

Herbicide resistance in *Bromus* spp.: a global review

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Review

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Abstract

This review summarizes what is currently known about herbicide resistance in *Bromus* spp. worldwide. Additional information on the biology and genetics of *Bromus* spp. is provided to further the understanding of resistance evolution and dispersal of the different species. Cases of herbicide resistance have been confirmed in *Bromus catharticus* Vahl., *Bromus commutatus* Schrad. (syn.: *Bromus racemosus* L.), *Bromus diandrus* Roth, *Bromus japonicus* Thunb. (syn.: *Bromus arvensis* L.), *Bromus madritensis* L., *Bromus rigidus* Roth (syn.: *Bromus diandrus* Roth ssp. *diandrus*), *Bromus rubens* L., *Bromus secalinus* L., *Bromus sterilis* L., and *Bromus tectorum* L. in 11 countries. *Bromus* spp. populations have evolved cross- and multiple resistance to six herbicide sites of action: acetyl-coenzyme A carboxylase, acetolactate synthase, photosystem II, very-long-chain fatty-acid, 5-enolpyruvylshikimate-3-phosphate synthase, and 4-hydroxyphe-nylpyruvate dioxygenase inhibitors. Resistance mechanisms varied from target-site to non-target site or a combination of both. *Bromus* spp. are generally highly self-pollinated, but outcrossing can occur at low levels in some species. *Bromus* spp. have different ploidy levels, ranging from diploid ($2n = 2x = 14$) to duodecaploid ($2n = 12x = 84$). Herbicide resistance in *Bromus* spp. is a global issue, and the spread of herbicide-resistance alleles primarily occurs via seed-mediated gene flow. However, the transfer of herbicide-resistance alleles via pollen-mediated gene flow is possible.

Introduction

Bromus (Poaceae) is a large genus of grasses that includes nearly 160 C_3 species with wide geographic distribution (Acedo and Llamas 2001). The genus contains annuals, biennials, and perennials either self- or cross-pollinated and adapted to a wide range of environmental conditions (Armstrong 1991). This genus is well known for its complex taxonomy (Acedo and Llamas 1999) due to morphological variation, plasticity, and hybridization (Fortune et al. 2008). Polyploidy and hybridization have played a major role in the evolution of this genus, resulting in a diversity of species with a different number of chromosomes and genome sizes (Stebbins 1981). The *Bromus* genus contains species with ploidy levels ranging from diploid ($2n = 2x = 14$) to duodecaploid ($2n = 12x = 84$) with the basic chromosome number $x = 7$ (Williams et al. 2011).

Bromus spp. have been treated in multiple ways by taxonomists because of the complexity of this genus. Tzvelev (1976) classified the species into five distinct genera: *Eubromus*, *Bromus*, *Ceratochloa*, *Neobromus*, and *Bromopsis*. Smith (1970) divided the species into six sections: *Genea*, *Bromus*, *Ceratochloa*, *Neobromus*, *Nevskiella*, and *Pnigma*. Stebbins (1981) took an intermediate position and distributed the species into seven subgenera: *Festucaria*, *Ceratochloa*, *Stenobromus*, *Bromus*, *Neobromus*, *Nevskiella*, and *Boissiera*. Smith's classification based on "sections" has been the most used since its publication in 1970. The sections are differentiated morphologically according to the number of nerves in the glumes, spikelet shape, and lemma and awn morphology, in addition to karyotypes, genome relationships (chromosome pairing), ploidy levels, and serological differences (Williams et al. 2011). Among the six sections, the major agricultural species are in the *Ceratochloa* (*Bromus catharticus* Vahl., *Bromus sitchensis* Trin.) and *Pnigma* (*Bromus inermis* Leyss.) sections, whereas several species in the *Genea* (*Bromus tectorum* L., *Bromus sterilis* L., *Bromus rubens* L., *B. madritensis* L., *Bromus rigidus* Roth [syn.: *Bromus diandrus* Roth ssp. *diandrus*]) and *Bromus* (*Bromus japonicus* Thunb. [syn.: *Bromus arvensis* L.], *Bromus secalinus* L., *Bromus commutatus* Schrad. [syn.: *Bromus racemosus* L.]) sections are troublesome weeds of both agricultural and nonagricultural systems (Williams et al. 2011).

Weeds are the main limiting factor in agricultural systems, because they reduce crop yield and profitability (Ghersa and Roush 1993; Patterson 1995; Swanton and Weise 1991).

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Herbicides are considered the most cost-effective available tool for achieving successful weed control (Heap 1997; Pleasant et al. 1994). However, the continuous reliance on weed management programs based heavily on herbicides has selected numerous herbicide-resistant weeds (Holt 1992; Moss and Rubin 1993; Powles and Howat 1990), including *Bromus* spp. (Table 1).

Herbicide-resistance mechanisms in weed species fall into two categories: (1) resistance conferred by mutations in the herbicide target enzyme or gene amplification (target-site resistance [TSR]) and (2) resistance conferred by mechanisms not involving the target enzyme (non-target site resistance [NTSR]) (Délye et al. 2013; Gaines et al. 2020). TSR is typically determined by monogenic traits (i.e., conferred by major alleles) (Délye et al. 2013; Scarabel et al. 2015). Conversely, NTSR can be under monogenic or polygenic control (i.e., governed by multiple alleles) (Busi et al. 2013; Scarabel et al. 2015). NTSR mechanisms can be the result of physiological and biochemical alterations such as reduced herbicide absorption and translocation, enhanced herbicide metabolism, and herbicide vacuolar sequestration (Jugulam and Shyam 2019; Yuan et al. 2007). NTSR is of particular concern, because it can confer resistance to herbicides from different chemical families across multiple sites of action (SOAs), including herbicides not commercially available (Ma et al. 2013; Petit et al. 2010; Preston 2003), thus limiting the herbicide options for weed control.

The evolution of herbicide resistance in *Bromus* spp. is of concern. Currently, there are 40 reports of herbicide resistance in the genus, including the diploids ($2n = 2x = 14$) *B. japonicus*, *B. sterilis*, and *B. tectorum*; the tetraploids ($2n = 4x = 28$) *B. commutatus*, *B. madritensis*, *B. rubens*, and *B. secalinus*; the hexaploids ($2n = 6x = 42$) *B. catharticus* and *B. rigidus*; and the octoploid ($2n = 8x = 56$) *B. diandrus* (Table 1). Herbicide resistance to six SOAs has been reported in *Bromus* spp.: acetyl-coenzyme A carboxylase (ACCase, Group 1), acetolactate synthase (ALS, Group 2), photosystem II (PSII, Groups 5 and 7), very-long-chain fatty-acid (VLCFA, Group 15), 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS, Group 9), and 4-hydroxyphenylpyruvate dioxygenase (HPPD, Group 27) inhibitors. Cross-resistance is prevalent in *Bromus* spp., with 20 reports confirmed in six countries, including Australia, the Czech Republic, France, Germany, the United Kingdom, and the United States. Instances of cross-resistance include resistance to ACCase and ALS inhibitors (Ball et al. 2007; Davies et al. 2020; Kumar and Jha 2017; Owen et al. 2012, 2015; Ribeiro et al. 2023; Sen et al. 2021). Multiple resistance is less common, with four cases confirmed in *Bromus* spp. In some regions, such as the United States Pacific Northwest, multiple resistance to two and four SOAs has been reported: the four SOAs were ACCase, ALS, PSII, and VLCFA (Mallory-Smith et al. 1999; Park et al. 2004; Park and Mallory-Smith 2004, 2005), and to two SOAs were ACCase and ALS inhibitors (Zuger and Burke 2020). The two other cases of multiple resistance were documented in Spain, with resistance to both ALS and EPSPS inhibitors (Escorial et al. 2011); and in China, with resistance to four SOAs: ACCase, ALS, PSII, and HPPD inhibitors (Lan et al. 2022).

Because of the worldwide importance of the *Bromus* genus and the increasing cases of herbicide resistance, a comprehensive review that summarizes what is known about herbicide resistance in *Bromus* spp. is needed. Therefore, the objective of this review is to provide an update on the status of herbicide resistance in *Bromus* spp. globally and what is known about the resistance mechanisms. Additionally, relevant information,

including the biology and genetics of *Bromus* spp., is provided to further the understanding of the resistance evolution and dispersal of the different species.

Bromus catharticus

Bromus catharticus, commonly known as prairie grass or rescue grass, is one of the major agricultural species of forage grass in the *Bromus* genus (Abbott et al. 2012). Native to South America, *B. catharticus* is an annual or short-lived perennial cool-season grass that has been introduced on a wide geographic scale, including Europe, Africa, Asia, Australia, New Zealand, and North America (Aulicino and Arturi 2002; Muzafar et al. 2016; Williams et al. 2011). This species is considered a valuable forage crop because of its high biomass production, fast growth rate during winter and spring, great adaptability, and ability to remain green after seed maturation (Sun et al. 2021). In the Pampas of Argentina, *B. catharticus* is cultivated as a winter forage crop for grazing, but it can also behave as a weed in several winter crops such as wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), and pea (*Pisum sativum* L.) (Poggio et al. 2004; Yannicari et al. 2021). *Bromus catharticus* typically germinates in midsummer and fall (Ahumada and Troiani 2016; Iroulart 2020), when applications of glyphosate are extensively performed for weed control before to planting winter cereals such as wheat and barley (Vigna et al. 2014). If not controlled preplanting, *B. catharticus* can cause yield losses of up to 70% in these crops (Iroulart 2020).

Biology and Genetics

Bromus catharticus reproduces entirely by seeds, and its inflorescences consist of drooping panicles with spikelets that are strongly laterally compressed and attached to 2- to 4-cm-long pedicels (Auld and Medd 1987). Lemmas have a short awn (<5 mm) arising right below the apex. *Bromus catharticus* can produce both cleistogamous (closed) and chasmogamous (open) flowers, but its reproduction is mainly through self-pollination, although outcrossing can occur (Gutierrez and Pensiero 1998; Naranjo 1992; Rosso et al. 2009; Table 2). The outcrossing rate for this species was estimated to be 1.8% (Morant et al. 1994). Flowering depends on flower morphology, photoperiod, and soil moisture (Ragonese and Marcó 1941, 1943). For instance, the chasmogamic flowering period typically happens at the beginning of spring, and the cleistogamic period at the end of spring and during the summer (Perez López 1975).

Bromus catharticus is a hexaploid species ($2n = 6x = 42$; AABBCC; 12.36-Gb genome size) in the *Ceratocloa* section (Stebbins and Tobgy 1944; Table 2), with a nuclear DNA content of 12.64 pg (Klos et al. 2009). This species has an allopolyploid origin that probably arose through hybridization between extinct diploid ($2x$) and tetraploid ($4x$) species (Stebbins 1956).

Despite being predominantly self-pollinated, hybridization between *B. catharticus* and other *Bromus* spp. is possible (Table 3). *Bromus catharticus* can hybridize with *Bromus bonariensis* Parodi & J.A. Cámara, *Bromus brevis* Nees ex Steud. (syn.: *B. catharticus*), *Bromus parodii* Covas & Itria (Naranjo 1992), *Bromus carinatus* Hook. & Arn. (Stebbins and Tobgy 1944), and *Bromus haenkeanus* (J. Presl) Kunth (syn.: *B. catharticus*) (Hall 1955). *Bromus catharticus* can produce fertile hybrids ($\leq 7.9\%$ pollen viability and $\leq 3.48\%$ flowers with mature seeds) when crossed with *B. brevis* (7.9% pollen viability and 2.8% flowers with mature seeds), *B. parodii* (6.8% pollen

Table 1. Herbicide-resistant *Bromus* spp. reported globally and reviewed in this study.

Species	Year	Country	Site	SOA (no.) ^a	Chemical family ^b	Active ingredient	Resistance mechanism ^c	Reference
<i>B. catharticus</i> Vahl.	2017	Argentina	Fallow Wheat Barley	EPSPS (9)	GLY	Glyphosate	NTSR	Yannicari et al. (2021)
<i>B. commutatus</i> Schrad.	2020	United Kingdom	Cereals	ALS (2)	SU TP	Mesosulfuron + iodosulfuron Pyroxsulam	TSR and NTSR	Davies et al. (2020)
<i>B. diandrus</i> Roth	1999	Australia	Cereals	ACCCase (1)	AOPP	Fluazifop, haloxyfop, quizalofop	NA	Boutsalis and Preston (2006)
<i>B. diandrus</i> Roth	2011	Australia	Winter pulses Wheat	ALS (2)	CHD SU TP	Clethodim and tepraloxym Mesosulfuron Pyroxsulam	NA	Boutsalis et al. (2012)
<i>B. diandrus</i> Roth	2011	Australia	Fencelines Wheat	EPSPS (9)	GLY	Glyphosate	TSR	Malone et al. (2016)
<i>B. diandrus</i> Roth	2011	Spain	Winter cereals	ALS (2) EPSPS (9)	SU GLY	Sulfosulfuron Glyphosate	NA	Escorial et al. (2011)
<i>B. diandrus</i> Roth	2015	Australia	Grain belt cereals	ACCCase (1)	AOPP CHD	Fluazifop Clethodim	NA	Owen et al. (2015)
<i>B. diandrus</i> Roth	2020	United Kingdom	Cereals	ALS (2)	SU TP	Mesosulfuron + iodosulfuron Pyroxsulam	NA	Davies et al. (2020)
<i>B. japonicus</i> Thunb.	2007	United States	Winter wheat	ALS (2)	IMI TAZN TP SU	Imazamox Propoxycarbazone Pyroxsulam	TSR	Heap (2022)
<i>B. japonicus</i> Thunb.	2022	China	Wheat	ALS (2) ACCCase (1) PSII (7) HPPD (27)	TAZN SU TP AOPP PU PY	Sulfosulfuron Flucarbazone Mesosulfuron Pyroxsulam Clodinafop Isoproturon Cypirafluone	TSR and NTSR	Lan et al. (2022)
<i>B. madritensis</i> L.	2018	Spain	Orchards Cereals	EPSPS (9)	GLY	Glyphosate	NA	Vázquez-García et al. (2023)
<i>B. rigidus</i> Roth	2005	Australia	Canola lupins	ACCCase (1)	AOPP	Quizalofop	NA	Heap (2022)
<i>B. rigidus</i> Roth	2007	Australia	Beans	ACCCase (1)	AOPP CHD	Fluazifop, haloxyfop, quizalofop Clethodim and tepraloxym	NA	Heap (2022)
<i>B. rigidus</i> Roth	2011	Australia	Wheat	ALS (2)	SU TP	Mesosulfuron Pyroxsulam	NA	Heap (2022)
<i>B. rigidus</i> Roth	2011	Australia	Wheat	ALS (2)	SU TP	Mesosulfuron Pyroxsulam	NA	Heap (2022)
<i>B. rigidus</i> Roth	2012	Australia	Grain belt cereals	ALS (2)	SU	Sulfometuron and sulfosulfuron	NTSR	Owen et al. (2012)
<i>B. rigidus</i> Roth	2015	Australia	Grain belt cereals	ALS (2)	SU	Sulfometuron and sulfosulfuron	NTSR	Owen et al. (2015)
<i>B. rubens</i> L.	2014	Australia	Fallow	EPSPS (9)	GLY	Glyphosate	NA	Heap (2022)
<i>B. rubens</i> L.	2018	Spain	Almonds Olives Other orchards	EPSPS (9)	GLY	Glyphosate	NA	Vázquez-García et al. (2021)
<i>B. secalinus</i> L.	2007	United States	Winter wheat	ALS (2)	IMI TAZN TP SU	Imazamox Propoxycarbazone Pyroxsulam Sulfosulfuron	TSR	Heap (2022)
<i>B. secalinus</i> L.	2009	United States	Wheat	ALS (2)	IMI TAZN TP SU	Imazamox Propoxycarbazone Pyroxsulam Sulfosulfuron	NA	Heap (2022)
<i>B. secalinus</i> L.	2020	United Kingdom	Cereals	ALS (2)	SU	Mesosulfuron + iodosulfuron	NA	Davies et al. (2020)
<i>B. sterilis</i> L.	2009	France	Wheat	ALS (2)	SU TAZN TP	Iodosulfuron and mesosulfuron Propoxycarbazone Pyroxsulam	NA	Heap (2022)
<i>B. sterilis</i> L.	2012	Germany	Cereals Rapeseed	ACCCase (1)	AOPP CHD	Propaquizafop Cycloxydim	NA	Heap (2022)

Table 1. (Continued)

<i>B. sterilis</i> L.	2017	Germany	Wheat	ALS (2)	TAZN	Propoxycarbazone	NA	Heap (2022)
<i>B. sterilis</i> L.	2017	Czech Republic	Wheat	ALS (2)	TAZN	Propoxycarbazone	TSR and NTSR	Sen et al. (2021)
					TP	Pyroxsulam		
					SU	Sulfometuron		
<i>B. sterilis</i> L.	2018	United Kingdom	Postharvest stubble	EPSPS (9)	GLY	Glyphosate	NA	Davies et al. (2019)
<i>B. sterilis</i> L.	2020	United Kingdom	Cereals	ALS (2)	SU	Mesosulfuron + iodosulfuron	NTSR	Davies et al. (2020)
					TP	Pyroxsulam		
<i>B. tectorum</i> L.	1981	France	Corn	PSII (5)	TZ	Atrazine	NA	Heap (2022)
<i>B. tectorum</i> L.	1990	Spain	Olive	PSII (5)	TZ	Simazine	TSR	Menendez et al. (2007)
<i>B. tectorum</i> L.	1990	Spain	Wheat	PSII (7)	PU	Chlortoluron	NTSR	Menendez et al. (2006)
<i>B. tectorum</i> L.	1997	United States	Kentucky bluegrass	ACCase (1)	AOPP	Fluazifop	TSR and NTSR	Mallory-Smith et al. (1999)
				ALS (2)	CHD	Clethodim		Park and Mallory-Smith (2004, 2005)
				PSII (5)	SU	Primisulfuron and sulfosulfuron		Park et al. (2004)
				PSII (7)	TAZN	Propoxycarbazone		
				VLCFA (15)	TZ	Atrazine		
					TAZ	Metribuzin		
					UR	Terbacil		
					PU	Diuron		
					BF	Ethofumesate		
<i>B. tectorum</i> L.	1998	United States	Kentucky bluegrass	ALS (2)	SU	Primisulfuron and sulfosulfuron	TSR	Park and Mallory-Smith (2004)
					TAZN	Propoxycarbazone		
<i>B. tectorum</i> L.	2005	United States	Creeping red fescue	ACCase (1)	CHD	Clethodim and sethoxydim	NA	Ball et al. (2007)
					AOPP	Fluazifop and quizalofop		
<i>B. tectorum</i> L.	2016	United States	Wheat	ALS (2)	IMI	Imazamox	TSR	Kumar and Jha (2017)
					TAZN	Procarbazone		
					TP	Pyroxsulam		
<i>B. tectorum</i> L.	2020	United States	Wheat	EPSPS (9)	GLY	Glyphosate	NA	Zuger and Burke (2020)
<i>B. tectorum</i> L.	2020	United States	Wheat	ACCase (1)	CHD	Clethodim	NA	Zuger and Burke (2020)
				ALS (2)	IMI	Imazamox		
					TAZN	Propoxycarbazone		
					TP	Pyroxsulam		
					SU	Mesosulfuron and sulfosulfuron		
<i>B. tectorum</i> L.	2020	United States	Fine fescues	ACCase (1)	AOPP	Fluazifop and quizalofop	TSR	Ribeiro et al. (2023)
					CHD	Clethodim and sethoxydim		
<i>B. tectorum</i> L.	2021	Canada	Canola	EPSPS (9)	GLY	Glyphosate	NA	Geddes and Pittman (2022)
<i>B. tectorum</i> L.	2021	United States	Wheat	ALS (2)	IMI	Imazamox	NA	Ribeiro et al. (2023, unpublished data)
					TAZN	Propoxycarbazone		
					TP	Pyroxsulam		
					SU	Mesosulfuron and sulfosulfuron		

^aHerbicide site of action (SOA): ACCase, acetyl-coenzyme A carboxylase (Group 1); ALS, acetolactate synthase (Group 2); EPSPS, 5-enolpyruvyl shikimate-3-phosphate synthase (Group 9); HPPD, 4-hydroxyphenylpyruvate dioxygenase (Group 27); PSII, photosystem II (Groups 5 and 7); VLCFA, very-long-chain fatty-acid (Group 15).

^bChemical family abbreviations: AOPP, aryloxyphenoxypropionate; BF, benzofuran; CHD, cyclohexanedione; GLY, glycine; IMI, imidazolinone; PU, phenylurea; PY, pyrazole; SU, sulfonylurea; TAZ, triazinone; TAZN, triazolinones; TP, triazolopyrimidine; TZ, triazine; UR, urea.

^cMechanisms: NA, not available; NTSR, non-target site resistance; TSR, target-site resistance.

Table 2. Biology and genetics of *Bromus* spp. globally reviewed in this study.

Scientific name	Common name	Section	Ploidy level	1C ^a	Genome size ^b	Life cycle	Pollination system
<i>B. catharticus</i> Vahl.	Prairie grass or rescue grass	<i>Ceratochloa</i>	$2n = 6x = 42$	12.64	12.36	Annual or short-lived perennial	Self- and cross-pollinated
<i>B. commutatus</i> Schrad.	Meadow brome or hairy chess	<i>Bromus</i>	$2n = 4x = 28$	10.90	10.66	Annual or biennial	Self- and cross-pollinated
<i>B. diandrus</i> Roth	Ripgut brome or great brome	<i>Genea</i>	$2n = 8x = 56$	11.90	11.64	Winter annual	Self-pollinated
<i>B. japonicus</i> Thunb.	Japanese brome	<i>Bromus</i>	$2n = 2x = 14$	5.50	5.38	Winter annual	Self-pollinated
<i>B. madritensis</i> L.	Compact brome	<i>Genea</i>	$2n = 4x = 28$	4.90	4.79	Winter annual	Self-pollinated
<i>B. rigidus</i> Roth	Rigid brome	<i>Genea</i>	$2n = 6x = 42$	8.60	8.41	Winter annual	Self- and cross-pollinated
<i>B. rubens</i> L.	Red brome	<i>Genea</i>	$2n = 4x = 28$	4.90	4.79	Winter annual	Self-pollinated
<i>B. secalinus</i> L.	Rye brome or cheat	<i>Bromus</i>	$2n = 4x = 28$	14.00	13.69	Annual or biennial	Self-pollinated
<i>B. sterilis</i> L.	Barren brome or poverty brome	<i>Genea</i>	$2n = 2x = 14$	2.98	2.91	Annual or biennial	Self-pollinated
<i>B. tectorum</i> L.	Downy brome or cheatgrass	<i>Genea</i>	$2n = 2x = 14$	3.30	3.23	Winter annual	Self- and cross-pollinated

^aNuclear DNA amount 1C values were obtained in the website: <https://cvalues.science.kew.org/search>.

^bGenome size was estimated based on the conversion of nuclear 1C DNA amount in picograms to the numbers of base pairs suggested by Doležel et al. (2007): 1 pg DNA = 0.978×10^9 bp.

Table 3. Interspecific hybridization of *Bromus* spp. reviewed in this study.

Hybridization	Ploidy level	Hybrids ^a	Reference
Within the section <i>Ceratochloa</i>			
<i>B. bonariensis</i> × <i>B. catharticus</i>	$(2n = 6x = 42) \times (2n = 6x = 42)$	Sterile	Naranjo (1992)
<i>B. catharticus</i> × <i>B. brevis</i>	$(2n = 6x = 42) \times (2n = 6x = 42)$	Fertile	Naranjo (1992)
<i>B. catharticus</i> × <i>B. parodii</i>	$(2n = 6x = 42) \times (2n = 6x = 42)$	Fertile	Naranjo (1992)
<i>B. catharticus</i> × <i>B. haenkeanus</i>	$(2n = 6x = 42) \times (2n = 6x = 42)$	Fertile	Hall (1955)
<i>B. catharticus</i> × <i>B. carinatus</i>	$(2n = 6x = 42) \times (2n = 8x = 56)$	Sterile	Stebbins and Tobgy (1944)
Within the section <i>Bromus</i>			
<i>B. arvensis</i> × <i>B. commutatus</i>	$(2n = 2x = 14) \times (2n = 4x = 28)$	NR	Jahn (1959)
<i>B. arvensis</i> × <i>B. secalinus</i>	$(2n = 2x = 14) \times (2n = 4x = 28)$	NR	Jahn (1959)
<i>B. mollis</i> × <i>B. commutatus</i>	$(2n = 4x = 28) \times (2n = 4x = 28)$	Sterile	Knowles (1944)
<i>B. commutatus</i> × <i>B. racemosus</i>	$(2n = 4x = 28) \times (2n = 4x = 28)$	Fertile	Smith (1973)
<i>B. macrostachys</i> × <i>B. commutatus</i>	$(2n = 4x = 28) \times (2n = 4x = 28)$	NR	Jahn (1959)
Within the section <i>Genea</i>			
<i>B. sterilis</i> × <i>B. fasciculatus</i>	$(2n = 2x = 14) \times (2n = 2x = 14)$	Fertile	Fortune et al. (2008), Oja (2002a)
<i>B. tectorum</i> × <i>B. fasciculatus</i>	$(2n = 2x = 14) \times (2n = 2x = 14)$	Fertile	Fortune et al. (2008), Oja (2002a)
Section <i>Bromus</i> × section <i>Genea</i>			
<i>B. mollis</i> × <i>B. madritensis</i>	$(2n = 4x = 28) \times (2n = 4x = 28)$	Sterile	Knowles (1944)
<i>B. mollis</i> × <i>B. rigidus</i>	$(2n = 4x = 28) \times (2n = 6x = 42)$	Sterile	Knowles (1944)
<i>B. mollis</i> × <i>B. rubens</i>	$(2n = 4x = 28) \times (2n = 4x = 28)$	Sterile	Knowles (1944)

^aNR, not reported. The study only indicated compatibility between species.

viability and 4.81% flowers with mature seeds) (Naranjo 1992), and *B. haenkeanus* (4% seed fertility) (Hall 1955). In contrast, *B. catharticus* × *B. bonariensis* (2.4% pollen viability and 0% flowers with mature seeds) and *B. catharticus* × *B. carinatus* hybrids are sterile (Naranjo 1992; Stebbins and Tobgy 1944).

Resistance in *Bromus catharticus*

Glyphosate-resistant *B. catharticus* was identified in 2017 in Argentina (Yannicari et al. 2021; Table 1). The resistant population was found in a fallow field that had been under wheat–soybean [*Glycine max* (L.) Merr.] and barley–soybean crop rotations for at least 8 yr with frequent use of glyphosate. This resistant population was 4-fold less sensitive to glyphosate compared with the susceptible population. No evidence of TSR or enhanced glyphosate metabolism was detected in the resistant population. Conversely, lower foliar retention of glyphosate ($138.34 \mu\text{l}$ solution g^{-1} dry weight

vs. $390.79 \mu\text{l}$ solution g^{-1} dry weight), reduced absorption (54.18% vs. 73.56%), and translocation (27.70% vs. 62.36%) of [^{14}C]glyphosate from the labeled leaf were observed in this glyphosate-resistant population. As a consequence, the resistant plants accumulated a 4.1-fold lower concentration of [^{14}C] glyphosate in the roots compared with the susceptible plants. Therefore, low foliar retention of glyphosate and reduced herbicide absorption and translocation were reported to be the major mechanisms endowing NTSR in *B. catharticus*. This is the only case of resistance reported in *B. catharticus*. Because of *B. catharticus*'s reproductive system and widespread occurrence and the number of sympatric, compatible species, the risk of transferring herbicide-resistance alleles from *B. catharticus* to other *Bromus* spp. exists and should be of concern. In the Pampas of Argentina, *B. bonariensis*, *B. brevis*, and *B. parodii* occur sympatrically with *B. catharticus*, and they are sexually compatible (Leofanti and Camadro 2017; Naranjo 1992);

therefore, hybridization under field conditions and spread of resistance alleles is possible.

Bromus commutatus

Bromus commutatus, known as meadow brome or hairy chess, is native to Europe and western Asia and has been introduced throughout North America (Pavlick 1995; Williams et al. 2011). In the United Kingdom, *B. commutatus* is a troublesome weed commonly found in field margins and headlands of winter cereal crops and rarely seen in spring crops (Cussans et al. 1994). This species has become more widespread and difficult to control in the United Kingdom because of the increased adoption of minimum tillage; restricted crop rotations, including mainly fall-sown crops; and limited effective herbicide options for control (Davies and Hull 2018). *Bromus commutatus* can have winter or spring annual or biennial life cycles (Finnerty and Klingman 1962; Table 2). Integrating cultural and mechanical practices, including late sowing (beyond the conventional fall window), spring crop rotation, and stubble management using improved mechanical weeders, is a key strategy to control *B. commutatus*, reduce herbicide dependence, and consequently, reduce herbicide-resistance evolution (Clarke et al. 2000).

Biology and Genetics

Bromus commutatus is largely self-pollinated and only reproduces by seeds (Table 2). *Bromus commutatus* produces flowers on a panicle with ascending branches (12- to 25-cm long) containing pediceled spikelets (1.8- to 3.3-cm long; 8 to 11 flowered) with awns (8- to 11-mm long) (Bryson and DeFelice 2010). In the United Kingdom, seed is usually shed between May and October, and seedling emergence takes place between July and November (Bayer Crop Science UK 2022). Research has shown that *B. commutatus* seeds should be left on the soil surface for approximately 28 d before any tillage, because warm temperatures minimize seed dormancy (Clarke et al. 2000). Subsequently, the utilization of mechanical control methods such as plowing becomes more effective, resulting in less viable seed after burial.

Bromus commutatus is an allotetraploid species ($2n = 4x = 28$; 10.66-Gb genome size) belonging to the *Bromus* section (Table 2), with a nuclear DNA content of 10.90 pg (Bennett and Smith 1976). The allopolyploid origin of this species has not been reported in the literature.

Although *B. commutatus* is predominantly self-pollinated, hybridization between *B. commutatus* and other *Bromus* spp. can occur (Armstrong et al. 2005; Table 3). *Bromus commutatus* (4x) and *Bromus racemosus* (4x) are interfertile, and naturally occurring hybrids are produced (Smith 1973). Hybrids of *B. arvensis* (2x) × *B. commutatus* (4x) and *Bromus macrostachys* Desf. (4x) × *B. commutatus* (4x) resulted in some chromosome pairing, suggesting a compatibility relationship between these genomes (Jahn 1959). *Bromus mollis* auct. Non L. (syn.: *Bromus hordeaceus* L. ssp. *hordeaceus*) (4x) and *B. commutatus* (4x) crossed readily, but F₁ hybrid seeds did not germinate (Knowles 1944).

Resistance in *Bromus commutatus*

A case of cross-resistance to ALS-inhibiting herbicides was reported in *B. commutatus* in the United Kingdom with resistance to mesosulfuron-methyl + iodosulfuron-methyl-sodium and

pyroxsulam (Davies et al. 2020; Table 1). This population was >16 times more resistant to mesosulfuron-methyl + iodosulfuron-methyl-sodium and pyroxsulam compared with the susceptible population. Molecular evidence suggested that cross-resistance to sulfonyleurea (mesosulfuron-methyl + iodosulfuron-methyl-sodium) and triazolopyrimidine (pyroxsulam) chemical families in *B. commutatus* resulted from both TSR and NTSR mechanisms. The *ALS* gene sequence analysis revealed an amino acid substitution from tryptophan to leucine at position 154 (Trp-154-Leu). Additionally, enhanced levels of the glutathione transferase phi (F) class 1 enzyme, referred to as AmGSTF1, were detected in the resistant population compared with the susceptible population (Davies et al. 2020). This enzyme has a functional role in regulating NTSR. Based on the reports of sexual compatibility between *B. commutatus* and other *Bromus* spp., the transfer of resistance alleles from herbicide-resistant *B. commutatus* to other *Bromus* spp. is possible. In the United Kingdom, a survey of growers and agronomists reported the occurrence of multiple *Bromus* spp., including *B. commutatus*, *B. diandrus*, *B. hordeaceus*, *B. secalinus*, and *B. sterilis*, across cereal-growing areas (Davies and Hull 2018). These species were present on 34,730 ha of cropland and were reported to occur in 39 of 168 fields surveyed. Although sexual compatibility among these species has not been documented in the literature, research on potential outcrossing among these species would be relevant, as they are locally distributed and co-occur.

Bromus diandrus

Bromus diandrus, known by the common names ripgut brome or great brome, is a winter annual species (Table 2) native to the Mediterranean region and widely introduced elsewhere in the world. This species is a highly competitive weed in cereal crops in different geographies including Europe, Asia, Africa, North America, and Oceania (Clapham et al. 1952; Kon and Blacklow 1989). Previous research has shown that a *B. diandrus* infestation of 100 plants m⁻² can cause a yield loss of 30% in wheat (Gill et al. 1987). Moreover, *B. diandrus* seed can contaminate harvested grain and cause injury to livestock if the awns become embedded in the animal's nose or mouth when grazing (Kon and Blacklow 1995). The increased cropping frequency through minimum tillage and the lack of effective herbicide options for selective *B. diandrus* control have resulted in a significant increase in the importance of this species in cereal crops in southern Australia (Gill and Blacklow 1985; Heenan et al. 1990; Kon and Blacklow 1988), Spain (Fernandez Garcia and García-Baudín 1997), and the United Kingdom (Davies and Hull 2018). This high incidence of *B. diandrus* in cereal crops under no-till systems may be associated with the germination behavior of this species, which increases the difficulty of its control (Kleemann and Gill 2013). *Bromus diandrus* germination is characterized by two distinct flushes when soil moisture and temperature are not limiting (Del Monte and Dorado 2011). The first and main flush typically occurs in fall with the first rains, originating from superficially buried or shaded (by the field stubble) seeds. The second flush occurs in spring and comes from seeds that remain on the soil surface. In this second flush, the seeds are directly exposed to light, and germination is inhibited by light; hence, the dormancy is prolonged until seeds lose their negative photoblastism and germination can occur. Therefore, delayed *B. diandrus* establishment allows this species to escape preplanting weed control tactics and infest crops where its selective control is more difficult.

Biology and Genetics

Bromus diandrus produces loose and drooping panicles, 150- to 200-mm long, with long spikelet branches (Kon and Blacklow 1988). The lemma of this species is short (≤ 1 mm) and rounded at the tips. *Bromus diandrus* plants are largely self-pollinated with outcrossing frequencies of less than 1% (Kon and Blacklow 1990; Table 2). Chasmogamy in *B. diandrus* commonly occurs under favorable conditions such as high soil moisture (Kon and Blacklow 1990). Under irrigated conditions, the anthers of *B. diandrus* in the chasmogamous florets (2- to 8-mm long) were longer than those in cleistogamous florets (< 2 mm). In the same study, attempts at hybridization between *B. diandrus* $\times$ *B. rigidus* failed, and there was no evidence of naturally occurring hybrids. Thus, further research is needed to investigate pollen viability under different levels of soil moisture, temperature, relative humidity, and flowering synchrony, as well as potential hybridization between *B. diandrus* and other species.

Bromus diandrus is an allooctoploid species ($2n = 8x = 56$; 11.64-Gb genome size) classified into the *Genea* section (Table 2), with a nuclear DNA content of 11.90 pg (Bennett and Smith 1976). *Bromus diandrus* may have originated from the hexaploid *B. rigidus* (female genome donor) and the diploid *B. sterilis* (male genome donor), and the proposed genomic formula for this species is either AABBCCDD (disomic inheritance) or AAAABBCC (disomic and tetrasomic inheritance) (Fortune et al. 2008).

Resistance in *Bromus diandrus*

Bromus diandrus populations have evolved resistance to three herbicide groups: ACCase inhibitors, ALS inhibitors, and the EPSPS inhibitor (glyphosate) (Table 1). The evolution of cross-resistance to ALS- and ACCase-inhibiting herbicides has been widely documented in *B. diandrus* populations in Australia (Boutsalis and Preston 2006; Boutsalis et al. 2012; Owen et al. 2015) and the United Kingdom (Davies et al. 2020). Boutsalis and Preston (2006) identified an ACCase-resistant population that exhibited high levels of resistance to fluzifop-P-butyl (resistance factor [RF] > 50) and haloxyfop-ethoxyethyl (RF = 24). Boutsalis et al. (2012) found five ACCase-resistant populations with prevalent resistance to fluzifop-P-butyl (RF = 4 to 16) and quizalofop-P-ethyl (RF = 8 to 16), and to a lesser extent to clethodim (RF = 4 to 10) and haloxyfop-ethoxyethyl (RF = 3 to 7), and two ALS-resistant populations exhibiting moderate levels of resistance to mesosulfuron-methyl (RF = 4 to 5) and pyroxsulam (RF = 3 to 4). The population reported by Owen et al. (2015) was cross-resistant to clethodim and fluzifop-P-butyl with $> 85\%$ survival when treated with the labeled rate of these herbicides and survived two times the labeled rate of both herbicides. The ALS-resistant population reported in the United Kingdom was > 5.8 and 2.7 times more resistant to mesosulfuron-methyl + iodosulfuron-methyl-sodium and pyroxsulam compared with the susceptible population, respectively (Davies et al. 2020). However, the mechanisms of resistance were not reported in the populations from Australia and the United Kingdom. Resistance to glyphosate was identified in two populations of *B. diandrus* in Australia (Malone et al. 2016). These populations were 4.7- to 4.9-fold more resistant to glyphosate than the susceptible population. The mechanism of resistance in these two glyphosate-resistant *B. diandrus* populations was conferred by EPSPS gene amplification. These populations contained 10 to 36 additional copies of EPSPS compared with the susceptible population. Increased EPSPS

expression was also observed in the resistant populations, but the levels were not correlated with the number of EPSPS copies. A case of multiple resistance in *B. diandrus* was documented in Spain with resistance to both glyphosate and sulfosulfuron, but the mechanism of resistance in this population was not elucidated (Escorial et al. 2011).

Bromus japonicus

Bromus japonicus, Japanese brome, is an indigenous Eurasian species commonly found along roadsides, in floodplain wetlands, and in agricultural areas, including wheat fields (Li 1998). This species is extensively dispersed in Asia, Australasia, Europe, Northern Africa, North America, and South America (Che et al. 2010). It is estimated that a *B. japonicus* infestation of 4 plants m^{-2} can result in 2.11% to 2.24% yield loss in wheat (Li et al. 2016).

Bromus japonicus is a winter annual (Table 2) with seedlings typically emerging in September and October, flowering occurs in early May, and seed dispersal starts in early October (Baskin and Baskin 1981). The optimum temperature for *B. japonicus* germination is between 25 and 30 °C (Li et al. 2015). The authors found that light and pH are not limiting factors in germination, except under highly acidic conditions ($pH \leq 4$). Seedling emergence is relatively greater (98%) when seeds are left on the soil surface compared with seeds buried at a depth of 5 cm (7%). Additionally, the authors found that seeds are tolerant to osmotic potential and salinity, with germination occurring under a wide range of salt concentrations (20 to 320 mM).

Biology and Genetics

Bromus japonicus is exclusively self-pollinated (Oja et al. 2003; Table 2). It reproduces only by seeds, and a single plant can produce an average of 1,885 seeds that can be dispersed by water or wind due to their light weight (Wang 1986). *Bromus japonicus* produces flowers on an open panicle, 17- to 30-cm long and 6- to 13-cm wide, with the lower branches drooping at maturity (Bryson and DeFelice 2010). Spikelets are 5 to 10 flowered, 2.0- to 3.2-cm long with awns. Glumes are 4.0- to 7.6-mm long, minutely scabrous, with the second glume longer than the first. The lemma is 7.2- to 9.1-mm long, scabrous, and tip bent-awned from between two teeth.

Bromus japonicus is a diploid species ($2n = 2x = 14$; 5.38-Gb genome size) in the *Bromus* section (Table 2), with a nuclear DNA content of 5.50 pg (Bennett and Smith 1976). Previous studies, including serological analysis (Smith 1972), isozyme analysis (Oja et al. 2003), and DNA analyses (Ainouche and Bayer 1997; Ainouche et al. 1999), showed that *B. japonicus* and *Bromus squarrosus* L. are closely related species. According to Oja and Paal (2007), these species can be reliably distinguished based on the lemma margin, where plants with conspicuously angled margins are identified as *B. squarrosus*.

Resistance in *Bromus japonicus*

Herbicide resistance in *B. japonicus* was first reported in the United States in 2007 (Heap 2022) and in China in 2022 (Lan et al. 2022; Table 1). In both cases, the reported populations were ALS resistant with broad-spectrum cross-resistance patterns. The population identified in China exhibited a 120-fold increase in flucarbazone-sodium resistance (Lan et al. 2022). The DNA sequence analyses of the ALS gene revealed a single nucleotide substitution of CCC to TCC at codon 197, resulting in a Pro-197-Ser mutation.

Additionally, the application of malathion + flucarbazone-sodium reduced the 50% growth inhibition rate (GR_{50}) value of this population by 60%, suggesting a cytochrome P450 monooxygenase (P450)-mediated metabolic resistance. This population was cross-resistant to mesosulfuron-methyl and pyroxusulam, with $\geq 95\%$ survival when treated with the labeled rate and two times the labeled rate of the herbicides. Multiple resistance to ACCase, PSII, and HPPD inhibitors was also observed in this population, with $\geq 90\%$ survival when treated with the labeled rates of clodinafop-propargyl, isoproturon, and cyprofluthione.

Bromus madritensis

Bromus madritensis, known as compact brome, originated in the Mediterranean region (Oja 2002b). This species is found in southern and western Europe, Northern Africa, the Middle East (Fortune et al. 2008), and North America (Oja 2002b). *Bromus madritensis* grows in a variety of disturbed environments (Warembourg and Estelrich 2001) and agricultural areas (Heap 2022). Because of its close morphological similarity to *B. rubens*, there is controversy as to whether *B. madritensis* and *B. rubens* should be treated as subspecies (Sales 1994) or as separate species (Oja 2002b). Population genetics analysis suggested independent origins of *B. madritensis* and *B. rubens* (Oja and Jaaska 1996). These species can also be differentiated based on their panicle and spikelet characteristics. *Bromus madritensis* typically has longer panicle branches and looser panicles, whereas *B. rubens* is distinguished by its brushlike condensed panicles (Oja 2002b).

Biology and Genetics

Bromus madritensis has a winter annual life cycle and is predominantly self-pollinating (Table 2). Its panicles are longer (3 to 15 cm) than they are wide (2 to 6 cm) and less dense; panicle branches are 1 to 3 cm, ascending to spreading, never drooping, containing 1 or 2 spikelets (Hitchcock et al. 2018; Roché et al. 2019). Spikelets are 30 to 50 mm, longer than the panicle branches, with parallel sides or widening distally, and are moderately laterally compressed with 6 to 10 florets (Hitchcock et al. 2018; Roché et al. 2019). Glumes are pilose with lower glumes (5 to 10 mm, 1-veined) shorter than the upper ones (10 to 15 mm, 3-veined) (Hitchcock et al. 2018; Roché et al. 2019). Lemmas are 12- to 20-mm long with a linear-lanceolate shape, pubescent, and with awns (12 to 23 mm) (Hitchcock et al. 2018; Roché et al. 2019).

Bromus madritensis is a tetraploid species ($2n = 4x = 28$; 4.79-Gb genome size) in the *Genea* section (Table 2), with a nuclear DNA content of 4.90 pg (Bennett and Smith 1976). It has an allopolyploid origin that possibly resulted from the hybridization of the diploids *Bromus fasciculatus* C. Presl (maternal parent) and *B. sterilis* (paternal parent) (Fortune et al. 2008; Oja 2002a; Oja and Jaaska 1996).

Despite *B. madritensis* being predominantly self-pollinated, hybridization with other *Bromus* spp. has been reported (Table 3). Attempted hybridizations between *B. mollis* $\times$ *B. madritensis* showed compatibility between these two species; however, F_1 hybrids were sterile (Knowles 1944). Compatibility with other species is unknown.

Resistance in *Bromus madritensis*

To date, there is only one report of herbicide resistance in *B. madritensis* (Vázquez-García et al. 2023; Table 1). In 2018, six glyphosate-resistant *B. madritensis* populations were identified in

orchards and cereal fields in Spain (Vázquez-García et al. 2023). The resistant populations accumulated $\leq 600 \mu\text{g g}^{-1}$ shikimic acid and had $RF > 4$ based on 50% death rate (LD_{50}) and GR_{50} values. Populations with higher RFs factors showed lower shikimic acid accumulation. The resistance mechanisms were not reported in the study.

Bromus rigidus

Bromus rigidus, rigid brome, is an indigenous Mediterranean species with a winter annual life cycle (Table 2) that has become a severe weed problem in cropping systems in Australia (Kon and Blacklow 1990), New Zealand (Dastgheib et al. 2003), and North America (Gleichsner and Appleby 1989). In southern Australia, *B. rigidus* is commonly found in cropping areas with >250 -mm annual rainfall and lighter, sandy soils (Kon and Blacklow 1995). In early vegetative growth stages, *B. rigidus* and *B. diandrus* are very similar morphologically, causing difficulties in identifying these species. *Bromus rigidus* differs from *B. diandrus* by having shorter and sparser hairs on the adaxial surface of the leaf blades (Kon and Blacklow 1988). The germination behavior of these two species is also an important distinguishing feature. *Bromus rigidus* has longer seed dormancy compared with *B. diandrus* (Gill and Carstairs 1988; Kleemann and Gill 2006; Kon and Blacklow 1988), and its seeds are more likely to persist in the soil from one growing season to the next (Kleemann and Gill 2009). The longer seed dormancy observed in *B. rigidus* is related to inhibition factors in the embryo (Gill and Carstairs 1988; Kleemann and Gill 2006). *Bromus rigidus* germination is strongly inhibited by light exposure (Kleemann and Gill 2006). Studies from Spain (Del Monte and Dorado 2011) and Australia (Kleeman and Gill 2013) have shown that *B. diandrus* seems to be photosensitive, with seeds having longer dormancy when exposed to light. These findings differ from previous Australian studies, which reported that *B. diandrus* populations have low levels of seed dormancy (Cheam 1986; Gill and Blacklow 1985; Gill and Carstairs 1988; Harradine 1986).

Biology and Genetics

Bromus rigidus is a predominantly self-pollinated species (Table 2) with minimal outcrossing (Kon and Blacklow 1990). The inflorescences of *B. rigidus* are erect and compact, 90- to 210-mm long, with short spikelet branches (Kon and Blacklow 1988). The lemma calluses are elongated (≥ 1 mm), compressed, and pointed; the abscission scars are elliptical. Seed production in *B. rigidus* varies from 1,156 to 2,908 seeds per plant.

Bromus rigidus is an allohexaploid species ($2n = 6x = 42$; 8.41-Gb genome size) in the *Genea* section (Table 2), with a nuclear DNA content of 8.60 pg (Bennett and Smith 1976). This species is closely related to *B. diandrus*, and they share the same maternal parent. Based on a molecular phylogenetic study, there are at least three different genomes involved in the parentage of *B. rigidus*, including the diploids *B. tectorum* (T clade; TT), *B. fasciculatus* (F clade; FF), and an unidentified third ancestor (X clade; XX) (Fortune et al. 2008). It is unknown whether *B. rigidus* (XXFFT) originated independently or from hybridization between a tetraploid ancestor (related to *B. rubens*) and an unidentified parent.

Previous research reported compatibility between *B. mollis* and *B. rigidus* (Knowles 1944; Table 3). In the same study, the cross between *B. mollis* $\times$ *B. rigidus* yielded a total of 10 seeds, but none germinated. Further research investigating the potential hybridization between *B. rigidus* and other *Bromus* spp. is needed.

Resistance in *Bromus rigidus*

Herbicide resistance to ACCase and ALS inhibitors was documented in *B. rigidus* populations in Australia, including single- and cross-resistance cases (Table 1). Because there are limited herbicide options for selective *B. rigidus* control in crops, the selection for resistance to these two herbicide SOAs is a loss for Australian growers. Owen et al. (2012) identified six *B. rigidus* populations that were resistant to the ALS inhibitors sulfometuron-methyl (RF ≥ 3) and sulfosulfuron (RF ≥ 6) from Western Australia. Similar findings were reported 3 yr later in the same region, showing that the continued selection in the field by the use of the ALS-inhibiting herbicides sulfometuron-methyl and sulfosulfuron resulted in 100% plant survival at the field rate (Owen et al. 2015). In both studies, resistance was reversed when the plants were treated with malathion, suggesting enhanced metabolism (NTSR) as mechanism of resistance. The ACCase resistance mechanisms and cross-resistance mechanisms for both ACCase and ALS were not elucidated.

A survey conducted in the Western Australian grain belt showed the presence of several *Bromus* spp. in this region, including *B. diandrus*, *B. rigidus*, and *B. rubens* (Owen et al. 2015). These species were present in 91 of 466 crop fields surveyed. *Bromus diandrus* (85%) occurrence was widespread in all agronomic regions of the Western Australian grain belt; *B. rigidus* (13%) occurred in the northern agricultural region; and *B. rubens* (2%) was confined to the drier areas of the eastern wheat belt. The overlap of *Bromus* spp. commonly occurs in this region, particularly between *B. diandrus* and *B. rigidus*. Moreover, the presence of herbicide-resistant *Bromus* spp. populations has been documented. Of the 91 *Bromus* spp. populations screened in this survey, 13% exhibited resistance to ALS-inhibiting herbicides, and only one population was resistant to ACCase-inhibiting herbicides. All ALS-resistant populations were identified as *B. rigidus*, and the ACCase-resistant population was identified as *B. diandrus*. Because of the overlap of these species in some agronomic regions of the Western Australian grain belt and the evolution of herbicide-resistant populations, research investigating the hybridization between these species and potential gene flow is warranted.

Bromus rubens

Bromus rubens, red brome, is a Mediterranean grass species with widespread occurrence. This species is found in Southern Africa, Australasia, Europe, North America, and South America (USDA-ARS 2022a). *Bromus rubens* thrives in a variety of disturbed and non-disturbed environments and relatively shallow soils and drier areas (Crampton 1968). In North America, *B. rubens* is a successful colonizer in the southwestern United States deserts (Salo 2004, 2005). *Bromus rubens* was introduced to the United States in 1980 and has since become dominant in areas of the Mojave (Beatley 1966; Hunter 1991), Sonoran (Burgess 1965; Burgess et al. 1991), and Great Basin deserts (Tausch et al. 1994). This species can also be found in cropland. In southern Spain, growers utilize *B. rubens* as a cover crop in perennial cropping systems, such as olive (*Olea europaea* L.) and almond (*Prunus amygdalus* Batsch) orchards; however, this species has also become a severe weed in these systems (Vázquez-García et al. 2021). In Australia, *B. rubens* is a competitive weed in cereal crops and is confined to the drier areas of the eastern wheat belt in Western Australia (Owen et al. 2015). This distinctive ability of *B. rubens* to adapt to different environments is driven by key strategies such as rapid growth rates, high propagule pressure, low soil-moisture requirements for

germination, and positive responses to disturbance, including fire (Beatley 1966; Salo 2004; Wu and Jain 1979). The optimal temperature for *B. rubens* germination is 19 °C, with a hydro-thermal-time constant of 38.9 MPa °C⁻¹ and water potential of -1.35 MPa (Horn et al. 2015). *Bromus rubens* does not have a persistent soil seedbank (Forcella and Gill 1986; Pake and Venable 1995), and seed viability is negatively impacted by burial depth and timing (Jurand et al. 2013). A relatively small proportion of *B. rubens* seed retained viability for 2 yr, and viable seed proportions were significantly lower at 5- and 10-cm burial depths.

Biology and Genetics

Bromus rubens is a winter annual, highly self-pollinating species (Table 2) with outcrossing rates of less than 0.1% (Wu 1974). *Bromus rubens* produces a dense and erect panicle (2- to 10-cm long by 2- to 5-cm wide), often reddish-brown; branches are 0.1 to 1 cm, ascending, never drooping, with 1 or 2 spikelets (Hitchcock et al. 2018; Roché et al. 2019). Spikelets are much longer than the panicle branches, ranging from 18 to 25 mm, densely crowded, subsessile, with parallel sides or widening distally, moderately laterally compressed, with 4 to 8 florets. Glumes are pilose; lower glumes and upper glumes are 5 to 8 mm and 8 to 12 mm in length, respectively. Lemmas are linear-lanceolate (10- to 15-mm long) and awned (12- to 23-mm long).

Bromus rubens is an allotetraploid ($2n = 4x = 28$; 4.79-Gb genome size) in the *Genea* section (Table 2), with a nuclear DNA content of 4.90 pg (Bennett and Smith 1976). *Bromus rubens* and *B. madritensis* are closely related species derived from same the maternal donor (*B. fasciculatus*) and different paternal species (*B. tectorum*, and *B. sterilis*, respectively) (Fortune et al. 2008; Oja 2002a). Despite the low outcrossing rates, hybridization between *B. rubens* $\times$ *B. mollis* can occur, but F₁ hybrids are sterile (Knowles 1944; Table 3). Further investigations into reproductive compatibility between *B. rubens* and other species are needed.

Resistance in *Bromus rubens*

Bromus rubens populations have evolved resistance to glyphosate (Table 1). The first case of glyphosate resistance in *B. rubens* was documented in a fallow field in Australia in 2014 (Heap 2022; Table 1). In 2018, 17 *B. rubens* populations were confirmed to be glyphosate resistant in perennial crops including almonds, olives, and other orchards in southern Spain (Vázquez-García et al. 2021). The RF in these populations varied from 4.35 to 7.61 (based on GR₅₀ values) compared with the susceptible population. The resistant populations had lower shikimic acid accumulation (1,200 to 1,700 $\mu\text{g g}^{-1}$ fresh weight) compared with the three susceptible populations (300 to 700 $\mu\text{g g}^{-1}$ fresh weight) when treated with glyphosate. No difference in glyphosate retention was detected between the resistant and susceptible populations in the foliar retention assays. Further investigations are needed to characterize the mechanisms of resistance in these populations.

Bromus secalinus

Bromus secalinus, also known as rye brome or cheat, is a native species to Eurasia that has spread widely into warm and temperate regions globally (Williams et al. 2011). This species is found on all continents except Antarctica (USDA-ARS 2022b). *Bromus secalinus* invades open waste areas, dry grasslands, limestone glades, grassy meadows, abandoned fields, field margins, roadsides, and railway tracks (Zech-Matterne et al. 2021). In croplands, *B. secalinus* is

a common weed in cereal fields, particularly winter wheat and winter rye (*Secale cereale* L.) (Koscelny et al. 1990; Pytlarz and Gala-Czekaj 2022), and other crops such as alfalfa (*Medicago sativa* L.) (Pike and Stritzke 1984). *Bromus secalinus* typically grows in more acidic and sandy soils, but it also grows in damp clay soils (Zech-Matterne et al. 2021). *Bromus secalinus* typically germinates in the fall and less frequently in spring (Adamczewski et al. 2015). Optimum germination in *B. secalinus* occurs at temperature variations of 20/30 °C. Seedling emergence is 89% to 92% when seeds are left on the soil surface and completely inhibited when seeds are located at 10-cm depth. The *B. secalinus* soil seedbank is relatively short-lived (2 to 3 yr). Because of its similar phenology to wheat, *B. secalinus* typically ripens simultaneously with this crop and can be a major contaminant of wheat grain during harvesting (Stone et al. 2001). Cultural practices such as row spacing, seeding rate, and planting date are the foundation for *B. secalinus* control in winter wheat, as selective herbicide options are limited (Koscelny et al. 1990, 1991).

Biology and Genetics

Bromus secalinus is a self-pollinated species and has an annual or biennial life cycle (Table 2). This species reproduces exclusively by seed, and a single plant can produce from 8,000 to 16,000 seeds (Adamczewski et al. 2015). The inflorescence of *B. secalinus* consists of an erect, loose, or contracted panicle, ranging from 5- to 23-cm long (Bryson and DeFelice 2010). The spikelets are 17- to 21-mm long, with 4 to 7 florets and pediceled. The first glume is 3- to 5-veined and is shorter in length (4 to 6 mm) than the second glume (6 to 8 mm). The lemma is 6- to 9-mm long with apical teeth, and the awn ranges from 1.5- to 9-mm long.

Bromus secalinus is an allotetraploid ($2n = 4x = 28$; 13.69-Gb genome size) in the *Bromus* section (Table 2), with a nuclear DNA content of 14.00 pg (Bennett and Smith 1976). Hybridization between *B. secalinus* and other *Bromus* spp. is not common but can occur (Table 3). Hybrids of *B. arvensis* ($2x$) $\times$ *B. secalinus* ($4x$) showed some chromosome pairing, indicating a relationship between the genome of these two species (Jahn 1959).

Resistance in *Bromus secalinus*

There are currently three confirmed cases of herbicide-resistant *B. secalinus* populations (Table 1). Two populations were identified in the United States in 2007 and 2009, respectively (Heap 2022), and one population was documented in the United Kingdom in 2020 (Davies et al. 2020). All populations are resistant to ALS-inhibiting herbicides. Both resistant populations reported in the United States had broad cross-resistance patterns including all four ALS herbicide chemical families, imidazolinone, triazopyrimidine, triazolinones, and sulfonylurea. The population identified in the United Kingdom was resistant to the sulfonylurea herbicide mesosulfuron + iodosulfuron-methyl-sodium (Davies et al. 2020). This population was 3.9-fold less sensitive to mesosulfuron + iodosulfuron-methyl-sodium compared with the susceptible population. The mechanisms of resistance in these populations were not reported.

Bromus sterilis

Bromus sterilis, commonly known as barren brome or poverty brome, is an annual or biennial grass species that originated in the Mediterranean and southwestern Asian region (Williams et al. 2011; Table 2) and has been introduced into several countries in

Australasia, North America, and South America (USDA-ARS 2023a). It naturally occurs in field margins and waste ground areas and has become a troublesome weed in cropland (Green et al. 2001). This species is a particular problem in cereal crops because of the increased adoption of minimum tillage and limited herbicide options for its control. Lack of *B. sterilis* control can result in yield losses ranging from 30% to 60% in winter wheat (Gehring et al. 2006).

Bromus sterilis typically germinates in early fall with winter cereals and its germination can occur within a broad range of temperatures varying from 5 to 35 °C (Žd'árková et al. 2014). The optimum temperature for its germination is between 20 and 30 °C (95% to 100%) and germination is greater in the dark than in the light regardless of temperature. The primary dormancy of *B. sterilis* is typically short and lasts about a month. Previous research showed that light induces dormancy in *B. sterilis* (Peters et al. 2000; Pollard 1982). Seedling emergence is marginally greater when seeds are buried at a 2-cm depth (58.5%) than when they are left on the soil surface (53%) (Žd'árková et al. 2014). *Bromus sterilis* seeds retain short viability in the soil (<2 yr), suggesting a short-lived soil seedbank (Davies et al. 2019; Žd'árková et al. 2014).

Biology and Genetics

Bromus sterilis is predominantly self-pollinated with low levels of outcrossing occurring occasionally (Green et al. 2001). The inflorescences of *B. sterilis* are open and nodding (10- to 20-cm long by 5- to 12-cm wide) with spreading branches typically longer than the spikelets (Meyers et al. 2015). It has 1 or 2 spikelets (20 to 35 mm), moderately laterally compressed, containing 5 to 9 florets. Glumes are smooth or scabrous; lower glumes (8 to 10 mm; 1- to 3-veined) are shorter than upper glumes (12 to 15 mm; 3- to 5-veined). Lemmas are 14 to 20 mm, narrowly lanceolate, pubescent, and 7- to 9-veined. Lemma awns are straight and range from 15 to 30 mm in length.

Bromus sterilis is a diploid ($2n = 2x = 14$; 2.91-Gb genome size) species in the *Genea* section (Table 2), with a nuclear DNA content of 2.98 pg (Pustahija et al. 2013). This species is closely related to *B. tectorum* based on chloroplast DNA sequences (Fortune et al. 2008). Evidence in the literature suggests possible hybridization between *B. sterilis* and other *Bromus* spp. (Table 3). Based on isoenzyme analysis, *B. sterilis* (male parent) and *B. fasciculatus* (female parent) are the most plausible progenitors of *B. madritensis* (Oja 2002a).

Resistance in *Bromus sterilis*

Herbicide resistance in *B. sterilis* has been reported in four countries, including the Czech Republic, France, Germany, and the United Kingdom (Table 1). Resistant *B. sterilis* populations were identified in cereals including wheat, postharvest stubble, and rapeseed/canola (*Brassica napus* L.) (Table 1). Resistance has been reported for ACCase inhibitors, ALS inhibitors, and for the EPSPS inhibitor glyphosate. An ACCase inhibitor-resistant *B. sterilis* population was documented in Germany and was cross-resistant to cycloxydim (cyclohexanedione [CHD]) and propaquizafop (aryloxyphenoxypropionate [AOPP]) (Table 1). Cases of cross-resistance to two and three ALS chemical families have been documented in resistant *B. sterilis* populations in the Czech Republic, France, and the United Kingdom. An ALS-resistant *B. sterilis* population found in a wheat field in the Czech Republic was 288 times less sensitive to pyroxsulam than a

susceptible population and was cross-resistant to propoxycarbazon-sodium (RF = 575) and sulfometuron-methyl (RF = 88). The resistance mechanisms in this population were associated with overexpression of the *ALS* gene (almost 2-fold overexpression; TSR) and enhanced metabolism via P450 enzymes (NTSR) (Sen et al. 2021). In the United Kingdom, Davies et al. (2020) reported *B. sterilis* populations with reduced sensitivity to the *ALS* inhibitors mesosulfuron + iodosulfuron-methyl-sodium (RF = 3.5 to 8.3) and pyroxsulam (RF = 2.9 to 16). Enhanced levels of AmGSTF1 proteins were observed in the resistant populations, suggesting the presence of an NTSR mechanism. Glyphosate-resistant *B. sterilis* populations were identified in postharvest stubble in the United Kingdom (Davies et al. 2019). The effective rate to control 50% (ED₅₀) of these resistant *B. sterilis* populations ranged from 420 to 810 g ha⁻¹, resulting in an RF of 1.6 to 4.5. The mechanisms of resistance were not reported.

Bromus tectorum

Bromus tectorum, commonly known as downy brome or cheatgrass, is a native species from the Mediterranean and southwest Asian region (Williams et al. 2011). *Bromus tectorum* has been introduced to northern Europe, North America, Japan, South Africa, Australia, New Zealand, South America, and in single localities in Iceland and Greenland (Mitich 1999; USDA-ARS 2023b). Genetic evidence suggests that *B. tectorum*'s introduction into North America occurred independently multiple times on both coasts (Bartlett et al. 2002; Novak and Mack 1993). The soil used as ballast in ships sailing from Eurasia into North America was probably one of the main carriers of *B. tectorum* seeds (Mitich 1999). The first report of *B. tectorum* in the United States was in Pennsylvania in 1790 (Muhlenberg 1793). By the end of the 19th century, *B. tectorum* had expanded throughout the western United States (Mack 1981). *Bromus tectorum* thrives in a variety of non-crop disturbed and cultivated habitats and can occur in locations with annual rainfall ranging from 150 to 560 mm, including different soil types, and at elevations as high as 2,700 m (Hull and Pechanec 1947). In the United States Pacific Northwest, *B. tectorum* is a problematic weed in dryland winter wheat fields (Rydrych 1974). In eastern Washington, fewer than 54 *B. tectorum* plants m⁻² reduced wheat yields by 28% on a field with very fine sandy loam soil that received annual precipitation of 250 mm (Rydrych and Muzik 1968). On a field with silt loam soil that received annual precipitation of 550 mm, more than 538 *B. tectorum* plants m⁻² reduced winter wheat yields by 92% (Rydrych and Muzik 1968). *Bromus tectorum* is a winter annual that typically germinates in the fall shortly after the first onset of rains (Morrow and Stahlman 1984). If fall moisture is limiting, *B. tectorum* can germinate in the spring (Hulbert 1955; Stewart and Hull 1949). Freshly produced seeds become dormant after dispersal in early summer and lose dormancy through after-ripening (Allen and Meyer 2002). Nondormant seeds can germinate at temperatures ranging from 5 to 30 °C (Evans and Young 1984). Seedling emergence is greater at 2- (100%) than at 4- (93%) or 6-cm depths (14%) (Hulbert 1955). Most *B. tectorum* seeds germinate (96% to 99%) in the first year after entering the soil seedbank (Burnside et al. 1996), with few persisting longer than 2 yr (Haferkamp et al. 2001; Smith et al. 2008). In a winter wheat–summer fallow rotation, *B. tectorum* seed viability was less than 2% by the third year (Rydrych 1974).

Biology and Genetics

Bromus tectorum reproduces solely by seeds (Hulbert 1955). It produces loose and drooping panicles between 4- to 18-cm long with a purplish cast when mature (Bryson and DeFelice 2010). Spikelets are 1.9- to 2.3-cm long including awns and contain 4 to 8 flowers. Glumes are pubescent or glabrous; the first glume ranges from 4- to 9-mm long (1-veined) and the second glume ranges from 7- to 13-mm long (3- to 5-veined). The lemma is 9- to 12-mm long, pubescent, with an awn of 10- to 18-mm long. The palea (1.2 to 2.1 mm) is shorter than the lemma and ciliates on nerves.

Bromus tectorum is a diploid species ($2n = 2x = 14$; 3.23-Gb genome size) in the *Genea* section (Table 2), with a nuclear DNA content of 3.30 pg (Bennett and Smith 1976). *Bromus tectorum* is predominantly self-pollinated, but outcrossing can occur (Ashley and Longland 2007; Meyer et al. 2013; Novak and Mack 2016). The estimated outcrossing rate for four wild *B. tectorum* populations from the western United States ranged from 0.27% to 1.33% (Meyer et al. 2013). Significant levels of genotypic and phenotypic variations have been detected in *B. tectorum* populations, which are major drivers of *B. tectorum* successful invasion across different environments (Ashley and Longland 2007). Based on chloroplast data, *B. tectorum* (paternal parent), and *B. fasciculatus* (maternal parent) were the progenitors of *B. rubens* (Fortune et al. 2008). Therefore, interspecific hybridization between *B. tectorum* and other *Bromus* spp. is possible (Table 3).

Resistance in *Bromus tectorum*

Bromus tectorum populations have evolved resistance to ACCase-, ALS-, and PSII-inhibiting herbicides, and to the EPSPS inhibitor glyphosate (Table 1). The first recorded case of herbicide resistance in *B. tectorum* was an atrazine-resistant population in a cornfield in France in 1981 (Table 1). In Spain, *B. tectorum* populations resistant to PSII inhibitors were found in an olive orchard (Menendez et al. 2007) and wheat fields (Menendez et al. 2006). The resistant population (ED₅₀ = 7.3 kg ai ha⁻¹) identified in simazine-treated olive groves was 73-fold less sensitive to simazine compared with a susceptible population (ED₅₀ = 0.1 kg ai ha⁻¹) (Menendez et al. 2007). Hill reaction assays showed the chloroplasts of the resistant population were >300 times less sensitive to simazine than the susceptible population, suggesting a target-site mutation (likely due to a mutation of the chloroplast *psbA* gene that encodes the D1 protein) as the molecular basis for resistance to simazine in this population (Menendez et al. 2007). The resistant population reported in a wheat field required 7.4 kg ai ha⁻¹ of chlortoluron to reduce growth by 50%, which was 3.4 times the rate required for the susceptible population (Menendez et al. 2006). Molecular investigations showed that chlortoluron metabolism in the resistant population decreased by 20% when treated with the P450 inhibitor 1-ABT, suggesting a non-target site based resistance via P450-mediated metabolism.

In the United States Pacific Northwest, resistance in *B. tectorum* is of increasing concern in grass seed production systems and dryland wheat-based cropping systems, where cross- or multiple-herbicide resistance is extensive (Table 1). In 1997, an ALS-resistant *B. tectorum* population was identified in Madras, OR, in Kentucky bluegrass (*Poa pratensis* L.) experimental plots (Mallory-Smith et al. 1999). This population was cross-resistant to three ALS chemical families, including sulfonylurea (primisulfuron-methyl and sulfosulfuron), triazolinones (propoxycarbazon-sodium), and imidazolinone (imazamox) (Park and Mallory-Smith 2004). There was a variation in the levels of resistance (based on GR₅₀

values) for primisulfuron-methyl (RF = 18), sulfosulfuron (RF = 9), propoxycarbazone-sodium (RF = 40), and imazamox (RF = 14). The resistance mechanism in this population was related to enhanced metabolism via P450 enzymes (Park et al. 2004). When [^{14}C]propoxycarbazone-sodium was applied with 1-aminobenzotriazole (1-ABTP; P450 inhibitor), metabolism decreased by 20% at 12 h after treatment (Park et al. 2004). ALS gene sequencing did not detect any mutation in this population (Park and Mallory-Smith 2004). Further investigations revealed that this population was multiple resistant to clethodim (RF = 2.3) and fluzifop-P-butyl (RF = 1.9) (ACCase inhibitors); atrazine (RF > 14), terbacil (RF = 4.6), metribuzin (RF > 20), and diuron (RF = 3.1) (PSII inhibitors); and ethofumesate (RF = 4.2) (VLCFA inhibitor) (Park and Mallory-Smith 2005). DNA sequence analysis of the *psbA* gene, the target site of PSII inhibitors, revealed a single amino acid substitution from serine (AGT) to glycine (GGT) at amino acid 264 in the D1 protein, indicating that resistance to the PSII inhibitors atrazine and metribuzin was due to a target-site mutation (Park and Mallory-Smith 2005). The mechanisms of resistance to clethodim, fluzifop-P-butyl, and ethofumesate were not investigated. In 1998, another ALS-resistant *B. tectorum* population was found in a Kentucky bluegrass field in Oregon (Park and Mallory-Smith 2004). This population was cross-resistant to two ALS chemical families, sulfonyleurea (primisulfuron-methyl and sulfosulfuron), and triazolinones (propoxycarbazone-sodium) (Park and Mallory-Smith 2004). The level of resistance calculated by the estimated GR_{50} values showed that this population was 317-, 263-, and 235-fold more resistant than the susceptible population to primisulfuron-methyl, sulfosulfuron, and propoxycarbazone-sodium, respectively. Resistance in this population was conferred by a single-nucleotide polymorphism (C to T) at amino acid position 197, resulting in a Pro-197-Ser substitution (Park and Mallory-Smith 2004).

Kumar and Jha (2017) identified an ALS-resistant *B. tectorum* population in an imidazoline-resistant wheat field in Montana, USA, with high-level resistance (RF = 110.1) to imazamox and low to moderate levels of cross-resistance to pyroxsulam (RF = 4.6) and propoxycarbazone (RF = 13.9). A target-site Ser-653-Asn mutation was detected in this population. In Washington, among 50 *B. tectorum* populations tested for resistance, 2% were multiple resistant to ACCase and ALS inhibitors, 52% were cross-resistant to multiple chemical families of ALS inhibitors, and 20% were resistant to a single chemical family of ALS-inhibiting herbicides (Zuger and Burke 2020). Additionally, three glyphosate-resistant *B. tectorum* populations (RF = 88 to 165) were confirmed but did not have resistance to any other herbicide SOA (Zuger and Burke 2020). Resistance to ALS inhibitors is also prevalent in *B. tectorum* populations in dryland winter wheat fields in Oregon, with cases of cross-resistance ranging from two to four ALS chemical families (Ribeiro et al. 2023, unpublished data). *Bromus tectorum* populations cross-resistant to ACCase inhibitors were reported in fine fescue (*Festuca L. spp.*) fields in Oregon (Ball et al. 2007; Ribeiro et al. 2023). In 2005, Ball et al. (2007) identified an ACCase-resistant *B. tectorum* population in a creeping red fescue (*Festuca rubra L. ssp. rubra* Gaudin) seed production field in Oregon. The population exhibited high levels of resistance to fluzifop-P-butyl (RF > 16) and sethoxydim (RF > 23) and low levels of resistance to clethodim (RF > 2) and quizalofop-P-ethyl (RF > 3). Fifteen years later, nine more ACCase-resistant *B. tectorum* populations were found in fine fescue seed production fields in the same area (Ribeiro et al. 2023). The levels of resistance varied among the populations for clethodim (RF = 5.1 to 14.5), sethoxydim

(RF = 18.7 to 44.7), fluzifop-P-butyl (RF = 3.1 to 40.3), and quizalofop-P-ethyl (RF = 14.5 to 36). The ACCase sequence analysis indicated that the Ile-2041-Thr and Gly-2096-Ala mutations were the molecular basis of resistance to the ACCase-inhibiting herbicides in these populations. In 2021, a glyphosate-resistant *B. tectorum* population was documented in a rapeseed/canola field in Alberta, Canada (Geddes and Pittman 2022). This population exhibited 8.3- to 9.5-fold resistance to glyphosate compared with two susceptible populations. The mechanism of resistance in this population was not elucidated. This population was the first glyphosate-resistant grass weed species confirmed in Canada.

In the United States, *B. tectorum* and other species such as *B. commutatus*, *B. japonicus*, *B. secalinus*, *B. sterilis*, and *B. diandrus* can occur in several agricultural systems, including wheat, alfalfa, and grass seed production fields (Finnerty and Klingman 1962; Koscelny et al. 1990, 1991). The presence of multiple *Bromus* spp. in the same field, particularly species with sexual compatibility, plays a key role in hybrid speciation as well as the spread of resistance alleles. Research on the risk of gene flow between herbicide-resistant and herbicide-susceptible populations is scarce. Therefore, further investigations into the risk of transferring herbicide-resistance alleles from *B. tectorum* to susceptible plants are needed, as outcrossing can occur.

Summary and Research Needs

Herbicide resistance in *Bromus* spp. is a global issue. Cases of resistance have been confirmed in *B. japonicus*, *B. sterilis*, *B. tectorum*, *B. commutatus*, *B. madritensis*, *B. rubens*, *B. secalinus*, *B. catharticus*, *B. rigidus*, and *B. diandrus*. *Bromus* spp. populations have evolved resistance to six known herbicide SOAs, ACCase (Group 1), ALS (Group 2), PSII (Groups 5 and 7), VLCFA (Group 15), EPSPS (Group 9), and HPPD (Group 27). Several mechanisms of resistance have been reported in *Bromus* spp., including TSR, NTSR, and combinations of both. The mechanisms of resistance in many *Bromus* spp. populations still need to be investigated. Knowledge about the mechanism of resistance and its genetic basis is important for designing suitable management strategies to address resistance management. High-throughput, rapid genetic assays have been developed for herbicide-resistance detection (Kersten et al. 2023), and their deployment will help improve the development of weed management plans to ensure the proper chemistry is chosen. Knowledge of resistance mechanisms is particularly important for populations exhibiting NTSR, because this type of resistance mechanism can be unpredictable. Most studies tested *Bromus* spp. populations against a short list of herbicides. Therefore, it is possible that some of the populations are also resistant to other chemistries.

Bromus spp. are predominantly self-pollinated with low outcrossing rates ($\leq 1.8\%$) occurring in some species. The outcrossing rate in some *Bromus* spp. has not been reported, although the literature indicates that sexual compatibility among species exists. Information on the hybridization of *Bromus* spp. is very limited and needs further investigation. Furthermore, environmental conditions can impact the outcrossing rates of other weed species, with increased temperatures enhancing the outcrossing rate (Matzrafi et al. 2020), and more information is needed for *Bromus* spp. in a climate change scenario. The transfer of herbicide-resistance alleles via pollen-mediated gene flow cannot be ruled out, as outcrossing can occur at low rates in some *Bromus* spp. Most research on hybridization between

Bromus spp. has been done within a controlled environment (e.g., greenhouse). However, hybridization needs to be studied under field conditions. Chances of hybridization may be much greater under field conditions, because the number of plants present is greater. In addition, more studies are necessary to further elucidate hybrid seed viability, as well as potential for heterosis, and competitive ability. Although most hybrids produced between *Bromus* spp. have been reported to be sterile, research on interspecific hybridization involving other self-pollinating species such as jointed goatgrass (*Aegilops cylindrica* Host) and wheat showed restoration of self-fertility in the second backcross between these species (Zemetra et al. 1998). Thus, this assumption of sterility of hybrids between *Bromus* spp. can be incorrect and needs further investigation. Because *Bromus* spp. are typically highly self-pollinating, the geographic spread of herbicide resistance occurs primarily by natural (water and wind) and anthropogenic seed dispersal. Therefore, research on tactics to reduce seed-mediated gene flow in *Bromus* spp., including practices such as harvest weed seed destruction, would be beneficial.

Although herbicide resistance has been reported for most *Bromus* spp., the underlying genetic, molecular, and physiological mechanisms of many species remain unknown. Because of the parallel evolution of herbicide resistance in diverse continents, cropping systems, and ecotypes, the *Bromus* genus provides an invaluable opportunity to understand convergent evolution under herbicide selection pressure.

The ploidy levels in *Bromus* spp. range from diploid ($2n = 2x = 14$) to duodecaploid ($2n = 12x = 84$). Self-pollination and polyploidization are important traits responsible for the colonization and invasion success of plant species in a wide range of habitats (Orsucci et al. 2020). Self-pollination provides reproductive insurance, allowing a single plant to initiate an invasion (Kreiner et al. 2018), while polyploidization confers partial sheltering from the negative effect of inbreeding, particularly by masking deleterious alleles (Beest et al. 2012). However, the scientific literature is limited regarding the influence of ploidy on herbicide-resistance mechanisms. Therefore, more in-depth research is needed to comprehend the complexities of herbicide resistance and evolution in *Bromus* spp.

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