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Weed Technology

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Transfer of resistance alleles from herbicide-resistant to susceptible grass weeds via pollen-mediated gene flow

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Review

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Nomenclature:
Barnyardgrass; *Echinochloa crus-galli* (L.) Beauv.; creeping bentgrass; *Agrostis stolonifera* L.; Italian ryegrass; *Lolium perenne* ssp. *multiflorum* (Lam.) Husnot; johnsongrass; *Sorghum halepense* (L.) Pers.; perennial ryegrass; *Lolium perenne* L.; rigid (annual) ryegrass; *Lolium rigidum* Geud.; sterile oat; *Avena sterilis* L.; wild oat; *Avena fatua* L.

Keywords:
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Abstract

The objective of this paper was to review the reproductive biology, herbicide-resistant (HR) biotypes, pollen-mediated gene flow (PMGF), and potential for transfer of alleles from HR to herbicide-susceptible grass weeds including barnyardgrass, creeping bentgrass, Italian ryegrass, johnsongrass, rigid (annual) ryegrass, and wild oats. The widespread occurrence of HR grass weeds is at least partly due to PMGF, particularly in obligate outcrossing species such as rigid ryegrass. Creeping bentgrass, a wind-pollinated turfgrass species, can efficiently disseminate herbicide resistance alleles via PMGF and movement of seeds and stolons. The genus *Agrostis* contains about 200 species, many of which are sexually compatible and produce naturally occurring hybrids and hybrids with species in the genus *Polypogon*. The self-incompatibility, extremely high outcrossing rate, and wind pollination in Italian ryegrass clearly point to PMGF as a major mechanism by which herbicide resistance alleles can spread across agricultural landscapes, resulting in abundant genetic variation within populations and low genetic differentiation among populations. Italian ryegrass can readily hybridize with perennial ryegrass and rigid ryegrass due to their similarity in chromosome numbers ($2n = 14$), resulting in interspecific gene exchange. Johnsongrass, barnyardgrass, and wild oats are self-pollinated species, so the potential for PMGF is relatively low and limited to short distances; however, seeds can easily shatter upon maturity before crop harvest, leading to wider dispersal. The occurrence of PMGF in reviewed grass weed species, even at a low rate, is greater than that of spontaneous mutations conferring herbicide resistance in weeds and thus can contribute to the spread of herbicide resistance alleles. This review indicates that the transfer of herbicide resistance alleles occurs under field conditions at varying levels depending on the grass weed species.

Introduction

Weeds are among the most economically important pests of agronomic crops worldwide and are a major constraint to optimum crop production (Jhala et al. 2014). Herbicides have become integral to weed control in agronomic crop production systems particularly after the commercialization and widespread adoption of herbicide-resistant (HR) crops (Norsworthy et al. 2012). The use of herbicides has provided economical and selective weed control in major agronomic crops in developed countries for many years (Duke 2015), although widespread and repeated use of herbicides has resulted in the evolution of HR weeds (Beckie 2006; Kniss 2018). As of 2021, there are at least 502 unique cases of HR weeds worldwide in 263 weed species, including 152 broadleaf and 111 grass weeds (Heap 2021). Grass weeds are usually more difficult to identify compared with broadleaf weeds, particularly at the seedling stage due to similar appearance and emergence as a single leaf (Sarangi and Jhala 2017). Because growers rarely proactively manage HR grass weeds, their widespread occurrence and interference in agronomic crop production fields present a challenge (Beckie 2007). The grass weed species, rigid ryegrass, has evolved resistance to at least 14 herbicides with different sites of action (SOAs) in more than 21 countries (Suzukawa et al. 2021).

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Pollen-mediated gene flow (PMGF) is the change in the frequency of alleles in a population due to the movement of pollen via wind, insect pollinators, or other means (Ganie and Jhala 2017) leading to gene introgression in the population (Jhala et al. 2021). While seed-mediated gene flow is very common in most weed species (Beckie et al. 2016), gene flow can also occur through the transfer of vegetative propagules in certain weed species such as creeping bentgrass (Mallory-Smith and Zapiola 2008). PMGF occurs, at least to some extent, in most flowering plants, including grass weeds, and usually creates genetic diversity through the exchange of alleles within and between populations (Jhala et al. 2021). The intensity of gene exchange between populations via PMGF primarily depends on the plant breeding system (Darmency 1996), the pollen migration dynamics of the donor and recipient populations (Busi et al. 2011; Délye et al. 2010), distance between populations (Busi et al. 2008), and plant density of the source population (Baker and Preston 2006; Rognli et al. 2000). If the pollen source population is large enough and has a high frequency of herbicide resistance alleles, PMGF can cause effective migration of genes to distant population with a low plant density (Mallory-Smith et al. 2015), as evidenced with isolated, herbicide-susceptible rigid ryegrass (Busi et al. 2008). Genetic variation among individuals within a population is required for adaptive evolution by natural selection. The abundant genetic variation detected within a species may explain why resistance to many different herbicide SOAs has evolved so rapidly in certain weed species such as Italian ryegrass.

The evolution of HR weeds can be explained by analyzing population genetic principles to understand the continuous trade-off between the intensity of herbicide selection, the in situ mutation rate endowing herbicide resistance alleles, and the pleiotropic fitness effects of resistance-endowing traits (Diggle and Neve 2001; Gressel 1978; Maxwell et al. 1990). These factors drive the rate of evolution of resistance or increase the frequency of resistance alleles in a population (Jhala et al. 2021). The movement of herbicide resistance alleles within or between fields is the gene flow that impacts the spread and distribution of HR weeds (Jasieniuk et al. 1996; Neve et al. 2014). Empirical studies have determined that PMGF in cross-pollinated species can be high even at long distances depending on the species (Levin and Kerster 1974) compared with self-pollinated species (Jhala et al. 2021). This phenomenon has been documented to occur over considerable distances at the landscape level at relatively high frequency in some wind-pollinated grasses (Watrud et al. 2004) such as creeping bentgrass (Zapiola and Mallory-Smith 2017) and has generally been modeled by a negative exponential decay distribution (Levin and Kerster 1974; Pfender et al. 2007).

PMGF and the spread of HR weeds into new agroecosystems is a concern because it introduces new HR alleles into weeds and makes them difficult to control with herbicides (Jhala et al. 2011; Jhala and Hall 2013). Beckie et al. (2019) reported that PMGF from HR crops has been extensively studied; however, PMGF from HR weeds is understudied. Jhala et al. (2021) reviewed PMGF from economically important HR broadleaf weeds to susceptible weeds; however, a comprehensive review of the scientific literature on PMGF from HR grass weeds has not been collated. The objective of this article was to review reproductive biology, HR biotypes, and the potential for herbicide resistance allele transfer via pollen from economically important and widely distributed HR grass weeds, including barnyardgrass, creeping bentgrass, Italian ryegrass, johnsongrass, rigid ryegrass, and wild oats (*Avena fatua* L. and *Avena sterilis* L.).



Figure 1. Ongoing pollination of a barnyardgrass inflorescence (photo credit: Jason Norsworthy).

Barnyardgrass

Barnyardgrass is the world's principal grass weed in rice (Mitich 1990). It is among the most troublesome weeds in crops grown in rotation with rice or crops grown in areas where moist soil or seasonal flooding is common. Barnyardgrass is native to Europe and Asia and is found in almost all the agricultural regions of the world (Mitich 1990). It is a C_4 semi-terrestrial summer annual grass weed with high fecundity (Bagavathiannan et al. 2012; Bosnic and Swanton 1997; Norris et al. 2001), rapid turnover of its soil seedbank (Bagavathiannan et al. 2011), and tremendous genetic diversity (Altop and Mennan 2011). In Asian countries where hand weeding of transplanted rice is a common practice, barnyardgrass has evolved to morphologically mimic rice, making its removal from the crop difficult (Barrett 1983). Research continues to show high morphological and genetic variability between individual barnyardgrass genotypes within geographic locations, which aids the adaptive nature of this weed (Altop and Mennan 2011; Rutledge et al. 2000).

Barnyardgrass Reproductive Biology

Barnyardgrass is a self-compatible and an autogamous grass weed species (Maun and Barrett 1986) that exhibits indeterminate flowering and production of panicles with reproduction mainly through selfing (Figure 1; Table 1), although outcrossing can occur, especially when plants are in close proximity (Bagavathiannan and Norsworthy 2014). There is no known published literature on the viability of barnyardgrass pollen, and gene flow is mostly associated with wind events.

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Table 1. Economically important herbicide-resistant grass weed species reviewed in this study, their chromosome numbers, and their likelihood of pollen-mediated gene flow.

Weed species	Scientific name	Chromosome numbers	Pollination trait	Likelihood of PMGF[a]
Barnyardgrass[b]	*Echinochloa crus-galli* (L.) Beauv.	$2n = 36$ to 72	Self-compatible; autogamous	Low
Creeping bentgrass[c]	*Agrostis stolonifera* L.	$2n = 4x = 28$	Self-incompatible; outcrossing	High
Italian ryegrass	*Lolium perenne* ssp. *multiflorum* (Lam.) Husnot	$2n = 14$	Self-incompatible; outcrossing	High
Johnsongrass[c]	*Sorghum halepense* (L.) Pers.	$2n = 4x = 40$	Self-pollinated	Low
Rigid ryegrass	*Lolium rigidum* Geud.	$2n = 14$	Obligate outcrossing	High
Wild oats[d]	*Avena fatua* L.; Avena *sterilis* L.	$2n = 6x = 42$	Self-pollinated	Low

[a]Likelihood of pollen-mediated gene flow (PMGF) was estimated based on reproductive biology and scientific literature.
[b]Chromosome numbers reported for barnyardgrass vary from 2n = 36, 42, 48, 54, and 72 (Aoki et al. 2008).
[c]Creeping bentgrass is an allotetraploid species; johnsongrass is a tetraploid species.
[d]Wild oats are hexaploid species.

Herbicide Resistance in Barnyardgrass

Barnyardgrass and the closely related junglerice [*Echinochloa colona* (L.) Link] have evolved resistance to 13 herbicide SOAs with resistance to as many as seven SOAs in some populations, making management of this weed challenging in many cropping systems (Rouse et al. 2018). It is one of the most HR-prone weed species, second to rigid ryegrass (Heap 2021). Based on results from simulation modeling, simultaneous application of two effective herbicides has a greater likelihood of mitigating resistance in barnyardgrass compared with the exhaustion of one effective herbicide followed by the use of another (Bagavathiannan et al. 2014).

Florpyrauxifen-benzyl, a synthetic auxinic herbicide, is the most recent novel herbicide commercialized for use in rice for barnyardgrass control. Prior to the commercialization of this herbicide, results from herbicide screening programs indicated that florpyrauxifen-benzyl was effective for controlling quinclorac-resistant barnyardgrass and for its resistance to other SOA herbicides (Miller et al. 2018). Recent findings, however, show that florpyrauxifen-resistant barnyardgrass is present in rice production fields, with the resistance mechanism appearing to be based on non-target sites (Hwang et al. 2022). Limited herbicide options in crops such as rice, the occurrence of multiple herbicide resistance involving non-target site resistance mechanisms in barnyardgrass, and the lack of discovery of novel herbicide target sites make the sustainability of existing herbicide programs questionable at the current rate of herbicide loss due to resistance.

PMGF from HR Barnyardgrass

As with other weeds, gene flow in barnyardgrass can occur via seed or pollen movement. In field studies conducted in Arkansas, the likelihood of PMGF from barnyardgrass was examined using a quinclorac-resistant population as a pollen source (Bagavathiannan and Norsworthy 2014). Wind was found to be the main factor aiding the movement of resistance alleles via pollen, with very low PMGF detected at 50 m (0.01%), the farthest distance studied. Based on these findings, the authors speculated that seed movement would most likely contribute to the landscape-level spread of herbicide resistance in barnyardgrass through rainfall events, birds, and human activities. Likewise, Rutledge et al. (2000) suggested that the spread of herbicide resistance in barnyardgrass is primarily a result of seed dispersal following the selection of independent mutation events.

Creeping Bentgrass

Creeping bentgrass is a perennial, cool season (C_3) turf grass often used on golf courses, especially putting greens, due to its ability to withstand repeated, low mowing and foot traffic (Ferguson 1969). More than 80% of creeping bentgrass seed sold globally is produced in Oregon. In 2019, 1.3 million kg with a market value of US$8.73 million were produced on approximately 2,000 ha (ODA 2020). Many of the species in the *Agrostis* genus, including creeping bentgrass, are weedy or invasive in managed and unmanaged sites (Ahrens et al. 2011; Hart et al. 2009; Reichman et al. 2006). The weed risk potential of creeping bentgrass is classified as high (USDA-APHIS 2014; Table 1). Creeping bentgrass is widespread globally and is reported in all states in the continental United States (MacBryde 2006). It is a known grass weed in roadsides, ditches, irrigation canals, turf, and pasture (Figure 2). In the United States, the genus includes both native and nonnative species (MacBryde 2006).

Creeping Bentgrass Reproductive Biology

Creeping bentgrass is an outcrossing, self-incompatible, wind-pollinated species that reproduces via seed and stolons (Bradshaw 1958; Kik et al. 1990). Creeping bentgrass produces flowers on a panicle and flowers over an extended period of time. Pollen grains of creeping bentgrass are approximately 35.4 µm in diameter and weigh on average 52 ng (Pfender et al. 2007). The seeds are very small, with about 13,500 seeds g^{-1}. The seeds are easily transported via human activity and natural vectors such as wind, water, and animals. Panicles in irrigation canals moved an average of 19 m min^{-1} (Zapiola and Mallory-Smith 2010; Figure 2). Creeping bentgrass seeds soaked in water for 17 wk (the limits of the study) at 4 and 20 C maintained germinability (Zapiola and Mallory-Smith 2010).

As a perennial species, once a plant is established, it can contribute PMGF over multiple years, and genes can also disperse via seeds and stolons. Seeds of glyphosate-resistant creeping bentgrass lines survived more than 4 yr of burial in Oregon (Hancock et al. 2015). In greenhouse and laboratory studies, plants were established from sections of stolons with one node buried at 15 cm, and stolons remained viable after 5 d of desiccation at 20 C or after being submerged in water up to 2 m at 4 C (Dysart and Mallory-Smith unpublished data).

The *Agrostis* genus contains about 200 species, many of which are sexually *A.* ×*murbeckii* compatible with creeping bentgrass. Naturally occurring intraspecific, interspecific, and intergeneric (most commonly with *Polypogon* ssp.) hybrids have been identified (MacBryde 2006). Some of the hybrids are sufficiently common to have been given a scientific name; for example, the hybrid *A.* ×*murbeckii* Fouill. is a cross between creeping bentgrass and *A. capillaris*. *Agrostis* ×*murbeckii* is sterile but reproduces via stolons and is reported to be more competitive than either parent

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Figure 2. Glyphosate-resistant creeping bentgrass established on an irrigation canal in 2016 near Ontario, Oregon (photo credit: Maria Zapiola).

(Bradshaw 1958). Many of the hybrids are fertile; even if sterile, the plants will likely persist because the parent species are perennial and reproduce vegetatively.

Herbicide Resistance in Creeping Bentgrass

Amitrole-resistant creeping bentgrass was identified in 1986 in Belgium (Bulke and Eelen 2000). The HR biotype was found in a pear orchard where long-term studies had been conducted. This is the only report of evolved resistance in this species. Although never commercialized, genetically engineered glyphosate-resistant and glufosinate-resistant creeping bentgrass have been grown. Glyphosate-resistant creeping bentgrass was produced by Scotts Company and Monsanto using the *CP4* 5-enolpyruvylshikimate-3-phosphate synthase (*EPSPS*) gene used in other glyphosate-resistant crops (Zapiola et al. 2008). Glyphosate-resistant creeping bentgrass was grown for seed production in field sites in Oregon in 2002 and Idaho in 2002 to 2005 (Zapiola and Mallory-Smith 2017).

Glufosinate-resistant creeping bentgrass was produced by several entities, often the result of using the *bar* gene as a marker in plant transformation (Asano et al. 1998; Hartman et al 1994; Lee et al. 1995, 2010; Wang et al. 2003). Lee et al. (2010) produced creeping bentgrass with resistance to both herbicides. The authors are unaware of reports of feral glufosinate-resistant creeping bentgrass occurring in the environment as there is with glyphosate-resistant creeping bentgrass (Zapiola et al. 2008); however, it would not be surprising to find such cases due to research being conducted in field experiments, and because there would be no expectation that the glufosinate-resistant plants would respond differently than glyphosate-resistant plants (Belanger et al. 2003a, 2003b; Lee et al. 1995; Wipff and Fricker 2000).

PMGF from HR Creeping Bentgrass

PMGF from both glyphosate- and glufosinate-resistant creeping bentgrass has been evaluated in greenhouse and field studies in Oregon. Greenhouse studies used the glufosinate resistance gene as a marker to determine the frequency of interspecific crosses between creeping bentgrass and four *Agrostis* species, velvet, dryland, and colonial bentgrasses, and redtop (Belanger et al. 2003b). Glufosinate-resistant hybrids were recovered from all four species. The number of resistant hybrids ranged from 8% to 22% depending on the maternal parent. Under field conditions, the hybrids produced in the greenhouse study were fertile and could backcross with the parental species.

Field studies have included experimental designs using either glyphosate- or glufosinate-resistant plants as pollen sources and compatible species as pollen receptor plants spaced at known distances from the pollen source (Belanger et al. 2003a; Christoffer 2003; Wipff and Fricker 2000). Several studies were conducted over relatively short distances, ranging from 15 m (Belanger et al. 2003a) to 350 m (Christoffer 2003). Christoffer (2003) used glyphosate-resistant creeping bentgrass as the pollen parent and 15 other species as pollen receptors, 12 *Agrostis* species and three *Polypogon* species. (Table 2). Hybrids were produced on all tested species with the exception of *A. nebulosi* and *Apera interrupta*. No interspecific or intergeneric hybrids were found beyond 50 m, whereas intraspecific hybrids were recovered at 354 m, which was the limit of the study. Belanger et al. (2003a) reported crosses between glufosinate-resistant creeping bentgrass and *A. capillaris* and *A. castellana*. Wipff and Fricker (2001) reported crosses between glufosinate-resistant creeping bentgrass and five *Agrostis* species (Table 2). Wipff and Fricker (2001) measured intraspecific gene flow from glufosinate-resistant creeping bentgrass to conventional bentgrass. They recovered resistant plants at 300 m, which was the limit of the study. These studies confirm the potential for herbicide resistance allele movement via pollen. In all cases, gene flow was confirmed at the farthest distance measured in the study. Wipff and Fricker (2000) used an exponential decay model to predict gene flow at a level of 0.02%, which estimated pollen movement of approximately 1,300 m.

Two large-scale studies were conducted in Oregon where glyphosate-resistant creeping bentgrass had been planted for seed production in Jefferson County in an area designated by the Oregon

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Table 2. *Agrostis* species reported to produce herbicide-resistant hybrids either in situ or in research trials.

Agrostis species[a]	Common name	Reference
Agrostis canina L.	velvet bentgrass	Belanger 2003a, 2003b; Christoffer 2003; Wipff and Fricker 2000
A. capillaris L.	colonial bentgrass	Belanger 2003b; Christoffer 2003; Wipff and Fricker 2000
A. castellana L.	dryland bentgrass	Belanger 2003b; Christoffer 2003; Wipff and Fricker 2000
A. gigantea Roth	Redtop	Belanger 2003a, 2003b; Christoffer 2003; Watrud 2004; Wipff and Fricker 2000; Zapiola and Mallory-Smith 2017
A. hyemalis var. *scabra* (Willd.) H.L. Blomq.	winter bentgrass	Christoffer 2003
A. idahoensis Nash	Idaho bentgrass	Christoffer 2003
A. pallens Trin.	seashore bentgrass	Christoffer 2003; Wipff and Fricker 2000
A. stolonifera L.	creeping bentgrass	Christoffer 2003; Watrud et al. 2004; Wipff and Fricker 2000; Zapiola and Mallory-Smith 2010
A. trinii Turcz		Christoffer 2003
A. vinealis Schreb	brown bentgrass	Christoffer 2003
Polypogon fugax Nees ex Steud.	Asia minor bluegrass	Christoffer 2003
P. monspeliensis L., Desf	annual rabbitsfoot	Christoffer 2003; Zapiola and Mallory-Smith 2017
P. viridis (Gouan) Breistr.	beardless rabbitsfoot	Christoffer 2003

[a]Many of these species have multiple synonyms for their scientific and common names.

State Department of Agriculture. In 2002, eight fields totaling 162 ha were planted with glyphosate-resistant creeping bentgrass within the 4,500 ha area. One study evaluated gene flow outside of the control area and the other evaluated gene flow within the control area (Watrud et al. 2004; Zapiola et al. 2008; Zapiola and Mallory-Smith 2012, 2017).

For the study outside of the control area, pollen receptor plants were used but were placed at much greater distances than in other studies, with glyphosate-resistant creeping bentgrass seed production fields serving as the pollen sources (Watrud et al. 2004). Seeds recovered from the receptor plants and in situ feral creeping bentgrass and redtop plants were tested for the presence of the *CP4 EPSPS* gene. Resistant seedlings were found on receptor plants and in situ creeping bentgrass plants at 21 and 8 km distance, respectively. Resistant seedlings were produced on redtop plants at a maximum distance of 14 km. In a follow-up study, in situ glyphosate-resistant plants were identified up to 3.8 km from the perimeter of the control area in non-agricultural sites (Reichman et al. 2006). The authors suggested that these plants could have resulted from both pollen and seed movement and provided evidence that creeping bentgrass plants would be established outside of cultivation. The distance that pollen moved in this study is an underestimation of the actual distance because the plants were placed based on the control area perimeter rather than an individual field.

In a second study, the PMGF within and around the seed production control area was assessed and documented over a 4-yr period (Zapiola et al. 2008). In 2006, 3 yr after the fields were taken out of production, 62% of the 585 creeping bentgrass tested in situ (established on irrigation ditches, canals, and roadsides) were glyphosate-resistant. The most distant resistant plants were found 4.6 km from the nearest seed production field. It was not possible to determine in all cases whether gene movement was due to pollen, seed, or stolons. Glyphosate-resistant hybrid seed of creeping bentgrass, *A. gigantea*, and *P. monspelienis* were produced on plants in situ (Zapiola et al. 2010; Zapiola and Mallory-Smith 2012, 2017). Hybrids between creeping bentgrass and *A. gigantea* produced both rhizomes and stolons, indicating a potential reproductive advantage over either parent (Zapiola and Mallory-Smith 2017). An intergeneric hybrid between glyphosate-resistant creeping bentgrass and the annual *P. monspelienis* (×*Agropogon littoralis*) was identified in the study (Zapiola and Mallory-Smith 2012, 2017; Figure 3). Although previously reported to be male sterile, the hybrid produced viable seed. In addition, the resulting hybrid was perennial and produced stolons, traits that *P. monspelienis* does not have, could increase gene flow. In 2016, in situ glyphosate-resistant hybrid plants of creeping bentgrass by *A. gigantea* (Jefferson County OR) and ×*Agropogon littoralis* (Malheur County OR) were identified (Mallory-Smith and Zapiola unpublished data). The plasticity in the *Agrostis* genus and the number of potential crosses that can occur make identifying hybrids in the field challenging if not impossible; therefore, molecular markers are needed to determine parentage (Zapiola et al. 2010). This difficulty in identifying hybrids may allow the gene to remain in the environment without detection.

Italian Ryegrass

Italian ryegrass is a highly competitive weed in cereal fields, vineyards, orchards, and natural grasslands in areas worldwide with temperate climate. The species is believed to be a native to the Mediterranean region of southern Europe, northwest Africa, and southwest Asia (Beddows 1973; Hubbard 1968) but is now distributed in temperate regions of the majority of continents (Clayton et al. 2021). Similar to rigid ryegrass, it was intentionally introduced and continues to be cultivated for pasture forage, turf, and erosion control in many regions of the world, where it escaped cultivation to become a major agricultural weed (CABI 2021). According to Lacefield et al. (2003), Italian ryegrass was first cultivated in northern Italy, followed by cultivation in France, Switzerland, and England. It was introduced into the United States in the early colonial migration and quickly became an important forage grass, especially in the South. Italian ryegrass is a major weed in cereal fields of the southeastern and south-central United States and in cereal fields, nut and fruit orchards, and vineyards in the Pacific Northwest. Italian ryegrass is a C_3 bunchgrass with a summer annual, winter annual, or biennial life cycle (Beddows 1973) depending on the climatic conditions of the

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Figure 3. (left to right) Spikes of glyphosate-resistant creeping bentgrass, intergeneric hybrid between glyphosate-resistant creeping bentgrass and annual rabbitsfoot, and annual rabbitsfoot (photo credit: Maria Zapiola).

geographical region it inhabits. High intra- and interspecific diversity has been reported in this species (Maity et al. 2021), allowing for high adaptive potential. It is especially invasive where ground cover is disturbed or discontinuous and requires fertile, well-drained soils, and moderate temperature and moisture conditions for vigorous growth and reproduction (Beddows 1973; CABI 2021).

Italian Ryegrass Reproductive Biology

Italian ryegrass is hermaphrodite and reproduces solely by sexual reproduction and seeds. Inflorescences consist of spikes 10 to 30 cm long that are comprised of spikelets 8 to 25 mm long, each with 5 to 20 laterally flattened fertile florets and smaller sterile florets at the apex (Beddows 1973; CABI 2021; Clayton et al. 2021). Spikelets alternate with one another along the rachis, which is recessed opposite each spikelet, and breaks up at maturity by disarticulating below each fertile floret. Each fertile floret has three yellow, occasionally tinged red, anthers and two feathery stigmas that protrude slightly before or at the same time as the anthers when the floret opens (Beddows 1973). Each floret produces one caryopsis (single-seeded fruit). Pollen is dispersed by wind.

Italian ryegrass is self-incompatible and outcrosses at extremely high levels (>99%; Fearon et al. 1983). Self-incompatibility is determined by two multi-allelic gene loci (*S* and *Z*) with gametophytic control of the incompatibility phenotype (Fearon et al. 1983). The incompatibility reaction takes place on the stigmatic surface. Incompatible pollen produces only short pollen tubes, whereas compatible pollen produces long tubes. Self-incompatibility, an extremely high outcrossing rate, and wind-mediated pollen dispersal results in abundant genetic variation within populations and low genetic differentiation among populations, as has been observed in Italian ryegrass in California (Karn and Jasieniuk 2017). Genetic variation among individuals within a population is required for adaptive evolution by natural selection. The abundant genetic variation detected within Italian ryegrass populations may explain why resistance to many different herbicide SOAs has evolved so rapidly in this species.

Herbicide Resistance in Italian Ryegrass

Italian ryegrass populations have evolved resistance to herbicides with at least nine different SOAs (Ghanizadeh et al. 2015; Heap 2021), including acetyl CoA carboxylase (ACCase) inhibitors (Bobadilla et al. 2021; Bravin et al. 2001; Kaundun 2010; Mahmood et al. 2016; Nandula et al. 2020; Rauch et al. 2010; Stranger and Appleby 1989), acetolactate synthase (ALS) inhibitors (Bobadilla et al. 2021; Délye et al. 2009; Mahmood et al. 2016; Rauch et al. 2010; Shimono et al. 2015), carotenoid biosynthesis inhibitors (Ghanizadeh et al. 2015), EPSPS inhibitor (glyphosate; Bobadilla et al. 2021; Dickson et al. 2011; Jasieniuk et al. 2008; Niinomi et al. 2013; Perez and Kogan 2003; Perez-Jones et al. 2005; Preston et al. 2009; Salas et al. 2012), glutamine synthase inhibitors (Avila-Garcia et al. 2011, 2012; Fernández et al. 2017; Ghanizadeh et al. 2015; Karn et al. 2018; Kurata et al. 2017), protoporphyrinogen oxidase (PPO) inhibitors (Fernández et al. 2017), photosystem I inhibitors (Brunharo and Hanson 2018; Tehranchian et al. 2018), photosystem II (PS II) inhibitors (Bobadilla et al. 2021; Liu et al. 2014), and very long chain fatty acid (VLCFA) inhibitors (Bobadilla et al. 2021; Liu et al. 2014, 2016; Rauch et al. 2010). Resistance to ACCase inhibitors and the EPSPS-inhibiting herbicide glyphosate are the most frequently reported types of resistance in Italian ryegrass (Heap 2021).

Multiple resistance to two, three, four, and five herbicide SOAs is becoming increasingly common in Italian ryegrass populations. Instances of multiple resistance to two SOAs include resistance to ACCase and ALS inhibitors (Bobadilla et al. 2021; Chandi et al. 2011; Kuk et al. 2000, 2008; Rauch et al. 2010; Singh et al. 2020), ACCase and EPSPS inhibitors (Bobadilla et al. 2021; Dickson et al. 2011), ALS and EPSPS inhibitors (Bobadilla et al. 2021; Henckes et al. 2019), and EPSPS and glutamine synthetase inhibitors (Avila-Garcia and Mallory-Smith 2011; Fernández et al. 2017; Karn et al. 2018; Kurata et al. 2017). Italian ryegrass populations with resistance to three herbicide SOAs have been confirmed (Bobadilla et al. 2021; Brunharo and Hanson 2018; Ghanizadeh et al. 2015; Liu et al. 2014, 2016; Rauch et al. 2010; Singh et al. 2020; Vázquez-García et al. 2020a; Tehranchian et al. 2018). Italian ryegrass populations with resistance to four herbicide SOAs include resistance to ACCase, ALS, PS II, and VLCFA inhibitors (Bobadilla et al. 2021; Liu et al. 2016); ACCase, ALS, EPSPS, and PS II inhibitors (Tehranchian et al. 2019); and ALS, EPSPS, PS II, and VLCFA inhibitors (Bobadilla et al. 2021). Recently, 15 of 75 Italian ryegrass populations surveyed in the Willamette Valley of Oregon were confirmed with resistance to five herbicide SOAs, i.e., ACCase, ALS, EPSPS, PS II, and VLCFA inhibitors (Bobadilla et al. 2021).

PMGF from HR Italian Ryegrass

The high genetic diversity admixture and low differentiation detected between California populations (Karn and Jasieniuk 2017) strongly suggest the spread of herbicide resistance alleles through PMGF; however, experimental studies of PMGF from

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HR Italian ryegrass are lacking. In contrast, several studies have been conducted for rigid and perennial ryegrass. Given the morphological and reproductive similarities, close genetic relatedness, and inter-fertility of the three species, the results of these studies are likely to be directly applicable to Italian ryegrass. Yanniccari et al. (2018) studied PMGF in perennial ryegrass from glyphosate-resistant to glyphosate-susceptible plants under field conditions in Argentina using a donor-receptor design, and PMGF of glyphosate resistance reached susceptible trap plants up to 35 m downwind from the source of pollen. Susceptible receptor plants grown at 15 and 25 m from the source of glyphosate resistance exhibited a 4-fold and 2-fold increase, respectively, in the frequency of glyphosate-resistant offspring, whereas no glyphosate-resistant plants were detected in the progeny of susceptible receptor plants located >35 m from donor resistant plants.

Interspecific Hybridization in Lolium Species

Italian ryegrass readily hybridizes with perennial ryegrass and rigid ryegrass to produce hybrids where the species co-occur (Charmet et al. 1996; Dinelli et al. 2002, 2004; Kloot 1983; Terrell 1966). All three species are diploid with $2n = 14$ chromosomes (Terrell 1966) (Table 1), have high rates of outcrossing due to self-incompatibility (Fearon et al. 1983), are highly variable morphologically (Bravin et al. 2001; Terrell 1968; Vasek and Ferguson 1963), and have the same basic karyotype (Bulinska-Radomska and Lester 1985; Malik and Thomas 1966).

Intergeneric hybridizations between Italian ryegrass and *Festuca* species have also been detected in nature (Dinelli et al. 2002, 2004; Zwierzykowski 1996). Interestingly, a significantly higher amount of *Festuca* DNA was detected in two diclofop-resistant Italian ryegrass biotypes than in a susceptible accession in Italy, suggesting the possibility of resistance gene flow from *Festuca* into Italian ryegrass via hybridization (Dinelli et al. 2004). However, based on the homology between chromosomes of certain *Lolium* and *Festuca* species, some authors have suggested that the two genera may share a monophyletic origin (Bulinska-Radomska and Lester 1988). Thus, the resistance trait shared by the interfertile genera (*Lolium* and *Festuca*) could have been inherited from a common ancestor. The evolution of resistance to diclofop in Italian ryegrass as a consequence of *Festuca* species gene introgression was also suggested by Martinez-Ghersa et al. (1997), but scientific support for the hypothesis is lacking.

Johnsongrass

Native to the Mediterranean, johnsongrass ($2n = 4x = 40$) has a wide geographical range between 55°N and 45°S, and is distributed in more than 53 countries across Asia, Africa, Australia, Europe, North America, and South America (Holm et al. 1977). Molecular genetic investigations suggest that *S. halepense* is a hybrid of *S. bicolor* ($2n = 2x = 20$) and *S. propinquum* ($2n = 2x = 20$; Paterson et al. 1995). Chromosome doubling in *S. propinquum* has been suggested as a possible origin of *S. halepense* (Defelice 2006). Johnsongrass was introduced into the United States in the late 1700s (McWhorter 1971), and molecular evidence suggests two geographically distinct introduction events (Ohadi et al. 2017; Uzay Sezen et al. 2016).

Being a perennial, rhizomatous, invasive, C_4 grass species, johnsongrass is a troublesome weed in summer crops in the southern United States (McWhorter 1989). Johnsongrass is a particularly problematic weed in sorghum fields (Figure 4) due to its genetic similarities to sorghum and, until recently, the lack of selective herbicide options. The weediness of johnsongrass is attributed to its rapid vegetative growth and biomass accumulation, vigorous rhizome production, high fecundity, seed dormancy, and seedbank longevity, among other factors (McWhorter 1989; Warwick and Black 1983). Plants show a high degree of intra-population variability for adaptive traits, which might contribute to its range expansion into northern environments (Burt and Wedderspoon 1971). The high relative growth rate and adaptation to water stress suggests increased frequency of johnsongrass occurrence under future climate change scenarios, especially under rainfed conditions (Leguizamon and Acciaresi 2014).

Johnsongrass Reproductive Biology

Johnsongrass reproduces via both seeds and underground rhizomes. The flowering stems (culms) grow up to 2.5 m tall and about 2.0 cm diameter (Warwick and Black 1983). It produces large, erect, open, spreading panicles that can extend up to 50 cm in length. The spikelets appear in pairs, except at the end of each branch where they occur in triplets. Seeds usually have awns (1.0 to 1.6 cm long), which are generally shed at maturity. The mature grains are oblong to ovate, reddish brown to shiny black and remain enclosed in the glumes even after complete maturity (Warwick and Black 1983).

A single johnsongrass plant can produce about 28,000 seeds (Horowitz 1973), which easily shatter upon maturity, leading to wide dispersal. In addition to seeds, a substantial number of rhizomes (up to about 90 m total length) can be produced in a growing season (McWhorter and Jordan 1976), which can account for up to 70% of the plant's total dry mass (Oyer et al. 1959). Each rhizome can grow up to about 2 m in length and several cm in diameter, with internodes covered with brown sheaths (Figure 5). The cut pieces of rhizomes can regenerate into individual plants, thus contributing to their spread. Liu et al. (2019) developed an individual-based model of johnsongrass that incorporated seed and rhizome propagation and revealed the important role of rhizome production in driving population dynamics.

Herbicide Resistance in Johnsongrass

As of 2020, 29 unique cases of herbicide resistance in johnsongrass have been reported in 12 countries worldwide, including Argentina, Australia, Chile, Greece, Hungary, Israel, Italy, Mexico, Serbia, Spain, the United States, and Venezuela (Heap 2021). Resistance has been reported for the EPSPS inhibitor glyphosate, ACCase inhibitors, ALS inhibitors, and the microtubule inhibitors. A case of multiple-herbicide resistance in johnsongrass was documented in Argentina with resistance to both glyphosate and haloxyfop-methyl. In the United States, HR johnsongrass biotypes have been reported in Arkansas, Indiana, Kentucky, Louisiana, Mississippi, Tennessee, Texas, Virginia, and West Virginia. In a multi-state johnsongrass survey conducted across northern Kansas, northwestern Missouri, and southern Nebraska, Werle et al. (2016) found that 8% of the populations (5 out of 59) were resistant to imazethapyr and 5% (3 out of 59) were resistant to nicosulfuron. Barrentine et al. (1992) reported johnsongrass resistance to fluazifop-P in two field populations in Mississippi. Smeda et al. (1997) further studied these populations and found they also exhibited resistance to quizalofop-P, along with reduced susceptibility to sethoxydim. Johnson et al. (2014) screened for the presence of herbicide resistance in 141 johnsongrass accessions collected during 2008–2010 across 14

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Figure 4. Infestation of johnsongrass in a grain sorghum production field in southeast Texas (photo credit: Muthukumar Bagavathiannan).



Figure 5. Vigorous rhizome production by johnsongrass in a field study conducted at College Station, Texas (photo credit: Muthukumar Bagavathiannan).

counties in Arkansas and found resistance in two accessions for glyphosate or imazethapyr. Riar et al. (2011) confirmed glyphosate resistance in a johnsongrass population collected from a field near West Memphis, AR, that had been under continuous soybean production for at least 6 yr with frequent use of glyphosate. This resistant population was 5-fold to 7-fold less sensitive to glyphosate compared to the susceptible population.

In Europe, Vázquez-García et al. (2020b) reported the first case of glyphosate-resistant johnsongrass in Cordoba, Spain, in railroad and freeway populations that were routinely exposed to glyphosate,

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wherein reduced herbicide translocation led to 4.2 to 9 times greater resistance compared to a susceptible population. Several johnsongrass biotypes have evolved resistance to glyphosate as a result of intensive use, especially across vast soybean production areas in Argentina (Vila-Aiub et al. 2007). The glyphosate-resistant accessions studied by Vila-Aiub et al. (2011) had less herbicide absorption and less translocation to root and stem meristems. An analysis using single sequence repeat markers among 46 glyphosate-resistant johnsongrass accessions collected across Argentina showed no clear pattern of association with geographical origin, suggesting multiple origins of resistance (Fernández et al. 2013).

PMGF from HR Johnsongrass

Johnsongrass is a highly self-pollinated species, but PMGF is possible between different johnsongrass biotypes. Maity and Bagavathiannan (2021) studied PMGF from nicosulfuron-resistant johnsongrass to susceptible (pollen recipient) johnsongrass biotypes in Texas. They found PMGF as high as 13.7% at the shortest distance of 5 m, and up to 2.3% at the farthest studied distance of 50 m. These levels of outcrossing are sufficient for transferring herbicide resistance alleles between adjacent field populations. Even at distances farther than those studied by Maity and Bagavathiannan (2021), PMGF can be greater than the rate of spontaneous mutation for conferring herbicide resistance in this species. Johnsongrass is also known to outcross with other compatible sorghum relatives across the agricultural landscape, with a potential for transferring herbicide resistance and other traits (Ohadi et al. 2017). Despite the ploidy barriers between johnsongrass ($2n = 40$) and cultivated sorghum ($2n = 20$), PMGF has been reported between the two species (Arriola and Ellstrand 1996; Hodnett et al. 2019; Sias et al. 2020; Subramanian et al. 2021). Historical exchange of alleles between johnsongrass and sorghum in agricultural landscapes has been documented by Morrell et al. (2005). Arriola and Ellstrand (1997) found no fitness differences between the F1 johnsongrass (female) × sorghum hybrids and wild johnsongrass. Gene flow involving johnsongrass has practical significance when it acts as either a male or a female parent (Ohadi et al. 2017).

Shattercane [*S. bicolor* (L.) Moench subsp. *drummondii* (Steud.) de Wet ex Davidse] ($2n = 20$) is a closely related species of sorghum present in sorghum production regions in the United States (Schmidt 2011). Shattercane is thought to be a feral form of cultivated sorghum (Ejeta and Grenier 2005) with a very high degree of genetic similarity with sorghum and sudangrass (*S. bicolor* ssp. *drummondii*), an annual forage sorghum species (Defelice 2006). Thus, the PMGF between shattercane × johnsongrass should be similar to that of sorghum × johnsongrass. The PMGF between sorghum (female) × johnsongrass was as high as 0.5% with certain sorghum genotypes and environments (Sias et al., unpublished data). Feral HR sorghum in agricultural landscapes may serve as conduits for the transfer of herbicide resistance and other traits between johnsongrass and sorghum in either direction (Ohadi et al. 2018). Currently, sorghum cultivars with non-transgenic herbicide resistance (Inzen™ sorghum with resistance to nicosulfuron; igrowth™ sorghum with resistance to imazamox; and DoubleTeam™ sorghum with resistance to quizalofop) are under commercial development. Likewise, PMGF between johnsongrass and shattercane or HR sorghum volunteers (or vice versa) in production fields can facilitate trait movement.

Rigid (Annual) Ryegrass

The genus *Lolium* belongs to the Poaceae family and includes eight diploid species with a chromosome number $2n = 14$ (Table 1). These species originated in Europe, North Africa, and temperate Asia and are distributed throughout the temperate regions of the world (Bennett et al. 2000). The genus contains species such as *L. multiflorum*, *L. perenne,* and *L. rigidum*, which are obligate outcrossing and wind-pollinated (Matzrafi et al. 2021). Rigid ryegrass is the most widespread and troublesome weed in Australia and is currently ranked as the number one weed worldwide for its ability to evolve resistance to a number of herbicides with different SOAs (Busi et al. 2020; Heap 2021).

Rigid Ryegrass Reproductive Biology

Rigid ryegrass is a self-incompatible, outcrossing species and a prolific pollen producer (Gill 1996; McCraw and Spoor 1983; Figure 6A). It has a high degree of genetic variability that helps it adapt to a range of climatic and edaphic conditions (Kloot 1983). In Australia, rigid ryegrass populations with large differences in phenological development have been documented, demonstrating adaptation to local environments (Gill et al. 1995). It also exhibits genotypic plasticity (Gill et al. 1995), creating the potential for PMGF that enables the spread of herbicide resistance traits (e.g., paraquat or glufosinate resistance in *Lolium*; Yu et al. 2004) or resistance to newly discovered herbicides (Brunton et al. 2021), favoring the evolution of multiple HR populations (Figure 6B).

Herbicide Resistance in Rigid Ryegrass

Rigid ryegrass is the most damaging weed in Australia, with an estimated cost of AUS$100 million annually (Llewellyn et al. 2016). Herbicide-resistant rigid ryegrass infests millions of hectares of the southern Australian cropping region (Busi et al. 2021; Busi and Beckie 2021).

Rigid ryegrass is an excellent example of the ability of a weed species to evolve resistance to herbicides with different SOAs (Heap 2021). This is a consequence of persistent herbicide selection leading to a steady increase in the frequency of cross-resistance and multiple resistance to ALS- and ACCase- inhibiting herbicides (Heap and Knight 1986; Owen et al. 2014; Figure 6B). In a recent study, Busi et al. (2021) showed that out of 600 rigid ryegrass populations tested across the Australian continent, only 9% were susceptible to all herbicides tested (Figure 6B). Conversely, more than 50% of the tested populations survived at least three different herbicides. One population of rigid ryegrass evolved resistance to at least 13 of the herbicides tested, including five different SOAs (ACCase, ALS, microtubule, lipid biosynthesis, and VLCFA inhibitors; Figure 6B). This confirms the formidable ability of rigid ryegrass to adapt and evolve resistance to herbicides (Heap 2021) and the accumulation of multiple resistance traits in self-incompatible cross-pollinated individuals (i.e., multiple HR field populations).

PMGF from HR Rigid Ryegrass

Loureiro et al. (2016) studied PMGF in rigid ryegrass under both greenhouse and field conditions using a diclofop-methyl-resistant biotype as the pollen donor. The maximum PMGF was 56.1% in the greenhouse. Data from the field study were fit to an exponential decay model to predict gene flow at increasing distances. When the model was based on data from all recipient plants in the study, it

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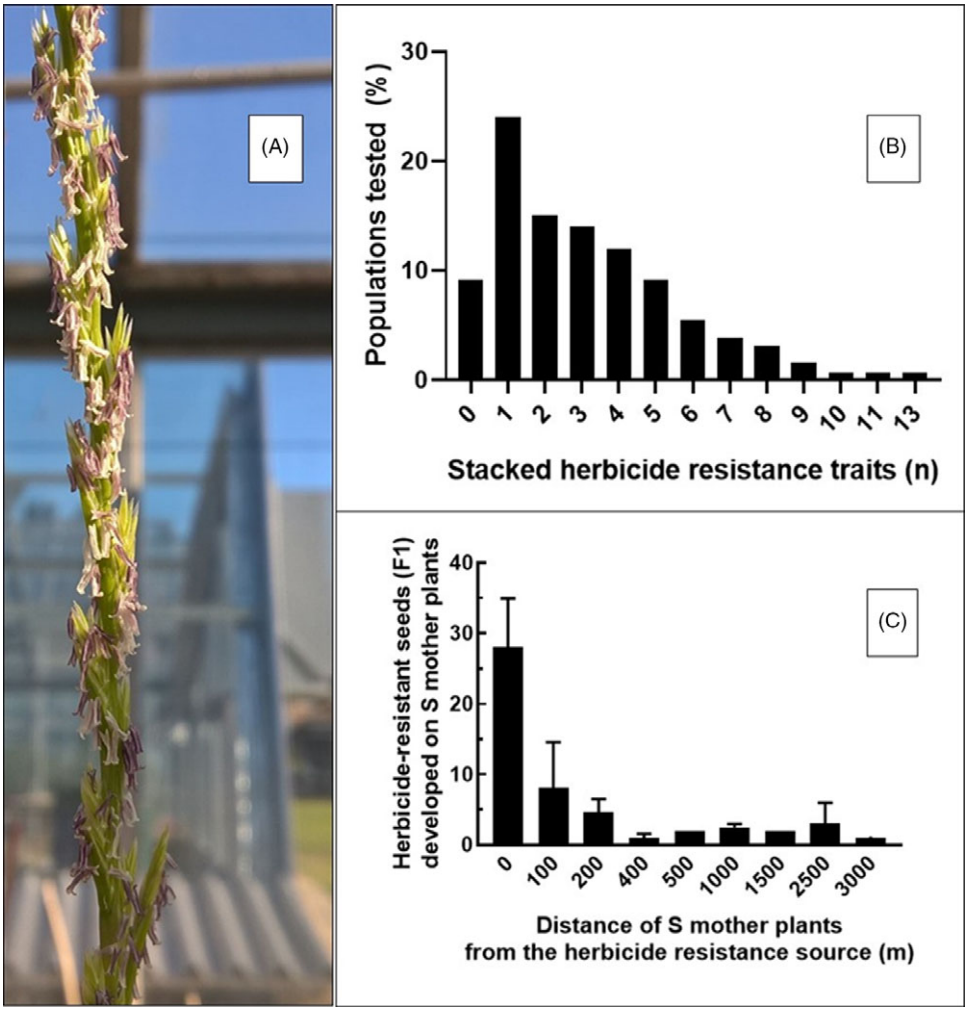


Figure 6. (A) Inflorescences of rigid ryegrass (*Lolium rigidum*) with extruded stamens (photo credit: Roberto Busi), (B) frequency (%) of tested rigid ryegrass populations (n = 600) exhibiting resistance to a number of herbicides, and (C) number of resistance seeds from herbicide-susceptible (S) rigid ryegrass mother plants placed at increasing distance from fields infested with herbicide-resistant rigid ryegrass.

predicted an average PMGF of 7.1% when the pollen donor and receptor plants were 0 m apart and a 50% reduction at 16.7 m from the pollen source regardless of the direction. When recipient plants were downwind of the pollen source, however, PMGF was 5.2% at 25 m, the farthest distance studied.

PMGF can occur over long distances in rigid ryegrass (4% at >3,000 m; Figure 6C) from large field sources infested by HR rigid ryegrass to isolated herbicide-susceptible population (Busi et al. 2008). Thus, the transfer of HR alleles from HR rigid ryegrass field populations can occur between fields and result in increased frequency of herbicide-resistant populations in a region (Beckie et al. 2019). In a subsequent study, this hypothesis was validated by studying the dynamics of PMGF from organic fields and neighboring conventional fields with persistent herbicide use. In organic fields, the frequency of HR rigid ryegrass (identical haplotypes) was much higher than could be explained by a background mutation frequency (Busi et al. 2011). For example, the frequency of field resistance to the herbicide diclofop-methyl was 3-fold to 10-fold greater than expected in unselected and genetically isolated rigid ryegrass populations (Neve and Powles 2005).

Wild Oats

Avena fatua originated in the western Mediterranean (Loskutov 2008) and has been introduced to most temperate regions globally. The species is found in Europe, the Middle East, western Asia, and North America (Beckie et al. 2012; USDA-NRCS 2020). *Avena fatua* occurs in a variety of non-crop disturbed (ruderal) and cultivated habitats, and prefers clay or clay loam soils (Beckie et al. 2012). *Avena sterilis* (sterile wild oat) likely spread as a weed in small-grain cereals from the Fertile Crescent (Middle East) 3,000 to 4,000 yr ago to its present native range throughout the Mediterranean region and southern Europe (Rosentrater and Evers 2018). It was subsequently introduced into central and eastern Europe and other continents via seed contamination of wool and grain (Stace 1997; Torner et al. 1991). *Avena sterilis* is well adapted to a wide range of climatic conditions and is commonly found in semi-arid, temperate, and sub-tropical regions globally; it occurs on all continents except Antarctica (Anonymous 2019; Floc'h 1991; Holm et al. 1979; O'Donnell et al. 2002). The species can be found in cropland, pastures, vineyards, and ruderal areas; it tends to prefer heavier-textured soils

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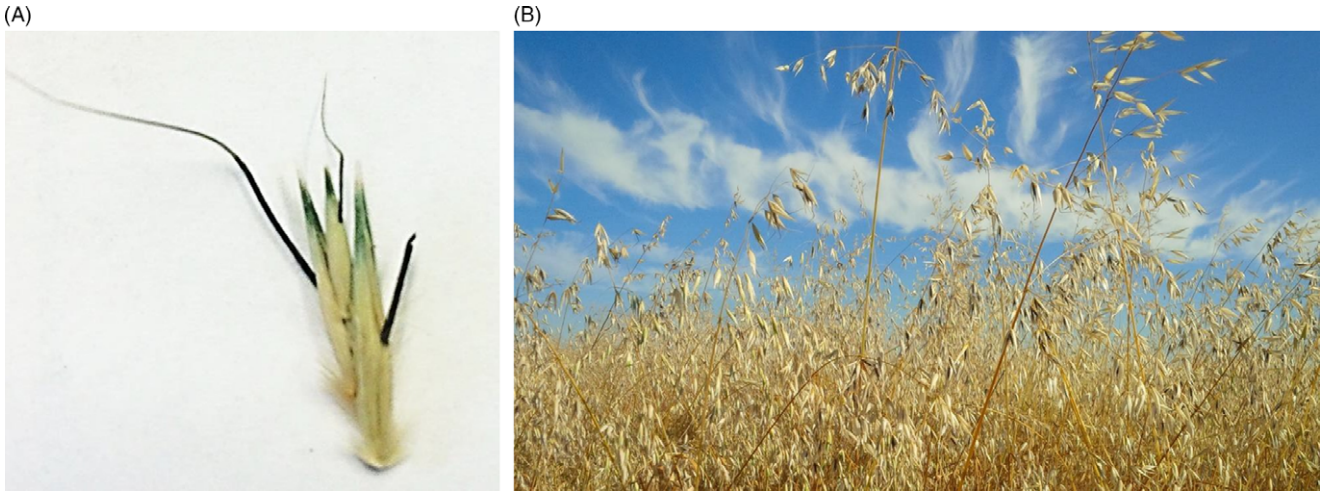


Figure 7. (A) Wild oat (*Avena fatua*): three florets/seeds and (B) wild oat mature plants in a crop canopy (photo by K.N. Harker, used with permission).



Figure 8. A wild oat panicle during anthesis with yellow anthers visible on some of the florets (photo credit: Breanne Tidemann).

compared with those favored by *A. fatua* (Stace 1997). In addition, *A. sterilis* can grow under drier conditions than *A. fatua* (Fernández-Quintanilla et al. 1990; Thurston 1951).

Wild Oats Reproductive Biology

Avena fatua and *A. sterilis* have an annual life cycle and grow up to 1.5 m high (Anonymous 2019; Beckie et al. 2012). The open loose panicle of *A. fatua* is 10 to 40 cm long, with spikelets that have two glumes 1.8 to 2.5 cm long containing three florets (Figure 7 A and B). The florets separate through disarticulation of the rachillas segments, and each floret has a twisted awn 3 to 4 cm long (Figure 8; Bajwa et al. 2017). The inflorescence of *A. sterilis* is an equilateral, pyramidal, or slightly one-sided loose panicle, 15 to 45 cm long and 8 to 25 cm wide (Stace 1997). Spikelets are 1.7 to 4.5 cm long without the awns, each with two to five florets of which only the lowest has a basal scar, disarticulating above the glumes but not between the florets. Glumes are equal or subequal, and 2.4 to 5.0 cm long. The lemma is 1.5 to 4.0 cm long, with the uppermost (third seed) being awnless and the lower two (first and second seeds) having a 3 to 9 cm long bent and twisted dorsal awn (Ivens 1989). The caryopsis length is 10 mm with a width of 0.2 to 0.25 cm.

Compared with *A. fatua*, the stem of *A. sterilis* is more prostrate, with more tillers at the maximum tillering stage. The panicles are lighter in weight because the spikelets have fewer and smaller florets, while the glume is longer, the awn is absent for the third seed, the spikelets are hard and do not break easily, and the seeds remain longer within the spikelet at maturity and are shed in units of 2 or 3 (Moss 2015; Stace 1997). *A. fatua* and *A. sterilis* are hexaploid, with a chromosome count of $2n = 42$ and genome AACCDD (Bajwa et al. 2017; Beckie et al. 2012).

Herbicide Resistance in Wild Oats

Herbicide resistance in *A. fatua* was first reported in Australia in 1985 and has since been reported in 17 countries, whereas resistance in *A. sterilis* has been documented in nine countries since first reported in 1989 (Heap 2021). Most HR populations are resistant to ACCase- or ALS-inhibiting herbicides. The incidence of herbicide resistance in *A. sterilis* is significantly less than that of *A. fatua* because of lower relative abundance and more restricted global distribution. While herbicide resistance in *A. sterilis* remains limited to ACCase and ALS inhibitors and microtubule inhibitors, flamprop-methyl, *A. fatua* populations in Canada and the United States have also exhibited resistance to lipid synthesis inhibitors or cell elongation inhibitors, microtubule inhibitors, VLCFAE inhibitors, and PPO inhibitors (Heap 2021; Mangin et al. 2017; O'Donovan et al. 1994). Five-way herbicide resistance was found in an *A. fatua* population from Manitoba, Canada (Mangin et al. 2017), which is the only *Avena* species population reported to exhibit resistance to VLCFAE- or PPO-inhibiting herbicides. In 2018, the first and only cases of glyphosate resistance in *A. fatua* and *A. sterilis* were identified in a chickpea (*Cicer arietinum* L.) field in New South Wales, Australia (Heap 2021; B. Chauhan pers.

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comm.). Although this biotype is not reported elsewhere, *A. fatua* was predicted to be at high risk of selection for glyphosate resistance in western Canada because of significant use of glyphosate (Beckie et al. 2013a).

The most recent (2014 to 2017) survey in western Canada identified HR *A. fatua* in 69% of 578 fields where samples were collected (Beckie et al. 2020), which was significantly higher than 44% of sampled fields in the previous survey (2007 to 2009; Beckie et al. 2013b). In the 2014 to 2017 survey, populations with resistance to ACCase inhibitors, ALS inhibitors, and both ACCase and ALS inhibitors occurred in 62%, 34%, and 27% of fields containing *A. fatua*, respectively (Beckie et al. 2020). There was a marked increase in resistance to ALS-inhibiting herbicides and resistance to both ACCase and ALS inhibitors in the most recent survey due to increased use of ALS inhibitors to manage ACCase inhibitor-resistant *A. fatua* populations (Beckie et al. 2020). In contrast, herbicide resistance in *Avena* species (*A. fatua* and *A. sterilis*) remained stable in Western Australia between 2005 and 2010, with the most recent survey of 128 populations in 2015 indicating resistance to ACCase inhibitors, ALS inhibitors, and both ACCase and ALS inhibitors in 48%, 2%, and 7% of populations, respectively (Owen and Powles 2009, 2016). A 2007 survey of 113 *Avena* species from New South Wales, Australia, found that 38% of populations were resistant to ACCase inhibitors, while no populations exhibited resistance to ALS inhibitors (Broster et al. 2011). In Greece, 81% of 104 *A. sterilis* populations in 2009 were ACCase inhibitor-resistant, whereas only 3% were ALS inhibitor-resistant (Travlos et al. 2011).

PMGF from HR Wild Oats

Both *Avena* species are highly self-pollinating. Flowering in *A. sterilis* occurs earlier than in *A. fatua* (Holm et al. 1979; Stace 1997). In *A. fatua*, anthesis within each spikelet occurs in order from the first to the third floret (Raju et al. 1985). Some pollens emitted by anthers are intercepted by adjacent branches of the stigma, with embryo development occurring 24 to 40 h after pollination. Anthesis continues within a panicle for 4 to 14 d. Florets are normally chasmogamous vs. cleistogamous. Insects or wind have not been reported as significant vectors in pollination (Murray et al. 2002).

There is a paucity of data regarding the extent of PMGF in *A. sterilis* under field conditions, although rates are expected to be similar among *Avena* species (Bajwa et al. 2017; Cavan et al. 1998; Darmency and Uludag 2018). The PMGF is limited in *A. fatua* (Sharma and Vanden Born 1978). Using ACCase inhibitor resistance as a marker, PMGF for *A. fatua* in a non-crop environment in western Canada ranged between 0% and 12.3% (mean of 5.2%; Murray et al. 2002). Distance from the pollen source (maximum 0.56 m) was a significant factor only for the high-density planting arrangement in flax (*Linum usitatissimum* L.). Therefore, intraspecific pollination is substantially reduced within crop canopies. In spring wheat (*Triticum aestivum* L.), PMGF in *A. fatua* at low density (19 plants m^{-2}) and high density (37 plants m^{-2}) was 0.08% and 0.05%, respectively; in the less competitive flax, PMGF averaged 0.07% and 0.16%, respectively (Murray et al. 2002). These results indicate that PMGF does contribute to the evolution and spread of herbicide resistance in *A. fatua* populations, although it is of minor importance compared with seed-mediated gene flow (Murray et al. 2002).

Hybridization can occur between *Avena* species. For example, *A. sterilis* hybridizes with *A. sterilis* sub-species and other *Avena* species such as *A. fatua* (Cavan et al. 1998), *A. sativa* L. (Mariot et al. 1999; Sereno-Tavares et al. 1995), and *A. nuda* L. (Yu et al. 1998). *A. fatua* can create fertile hybrids when crossed with *A. sterilis* (Cavan et al. 1998). Sterile hybrids have been recorded between *A. fatua* and *A. strigose* Schreb., *A. barbata* Pott ex Link, *A. magna* H.C. Murphy & Terrell, and *A. murphyi* Ladiz. (Rajhathy and Thomas 1974).

Avena fatua can produce up to 1,070 seeds per plant in non-crop conditions; however, 20 to 150 seeds per plant are more common in competitive environments (Beckie et al., 2012). *Avena fatua* seed shatters before most crops mature. For example, studies have reported that 30% to 70% of *A. fatua* seed shattered before wheat harvest in western Canada (Burton et al. 2016, 2017; Shirtliffe et al. 2000; Tidemann et al. 2017). This variability in percent seed shatter is likely affected by genetic heterogeneity and phenotypic plasticity. Seed shatter from panicles may begin 2 to 3 wk before the typical wheat harvest in India (Balyan et al. 1991). Seed dispersal primarily occurs near the parent plant (Beckie et al. 2012); however, combine harvesters can spread seeds over distances up to 145 m (Shirtliffe and Entz 2005). In addition, seed dispersal occurs via birds or other animals, although the scale of anthropogenic dispersal via grain seedlot mixture, hay, or farm equipment is considerably greater (Stace 1997; Terry 1984). *Avena sterilis* can produce up to 200 seeds $plant^{-1}$, although substantially less seed is produced under inter- or intraspecific competition (Fernández-Quintanilla et al. 1986).

Summary and Research Needs

Reviewing the literature on reproductive biology, HR biotypes, and PMGF studies of the economically important HR grass weeds, barnyardgrass, creeping bentgrass, Italian ryegrass, johnsongrass, rigid ryegrass, and wild oats, confirms that transfer of HR alleles is possible. Rigid ryegrass and Italian ryegrass are self-incompatible, outcrossing species with the potential for long-distance PMGF and transfer of herbicide resistance alleles. In addition, Italian ryegrass readily hybridizes with rigid ryegrass as well as perennial ryegrass and produces hybrids, thereby increasing chances of PMGF and transfer of resistance alleles in *Lolium* species.

Genetically engineered glyphosate-resistant feral hybrids between creeping bentgrass and compatible species have been identified multiple times in situ in Oregon and Idaho. The plants were found in agricultural fields, irrigation canals, and non-agricultural sites. Due to its reproductive biology, widespread occurrence, and the number of sympatric, compatible species, the risk of PMGF and transfer of HR alleles in creeping bentgrass is high. Experience has shown that the HR trait in creeping bentgrass cannot be contained once it is released, nor is the appearance of the gene likely to decline over time because no fitness penalty from the gene has been documented. Glyphosate was used for the control of weeds along irrigation systems but is no longer effective for the control of glyphosate-resistant creeping bentgrass, which can clog waterways and slow water movement (Figure 2). Further studies are needed to monitor the resistance gene over time to determine its spread and stability in hybrids. Johnsongrass is a highly self-pollinating species; however, PMGF up to 2.3% has been reported in Texas from nicosulfuron-resistant to -susceptible johnsongrass at 50 m from the pollen source. With respect to herbicide resistance traits, PMGF between johnsongrass, shattercane, and HR sorghum poses challenges for HR trait sustainability. Therefore, research is needed to rotate sorghum with other crops to reduce PMGF.

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Barnyardgrass is an autogamous species with a low level of PMGF, thus seed movement would most likely contribute more to the landscape-level spread of herbicide resistance compared to PMGF. Herbicide resistance in wild oats is a global issue, but cross- or multiple-herbicide resistance is most extensive in the northern Great Plains of North America. Gene flow studies in wild oats have confirmed that PMGF is possible; however, because both wild oat species (*A. fatua* and *A. sterilis*) are highly self-pollinating, the spread of herbicide resistance alleles has been mediated primarily by natural or anthropogenic seed dispersal. Therefore, research is needed to reduce seed-mediated gene flow in barnyardgrass and wild oats by developing best management practices such as harvest weed seed destruction.

The scientific literature is limited regarding the reproductive biology of grass weed species. Therefore, research is needed to investigate pollen viability affected by varying levels of temperature, moisture, and relative humidity, flowering synchrony among and between economically important grass weeds, and the possibility of PMGF. Landscape-level PMGF has been studied in rigid ryegrass and creeping bentgrass. This type of study is needed for other HR grass weed species such as barnyardgrass, Italian ryegrass, johnsongrass, and others in different environments. Studies of PMGF are usually focused on moderately to highly outcrossing weed species and neglect low outcrossing species. Dense populations of the latter species can elevate the importance of PMGF relative to seed movement that needs to be investigated. Climate change and unfavorable weather events such as flood, tornado, and high wind are likely to bring further shifts in weed species occurrence and distribution; therefore, research is needed on how climate change may affect PMGF in economically important grass weed species. For example, higher temperatures during pollination and greater precipitation variability in the future may exacerbate or mitigate the contribution of PMGF to movement of herbicide resistance alleles among weed populations.

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