease to 41% at 28 d after the

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Table 3. Significant differences (P-value < 0.05) in the seed-shattering rate (c) and in the percentage of seed retention at the beginning of harvest (Y_o) between pairs of locations/years per species according to the mixed model analysis for c and according to the analysis of variance for Y_o.[a]

Bromus tectorum		*Secale cereal*	Vulpia myuros	
c	Y_o	c	c	Y_o
P. Rock 2016–CBARC 2018	P. Rock 2016–Adams 2018	P. Rock 2016–Echo 2017	P. Rock 2016–Dixie 2017	P. Rock 2016–Dixie 2017
CBARC 2016–Dixie 2017	P. Rock 2016–Dixie 2018	P. Rock 2016–Dixie 2018	P. Rock 2018–Dixie 2017	
CBARC 2016–Dixie 2018	CBARC 2016–Dixie 2018	P. Rock 2016–P. Rock 2018	CBARC 2018–Dixie 2017	
CBARC 2016–Adams 2018	CBARC 2016–Adams 2018			
Adams 2016–CBARC 2018	Adams 2016–Adams 2018			
CBARC 2017–CBARC 2018	P. Rock 2018–Adams 2018			
CBARC 2017–P. Rock 2018	P. Rock 2018–Dixie 2018			
Dixie 2017–CBARC 2018	CBARC 2018–Dixie 2018			
Dixie 2017–P. Rock 2018	CBARC 2018–Adams 2018			
Echo 2017–CBARC 2018	Adams 2018–Echo 2018			
P. Rock 2018–Dixie 2018				
P. Rock 2018–Adams 2018				
P. Rock 2018–Echo 2018				
CBARC 2018–Dixie 2018				
CBARC 2018–Echo 2018				
CBARC 2018–Adams 2018				

[a]CBARC, Oregon State University Columbia Basin Agricultural Research Center; P. Rock, Pilot Rock; WSUCAF, Washington State University Cook Agronomy Farm. No significant differences were found in studied species not listed.

beginning of harvest). In the Great Plains, Soni et al. (2020) reported that *B. tectorum* averaged 75% seed retention at harvest, with a range of 20% to 95%. The high variability in *B. tectorum* seed retention at harvest time in the PNW and the central Great Plains makes it difficult to determine the efficacy of HWSC for this species.

The height of the inflorescence in this species varied between 16 and 93 cm, with the tallest plants found at Adams and CBARC farms (with more productive crops) and the shortest at Echo Farm (with less productive crops) (Table 2). This result is in line with previous observations of Walsh et al. (2018a), who noted that the greater the crop competition, the more upright the weed growth. Agronomic conditions seem to condition the effectiveness of HWSC practices, as plants with higher inflorescences are less likely to contribute to the seedbank.

Thermal characteristics of locations might not be the only factor affecting shattering of seeds. In addition to the effect observed for wet years, herbicide applications might cause a delay in seed-shattering patterns if the infestation comes mostly from plants with a late germination pattern or plants that recovered after a growth pause. In this study, only populations collected in 2018 seemed to reflect this potential effect. However, the lack of evident herbicide effect in the seed-shattering pattern between treated and untreated populations/locations in 2016 and 2017 could have been due to different reasons. It is possible that the herbicide failed to control most of the population due to the presence of resistant biotypes. Resistance to group 2 herbicides (acetolactate synthase inhibitors), such as pyroxsulam, has been reported to be common in the area (Barroso 2019). Alternatively, the herbicide may have been applied to larger than preferred plants with a consequently poor effect, or it could be that there may not be much difference in seed shattering between plants that germinate in spring after the herbicide application and plants that germinate in the fall. Further research would be necessary to clarify the effects of herbicide resistance and germination time on *B. tectorum* seed-shattering pattern.

The wind could also play an important role in panicle movement and seed shattering of *B. tectorum*, as was indicated by Rew et al. (1996) for poverty brome (*Bromus sterilis* L.). Wind speed likely varied among locations and differentially impacted seed shattering depending on crop competitiveness, interrow space, and seed maturity at the time strong wind conditions occurred. A potential low rate of shattering observed in the population collected at Adams Farm in 2018 could have been the result of the dense wheat stand (15.3-cm interrow space). Locations with greater interrow spaces (Pilot Rock and Echo) could have led to greater wind exposure of *B. tectorum* plants, favoring seed shattering. However, further research is needed to evaluate and differentiate the impact of different biotic and abiotic factors on seed retention and seed-shattering rate.

Secale Cereale

Secale cereale was collected at one, two, and three locations in 2016, 2017, and 2018, respectively. For *S. cereale*, the shattering rate was not significantly different among locations in a particular year, but it was different between years and certain locations (Table 3). The population collected at Pilot Rock in 2016 had the lowest seed-shattering rate, which was significantly different from the populations collected at Echo Farm in 2017 (with the highest shattering rate), Dixie Farm in 2018, and Pilot Rock Farm in 2018. The beginning of shattering started around 2,150 accumulated GDD on average, with the earliest population (Pilot Rock 2018) starting at 1,840 and the latest population (Dixie 2018) starting at 2,420 (Figure 2). Despite some differences in the shattering rate and beginning of shattering, the percentage of seed retained by July 15 was not significantly different between years and locations, ranging from 34% at Pilot Rock 2018 to 70% at Dixie 2017. The lack of differences in seed retention at the beginning of harvest could be due to several reasons. For instance, at Echo, later seed shattering in 2017 compared with 2018 may have compensated for a more rapid shattering rate in 2017. However, the high variability in the number of seeds per plant was probably the main cause of differences not being found. The population collected at Dixie Farm, the northernmost location and the one with the highest annual precipitation, consistently had the highest seed retention at harvest.

Thermal time (accumulated GDD), year, and location seemed to be impacting seed shattering in *S. cereale*, as was observed for *B. tectorum*. Retained seed at the beginning of harvest was not greater than 70% for any year or location, contrasting with an

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average 90% seed retention rate found for this species in Colorado (Soni et al. 2020). Differences in averaged seed retention between Colorado and Oregon populations could be due to different methodologies. However, it is probable that differences may also be the result of the quick local adaptability of this species (Buger and Ellstrand 2014). Buger and Ellstrand found that feral populations of *S. cereale* have diverged regionally in North America and exhibit a greater range of phenotypes than rye cultivars.

Although the seed retention percentage at the beginning of harvest in this study might not be enough to control *S. cereale* in the short term, HWSC practices should be helpful for reducing *S. cereale* seeds in the soil seedbank. Given the limited herbicide options, *S. cereale*'s seed height above the crop canopy (Table 2), and its high competitiveness with wheat (Atri et al. 2008), HWSC practices should be included in integrated strategies to control this weed.

Lolium Perenne Ssp. Multiflorum

Lolium perenne ssp. *multiflorum*, another economically important grass species in the PNW (Bailey and Wilson 2003; Ball et al. 1995), was collected in Washington State at three locations over 2 yr. No significant differences were found in the seed-shattering rate or percentage of seed retention at the beginning of harvest between locations and years. In both years (2017 and 2018), seed shattering started earlier at Dixie than at Albion and WSUCAF (the two latter locations had the highest latitude and elevation among locations in the study and lower values of accumulated GDD; Figure 3). By July 15, on average, *L. perenne* plants retained about 42% of their seeds at Dixie, which was similar to the retained seeds by August 1 at Albion and WSUCAF (48% and 31%, respectively).

Studies on rigid ryegrass (*Lolium rigidum* Gaudin), a similar species, reported greater seed retention at the beginning of harvest: 85% in Australia (Walsh and Powles 2014) and more than 90% in Spain (Blanco-Moreno et al. 2004). It seems that *L. perenne* spp. *multiflorum* in the PNW is less suitable for HWSC than *L. rigidum* in Australia and Spain because of its earlier and more rapid seed-shattering pattern. However, similar to *S. cereale*, *L. perenne* culms are present above the crop canopy, leading to an easier collection of seeds by harvesters using HWSC practices. HWSC practices will contribute to reducing the seedbank of this species, but due to the modest seed retention observed (around 40%), additional control practices will probably be needed to attain control in the long term.

Vulpia Myuros

Vulpia myuros was sampled at one location in 2016 and 2017 and two locations in 2018. A slower seed-shattering rate in this species was found for the population collected at Dixie Farm in 2017 compared with the other locations (Table 3; Figure 4). Based on calendar days, the population at Dixie Farm in 2017 also started shattering later than the other populations. However, based on accumulated GDD, the beginning of seed shattering for Dixie in 2017 (2,255 GDD) was only later than for populations collected in 2018 (1,865 GDD). Despite differences in the shattering rate between Dixie and the other sites/years, seed retention at Dixie in 2017 (87%) at the beginning of harvest was only significantly higher than seed retention at Pilot Rock in 2016 (12.8%) and marginally higher ($P < 0.1$) than seed retention at Pilot Rock in 2018 (23.5%) (Table 3) due to enormous experimental variability. As observed for other species, the cooler, wet conditions at Dixie Farm in 2017 (Table 2) may explain the greater seed retention (87%) and lower rate of seed shattering found at this location.

Vulpia myuros is adapted to dry habitats (Cordeau et al. 2018), and in those environments, it seems to develop and shatter seeds earlier than in cooler and wetter environments, possibly explaining the lower seed retention percentages at Pilot Rock and CBARC farms, which were the southernmost locations. Another factor potentially affecting seed-shattering rate, the beginning of seed shattering, and consequently the percentage of seed retained at harvest at Dixie Farm could have been the use of imazamox at this location (Table 1) (no herbicides were applied in the other locations). Ball et al. (2007) reported 58% control of *V. myuros* with imazamox in field trials near Pendleton, OR, and Pullman, WA. Most of the collected plants could have been late-germinating plants or plants that survived the herbicide treatment but had their development delayed. Greater rainfall during the seed-shattering period at Pilot Rock could have caused more rapid seed-shattering rates in this location (Table 2).

Vulpia myuros is a relatively short plant. The bottom part of the inflorescence is often less than 30 cm above the soil surface (Table 2), the regular wheat cutting height. Plants collected at Pilot Rock Farm in 2016 and 2018 had 0% and 47% of the inflorescence above the cutting height, respectively, while plants collected at CBARC had most of the inflorescence (88.9%) above the regular cutting height. The high density of *V. myuros* at Dixie resulted in lodging of many of the plants, which made them uncollectable. The lodging behavior of *V. myuros* has been observed in other fields and years in the region (JB, personal observations). The low percentage of seed retention observed at all locations except Dixie, the low height of this species, and a potential lodging problem at high densities make *V. myuros* a poor candidate for HWSC in the PNW.

All the studied species had quicker seed shattering early in the harvest season rather than later. This indicates that harvesting as early as possible after crop is at harvest maturity is critical to the success of HWSC in the PNW. Besides harvest time, the efficacy of HWSC practices in the PNW will depend primarily on environmental conditions and weed species, and to a lesser extent on specific growing conditions in each field and the influence of herbicide applications. Taking those factors into consideration and considering an early and feasible harvest, it seems that among the studied species, *S. cereale* had the greatest potential for HWSC systems in the PNW due to slower shattering rates and higher seed retention (54%) on average. *Vulpia myuros* seems to be a poorly suited species for HWSC, with a 38% seed retention on average and double the shattering rate of *S. cereale*. *Bromus tectorum* and *L. perenne* ssp. *multiflorum* had slightly higher seed retention percentages (43% and 41%, respectively) than *V. myuros*, but the seed height in these two species offers better potential for HWSC.

Due to the differences found among years for *B. tectorum*, *S. cereale*, and *V. myuros*, and among years and locations in 2018 for *B. tectorum*, more research is needed to advance the understanding on how agronomic factors, abiotic factors, and their interactions can help to delay seed shattering in problematic weeds and increase HWSC potential. In addition, due to the modest and variable seed retention percentages observed in the studied species, short-term control should not be expected with HWSC practices in the PNW. Further research is needed to evaluate these practices over the long term.

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