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High Seed Retention at Maturity of Annual Weeds Infesting Crop Fields Highlights the Potential for Harvest Weed Seed Control

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Seed production of annual weeds persisting through cropping phases replenishes/establishes viable seed banks from which these weeds will continue to interfere with crop production. Harvest weed seed control (HWSC) systems are now viewed as an effective means of interrupting this process by targeting mature weed seed, preventing seed bank inputs. However, the efficacy of these systems is directly related to the proportion of total seed production that the targeted weed species retains (seed retention) at crop maturity. This study determined the seed retention of the four dominant annual weeds of Australian cropping systems - annual ryegrass, wild radish, brome grass, and wild oat. Beginning at the first opportunity for wheat harvest and on a weekly basis for 28 d afterwards the proportion of total seed production retained above a 15 cm harvest cutting height was determined for these weed species present in wheat crops at nine locations across the Western Australian (WA) wheat-belt. Very high proportions of total seed production were retained at wheat crop maturity for annual ryegrass (85%), wild radish (99%), brome grass (77%), and wild oat (84%). Importantly, seed retention remained high for annual ryegrass and wild radish throughout the 28 d harvest period. At the end of this period, 63 and 79% of total seed production for annual ryegrass and wild radish respectively, was retained above harvest cutting height. However, seed retention for brome grass (41%) and wild oat (39%) was substantially lower after 28 d. High seed retention at crop maturity, as identified here, clearly indicates the potential for HWSC systems to reduce seed bank replenishment and diminish subsequent crop interference by the four most problematic species of Australian crops.

Nomenclature: Annual ryegrass, *Lolium rigidum* Gaud. LOLKRI; wild radish, *Raphanus raphanistrum* L. RAPRA; wild oat, *Avena fatua* L. AVEFA; Brome grass, *Bromus* spp. Roth, BRODI; wheat, *Triticum aestivum* L.

Keywords: Weed seed retention, herbicide resistance, seed bank

La producción de semilla de malezas anuales, que persisten a lo largo de las fases de la producción de cultivos, repone/establece bancos de semilla viables a partir de los cuales estas malezas continuarán interfiriendo con la producción de cultivos. El control de semillas de malezas mediante sistemas de cosecha (HWSC) es ahora visto como un medio efectivo para interrumpir este proceso al enfocarse en semillas maduras de malezas, previniendo la entrada de nuevas semillas en el banco de semillas. Sin embargo, la eficacia de estos sistemas está directamente relacionada a la proporción del total de semilla producida que la especie de maleza retiene (retención de semilla) al momento de la madurez del cultivo. Este estudio determinó la retención de semilla de cuatro malezas anuales dominantes en sistemas de cultivos Australianos -*Lolium rigidum*, *Raphanus raphanistrum*, *Bromus* spp., y *Avena fatua*. Empezando en la primera oportunidad de cosecha de trigo, y siguiendo intervalos semanales durante 28 d, se determinó la proporción del total de la semilla producida que fue retenida sobre 15 cm (altura de corte de la cosechadora) para estas especies de malezas presentes en campos de trigo, en nueve localidades a lo largo de la faja de trigo en el oeste de Australia (WA). Proporciones muy altas de la semilla total producida fue retenida al momento de la madurez del trigo para *L. rigidum* (85%), *R. raphanistrum* (99%), *Bromus* spp. (77%), y *A. fatua* (84%). Importantemente, la retención de semilla se mantuvo alta para *L. rigidum* y *R. raphanistrum* durante los 28 d del período de cosecha. Al final de este período, se retuvo 63 y 79% del total de la semilla producida de *L. rigidum* y *R. raphanistrum*, respectivamente, por encima de la altura de corte de cosecha. Sin embargo, la retención de semilla para *Bromus* spp. (41%) y *A. fatua* (39%) fue sustancialmente menor después de 28 d. Alta retención de semilla al momento de la madurez del cultivo, como se identificó aquí, claramente indica el potencial de los sistemas HWSC para reducir la recuperación del banco de semillas y disminuir así la interferencia con el cultivo de cuatro de las especies de enivos reponecciones ar el daño que persisten a lo largo de las fases de la producci de daño para hacer proyecciones ar el daño enmalezas más problemáticas en cultivos Australianos.

Crop production across the large (30 M ha per annum) southern Australian rain-fed cropping region occurs within a short, moisture-limited growing season (Mediterranean type climate). Crop

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breeding and agronomy aim to develop productive crops adapted to these constraints as they occur across this large and diverse cropping region (Angus 2001; Donald 1965). Concomitantly, there has been a similarly successful natural adaptation to these crop production environments by the dominant infesting annual weed species, annual ryegrass (Kloot 1983), wild radish (Bhatti 2004), brome grass (Kon and Blacklow 1989), and wild oat (Paterson 1976). A consequence is a form of crop mimicry, evident as synchronous growth, reproductive development, and seed maturity of annual weed species with the crops they infest.

Concurrent maturity of crops and infesting annual weeds means that commercial crop harvest can result in the "harvesting" and subsequent redistribution to the soil surface of seed of weed species such as annual ryegrass, wild radish, brome grass, and wild oat. These problematic annual weeds produce mature seed on upright plant structures at the time of crop harvest. Of these four weed species, high seed retention levels at wheat harvest have been recorded for annual ryegrass in Australia (80%) (Walsh and Powles 2007) and Spain (96%) (Blanco-Moreno et al. 2004). Variable levels of wild oat seed retention at wheat maturity have been documented in Canada (20 to 50%) (Feldman and Reed 1974; Shirtliffe et al. 2000) and the UK (20%) (Barroso et al. 2006). For brome grass and wild radish, studies indicate 40 to 50% seed retention at wheat crop maturity in the UK (Howard et al. 1991) and Italy (Balsari et al. 1994) for these species. At grain harvest, retained seed of these weed species enter the front of the harvester, are processed and separated from the collected grain and subsequently exit the harvester, predominantly in the chaff fraction (Balsari et al. 1994; Barroso et al. 2006; Blanco-Moreno et al. 2004; Rew et al. 1996; Shirtliffe and Entz 2005; Walsh and Powles 2007). The harvest residue spreading systems fitted to commercial harvesters ensure that the weed seed bearing chaff fraction is evenly redistributed across the crop field. Ironically, this is a practice contributing to the persistence and expansion of weed populations (Barroso et al. 2006; Blanco-Moreno et al. 2004).

Targeting weed seed at grain harvest is largely an ignored opportunity to minimize the replenishment/establishment of the weed seed bank. HWSC systems have been specifically developed and adopted in Australia to target weed seed exiting the harvester during commercial grain crop harvest (Walsh et al. 2013). Although HWSC systems have proven efficacy in destroying the weed seed bearing chaff fraction (Walsh et al. 2012; Walsh and Newman 2007; Walsh and Powles 2007), the efficacy of these systems is completely dependent on the amount of weed seed retained on standing plants at crop harvest. This seed retention is speculated to vary according to climatic conditions (Shirtliffe et al. 2000; Taghizadeh et al. 2012) and will likely vary across differing agro-ecosystems. This study determined the seed retention levels of the four dominant annual weeds of Australian cropping systems, annual ryegrass, wild radish, brome grass, and wild oat, during the first month of wheat harvest at nine widely separated locations across the Western Australian grain belt.

Materials and Methods

Site Details. Weed populations were identified in commercial wheat crops at nine locations across the Western Australia (WA) grain-belt at the end of the 2008 growing season (Table 1). Within these wheat fields, uniform areas of low to medium population densities (1 to 40 plants m^{-2}) of annual ryegrass, wild radish, brome grass, or wild oat were chosen for sampling. Weed infestations were selected from areas that would have likely received typical weed control and crop management treatments throughout the growing season. At each site, growers provided information on crop seeding date and seasonal rainfall. Site temperature data was sourced from the nearest available weather station (BOM 2008). Daily maximum and minimum temperature data were used to calculate growing degree days (GDD) over the growing season (seeding to harvest) and through harvest using the following equation.

$$GDD = \sum_{S1}^{S2} (Tm - b0) \qquad [1]$$

where Tm is the mean daily temperature, b0 is the base temperature (0 C), and S1 and S2 are the time (d) of crop seeding and first opportunity to harvest, respectively. Thus GDD is a summation of the accumulated degrees for every day from seeding to harvest.

Table 1. Wheat crop production and growing season details for nine locations where seed retention of, annual ryegrass, wild radish, brome grass, and wild oat present in wheat crops was assessed over the first 28 d of crop harvest in 2008.

Location	Wheat biomass	Wheat grain yield	Crop sowing to maturity	Rainfall		Growing degree days	
				Growing season	28 d harvest period	Growing season	28 d harvest period
	t ha^{-1}		d	mm		C base T	
Mullewa	3.2	1.4	169	194	6	2758	550
Yuna	2.8	1.2	137	189	10	2474	597
Mingenew	2.9	1.2	138	168	8	2564	588
Marchagee	3.9	1.9	162	217	0	2472	585
Toodyay	3.0	1.4	150	327	14	1890	550
Lake Varley	1.8	0.8	180	271	71	2264	507
Quairading	4.6	1.4	189	222	17	2041	565
Woodanilling	2.6	0.8	177	230	20	2160	532
Wyalkatchem	2.0	0.7	153	116	9	1978	565
LSD (P = 0.05)	0.31	0.16					

Collection Procedures. Weed and wheat plant samples were collected beginning at crop maturity, with subsequent collection every 7 d for 28 d, covering the first half of the typical harvest period. At each time of collection, annual ryegrass, wild oat, and brome grass plants were counted and sampled from within 3 by 0.1 m^2 quadrat areas. Wild radish plants were present at lower densities and were sampled from within a single 1.0 m^2 quadrat at each time of sampling. Care was taken to ensure the collection of all shed seed from sampled plants by placing quadrats beneath the entire plant canopy area or beneath representative canopy areas. Crop and weed plants were cut 15 cm above the soil surface, removed, and placed in paper bags taking care to avoid any weed seed shed. To allow the determination of total crop and weed plant biomass as well as total seed production, plant material, including lodged seed bearing plant parts, below 15 cm were collected. The soil surface within the quadrat was then carefully swept with a dustpan and brush to collect any seed or seed heads shed prior to sampling. Plant and soil surface samples were placed in a separate sample bag. Collected samples were stored in a hot (30 to 40 C) dry glasshouse for 6 to 12 mo until processed. Wheat plant and weed plant material were separated, plant material was weighed, and seed heads of each species were threshed with wheat grain weighed and weed seed counted. Wheat plant and grain weights were converted to biomass and grain yields, respectively.

Determination of Viable Seed Number. For grass weed species the number of viable seed in each sample was determined by placing three replicates of 100 seed on 1% (w/v) agar-solidified in petri dishes and incubated for 14 d at 12 h alternating temperatures of 25/15 C and a 12 h photoperiod. Seed were classified as viable if they germinated. Seed were also considered viable but dormant if they did not germinate but did not decay. The resulting average proportion of viable seed was used to convert total seed number to total viable seed number. Wild radish seed viability was determined by counting collected pod segments for each sample then separating seed from three replicate lots of 100 segments. These seed were then planted at 1 cm depth in 25 cm by 25 cm trays filled with potting mix (25% moss peat, 25% sand, and 50% mulched pine bark). The trays were placed in a glasshouse for 28 d at day temperatures of 20 to 25 C and night temperatures of 10 to 15 C, with an approximate 10 h photoperiod. The trays were kept well watered and emerging seedlings counted and removed daily. Seed germination and emergence was then used to convert pod segment number to viable wild radish seed number.

Data Analysis. Viable seed number data were converted to seed retention values, calculated as the proportion of total viable seed production retained on the upright portions of plants above 15 cm from the soil surface (harvest cutting height). An ANOVA using SAS statistical software (SAS Institute, Inc., Cary NC 27513) was conducted on seed retention data for annual ryegrass, brome grass, and wild oats. ANOVA could not be used to compare the site effects on wild radish at each time of sampling as replicated wild radish seed retention data was not collected for each sampling time. As

Table 2. *P*-values from analysis of variance of location effects on seed retention for four weed species at crop maturity and at weekly intervals over the first 28 d of crop harvest in 2008.

	Time past wheat crop maturity (d)				
Species	0	7	14	21	28
Annual ryegrass	0.087	0.165	0.069	0.02	0.683
Brome grass	0.014	0.437	0.469	0.9	0.639
Wild oat	0.007	0.013	0.048	0.12	0.013

there were only two instances where there were differences ($P < 0.05$) between sites at each time of collection for annual ryegrass (21 d) and brome grass (0 d), regression analyses were conducted on the pooled seed retention data from the nine sampling sites for wild radish (Table 2). For wild oat, there were differences ($P < 0.05$) between one site (Lake Varley) and the other eight sites. The low seed retention values at this site was most likely a result of rainfall received immediately prior to (43 mm) and during harvest (71 mm). The exclusion of these data resulted in no site differences and allowed the regression analysis of average wild oat seed retention data across the remaining eight sites. A linear relationship was found to fit the data for each species (Equation 2) (SigmaPlot Version 12, Systat Software Inc., 1735 Technology Drive, Suite 430, San Jose, CA 95110):

$$Y = A + Bx \qquad [2]$$

where Y represents the proportion of seed retention, A is seed retention (%) at the commencement of crop harvest, B is the rate of seed shed (% d^{-1}), and x is time (d) past the commencement of harvest. A test for equality of slopes of the lines plotting seed retention over harvest for the four weed species was performed (SigmaPlot Version 12).

Results and Discussion

Seed Production of Weeds Surviving in Wheat. Annual weed populations in crop fields persist from one season to the next via the production of seed by plants surviving to maturity despite earlier in-season weed control practices. In this study, the potential for weed persistence was clearly demonstrated in the seed production levels of four annual weed species present in wheat crops across nine locations of the WA wheat-belt (Table 3). There were consistently high seed production levels on mature annual ryegrass, wild radish, brome grass, and wild oat plants infesting wheat crops at maturity (Table 3). On average, infestations of annual ryegrass (27 plants m^{-2}), and brome grass (30 plants m^{-2}) resulted in very large seed production levels of 8,000 and 3,000 seed m^{-2}, respectively. Wild radish plants, although generally occurring at lower densities (2 plants m^{-2}), had substantial seed production (1,246 seed $plant^{-1}$). Wild oat plants, although present at similar densities (25 plants m^{-2}) as annual ryegrass, and brome grass, were the least fecund with lower seed densities (663 seed m^{-2}) (Table 3). Similar seed production levels have previously been recorded in Australian wheat crops for annual ryegrass (Reeves 1976), wild radish (Reeves et al. 1981; Walsh and Minkey 2006), brome grass (Kleemann and Gill 2009), and wild oat (Radford et al. 1980; Walker et al. 2002). Thus, despite the influence of routine weed control practices and crop competition weed populations persist to produce large numbers of viable seed, ensuring the replenishment/establishment of viable seed banks.

Seed Retention at Crop Maturity. The amount of total seed production retained on mature weed plants at crop maturity establishes the potential for HWSC. The average proportion of total seed production retained at crop maturity above a 15 cm harvest height was for annual ryegrass, 85%, wild radish, 99%, brome grass, 77%, and wild oat, 84% (Figure 2). Similarly high levels of seed retention at wheat maturity have previously been reported for annual ryegrass (96%) (Blanco-Moreno et al. 2004) and wild oat (84%) (Wilson 1970). The high levels of seed retention recorded here for these four weed species indicates that high proportions of total seed production can be collected (harvested) during crop harvest. Modern grain harvesters are highly efficient at processing and sorting crop grain from other collected material. Thus any collected weed seed are expelled from the harvester in the chaff fraction to enter the seed bank perpetuating

Table 3. Plant density, total seed production, and plant seed production for sampled annual ryegrass, wild radish, brome grass, and wild oat populations present in wheat crops at maturity at nine locations across the Western Australian wheat-belt in 2008.

	Annual ryegrass			Wild radish			Brome grass			Wild oat		
Location	plants m^{-2}	seed m^{-2}	seed $plant^{-1}$	plants m^{-2}	seed m^{-2}	seed $plant^{-1}$	plants m^{-2}	seed m^{-2}	seed $plant^{-1}$	plants m^{-2}	seed m^{-2}	seed $plant^{-1}$
Mullewa	17	15,913	1,277	1	4764	2,988	—	—	—	18	601	28
Yuna	13	10,123	844	1	832	832	41	4,045	113	17	136	10
Mingenew	53	6,049	128	3	671	110	36	2,674	55	39	409	13
Marchagee	31	10,799	349	1	1,386	1,386	37	2,119	49	39	79	3
Toodyay	37	4,553	124	1	231	226	—	—	—	15	606	18
Lake Varley	42	12,592	335	3	1,093	634	31	4,059	183	36	2,668	69
Quairading	13	4,847	418	2	3,015	2,139	—	4,373	—	11	387	33
Woodanilling	22	4,029	320	2	699	376	23	3,300	192	23	682	32
Wyalkatchem	14	7,133	484	1	3,311	2,524	12	2,374	146	30	130	5
Average	27	8,449	475	2	1,778	1,246	30	3,278	123	25	633	23
LSD ($P = 0.05$)	14	5,021	416	1	1,172	836	22	2,669	74	14	614	11

ongoing weed infestations (Walsh and Powles 2007). Thus, high levels (> 75%) of weed seed retention at crop maturity create an opportunity during crop harvest to severely restrict seed bank inputs and future weed infestations.

The greatest potential impact for HWSC systems on the problematic weeds infesting crops will occur with the commencement of crop harvest. At wheat crop maturity, annual ryegrass, wild radish, brome grass, and wild oat retained 80% or greater proportions of total seed production above harvest height (15 cm). However, weed seed rain (shedding) occurred over the harvest period for these four weed species (Figure 2). For annual ryegrass and wild radish, seed rain over the 28 d sampling period resulted in approximately 20% reductions in seed retention. Annual ryegrass seed retention remained high at 63% of total seed production after this time. Even more encouraging was the high level of seed retention ($P < 0.05$) of wild radish throughout the 28 d study period (Figure 2). For this species, almost all seed was retained over the first 14 d of harvest with 80% seed retention 28 d after the commencement of wheat crop harvest. Wild oat and brome grass exhibited high seed shedding with 39 and 41% of seed production respectively retained at the end of the 28 d sampling period.

The higher rates of seed shedding for brome grass and wild oat indicate that these species, if dominant, need to be targeted with HWSC systems at the earliest opportunity during the harvest program. Weed seed shedding over the 28 d harvest period followed a linear relationship for all four annual species (Table 4). The slopes of these relationships identified the average daily rate of seed shedding. As expected the rate of seed shedding was greatest for wild oat which on average lost 1.5 % per day. Brome grass had the next highest rate of shedding (1.2 % day^{-1}) while annual ryegrass and wild radish

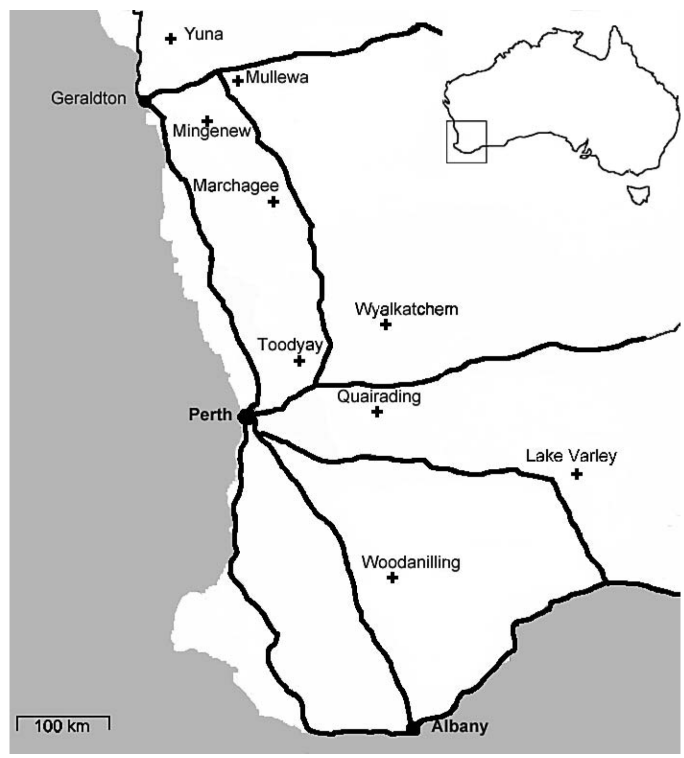

Figure 1. Location of nine sites in the Western Australian wheat-belt where weed seed retention was determined for of annual ryegrass, wild radish, brome grass, and wild oat plants present in wheat crops at maturity during the 2008 harvest.

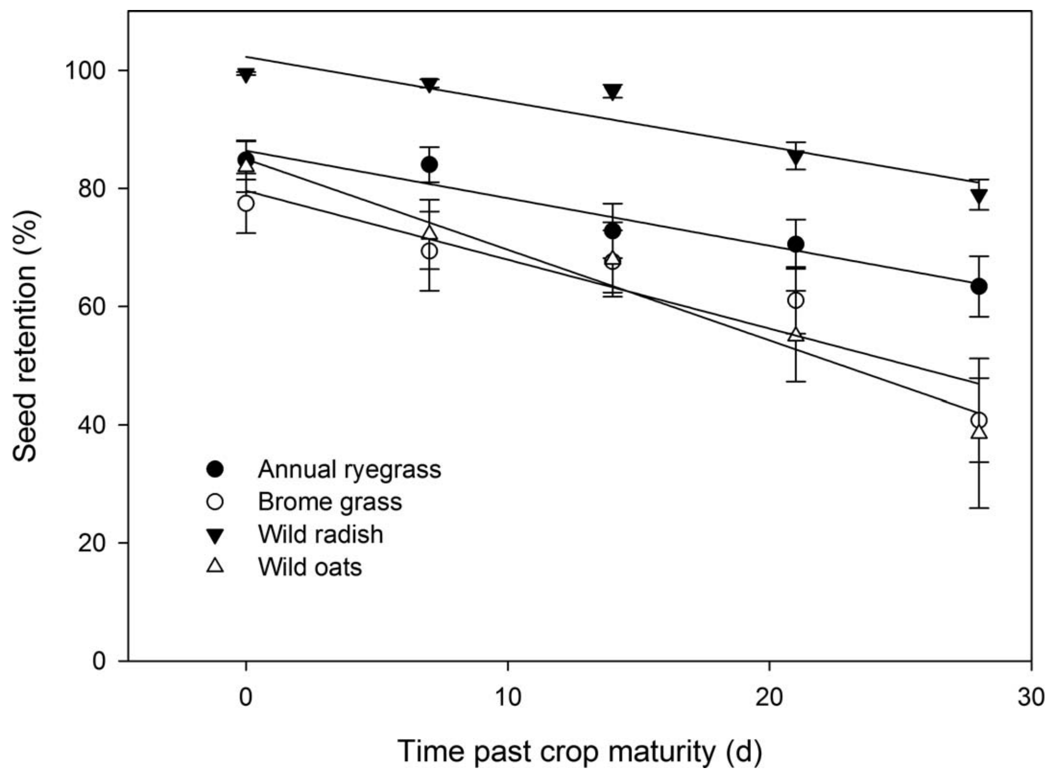

Figure 2. Seed retention above harvest cutting height for four species averaged across nine sites at wheat crop maturity and at 7 d intervals for 28 d. Lines represent the fitted linear model [1], equation parameters and Adjusted R^2 values for each line are presented in Table 3. Capped bars on symbols represent standard errors around the mean of three replicates and nine sites.

had the lowest rates at around 0.8 % day^{-1}. Therefore, to maximize the efficiency of HWSC systems crops infested with species with the highest rates of seed shedding (brome grass and wild oat) should be harvested initially. The lower rates of seed shedding for annual ryegrass and wild radish indicate that HWSC systems will remain effective in targeting the seed production of these species throughout much of the harvest period.

Effect of Location on Seed Retention. Despite widely dispersed locations and contrasting seasonal conditions, similar patterns of seed retention were observed for each weed species across nine distinct locations. Weed populations at each site grew to maturity under markedly different climatic conditions where temperature, rainfall, and growing season length varied markedly (Figure 1; Table 1). Additionally, these weed populations were exposed to contrasting agronomic influences including crop competition and weed population density (Tables 1 and 3). However, there was high consistency in the amount and pattern of weed seed retention across these locations ($P < 0.05$) (Table 2). Of the four weed species investigated, wild oat seed retention was the most affected by environmental conditions. The location effect observed for this species was

Table 4. Parameter estimates and standard errors in parentheses for linear regression model (Equation 1) for seed retention of four weed species over the initial 28 d of crop harvest at nine locations across the Western Australian wheat-belt in 2008.

	Parameter estimates				
	A (%)	P	Seed shed (% d^{-1})	P	R^2
Annual ryegrass	86.4 (2.0)	0.0062	−0.81 (0.12)	< 0.0001	0.94
Wild radish	100 (2.7)	< 0.0001	−0.76 (0.16	0.0172	0.88
Brome grass	79.6 (4.4)	0.0004	−1.17 (0.27)	0.021	0.87
Wild oat	84.9 (2.9)	< 0.0001	−1.53 (0.2)	0.0029	0.96

because of seed retention being lower ($P < 0.05$) at the Lake Varley than at the other eight sites. At this location large rainfall events prior to and during harvest were likely responsible for lower ($P < 0.05$) seed retention levels (Table 1). The only other study examining location effects on seed retention of any of the four species examined was also for wild oat maturing in spring wheat crops in Canada (Shirtliffe et al. 2000). This study compared seed retention levels at two sites over consecutive seasons and proposed that seed retention was related to thermal time. Despite large differences in GDDs among sites surveyed in this experiment, there was no apparent relationship between GDD and wild oat seed retention.

Weed Seed Retention in Cropping Systems. High seed retention levels at crop maturity for the four most problematic species of Australian cropping clearly defines the potential for HWSC systems to impact weed populations. HWSC offers an additional weed control strategy to complement our current herbicide focused programs that are threatened by herbicide resistance (Boutsalis et al. 2012; Broster and Pratley 2006; Owen et al. 2014; Walsh et al. 2007) and diminished herbicide discoveries (Duke 2012). HWSC systems are now being viewed as effective strategies for targeting the seed production of in-crop weeds surviving to maturity, thereby minimizing fresh inputs to the seed bank (Walsh et al. 2013). However, the efficacy of these systems is reliant on the retention of significant proportions of seed production for the targeted weed species at crop maturity. As shown here, very high proportions (> 75%) of total seed production are retained at maturity in wheat cropping systems for the four dominant weeds species annual ryegrass, wild radish, brome grass and wild oat. Additionally, for the two most problematic of these species, annual ryegrass and wild radish, high seed retention levels persist through the first 28 d of harvest.

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