Weed Science

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Concurrent evolution of seed dormancy and herbicide resistance in field populations of dominant weed species in Western Australian cropping systems

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Research Article

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Abstract

Herbicide resistance, documented in many economically damaging weed species, is a major threat to global crop production. The injudicious use of herbicides, often in the absence of diverse weed control strategies, poses an immense selection pressure on weed communities for resistance evolution and weed adaptive traits such as high seed dormancy. This study evaluates the interaction among developing herbicide resistance, seed size, and seed dormancy of ripgut brome (*Bromus diandrus* Roth), wild oat (*Avena fatua* L.), and hare barley [*Hordeum leporinum* Link; syn. *Hordeum murinum* L. ssp. *leporinum* (Link) Arcang.] collected from within intensively managed fields (in-crop) in comparison with populations in surrounding ruderal (non-crop disturbed) areas with no history of exposure to herbicides within the Western Australian grainbelt. Seed size of the three species varied by farming system (continuous cereal-intensive annual crops, diverse annual crops, pasture based) and habitat (in-crop, ruderal). Field populations of *H. leporinum* and *B. diandrus* tended to have greater seed size compared with ruderal populations. Larger seeds had significantly more dormancy in all three weed species. Field-collected populations that were exposed to herbicide applications for at least the past 5 yr exhibited significantly greater seed dormancy compared with their counterparts present in ruderal areas within the same geographic area. The association between increased seed dormancy and developing multiple herbicide resistance further complicates effective weed management.

Introduction

Weed adaptation is an inevitable and damaging consequence of modern agricultural practices that involve high cultivation intensity of the same annual crops and overreliance on herbicides. The evolutionary adaptation of weeds has indirectly but largely been influenced by the process of crop domestication that has selected for weeds acclimatized to specific or diverse new ecosystems (Baucom 2019). The ecological fitness advantages of weeds, mainly driven by their genetic architecture, have enabled multiple adaptation strategies such as prolonged seed dormancy, rapid growth rates, ease of dispersal, stress tolerance, and herbicide resistance—collectively known as agricultural weed syndrome (Guo et al. 2018; Vigueira et al. 2013). Modern farming practices that heavily and persistently rely on herbicides under high cropping intensity have exerted selective forces on arable weeds, resulting in the aggravation of this syndrome and leading to widespread selection and evolution of herbicide-resistant individuals that can thrive in the managed environment (Beckie 2006; Murphy and Lemerle 2006; Owen et al. 2015a; Sun et al. 2021).

Apart from widespread herbicide resistance, multiple adaptive strategies have been reported to evolve in weed populations that are linked to various farming operations across agricultural systems. For example, hand weeding led to crop mimicry, reaping led to dwarf stature (reviewed in Barrett 1983), intensive cropping led to delayed germination (Kleemann and Gill 2006), repeated mowing led to prostrate growth habit (Warwick and Briggs 1979), and weed seed

destruction may lead to early flowering and reduced podding height on the stem to evade capture at crop harvest (Ashworth et al. 2016). Moreover, weed adaptation in response to repetitive herbicide exposure has emerged as an unparalleled global threat to crop production. In contrast, the ruderal (non-crop disturbed) or natural areas surrounding intensively cultivated fields exhibit limited selection and evolution for herbicide resistance and life cycle or trait adaptations, indicating the prominent role of recurrent agronomic practices in directing the evolutionary patterns in weed adaptive traits (Owen et al. 2015a).

Since the 1990s, a number of studies have reported differential fitness costs in agricultural weeds that are resistant to one or multiple herbicides such as the inhibitors of acetyl CoA carboxylase (ACCase), acetolactate synthase (ALS), and 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) (Maity et al. 2021a, 2021b; Martinez-Ghersa et al. 2000; Mortimer 1997). Various plant adaptive traits such as plant height, biomass, tiller number, leaf area index, regrowth rate, photosynthetic rate, and seed production potential have shown divergent responses in herbicide-resistant populations as opposed to their less intensively managed or non-cropland counterparts (Darmency et al. 2017; Gundel et al. 2008; Jasieniuk et al. 1996; Watkinson and White 1985). For example, Ghanizadeh and Harrington (2019) reported reduced plant height and plant biomass in triazine-resistant common lambsquarters (*Chenopodium album* L.) phenotypes as compared with a susceptible cohort. Henckes et al. (2019) reported that Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot] biotypes resistant to glyphosate, iodosulfuron, and pyroxsulam produced taller plants with increased shoot dry matter and absolute growth rate; these plants, however, had fewer tillers and reduced leaf area ratio when compared with the susceptible biotypes.

Seed size and dormancy are two important plant adaptive traits that have affected the colonization and persistence of weed species and plant evolution in general, especially under human-influenced plant domestication regimes (Rees 1996). Unsurprisingly, both of these seed traits have coadapted to different weed management practices along with other adaptation strategies such as widespread evolution of herbicide resistance (Kleemann and Gill 2006; Maity et al. 2021a; Owen et al. 2015a). Some studies failed to establish an association between altered weed seed traits and herbicide resistance (Harris et al. 1995; Holt and Thill 1994; Park et al. 2004; Wiederholt and Stoltenberg 1996). However, a number of studies have found that weed populations resistant to various herbicides exhibit alterations in their seed morphophysiological traits such as size, speed of germination, seed dormancy, and seedling vigor (Darmency et al. 2017; Ghersa et al. 1994; Maity et al. 2021a; Nandula et al. 2009; Owen et al. 2015a, 2015b; Yanniccari et al. 2016). These alterations may enhance the fitness of herbicide-resistant individuals. For example, altered seed dormancy can change the expected weed emergence patterns under field conditions, with cohorts evading control by soil-residual preemergence herbicides or being less controlled by postemergence herbicide applications.

Australian cropping systems, particularly in Western Australia (WA), have high adoption of no or minimum tillage (Llewellyn et al. 2012). Although conservation tillage has provided enormous benefits in improving soil properties, elimination of tillage as a weed control measure has resulted in overreliance on herbicides, leading to changes in weed dynamics and adaptation strategies (Chauhan et al. 2006; Owen et al. 2015a). Rigid ryegrass (*Lolium rigidum* Gaudin) infests most southern Australian cropping systems; brome grass (*Bromus* spp.), hare and smooth barley [*Hordeum leporinum* Link; syn. *Hordeum murinum* L. ssp. *leporinum* (Link) Arcang.; and *Hordeum glaucum* Steud.; syn. *Hordeum murinum* L. ssp. *glaucum* (Steud.) Tzvelev, respectively], and wild oat (*Avena fatua* L.) are also abundant and cause significant crop yield loss (Llewellyn et al. 2016). For example, Poole and Gill (1987) reported a 30% yield loss in wheat (*Triticum aestivum* L.) from *Bromus* spp. at densities of 100 plants m^{-2} in southern Australia; Dastheib et al. (2003) reported a 25% to 30% yield loss in wheat and barley (*Hordeum vulgare* L.) in New Zealand.

In general, seeds of *Bromus* spp. can remain substantially dormant for more than 2 mo (Kleeman and Gill 2006), seeds of *H. leporinum* for 3 mo (Bolger et al. 1999), and seeds of *A. fatua* for 3 to 4 mo (Paterson 1976) when stored at ambient room temperature after maturity. A number of studies in WA and other regions have confirmed the presence of field populations of these species resistant to one or multiple herbicides, and an association of seed traits, especially dormancy, with herbicide resistance (Owen and Powles 2016; Owen et al. 2011, 2015b). We hypothesize that intensive cropping practices have divergently influenced field populations of these species for seed trait expression and response to commonly used herbicides as compared with adjacent ruderal populations. In-crop weed populations with larger seed size and enhanced seed dormancy may have a fitness advantage (e.g., greater emergence, growth, fecundity) relative to their nonmanaged ruderal counterparts, which could exacerbate management efficacy. Therefore, the aim of this study was to investigate whether field and adjacent ruderal populations of *B. diandrus*, *H. leporinum*, and *A. fatua* differ in seed size and dormancy in relation to herbicide susceptibility.

Materials and Methods

Seed Collection

Weed populations were collected from different farms (two populations per farm: cropland and ruderal habitat) randomly selected across a variety of farming systems (continuous, diverse, and pasture) in different agroclimatic cropping zones within the WA grainbelt (Table 1). The continuous farming system comprised wheat and barley crops, whereas the diverse system comprised crop sequences of cereals (wheat, barley, and oat [*Avena sativa* L.]), canola (*Brassica napus* L.), and lupin (*Lupinus angustifolius* L.). Multiyear pastures (subterranean clover [*Trifolium subterraneum* L.]) in rotation with cereal, oilseed, and pulse crops listed above constituted the pasture farming system. Glyphosate and paraquat were applied as burndown herbicides before seeding. Soil-residual herbicides such as triallate, trifluralin, and prosulfocarb were frequently applied preemergence before seeding or at the time of seeding. Both ACCase- and ALS-inhibiting herbicides were commonly applied postemergence in the annual crops and pasture establishment year. For *H. leporinum*, 12 populations were from continuous (6 in-crop and 6 ruderal) and 36 from pasture (18 in-crop and 18 ruderal) farming systems. For *B. diandrus*, 30 populations were from diverse (15 in-crop and 15 ruderal) and 12 from pasture (6 in-crop and 6 ruderal) systems. For *A. fatua*, 6 populations each from continuous and pasture (3 in-crop and 3 ruderal) and 12 populations from diverse (6 in-crop and 6 ruderal) systems were collected. Samples from mature seed heads for each population were collected from 40 to 50 plants randomly selected at each location (50 to 200 ha field area) during June 2018 before crop harvest. Collected seeds were threshed and cleaned from the chaff by aspiration, sieving, and forced-air separation.

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Table 1. Farming systems and habitats investigated in this study.

Factors	Type	Characteristics
Farming system (FS)	Continuous	Seed samples from continuous annual cropping systems (cereal intensive)
	Diverse	Samples from rotations consisting of cereal, *Brassica*, and legume species (no pastures)
	Pasture	Samples from rotations with multi-year pastures in rotation with cereal, *Brassica*, or legume crop species
Habitat within FS	In-crop/ cropland	Samples from within the field that received common weed management practices for more than 5 yr
	Ruderal	Samples from adjacent ruderal (non-cropland) area of similar soil type located within 2 km of the corresponding in-crop sample site (e.g., roadsides or bushlands)

Seed Size and Dormancy Evaluation

Immediately following collection, harvested seeds were placed in permeable paper bags and stored at ambient conditions (25 C in the dark). For each population, three replicate samples each comprising 100 seeds were weighed 12 mo after collection to assess relative seed size (mass), expressed as 100-seed weight (mg). A periodic evaluation of monthly (every 4 wk) seed dormancy release for 9 consecutive months after collection was performed using a standard test to assess germination. For each population, three replicates of 50 seeds each were subsampled every month. The subsampled seeds were sterilized in a 1:16 ratio of 12.5% sodium hypochlorite solution and then placed in 750-ml rectangular plastic trays (50 seeds per tray) containing 1% (10 g L^{-1}) agar dissolved in deionized water. Trays were immediately transferred to a plant growth cabinet (Conviron® A1000; Conviron Australasia, Grovedale, Victoria 3216, Australia) that was set at environmental conditions conducive for seed germination: 12-h day at 20 C with white fluorescent light (30 to 60 µmol $m^{-2}s^{-1}$)/12-h night (dark) cycle at 11 C. Seed germination was evaluated daily for 4 wk after subsampling, with the criterion for germination being visible radicle protrusion (>1 mm) from the seed (Figure 1). Germinated seed was removed from the tray after each evaluation. At the end of the germination test, the remaining nongerminated seeds were assessed for viability by making a transverse section to expose the endosperm and incubating in 1% (10 g L^{-1}) solution of 2,3,5-triphenyltetrazolium chloride for 24 h at 30 C. Evidence of pink staining of the embryo scored a seed as being viable; seeds with unstained embryos were considered nonviable (Verma and Majee 2013). Nonviable seeds were not included in the calculation of total seed count. Dormancy was calculated by the following formula (Equation 1):

$$\text{Dormancy}\ (\%) = [(\text{total viable seed count}_{t(x)} - \text{germinated seed count}_{g(x)})/ \text{total viable seed count}_{t(x)}] \times 100 \quad [1]$$

where t(x) is the total viable seed count and g(x) is the total germinated seed count at evaluation time x, that is, after 4 wk from the start of a test.

Herbicide-Resistance Screening

Herbicide-resistance screening for *B. diandrus* and *H. leporinum* was conducted between June and August during the normal growing season in the Southern Hemisphere. Seeds of each population were germinated in 1% (10 g L^{-1}) agar–water, as described earlier before being transplanted into plastic trays (40 cm by 30 cm by 10 cm) containing potting mix (50% composted pine bark, 25% peat, and 25% river sand). Plants were maintained outside with adequate light and soil moisture at the University of Western Australia until the 2- to 3-leaf stage. Fifty plants per herbicide for each population were sprayed with the upper range of the recommended dose of the herbicides as listed in Table 2, using a custom-built dual-nozzle (TeeJet® XR11001 flat fan, Springfield, IL, USA) cabinet sprayer (for details of spray application, see Owen et al. 2015b). Known herbicide-susceptible (100% mortality) and herbicide-resistant (<10% mortality) populations of each species were included as negative and positive controls, respectively, and the experiment was repeated. Herbicide efficacy was assessed by determining seedling mortality at 21 d after herbicide treatment (dead or alive). Flamprop-methyl was applied at the 4-leaf stage

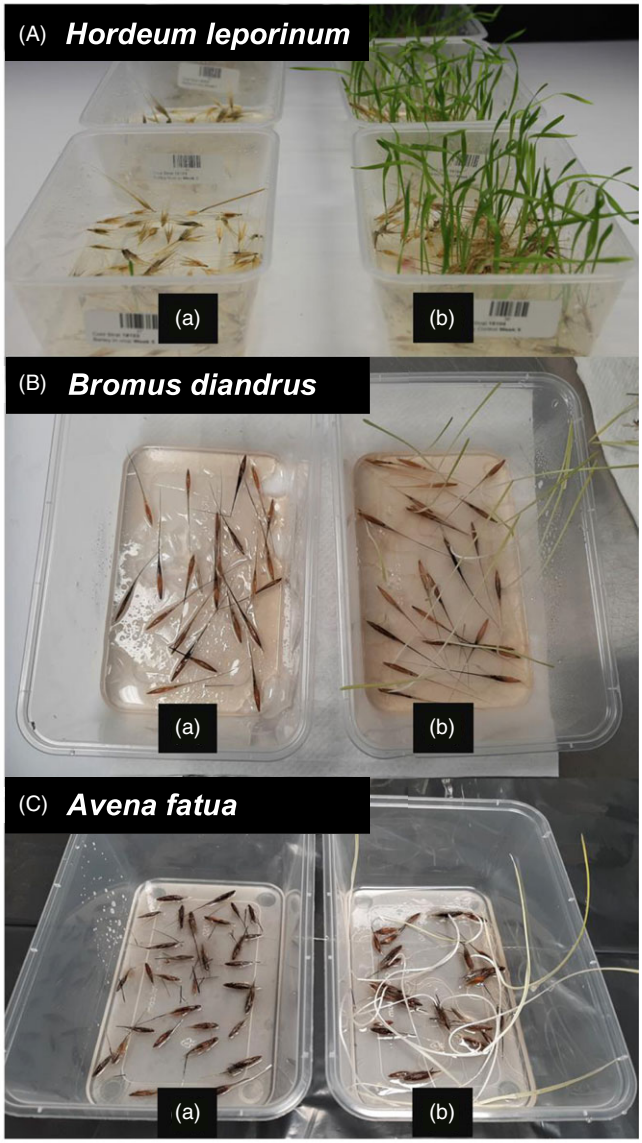

Figure 1. Difference in seed germination of in-crop (a) and ruderal samples (b) collected from a single farming system of *Hordeum leporinum* (A), *Bromus diandrus* (B), and *Avena fatua* (C).

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Table 2. Herbicides and rates used for resistance screening of *Hordeum leporinum*, *Bromus diandrus*, and *Avena fatua* populations.

Site of action: inhibitor of[a]	Active ingredient	Trade name	Field rate[b]	
			H. leporinum/ *B. diandrus*	*A. fatua*
			g ai or ae ha^{-1}	
ACCase	Clethodim	Sequence®, Syngenta, Macquarie Park, New South Wales 2113, Australia	60	—
ACCase	Fluazifop	Fusilade Forte®, Syngenta (as above)	78	—
ACCase	Diclofop-methyl	Hoegrass®, Bayer CropScience, Hawthorn East, Victoria 3123, Australia	—	500
ACCase	Fenoxaprop	Wildcat®, Bayer CropScience (as above)	—	110
ACCase	Pinoxaden	Axial®, Syngenta (as above)	—	100
ACCase	Sethoxydim	Sertin®, Bayer CropScience (as above)	—	186
ACCase	Tralkoxydim	Achieve®, Syngenta (as above)	—	200
ALS	Sulfometuron	Mako®, Nufarm, Kwinana Beach, Western Australia 6167, Australia	15	—
ALS	Sulfosulfuron	Titan, Titan Ag Pty Ltd., Newport, New South Wales 2106, Australia	37.5	—
ALS	Imazamox + imazapyr	Intervix®, Nufarm (as above)	23+10.5	13+6
ALS	Mesosulfuron	Atlantis®, Bayer CropScience (as above)	—	30
EPSPS	Glyphosate	Roundup Powermax®, Nufarm (as above)	400	705
Lipid synthesis	Triallate	Avadex® Xtra, Nufarm (as above)	—	500
Mitosis	Flamprop-methyl	Mataven®, Nufarm (as above)	—	90
Photosystem I	Paraquat	Gramoxone, Syngenta (as above)	300	250

[a]Abbreviations: ACCase, acetyl Co-A carboxylase; ALS, acetolactate synthase; EPSPS, 5-enolpyruvylshikimate-3-phosphate synthase.
[b]A dash (—) indicates specific herbicide was not used for screening resistance in the species.

and evaluated for mortality at 28 d after application. The proportion of survivors for each population for a particular herbicide was determined based on the number of plants that survived the herbicide application out of the total number of plants sprayed. The preemergence triallate treatment was applied to the soil surface, and 10 mm of untreated soil was immediately placed on the soil surface to prevent volatilization; mortality was assessed at 21 d after treatment. Although a single discriminating herbicide dose, based on previous dose–response experiments, is commonly used to classify weed populations collected in field surveys as herbicide resistant when both positive and negative controls are included (e.g., Owen et al. 2015a, 2015b), survivorship in this study denotes "developing herbicide resistance" (DHR) to conservatively indicate reduced sensitivity or potentially herbicide resistant.

Data Analysis

Experiments were conducted under controlled growth chamber (germination test) or net house conditions (herbicide screening) in a factorial randomized complete block design, with main factors being farming system (continuous, diverse, or pasture), weed population habitat (in-crop vs. ruderal), and weed species. Each farm was considered a replicated experimental site. Before statistical tests were conducted, data were checked for normality using the Shapiro-Wilk *W* test. No transformations were required. ANOVA (see Table 3 for response variables) and Pearson nonparametric correlation (ordinal variable) were performed using JMP v. 15.0 (SAS Institute, Cary, NC). Interactions of interest are detailed in Tables 4 and 5 and Figures 2 and 3 (significance denoted at $P < 0.05$, $P < 0.01$, or $P < 0.001$). In the few cases where standard errors were zero for a population (Table 5), that is, all replicates were equal to the population mean, no specific statistical tests could be conducted; the arithmetic difference between means was considered consistent and reportable in the absence of dispersion of the sample means. Statistical graphs were created using SigmaPlot v. 14.0 (Systat Software, San Jose, CA).

Table 3. Significance of the experimental factors on various traits of the *Hordeum leporinum*, *Bromus diandrus*, and *Avena fatua* populations.

Traits	Factors[a]		
	Species	Farming system	Habitat
Seed dormancy (%)	***	***	**
Seed dormancy release rate (D_{50})[b]	**	***	***
Seed size (100-seed weight)	***	**	**
Developing herbicide resistance (% survival)	*	**	**

[a]Level of significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
[b]D_{50}, time (months) required for 50% dormancy release.

Time (months) required for 50% dormancy release (D_{50}) across the populations was estimated using a three-parameter sigmoidal model (Equation 2) on cumulative seed germination data collected over a 4-wk period. The model was constructed using SigmaPlot v. 14.0 and is described by Equation 2:

$$y = \frac{a}{1+e^{\left[\frac{-(x-x_0)}{b}\right]}} \quad [2]$$

where y is cumulative germination (%) on the xth day, a is maximum germination (%), x_0 is days to 50% germination, and b = slope at x_0. Pearson correlation analysis was conducted in JMP PRO 14 to examine correlations between DHR to individual herbicides and seed size and dormancy. For this purpose, data on percent survival for each population in response to the different herbicides and percent dormancy (observed in the first-month evaluation) were used. Seed dormancy release rate can be influenced by numerous factors, including storage conditions. Percent seed dormancy represents a relatively consistent measurement of a population and hence is preferable to dormancy release rate for this correlation analysis. Due to the significant main effect of weed species on seed dormancy, seed size, and DHR, data are presented by species.

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Table 4. Mean time (months; SE in parentheses) required for 50% dormancy release (D_{50}) of the *Hordeum leporinum* (HL), *B. diandrus* (BD), and *Avena fatua* (AF) seeds collected from three farming systems and two habitats across Western Australia.[a]

	Continuous		Diverse		Pasture	
Weed	In-crop	Ruderal	In-crop	Ruderal	In-crop	Ruderal
HL	∞ *n* = 6	2.8 (0.14) y *n* = 6	—	—	3.1 (0.25) A *n* = 18	3.3 (0.31) A,x *n* = 18
BD	—	—	2.6 (0.26) A,b *n* = 15	2.3 (0.49) A,x *n* = 15	4.7 (0.23) A,a *n* = 6	1.5 (0.19) B,y *n* = 6
AF	4.3 (0.21) A,b *n* = 3	2.7 (0.28) B,y *n* = 3	5.9 (0.14) A,a *n* = 6	3.4 (0.49) B,x *n* = 6	3.3 (0.11) A,c *n* = 3	2.7 (0.53) B,y *n* = 3

[a]Symbols: ∞, seed dormancy did not release during the study period; —, the study did not include any population of the weed species from the specific farming system or habitat (*n* = no. of populations). Capital letters A and B indicate significant difference ($P < 0.05$) between weed habitats (in-crop vs. ruderal) for each weed species within a farming system; lowercase letters indicate significant difference for in-crop populations among farming systems (a, b, and c) and for ruderal populations (x and y).

Table 5. Effect of farming system (continuous, diverse, or pasture) and weed population habitat (in-crop vs. ruderal) on survival (SE in parentheses) of *Hordeum leporinum*, *Bromus diandrus*, and *Avena fatua* in response to herbicide treatment.[a]

	Continuous		Diverse		Pasture	
Weed species	In-crop	Ruderal	In-crop	Ruderal	In-crop	Ruderal
Survival (%)						
Hordeum leporinum	*n* = 12	*n* = 12	*n* = 7	*n* = 7	*n* = 18	*n* = 18
Clethodim*	0.0	0.0	—	—	4.1(0.8)	0.85(0.1)
Fluazifop	0.0	0.0		—	14.7(1.5)	0.0
Glyphosate	0.0	0.0	—	—	0.0	0.0
Imazamox + imazapyr	0.0	0.0	—	—	0.0	0.0
Paraquat	0.0	0.0	—	—	0.0	0.0
Sulfometuron**	96.2 (16.5)	0.0	—	—	33.4 (6.7)	0.0
Sulfosulfuron**	66.7 (12.2)	0.0	—	—	35.6 (6.5)	0.0
Bromus diandrus			*n* = 15	*n* = 15	*n* = 6	*n* = 6
Clethodim	—	—	0.0	0.0	0.0	0.0
Fluazifop	—	—	0.0	0.0	0.0	0.0
Glyphosate	—	—	0.0	0.0	0.0	0.0
Imazamox + imazapyr	—	—	0.0	0.0	0.0	0.0
Paraquat	—	—	0.0	0.0	0.0	0.0
Sulfometuron**	—	—	37.5(5.7)	0.0	100.0(0)	0.0
Sulfosulfuron**	—	—	100.0(0)	0.0	37.5(6.3)	0.0
Avena fatua	*n* = 3	*n* = 3	*n* = 6	*n* = 6	*n* = 3	*n* = 3
Diclofop-methyl*	12.4 (2.3)	0.0	24.1 (3.7)	0.0	39.1 (7.7)	0.0
Fenoxaprop	0.0	0.0	0.0	0.0	0.0	0.0
Flamprop-methyl	60.0 (5.7)	0.0	0.0	0.0	0.0	0.0
Glyphosate	0.0	0.0	0.0	0.0	0.0	0.0
Imazamox + imazapyr	0.0	0.0	0.0	0.0	0.0	0.0
Mesosulfuron	82.8 (10.7)	0.0	80.8 (11.3)	0.0	100.0 (0)	0.0
Paraquat	0.0	0.0	0.0	0.0	0.0	0.0
Pinoxaden	0.0	0.0	0.0	0.0	0.0	0.0
Sethoxydim	10.0 (1.4)	00	0.0	0.0	0.0	0.0
Tralkoxydim	0.0	0.0	0.0	0.0	0.0	0.0
Triallate	100.0 (0)	0.0	86.4 (9.3)	0.0	100.0 (0)	0.0

[a]A dash (—) indicates the study did not include any population of the weed species from the specific farming system or habitat. Significant difference between weed population habitat among farming systems at *$P < 0.05$ or **$P < 0.01$. Where SE is 0, arithmetic difference between habitats and/or farming systems was considered consistent and valid.

Results and Discussion

Seed dormancy of all three weed species differed among the two habitats assessed in this study (Table 3; Figure 2). Populations collected from within weed-managed fields (in-crop) exhibited greater seed dormancy compared with the corresponding population collected from an unmanaged ruderal location (Figure 2). At 7 mo after harvest, *H. leporinum* in-crop populations exhibited 52% to 100% seed dormancy compared with 17% to 24% for populations collected from the corresponding ruderal locations. After the same 7-mo duration, *B. diandrus* populations collected from in-crop locations had a dormancy range of 13% to 61% compared with 0% to 14% in the populations collected from ruderal locations. The *A. fatua* in-crop populations exhibited 5% to 49% seed dormancy compared with 4% to 17% dormancy in ruderal populations ($P < 0.05$). Results indicate that there was also an effect of farming system on seed dormancy (Table 3; Figure 2). Populations of *H. leporinum*, *B. diandrus*, and *A. fatua* from the farming systems with annual crops, whether continuous or diverse, exhibited greater seed dormancy compared with the pasture-intensive farming system.

Rate of seed dormancy release was greatly impacted by both farming system and habitat (Table 4; Figure 2). In-crop populations released seed dormancy at a significantly slower rate than their ruderal counterparts, except for *B. diandrus* from the diverse system and *H. leporinum* from the pasture system. The time required for 50% dormancy release (D_{50}) for *H. leporinum* was 3.1 mo or more for in-crop populations compared with 2.8 to

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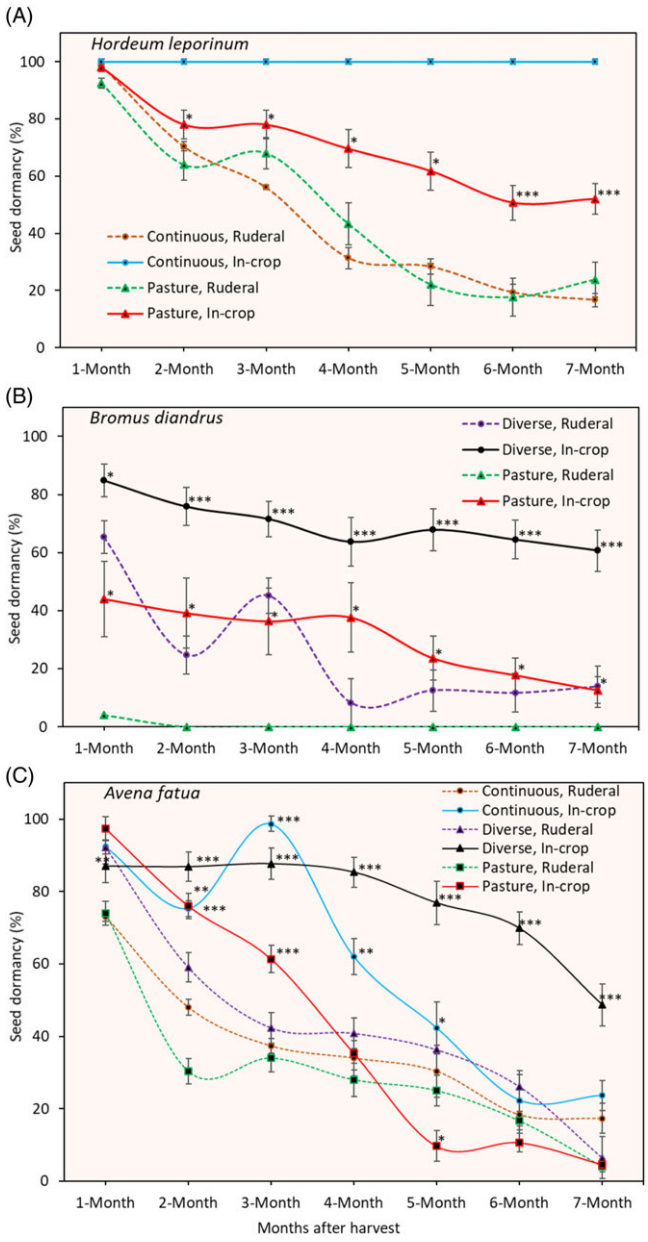

Figure 2. Effect of farming system (continuous, diverse, or pasture) and weed population habitat (in-crop vs. ruderal) on monthly seed dormancy (means ± SE) release after harvest of (A) *Hordeum leporinum*, (B) *Bromus diandrus*, and (C) *Avena fatua*. Asterisks denote significant difference between means of weed population habitat within a specific farming system: *P < 0.05; **P < 0.01; ***P < 0.001.

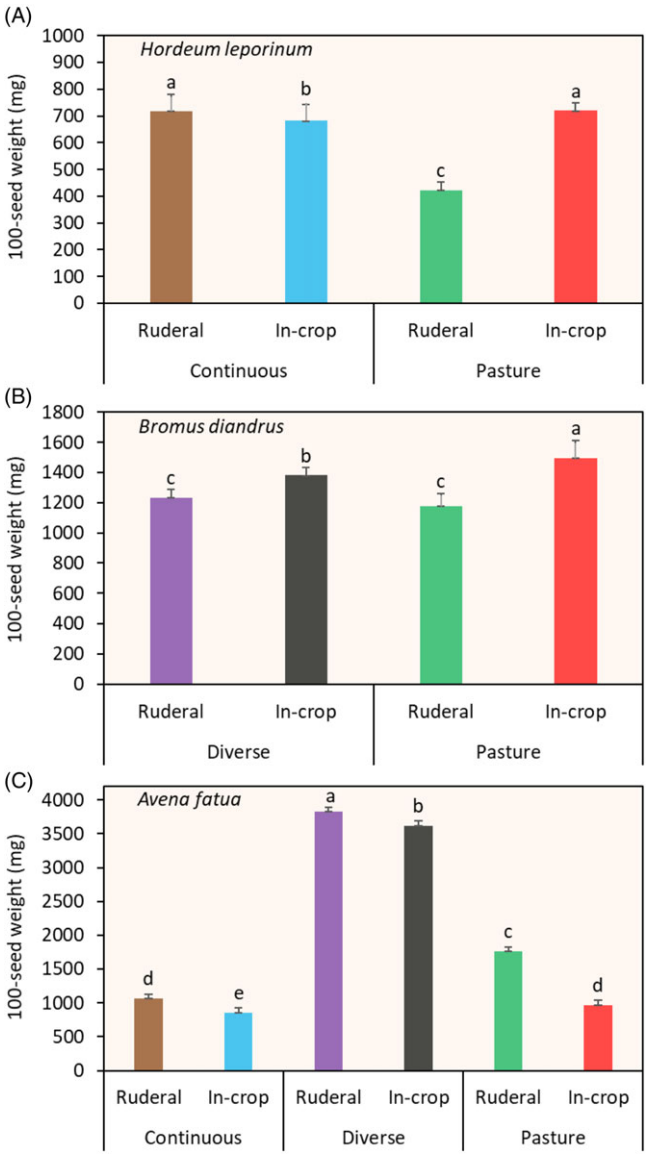

Figure 3. Effect of farming system (continuous, diverse, or pasture) and weed population habitat (in-crop vs. ruderal) on 100-seed weight of (A) *Hordeum leporinum*, (B) *Bromus diandrus*, and (C) *Avena fatua*. Different letters indicate significant differences between habitat among the farming systems at P < 0.05 (bars indicate SE).

3.3 mo for ruderal populations. For *B. diandrus*, D_{50} ranged from 2.6 to 4.7 mo for in-crop populations as compared with 1.5 to 2.3 mo for ruderal populations; D_{50} of *A. fatua* ranged from 3.3 to 5.9 mo for in-crop populations and 2.7 to 3.4 mo for ruderal populations (Table 4). There was no consistent effect of farming system on dormancy release rate. Farming system had a significant influence on D_{50} (Table 3), particularly for in-crop populations (Table 4). The *A. fatua* in-crop populations from the pasture system released seed dormancy faster (D_{50} of 3.3 mo) than the continuous (D_{50} of 4.3 mo) and diverse systems (D_{50} of 5.9 mo; P < 0.05). In contrast, *B. diandrus* in-crop populations from the diverse system released seed dormancy faster than in-crop populations from the pasture system (Table 4).

Seed size as inferred from 100-seed weight of the in-crop populations differed from their ruderal counterparts across farming systems. This study also found that farming system had a substantial influence on seed size (Table 3). In-crop *B. diandrus* populations had greater 100-seed weight than ruderal populations from the pasture and diverse systems (Figure 3). Additionally, the 100-seed weight of in-crop *H. leporinum* populations from the pasture system was 70% greater than for ruderal populations. The trend was consistent for *B. diandrus*, with 26% greater seed size for in-crop compared with ruderal populations from the same system. However, *H. leporinum* from the continuous system and *A. fatua* from all three systems showed the opposite trend. Under the continuous system, in-crop populations had lighter seeds than the ruderal populations for *H. leporinum* and *A. fatua*. *Avena fatua* from the pasture system showed a similar trend (P < 0.05; Figure 3). However, *B. diandrus* in-crop populations had greater seed weight than ruderal populations in the diverse

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Table 6. Association of seed dormancy (%) with 100-seed weight and developing herbicide resistance status of the three weed species in response to weed population habitat across farming systems.[a]

	Correlation (r) with seed dormancy[b]		
Herbicides/crops	*Hordeum leporinum* (*n* = 48)	*Bromus diandrus* (*n* = 42)	*Avena fatua* (*n* = 24)
100-seed weight	0.79****	0.85*	0.37**
Diclofop-methyl	—	—	0.84**
Mesosulfuron	—	—	0.74[c]
Pinoxaden	—	—	—
Sulfometuron[d]	0.72**	0.83*	—
Sulfosulfuron	0.90**	0.85*	—

[a]A dash (—) indicates the study did not include any population or the populations did not show significant correlation for these specific scenarios (*n* = no. of populations).
[b]Significance level of the correlation between herbicide resistance or 100-seed weight and seed dormancy: *P < 0.05; **P < 0.01, ****P < 0.0001.
[c]P < 0.09.
[d]Correlation between *B. diandrus* survival (%) to sulfometuron and 100-seed weight was 0.75* (P < 0.05).

farming system, but *A. fatua* in-crop populations had lighter seeds than their ruderal counterparts from the same system.

Developing herbicide resistance, assessed as the survival of plants following herbicide exposure, varied significantly among species, farming systems, and habitats (Tables 3 and 5). Overall, all ruderal populations of the three species did not survive the field rate of these herbicides, except for <1% of plants of *H. leporinum* when treated with clethodim (Table 5). *Hordeum leporinum* in-crop populations from the continuous system had greater DHR to ALS inhibitors than populations from the pasture system: sulfometuron (96% vs. 33%, respectively) and sulfosulfuron (67% vs. 36%, respectively) (P < 0.05). Moreover, *H. leporinum* in-crop populations in the pasture system showed low levels of DHR to clethodim (4%) and fluazifop (15%).

Bromus diandrus in-crop populations collected from the diverse system showed greater DHR to sulfosulfuron compared with populations collected from the pasture system (100% vs. 38%, respectively; P < 0.05). However, the opposite trend was evident for sulfometuron (38% vs. 100%, respectively) (Table 5). *Avena fatua* in-crop populations from the continuous farming system had DHR to diclofop-methyl (ACCase inhibitor), sethoxydim (ACCase inhibitor), flamprop-methyl (mitosis inhibitor), mesosulfuron (ALS inhibitor), and triallate (lipid synthesis inhibitor) (Table 5). In-crop populations of this weed in the diverse and pasture systems showed a similar DHR profile, except to flamprop-methyl and sethoxydim (i.e., susceptible).

Seed size, expressed as 100-seed weight, exhibited strong positive correlation with seed dormancy, irrespective of the farming system and habitat (Table 6). The correlation (r) was 0.79 for *H. leporinum* (P < 0.0001) and 0.85 for *B. diandrus* (P < 0.05). *Avena fatua* showed a low yet significant correlation (r = 0.37: P < 0.01) between seed size and dormancy. The seed size of *B. diandrus* was significantly correlated with sulfometuron DHR (r= 0.75; P < 0.05) (Table 6); however, this correlation was not evident for any other herbicides tested in this study (data not shown).

Populations with greater seed dormancy also exhibited greater DHR in the three weed species. This association was particularly evident for sulfometuron (r = 0.72, P < 0.01, and r = 0.83, P < 0.05, in *H. leporinum* and *B. diandrus*, respectively) and sulfosulfuron (r = 0.90, P < 0.01, and r = 0.85, P < 0.05, in *H. leporinum* and *B. diandrus*, respectively). This correlation was not significant for the other herbicides investigated for these two species (data not shown). A similar correlation between seed dormancy and DHR was identified in *A. fatua* populations for the ACCase inhibitor diclofop-methyl (r = 0.84, P < 0.01), but a weak correlation was seen with resistance to the ALS inhibitor mesosulfuron (r = 0.74, P < 0.09) (Table 6).

This study found that *H. leporinum*, *B. diandrus,* and *A. fatua* present in intensively managed situations such as continuously cropped fields exhibit a higher level of seed dormancy compared with their counterparts from surrounding ruderal areas. Moreover, the annual crop populations of *H. leporinum* and *B. diandrus* tended to have greater seed size compared with ruderal populations. Several factors related to plant genetics as well as cropping practices might contribute to these differences observed between populations in cropped and non-cropped areas. While genotype plays a critical role in determining seed size and dormancy across plant species (Baskin and Baskin 2001; Fenner 1991), soil moisture stress and other stresses at any critical growth stage can alter or reduce seed size and can also reduce seed dormancy level, as determined in *L. rigidum* (Goggin et al. 2010; Steadman et al. 2004). Intensive cropping in semiarid (nonirrigated) arable land often leads to faster uptake of soil moisture by successive, early-maturing crops compared with natural grassland situations (Liu et al. 2015; Niu et al. 2015), creating a relative drought condition for weed seed production. This situation may lead to increased seed dormancy or reduced seed germination, as reported by Cici (2017) in cowcockle [*Vaccaria hispanica* (Mill.) Rauschert]. Such a cropping practice–induced survival strategy may decrease the risk of reproductive failure in weeds and increase their persistence in arable lands, especially under temporal environmental uncertainty.

We report that larger seeds had significantly more dormancy in all three weed species in the study. Gardarin and Colbach (2014) analyzed the seed size and dormancy in a number of weed species, including smooth pigweed (*Amaranthus hybridus* L.), and reported that larger seeds had higher levels of dormancy, in agreement with Grime et al. (1981), who analyzed more than 400 species collected in Sheffield, UK. Although Maity et al. (2021b) did not observe any strong correlation between *L. perenne* ssp. *multiflorum* seed size and dormancy, Rubio de Casas et al. (2017) and Chen et al. (2020) noted that plant species with large seeds usually exhibit reduced dormancy and can thrive in relatively unfavorable growing conditions. Their latter conclusion regarding stressful growing conditions agrees with findings in the present study in that the high dormant populations (correlated with large seed size) showed increased survivability to herbicide application, an imposed plant stress.

Larger seed size can promote increased vigor of the emerging seedlings leading to more robust plants in general (Bean 1972; Bebawi et al. 1984; Marcos-Filho 2015; Naylor and Jana 1976), which ultimately strengthens a weed's ability to persist in adverse environments (Bu et al. 2007; Buckley et al. 2003; Guillemin and Chauvel 2011). Weeds with greater seed mass or weight also facilitate range expansion potential, as reported by Daws et al. (2007) in a meta-analysis of 376 species and by Anderson (1990) investigating narrowleaf hawksbeard (*Crepis tectorum* L). Nurse and DiTommaso (2005) observed fewer velvetleaf (*Abutilon theophrasti* Medik) seeds produced in-crop under high corn (*Zea mays* L.) competition as compared with the field edges. Conditions leading to a reduction in the number of seeds often results in the production of larger seeds due to higher resource allocation per seed that may aid population persistence (Gallagher et al. 2013; Sawhney and Naylor 1982). Larger seeds promote faster growth, which may facilitate plants to develop to an advanced stage of growth that is less than optimum for effective herbicidal control.

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Consequently, the larger plants likely receive a lower dose than required for control, which can gradually lead to quantitative herbicide resistance evolution (Manalil et al. 2011). Although larger seed size was not generally associated with high DHR in this study, sulfometuron DHR in *B. diandrus* showed considerable positive correlation with seed size. Maity et al. (2021a) reported that *L. perenne* ssp. *multiflorum* seeds with larger size exhibited significantly greater resistance to multiple herbicides. Conducting additional studies with globally important weed species will provide further insights into this association.

There is a substantial level of DHR to multiple herbicide chemistries in all three weed species in this study. Widespread evolution of herbicide-resistant weed populations is now common in Australia for the major arable weeds, including *Avena* spp., *Bromus* spp., and *Hordeum* spp. (Broster et al. 2011; Heap 2021; Owen and Powles 2009, 2016). As ACCase and ALS inhibitors are the most frequently used herbicides to selectively control these weed species in a crop, resistance evolution to these high-risk herbicides is an inadvertent but expected outcome of their recurrent usage.

We found a direct and positive correlation between DHR (in-crop habitat) and seed dormancy of populations of the three species in this study. This finding substantiates a widespread view that weed populations in intensive cropping systems exhibit greater seed dormancy than those populations inhabiting pasture or non-cropped areas (Gundel et al. 2008; Owen et al. 2011; Vila-Aiub et al. 2005). Owen et al. (2015a, 2015b) reported a consistent trend of higher seed dormancy in *L. rigidum* and *Bromus* spp. populations from within intensively cropped fields that exhibited substantial resistance to different ACCase and ALS inhibitors. They postulated that the dormant cohort of a weed population escapes the pre-sowing weed management tools (preemergence herbicides or tillage) and thus augments the population with dormant individuals. These later-emerging individuals are exposed to repeated application of selective postemergence herbicides and eventually evolve resistance (Maity et al. 2021a). Similar phenomena were observed in *Hordeum* spp. in response to ALS-inhibiting and bipyridyl herbicides in WA (Owen et al. 2012; Yu et al. 2007), ACCase-inhibiting herbicides in southern Australia (Shergill et al. 2015), and ACCase-inhibiting and bipyridyl herbicides in eastern Australia (Heap 2021; Tucker and Powles 1991), and in *A. fatua* in response to herbicides of multiple sites of action including ALS inhibitors in Montana, USA (Lehnhoff et al. 2013) and WA (Owen and Powles 2016). However, these studies did not focus on quantifying the degree of correlation between the levels of seed dormancy and herbicide resistance.

The in-crop weed populations in this study were exposed to similar herbicide chemistries for at least 5 yr. Weed control measures are often applied repetitively at the same growth stage of the weeds, which may lead to a gradual but steady evolutionary shift to evade such measures (Sun et al. 2021). Co-occurrence of higher seed dormancy and DHR in the in-crop populations of *H. leporinum*, *B. diandrus*, and *A. fatua* tested in this study supports this assumption. However, coevolution or coexistence of herbicide resistance and seed dormancy observed in recent studies is a complex ecological phenomenon to decipher. Selection of resistance with recurrent herbicide use may not directly lead to an increase in seed dormancy (Gundel et al. 2008) or vice versa.

Darmency et al. (2017) surmised that the linkage between seed dormancy and herbicide resistance may arise through selection of both traits simultaneously (pleiotropy). Two traits can arise simultaneously via separate mechanisms: the production by a single gene of two or more apparently unrelated effects (Gundel et al. 2008) or linkage between two separate genes conferring dormancy and resistance (Jordan 1999), though the latter is a rare process (Délye et al. 2013b). Délye et al. (2013a) postulated that single-locus mutations (similar to target-site mutations) and complex multigenic stress responses (similar to non–target site mutations) in weeds may underlie the simultaneous evolution of multiple traits. In recent studies, single-locus resistance mutations have sometimes been linked to seed biochemical compositions that alter seed germination dynamics, such as fatty acids (Tremolières et al. 1988), abscisic acid (Topuz et al. 2015; Touraud et al. 1987), and branched-chain amino acids (Eberlein et al. 1999). However, *ALS* mutations are expected to promote faster germination because of lower abscisic acid content (Topuz et al. 2015), as abscisic acid is associated with higher dormancy (Kermode 2005). Yet evolution of weed populations with greater seed dormancy and tolerance to ALS-inhibiting herbicides, as evident from multiple recent studies including the present study, contradicts these assumptions. Much more research is required to understand the causal factors influencing this association. In general, epistatic interactions between alleles at different loci may impact the selection of weed traits that enhance fitness (Leon et al. 2021).

It has been clearly demonstrated that along with the widespread evolution of herbicide resistance, herbicide-dependent farming systems also select for weed life cycle traits that enable weeds to evade control practices. This study illustrates the ability of in-crop *H. leporinum*, *B. diandrus*, and *A. fatua* populations exposed to recurrent herbicide selection to escape early-season herbicide application through enhanced dormancy, as previously documented (Fleet and Gill 2012; Kleemann and Gill 2006; Owen et al. 2011). The combination of increased seed dormancy and herbicide resistance poses a tremendous ecological and agronomic challenge as populations with greater seed dormancy are able to evade the use of preseeding tillage or effective preemergence herbicide applications. These attributes can lead to increased usage of postemergence herbicides and limit the diversity of weed control tactics applied later in the crop season, which may lead to an increased selection intensity for herbicide resistance. In Australia, the net effect of prolonged weed seed dormancy on crop and weed growth and seed yield will depend on the duration of preemergence herbicide bioactivity in soil (e.g., pyroxasulfone greater than trifluralin), competitiveness of the crop species (e.g., cereals more competitive than pulses), period of the growing season (time required for crop canopy closure, emergence time differential between crop and dormant weeds, duration of crop growth advantage as soils cool going into winter), and timing of precipitation events.

While this study demonstrates that simultaneous evolution of both weed seed traits and DHR is occurring, such widespread adaptations need not be inevitable. The application of sufficient weed control diversity involving cultural, physical/mechanical, and herbicidal weed control tools within a crop–weed competitive environment has been demonstrated to reduce weed seedbanks to low and manageable levels (Sun et al. 2021; Walsh et al. 2017). Weed management diversity should help mitigate unidirectional selection pressures driving weed-trait adaptations. By minimizing weed seedbanks through maximizing crop competition, preharvest nonselective herbicide application (spray topping) when required, and harvest weed seed control (destroying or removing weed seeds in the chaff fraction of harvested crop residue), growers can limit the number of weeds under selection and thereby help mitigate

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further shifts in resistance evolution in response to herbicide exposure and physiological or phenological adaptations to evade weed control practices.

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References

Anderson S (1990) The relationship between seed dormancy, seed size and weediness in *Crepis tectorum* (Asteraceae). Oecologia 83:277–280

Ashworth MB, Walsh MJ, Flower KC, Vila-Aiub MM, Powles SB (2016) Directional selection for flowering time leads to adaptive evolution in *Raphanus raphanistrum* (wild radish). Evol Appl 9:619–629

Barrett SCH (1983) Crop mimicry in weeds. Econ Bot 37:255–282

Baskin CC, Baskin JM (2001) Seeds: ecology, biogeography, and evolution of dormancy and germination. Nordic J Bot 20:598–598

Baucom RS (2019) Evolutionary and ecological insights from herbicide-resistant weeds: what have we learned about plant adaptation, and what is left to uncover? New Phytol 223:68–82

Bean EW (1972) Seed Quality: Its Variation, Control and Importance in Breeding and Varietal Assessment. Report of the Welsh Plant Breeding Station. Penglais, Ceredigion, U.K: Aberystwyth University. 194 p

Bebawi FF, Eplee RE, Norris RS (1984) Effects of seed size and weight on witchweed (*Striga asiatica*) seed germination, emergence, and host-parasitization. Weed Sci 32:202–205

Beckie H (2006) Herbicide-resistant weeds: management tactics and practices. Weed Technol 20:793–814

Bolger TP, Chapman R, Le Coultre IF (1999) Seed dormancy release in three common pasture grasses from a Mediterranean-type environment under contrasting conditions. Aust J Exp Agric 39:143–147

Broster JC, Koetz EA, Wu H (2011) Herbicide resistance in wild oats (*Avena spp.*) in southern New South Wales. Plant Prot Q 26:106–107

Bu H, Chen X, Xu X, Liu K, Jia P, Du G (2007) Seed mass and germination in an alpine meadow on the eastern Tsinghai-Tibet plateau. Plant Ecol 191:127–149

Buckley YM, Downey P, Fowler SV, Hill R, Memmot J, Norambuena H, Pitcairn M, Shaw R, Sheppard AW, Winks C, Wittenberg R, Rees M (2003) Are invasives bigger? A global study of seed size variation in two invasive shrubs. Ecology 84:1434–1440

Chauhan BS, Gill G, Preston C (2006) Influence of tillage systems on vertical distribution, seedling recruitment and persistence of rigid ryegrass (*Lolium rigidum*) seed bank. Weed Sci 54:669–676

Chen SC, Poschlod P, Antonelli A, Liu U, Dickie JB (2020) Trade-off between seed dispersal in space and time. Ecol Lett 23:1635–1642

Cici SZH (2017) Maternal environment modulates dormancy and germination in *Vaccaria hispanica.* Agrotechnology 6:e1000154

Darmency H, Colbach N, Corre VL (2017) Relationship between weed dormancy and herbicide rotations: implications in resistance evolution. Pest Manag Sci 73:1994–1999

Dastheib F, Rolston MP, Archie WJ (2003) Chemical control of brome grasses (*Bromus* spp.) in cereals. New Zealand Plant Prot 56:227–232

Daws MI, Hall J, Flynn S, Pritchard HW (2007) Do invasive species have bigger seeds? Evidence from intra- and inter-specific comparisons. S Afr J Bot 73:138–143

Délye C, Jasieniuk M, Le Corre V (2013a) Deciphering the evolution of herbicide resistance in weeds. Trends Genet 29:649–658.

Délye C, Menchari Y, Michel S, Cadet E, Le Corre V (2013b) A new insight into arable weed adaptive evolution: mutations endowing herbicide resistance also affect germination dynamics and seedling emergence. Ann Bot 111:681–691

Eberlein CV, Guttieri MJ, Berger PH, Fellman JK, Mallory-Smith CA, Thill DC, Baerg RJ, Belknap WR (1999) Physiological consequences of mutation for ALS-inhibitor resistance. Weed Sci 47:383–392

Fenner M (1991) The effects of the parent environment on seed germinability. Seed Sci Res 1:75–84

Fleet B, Gill G (2012) Seed dormancy and seedling recruitment in smooth barley (*Hordeum murinum* ssp. *glaucum*) populations in southern Australia. Weed Sci 60:394–400

Gallagher RS, Granger KL, Snyder AM, Pittmann D, Fuerst EP (2013) Implications of environmental stress during seed development on reproductive and seed bank persistence traits in wild oat (*Avena fatua* L.). Agronomy 3:537–549.

Gardarin A, Colbach N (2014) How much of seed dormancy in weeds can be related to seed traits? Weed Res 55:14–25

Ghanizadeh H, Harrington KC (2019) Ecological evidence for the fitness trade-off in triazine resistant *Chenopodium album* L.: can we exploit the cost of resistance? Agronomy 9:e9090523

Ghersa CM, Martınez-Ghersa MA, Brewer TG, Roush ML (1994) Selection pressures for diclofop-methyl resistance and germination time of Italian ryegrass. Agron J 86:823–828

Goggin DE, Emery RJN, Powles SB, Steadman KJ (2010) Initial characterization of low and high seed dormancy populations of *Lolium rigidum* produced by repeated selection. J Plant Physiol 167:1282–1288

Grime JP, Mason G, Curtis AV, Rodman J, Band SR, Mowforth MAG, Neil AM, Shaw S (1981) A comparative study of germination characteristics in a local flora. J Ecol 69:1017–1059

Guillemin J, Chauvel B (2011) Effects of the seed weight and burial depth on the seed behavior of common ragweed (*Ambrosia artemisiifolia*). Weed Biol Manag 11:217–223

Gundel PE, Martinez-Ghersa MA, Ghersa CM (2008) Dormancy, germination and ageing of *Lolium multiflorum* seeds following contrasting herbicide selection regimes. Eur J Agron 28:606–613

Guo L, Qiu J, Li LF, Lu B, Olsen K, Fan L (2018) Genomic clues for crop-weed interactions and evolution. Trends Plant Sci 23:1102–1115

Harris JR, Gosset BJ, Toler JE (1995) Growth characteristics of selected dinitroaniline-resistant and -susceptible goosegrass (*Eleusine indica*) populations. Weed Technol 9:561–567

Heap IM (2021) The International Herbicide-Resistant Weed Database. http://www.weedscience.org. Accessed: November 4, 2021

Henckes JR, Cechin J, Schmitz MF, Piasecki C, Vargas L, Agostinetto D (2019) Fitness cost and competitive ability of ryegrass susceptible and with multiple resistance to glyphosate, iodosulfuron-methyl, and pyroxsulam. Planta Daninha 37:e019197532

Holt JS, Thill DC (1994) Growth and productivity of resistant plants. Pages 299–316 *in* Powles SB, Holtum JAM, eds. Herbicide Resistance in Plants. Biology and Biochemistry. Boca Raton, FL: Lewis Publishers

Jasieniuk M, Brulé-Babel AL, Morrison IN (1996) The evolution and genetics of herbicide resistance in weeds. Weed Sci 44:176–193

Jordan N (1999) Fitness effects of the triazine resistance mutation in *Amaranthus hybridus*: relative fitness in maize and soybean crops. Weed Res 39:493–505

Kermode AR (2005) Role of abscisic acid in seed dormancy. J Plant Growth Regul 2:319–344

Kleemann SGL, Gill GS (2006) Differences in the distribution and seed germination behaviour of populations of *Bromus rigidus* and *Bromus diandrus* in South Australia: adaptations to habitat and implications for weed management. Aust J Agric Res 57:213–222

Lehnhoff EA, Keith BK, Dyer WE, Peterson RK, Menalled F (2013) Multiple herbicide resistance in wild oat and impacts on physiology, germinability, and seed production. Agron J 105:854–862

Leon RG, Dunne JC, Gould F (2021) The role of population and quantitative genetics and modern sequencing technologies to understand evolved herbicide resistance and weed fitness. Pest Manag Sci 77:12–21

Liu Y, Pan Z, Zhuang Q, Miralles DG, Teuling AJ, Zhang T, An P, Dong Z, Zhang J, He D, Wang L, Pan X, Bai W, Niyogi D (2015) Agriculture intensifies soil moisture decline in Northern China. Sci Rep 5:e11261

Llewellyn R, D'Emden F, Kuehne G (2012) Extensive use of no-tillage in grain growing regions of Australia. Field Crops Res 132:204–212

https://doi.org/10.1017/wsc.2022.15 Published online by Cambridge University Press

Llewellyn RS, Ronning D, Ouzman J, Walker S, Mayfield A, Clarke M (2016) Impact of Weeds on Australian Grain Production: the Cost of Weeds to Australian Grain Growers and the Adoption of Weed Management and Tillage Practices. Report for GRDC. Canberra, ACT, Australia: CSIRO. 112 p

Maity A, Singh V, Jessup R, Bagavathiannan M (2021a) Seed traits correlate with herbicide resistance in Italian ryegrass (*Lolium perenne* spp. *multiflorum*). Pest Manag Sci 77:2756–2765

Maity A, Singh V, Martins MB, Ferreira PJ, Bagavathiannan M (2021b) Species identification and morphological trait diversity assessment in ryegrass (*Lolium* spp.) populations from Texas Blacklands. Weed Sci 69:379–392

Manalil S, Busi R, Renton M, Powles S (2011) Rapid evolution of herbicide resistance by low herbicide dosages. Weed Sci 59:210–217

Marcos-Filho J (2015) Seed vigor testing: an overview of the past, present and future perspective. Sci Agric 72:363–374

Martinez-Ghersa MA, Ghersa CM, Benech-Arnold RL, Mac Donough R, Sanchez RA (2000) Adaptive traits regulating dormancy and germination of invasive species. Plant Spec Biol 15:127–137

Mortimer AM (1997) Phenological adaptation in weeds—an evolutionary response to the use of herbicides? Pestic Sci 51:299–304

Murphy CE, Lemerle D (2006) Continuous cropping systems and weed selection. Euphytica 148:61–73

Nandula VK, Poston DH, Reddy KN (2009) Seed germination differences between glyphosate- resistant and -susceptible Italian ryegrass populations. Seed Technol 31:123–133

Naylor JM, Jana S (1976) Genetic adaptation for seed dormancy in *Avena fatua*. Can J Bot 54:306–312

Niu CY, Musal A, Liu Y (2015) Analysis of soil moisture condition under different land uses in the arid region of Horqin sandy land, northern China. Solid Earth 6:1157–1167

Nurse RE, DiTommaso A (2005) Corn competition alters the germinability of velvetleaf (*Abutilon theophrasti*) seeds. Weed Sci 53:479–488

Owen MJ, Goggin DE, Powles SB (2012) Identification of resistance to either paraquat or ALS- inhibiting herbicides in two Western Australian *Hordeum leporinum* biotypes. Pest Manag Sci 68:757–763

Owen MJ, Goggin DE, Powles SB (2015a) Intensive cropping systems select for greater seed dormancy and increased herbicide resistance levels in *Lolium rigidum* (annual ryegrass). Pest Manag Sci 71:966–971

Owen MJ, Martinez NJ, Powles SB (2015b) Herbicide resistance in *Bromus* and *Hordeum* spp. in the Western Australian grain belt. Crop Pasture Sci 66:466–473

Owen MJ, Michael PJ, Renton M, Steadman KJ, Powles SB (2011) Towards large-scale prediction of *Lolium rigidum* emergence. II. Correlation between dormancy and herbicide resistance levels suggests an impact of cropping systems. Weed Res 51:133–141

Owen MJ, Powles SB (2009) Distribution and frequency of herbicide-resistant wild oat (*Avena* spp.) across the Western Australian grain belt. Crop Pasture Sci 60:25–31

Owen MJ, Powles SB (2016) The frequency of herbicide-resistant wild oat (*Avena* spp.) populations remains stable in Western Australian cropping fields. Crop Pasture Sci 67:520–527

Park KW, Mallory-Smith CA, Ball DA, Mueller-Warrant GW (2004) Ecological fitness of acetolactate synthase inhibitor-resistant and -susceptible downy brome (*Bromus tectorum*) biotypes. Weed Sci 52:768–773

Paterson JG (1976) Wild oats in Western Australia. J Dept Agric Western Australia 17:90–95

Poole ML, Gill GS (1987) Competition between crops and weeds in southern Australia. Plant Prot Q 2:86–96

Rees M (1996) Evolutionary ecology of seed dormancy and seed size. Phil Trans R Soc London B351:1299–1308

Rubio de Casas R, Willis CG, Pearse WD, Baskin CC, Baskin JM, Cavender-Bares J (2017) Global biogeography of seed dormancy is determined by seasonality and seed size: a case study in the legumes. New Phytol 214:1527–1536

Sawhney R, Naylor JM (1982) Dormancy studies in seed of *Avena fatua* 13: influence of drought stress during seed development on the duration of seed dormancy. Can J Bot 60:1016–1020

Shergill LS, Malone J, Boutsalis P, Preston C, Gill G (2015) Target-site point mutations conferring resistance to ACCase-inhibiting herbicides in smooth barley (*Hordeum glaucum*) and hare barley (*Hordeum leporinum*). Weed Sci 63:408–415

Steadman KJ, Ellery AJ, Chapman R, Moore A, Turner NC (2004) Maturation temperature and rainfall influence seed dormancy characteristics of annual ryegrass (*Lolium rigidum*). Aust J Agric Res 55:1047–1057

Sun C, Ashworth MB, Flower K, Vila-Aiub MM, Rocha RL, Beckie HJ (2021) The adaptive value of flowering time in wild radish (*Raphanus raphanistrum*). Weed Sci 69:203–209

Topuz M, Nemli Y, Fatima T, Mattoo AK (2015) Seed dormancy is modulated in recently evolved chlorsulfuron-resistant Turkish biotypes of wild mustard (*Sinapis arvensis*). Front Chem 3:46

Touraud G, Leydecker MT, Darmency H (1987) Abscisic acid in triazine-resistant and susceptible *Poa annua*. Plant Sci 49:81–83

Tremolières A, Darmency H, Gasquez J, Dron M, Connan A (1988) Variation of transhexadecenoic acid content in two triazine resistant mutants of *Chenopodium album* and their susceptible progenitor. Plant Physiol 86:967–970

Tucker ES, Powles SB (1991) A biotype of hare barley (*Hordeum leporinum*) resistant to paraquat and diquat. Weed Sci 39:159–162

Verma P, Majee M (2013) Seed germination and viability test in tetrazolium (TZ) assay. Bio- protocol 3:e884

Vigueira C, Olsen K, Caicedo A (2013) The Red Queen in the corn: agricultural weeds as models of rapid adaptive evolution. Heredity 110:303–311

Vila-Aiub MM, Neve P, Powles SB (2005) Resistance cost of a cytochrome P450 herbicide metabolism mechanism but not an ACCase target site mutation in a multiple resistant *Lolium rigidum* population. New Phytol 167:787–796

Walsh MJ, Broster JC, Schwartz-Lazaro LM, Norsworthy JK, Davis AS, Tidemann BD, Beckie HJ, Lyon DJ, Soni N, Neve P, Bagavathiannan MV (2017) Opportunities and challenges for harvest weed seed control in global cropping systems. Pest Manag Sci 74:2235–2245

Warwick SI, Briggs D (1979) Genecology of lawn weeds. 3. Cultivation experiments with *Achillea millefolium* L., *Bellis perennis* L., *Plantago lanceolata* L., *Plantago major* L. and *Prunella vulgaris* L. collected from lawns and contrasting grassland habitats. New Phytol 83:509–536

Watkinson AR, White J (1985) Some life-history consequences of modular construction in plants. Phil Trans R Soc London Ser B 313:31–51

Wiederholt RJ, Stoltenberg DE (1996) Similar fitness between large crabgrass (*Digitaria sanguinalis*) accessions resistant or susceptible to acetyl-coenzyme A carboxylase inhibitors. Weed Technol 10:42–49

Yanniccari M, Vila-Aiub MM, Istilart C, Acciaresi H, Castro AM (2016) Glyphosate resistance in perennial ryegrass (*Lolium perenne* L.) is associated with a fitness penalty. Weed Sci 64:71–79

Yu Q, Nelson K, Zheng MQ, Jackson M, Powles S (2007) Molecular characterisation of resistance to ALS-inhibiting herbicides in *Hordeum leporinum* biotypes. Pest Manag Sci 63:918–927

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