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Pollen-mediated gene flow and transfer of resistance alleles from herbicide-resistant broadleaf weeds

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Review

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Nomenclature:
Common lambsquarters, *Chenopodium album* L.; giant ragweed, *Ambrosia trifida* L.; horseweed, *Erigeron canadensis* (L.) Cronquist; kochia, *Bassia scoparia* (L.) A.J. Scott; Palmer amaranth, *Amaranthus palmeri* S. Watson.; waterhemp, *Amaranthus tuberculatus* (Moq.) Sauer

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Abstract

Pollen-mediated gene flow (PMGF) refers to the transfer of genetic information (alleles) from one plant to another compatible plant. With the evolution of herbicide-resistant (HR) weeds, PMGF plays an important role in the transfer of resistance alleles from HR to susceptible weeds; however, little attention is given to this topic. The objective of this work was to review reproductive biology, PMGF studies, and interspecific hybridization, as well as potential for herbicide resistance alleles to transfer in the economically important broadleaf weeds including common lambsquarters, giant ragweed, horseweed, kochia, Palmer amaranth, and waterhemp. The PMGF studies involving these species reveal that transfer of herbicide resistance alleles routinely occurs under field conditions and is influenced by several factors, such as reproductive biology, environment, and production practices. Interspecific hybridization studies within *Amaranthus* and *Ambrosia* spp. show that herbicide resistance allele transfer is possible between species of the same genus but at relatively low levels. The widespread occurrence of HR weed populations and high genetic diversity is at least partly due to PMGF, particularly in dioecious species such as Palmer amaranth and waterhemp compared with monoecious species such as common lambsquarters and horseweed. Prolific pollen production in giant ragweed contributes to PMGF. Kochia, a wind-pollinated species can efficiently disseminate herbicide resistance alleles via both PMGF and tumbleweed seed dispersal, resulting in widespread occurrence of multiple HR kochia populations. The findings from this review verify that intra- and interspecific gene flow can occur and, even at a low rate, could contribute to the rapid spread of herbicide resistance alleles. More research is needed to determine the role of PMGF in transferring multiple herbicide resistance alleles at the landscape level.

Introduction

The development and commercial cultivation of herbicide-resistant (HR) corn (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] in the mid-1990s stimulated intense public awareness and scientific interest in gene flow from HR crops to conventional or organic crops, as well as to their wild and weedy relatives (Snow 2002; Stewart et al. 2003). The frequency of pollination between crops and adjacent sexually compatible species at various spatial scales was an important issue in risk assessment of genetically engineered crops (Jhala and Hall 2013; Jhala et al. 2009; Wolfenbarger and Phifer 2000). Studies to detect pollen-mediated gene flow (PMGF) from genetically engineered crops to conventional or organic crops confirmed that transfer of herbicide-resistance alleles is possible at varying levels under field conditions, even in self-pollinated crops such as flax (*Linum usitatissimum* L.) (Jhala et al. 2011) and wheat (*Triticum aestivum* L.) (Rieben et al. 2011). In addition, studies of gene flow from HR crops to closely related species were conducted in several commodities such as canola (*Brassica napus* L.) (Légère 2005; Warwick et al. 2003), corn (Ma et al. 2004), flax (Jhala et al. 2008), soybean

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Table 1. Economically important broadleaf weed species selected in this study, their family, and chromosome numbers to determine the potential for PMGF and transfer of herbicide-resistance alleles.

Weed species	Scientific name	Family[a]	Chromosome number	Likelihood of PMGF[b,c]
Common lambsquarters	*Chenopodium album* L.	Amaranthaceae	$2n = 54$	Low
Giant ragweed	*Ambrosia trifida* L	Asteraceae	$2n = 24$	Medium
Horseweed	*Erigeron canadensis* L.	Asteraceae	$2n = 18$	Low
Kochia	*Bassia scoparia* (L.) A. J. Scott	Amaranthaceae	$2n = 18$	Medium
Palmer amaranth	*Amaranthus palmeri* S. Watson	Amaranthaceae	$2n = 34$	High
Waterhemp	*Amaranthus tuberculatus* (Moq.) Sauer	Amaranthaceae	$2n = 32$	High

[a]Common lambsquarters and kochia previously were classified in the Chenopodiaceae, which has been reassigned as Amaranthaceae in recent years in the order Caryophyllales.
[b]Abbreviation: PMGF, pollen-mediated gene flow.
[c]Likelihood of PMGF as estimated on the basis of reproductive biology and previous studies.

(Kim et al. 2019), and wheat (Gandhi et al. 2006; Hanson et al. 2005; Martins et al. 2016) [and see reviews by Gressel (2015); Ellstrand et al. (1999); Jhala et al. (2017b)].

Herbicides are an important component of weed management in most agronomic crops, particularly in developed countries, including the United States. Reliance on herbicides is especially prevalent in HR corn-soybean cropping systems in the midwestern United States (Jhala et al. 2014) as well as in several other cropping systems and in noncrop areas. Adoption of no-tillage production practices significantly reduced the use of tillage for weed management and further increased the dependence on herbicides (Bhowmik and Bekech 1993; Sarangi and Jhala 2018), contributing to the evolution of HR weeds (Beckie 2006). As of 2020, there are 514 unique cases of HR weeds globally in 93 crops in 70 countries (Heap 2020a).

Independent evolution of herbicide resistance due to selection pressure from the same herbicide site of action (SOA) in the same field is a primary contributing factor to the regional occurrence of HR weeds (Beckie 2006); however, once resistance has evolved, HR alleles can spread via seed and pollen movement (Jhala and Knezevic 2017). Weed-seed dispersal has the potential to affect movement of herbicide-resistance alleles on a much larger scale than pollen flow. Movement of HR seed among fields or regionally via equipment, manure, commercial seed stocks, feed, crop residues, plant byproducts, or irrigation water is often greater than via natural seed dispersal (Beckie et al. 2019a). Farmer et al. (2017) confirmed that migratory waterfowl consume seeds of several agronomically important weed species that can remain viable after passage through digestive tracts and have the potential to be dispersed over long distances. The commercial bird-feed trade has been recognized as a pathway for long-distance weed-seed dispersal to new areas. Recent analysis of commercially available bird-feed mixes in the eastern United States found 29 weed species in the mixes (Oseland et al. 2020). *Amaranthus* species were the most common, found in 96% of the mixes; common lambsquarters seed was identified in 10% of the mixes.

Invasions are usually associated with the movement of regenerative propagules into new habitats; a less commonly explored aspect is the introduction of a unique, but advantageous, allele into a locally adapted genetic pool (Petit 2004). Herbicide-resistance alleles from HR weeds can spread, via pollen, both intra- and interspecifically in certain species, such as *Amaranthus* (Gaines et al. 2012; Sarangi et al. 2017; Sosnoskie et al. 2012) and *Ambrosia* (Ganie and Jhala 2017; Vincent et al. 1988). PMGF of herbicide-resistance alleles in kochia is an important vector for proximal dispersal, such as within fields. The PMGF in kochia can contribute to rapid accumulation of herbicide-resistance alleles in an individual or population. For example, an individual plant may accumulate different target-site mutations conferring resistance to acetolactate synthase (ALS)-inhibiting herbicides (Beckie et al. 2011) or multiple mechanisms conferring herbicide resistance to multiple SOAs. A kochia population in Kansas was confirmed to be resistant to four SOA: ALS inhibitors, photosystem-II (PS II) inhibitors, glyphosate, and synthetic auxins (Varanasi et al. 2015).

The spread of HR weeds into new agroecosystems is a concern for growers and includes the potential of pollen-mediated gene introgression of herbicide-resistance traits into indigenous weed species. Beckie et al. (2019a) stated that PMGF from HR weeds is underestimated and underappreciated. To better quantify the nature of pollen movement and transfer of resistance alleles, more information is needed about the reproductive biology, cytogenetics, and occurrence of gene transfer in economically important weed species (Table 1). Our objective for this article was to review reproductive biology, PMGF studies, interspecific hybridization, and potential of herbicide-resistance allele transfer via pollen from HR plants to susceptible plants in economically important and widely distributed broadleaf weeds, including common lambsquarters, giant ragweed, horseweed, kochia, Palmer amaranth, and waterhemp.

Common Lambsquarters

Common lambsquarters is one of the most widely distributed and economically important weeds in the world (Bassett and Crompton 1978; Holm et al. 1977). The *Chenopodium* genus has a worldwide distribution of at least 150 species, with the highest species diversity in temperate areas (Krak et al. 2016). The origin of common lambsquarters is unclear (Holm et al. 1977). Common lambsquarters has been reported to be native to western Asia, but its native range likely includes most of Europe (Bajwa et al. 2019; CABI-ISC 2019). It is widely naturalized elsewhere, including North America. Common lambsquarters is adapted to many cropping systems and is competitive with at least 40 crop species (Bajwa et al. 2019; Holm et al. 1977). In the United States and Canada, common lambsquarters is perceived as the most common and the fifth most troublesome (i.e., difficult to control) weed in corn (Van Wychen 2017). In soybean, common lambsquarters is the third most common and sixth most troublesome weed (Van Wychen 2019).

Reproductive Biology of Common Lambsquarters

Common lambsquarters has an annual life cycle with peak seed germination and seedling emergence occurring in early to mid spring, but subsequent cohorts can emerge during summer and fall (Holm et al. 1977). Plants can grow to a height of 2 m or more and

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have ascending branches and simple, alternate leaves (Holm et al. 1977). Inflorescences are a spiked panicle in leaf axils or at the terminus of stems and branches, with small, dense flower clusters. Plants are monoecious (i.e., male and female flowers on the same plant); flowers are perfect, green, small, sessile, in irregular spikes and without petals (Bassett and Crompton 1978).

Common lambsquarters flowers at any day length, but short days hasten flowering and maturity (Holm et al. 1977). The time of anthesis varies from a few days to several weeks. Common lambsquarters is self-compatible and reproduces both by self- and cross-pollination (Bassett and Crompton 1978). Flowers are mainly wind pollinated, but insects may play a role in pollination. A mature plant produces approximately 20,000 pollen grains in a season (Bajwa et al. 2019). Average-sized plants have been reported to produce more than 70,000 seeds (Bassett and Crompton 1978), although large plants have been reported to produce 500,000 seeds (Holm et al. 1977). Because common lambsquarters does not have a natural seed dispersal mechanism, most seeds drop to the ground near the mother plant.

Herbicide Resistance in Common Lambsquarters

Common lambsquarters has evolved resistance to PS-II inhibitors, ALS inhibitors, and synthetic auxins (Heap 2020a; Warwick and Marriage 1982). Resistance to PS-II inhibitors (including atrazine, simazine, metribuzin, and metamitron) is the most widespread resistance ($n = 42$ cases globally). Resistance to ALS inhibitors in common lambsquarters has been confirmed in a total of six cases (three in Canada, two in the United States, and one in Finland). The only report of resistance to synthetic auxin herbicides (namely, aminopyralid, clopyralid, and dicamba) in common lambsquarters is from New Zealand in 2005.

Glyphosate-resistant (GR) common lambsquarters has not yet been reported; however, some populations have shown variable or inconsistent responses to glyphosate across a wide geographic range in the United States (Hite et al. 2008; Kniss et al. 2007; Sivesind et al. 2011; Westhoven et al. 2008). Glyphosate efficacy on common lambsquarters can be affected by plant size (DeGreeff et al. 2018; Schuster et al. 2007) and environmental conditions (DeGreeff et al. 2018; Sivesind et al. 2011), but in other instances, reduced efficacy has been attributed to reduced sensitivity (Hite et al. 2008; Kniss et al. 2007; Westhoven et al. 2008). A subsequent investigation showed that reduced translocation of glyphosate plays an important role in conferring reduced sensitivity (Yerka et al. 2013).

PMGF from HR Common Lambsquarters

The PMGF in common lambsquarters decreases rapidly with increasing distance from the pollen source. Gasquez (1985) estimated that PMGF was 50% between plants spaced 0.2 m apart, whereas it decreased logarithmically to 5% at a plant spacing of 2.0 m. The results were likely indicative of common lambsquarter's PMGF in sugar beet (*Beta vulgaris* L.), which is a relatively short species, whereas the expected PMGF among common lambsquarters plants in corn would likely be much lower because of the tall stature of crop plants impeding pollen movement by wind (Darmency and Gasquez 1990).

Yerka et al. (2012) quantified PMGF in common lambsquarters in field experiments using magenta spreen (*Chenopodium giganteum* D. Don; $2n = 54$), which has a dominant magenta phenotypic marker, as the pollen source. A wild-type accession of common lambsquarters ($2n = 54$) served as pollen-receptor plants that were grown in a soybean stand and arranged in concentric circles 2 to 15 m from the center that contained 24 pollen-source plants. The concentric circles were divided into eight cardinal directions. Pollen movement was analyzed by determining the percentage of progeny with the magenta phenotype from the pollen-receptor plants. Average PMGF across directions was greatest (3.0%) at 2 m and decreased exponentially to low levels (0.16%) 15 m from the edge of pollen source. The PMGF was greatest in the south-southwest, west-southwest, and west-northwest directions, approximately 180° from the prevailing wind direction during the time of pollen shed (Figure 1). Because common lambsquarters does not have an active seed-dispersal mechanism, the results suggested PMGF may play an important role in the short-distance transfer and frequency of resistance alleles within and between populations.

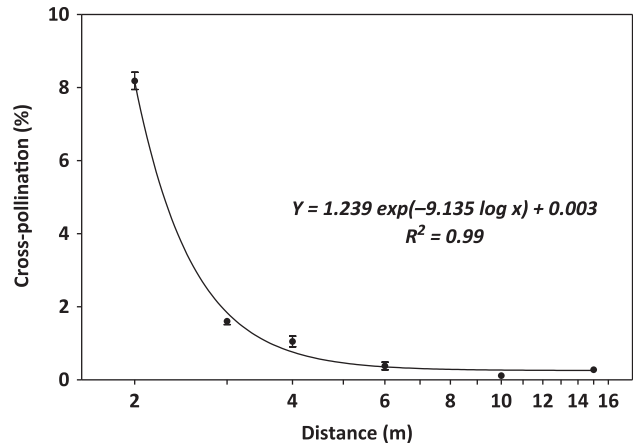

Figure 1. Empirical model of pollen-mediated gene flow in common lambsquarters under field conditions (Yerka et al. 2012). The maximum observed cross-pollination percentage between wild-type *Chenopodium album* and *C. giganteum* was described by a negative exponential function using the two highest values at each distance from the south-southwest, west-southwest, and/or west-northwest sectors (generally 180° from the prevailing wind direction during the time of pollen shed). Mean values of the maximum cross-pollination percent (±SE) are shown.

Resistance to PS-II inhibitors is the most reported resistance in common lambsquarters (Heap 2020a). Consequently, research on gene flow of resistance alleles in this species has focused on PS-II inhibitors. Soon after the first report of triazine resistance in common lambsquarters (Bandeen and McLaren 1976), it was determined that the inheritance of atrazine resistance was uniparental (maternal) (Warwick and Black 1980). This discovery was critical for understanding the importance of seed-mediated gene flow of atrazine-resistance alleles in common lambsquarters.

In a study that assessed the spread of metamitron-resistant common lambsquarters patches in sugar beet and corn fields across four farms, using amplified fragment length polymorphism markers, Aper et al. (2012) found significant genetic variation among farm locations and among patches within farm locations. They also found a positive correlation between genetic distance and geographic distance, suggesting isolation by distance. However, the genetic similarity between patches from different fields indicated that seed transport by agricultural machinery and manure was likely to have played an important role in the spread of resistance.

Interspecific Hybridization and Gene Flow in Chenopodium Species

Common lambsquarters is a hexaploid ($2n = 54$) (Bassett and Crompton 1978). Recent research suggests that hexaploid

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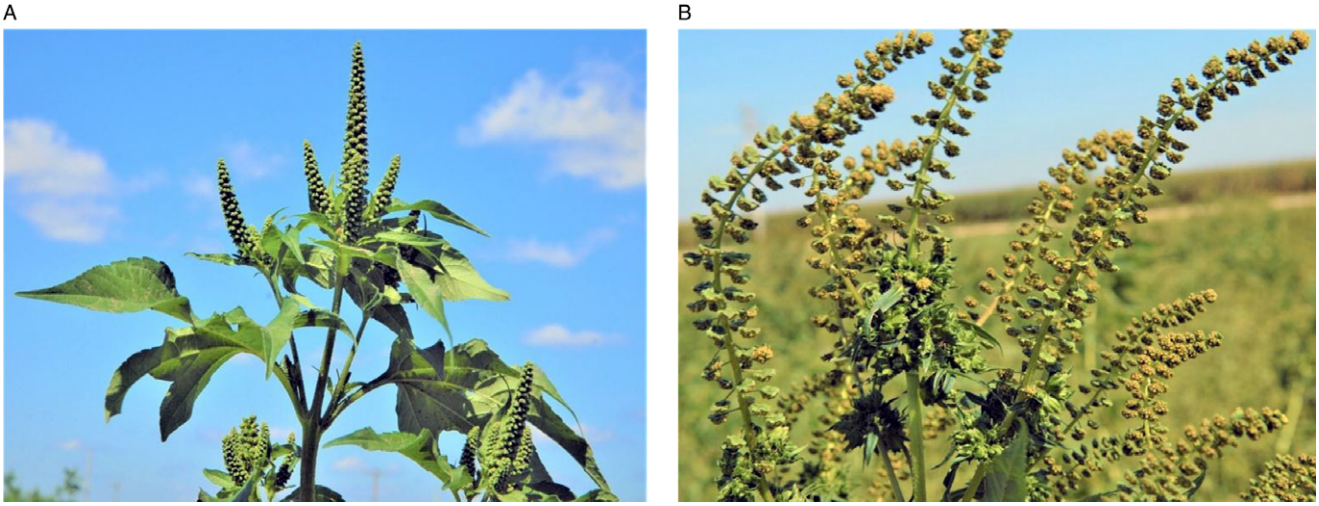

Figure 2. Giant ragweed inflorescence. (A) Initiation of male flowers and (B) seed clusters at the base of the flower heads.

Chenopodium species originated by hybridization between diploid ($2n = 18$) and tetraploid ($2n = 36$) *Chenopodium* species (Krak et al. 2016; Mandák et al. 2018). Common lambsquarters hybridizes with other hexaploid *Chenopodium* species, including the aforementioned magenta spreen (Yerka et al. 2012) and seaport goosefoot (*C. opulifolium* Shrad. ex W.D.J. Koch & Ziz) (CABI-ISC 2019; Mandák et al. 2018). Although experimental evidence suggests that *Chenopodium* species do not hybridize freely across ploidy levels (Mandák et al. 2012), common lambsquarters has been reported to hybridize with diploid and tetraploid species within the *Chenopodium* genus, including figleaf goosefoot (*C. ficifolium* Sm.; $2n = 18$), Swedish goosefoot (*C. suecicum* Murr.; $2n = 18$), and netseed lambsquarters or pitseed goosefoot (*C. berlandieri* Moq.; $2n = 36$) (CABI-ISC 2019; Mandák et al. 2018).

Giant Ragweed

Giant ragweed, a native of North America, is a summer annual dicotyledonous weed belonging to the Asteraceae (sunflower) family (Bassett and Crompton 1982). It is widely distributed in the United States, primarily in the eastern Corn Belt, and in southern Canada (Bassett and Crompton 1982) and in several countries in Asia and Europe (Makra et al. 2015). Giant ragweed is an economically important weed because of its allergenic pollen and its competitiveness with agronomic crops, including corn, soybean, and wheat (Ganie et al. 2016; 2017b; Mahoney et al. 2015). Early emergence, rapid growth rate, and a high leaf-area index enable giant ragweed to assume a dominant role in the plant community; it often becomes invasive, reducing species diversity in the infested landscape (Abul-Fatih and Bazaz 1979a). Giant ragweed grows erect, with plasticity evident in branching and plant height according to habitat (crop or noncrop) and competing crop or weed species (Abul-Fatih and Bazaz 1979b).

Reproductive Biology of Giant Ragweed

Giant ragweed is a monoecious species with imperfect flowers; the main stem and branches of giant ragweed culminate in an inflorescence bearing male flowers; female flowers are usually present at the base of the male inflorescence or at the leaf axils in clusters of three or more sessile seed-bearing involucres (Figure 2) (Abul-Fatih and Bazaz 1979a; Bassett and Crompton 1982). Giant ragweed is a protogynous species, meaning stigmas in female flowers protrude and become receptive before the male flowers on the same plant start shedding pollen grains (Bassett and Crompton 1982). Giant ragweed is anemophilous (i.e., wind pollinated) and each plant can produce approximately 1 billion pollen grains during a normal growing season. It has been estimated that during peak flowering time, a single giant ragweed plant can release 1 million pollen grains day^{-1} (Bassett and Crompton 1982). Ragweed pollen is relatively small (18–25 μm) and flat to nearly spherical, covered with miniature spine-like projections that likely support a low rate of deposition (0.02 to 0.06 m s^{-1}) (Barnes et al. 2001; Kanter et al. 2013). In addition, self-incompatibility has been documented in giant ragweed, which promotes PMGF despite being monoecious. Bassett and Crompton (1982) reported flower heads bagged before flowering produced viable seeds after self-pollination, although plants generated from self-pollinated seeds had reduced vigor compared with seeds resulting from cross-pollination.

Herbicide Resistance in Giant Ragweed

Giant ragweed has evolved resistance to ALS-inhibiting herbicides (Heap 2020a; Marion et al. 2017; Patzoldt and Tranel 2002), 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS)-inhibiting herbicide glyphosate (Harre et al. 2017; Regnier et al. 2016) and multiple resistance to ALS and EPSPS inhibitors (Regnier et al. 2016). Resistance to ALS inhibitors in giant ragweed is due to a tryptophan-to-leucine substitution at the 574 amino acid position (W574L position relative to *Arabidopsis thaliana*) (Marion et al. 2017; Patzoldt and Tranel 2002). The GR giant ragweed biotypes have two distinct phenotypes: a rapid response phenotype in which cell death or necrosis occurs within hours after glyphosate application in fully expanded mature leaves; and a nonrapid response phenotype that results in chlorosis in the meristematic tissues during the first week or cessation of normal growth with no visible symptoms (Moretti et al. 2018; Van Horn et al. 2018). The precise mechanism of glyphosate resistance in ragweed is not known (Ganie et al. 2017a; Wilson et al. 2020); however, in collaborative studies conducted with several GR populations across the United States and Canada, researchers concluded that the mechanism of

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glyphosate resistance in the rapid-response biotype appears to be different compared with the known target-site or non–target-site resistance mechanisms and involves production of reactive oxygen species (Moretti et al. 2018; Van Horn et al. 2018). A recent study revealed that a novel mechanism confers glyphosate resistance in non–rapid-response type giant ragweed from Wisconsin and more investigation is needed (Wilson et al. 2020).

PMGF from HR to Susceptible Giant Ragweed

PMGF has been reported in giant ragweed. Ganie and Jhala (2017) used glyphosate resistance (nonrapid-response type) as a selective marker to quantify the PMGF and the dissemination of resistance alleles from a GR population (a pollen source) to a glyphosate-susceptible population (a pollen receptor). In this 2-yr study, PMGF ranged from 43% to 60% at less than 0.5 m and 3% to 4% at 50 m from the edge of pollen source. In the same study, a double exponential-decay model predicted 90% reduction in PMGF at 49.5 m in year 1 and 106.6 m in year 2. Similarly, Brabham et al. (2011) reported 31% PMGF between GR (rapid-response type) and glyphosate-susceptible giant ragweed planted in rows at 0.76 m apart. These studies provided empirical gene flow rates and experimental evidence to support the hypotheses of spread of resistance alleles through PMGF. High rates of PMGF explain the high level of phenotypic plasticity and genetic diversity in this species and should be considered when implementing management plans before plants reach the reproductive stage.

With little fitness cost associated with cloransulam or glyphosate resistance in giant ragweed (Glettner and Stoltenberg 2015; Marion et al. 2017), herbicide-resistance traits may have a greater likelihood for wide dissemination due to PMGF and possible introgression (i.e., permanent fixation of the trait in the gene pool of natural, wild populations) over time (Ellstrand et al. 1999; Stewart et al. 2003). Surveys in Indiana showed that GR giant ragweed spread from 15% to 39% of Indiana counties from 2006 to 2014 (Harre et al. 2017). Furthermore, it is possible that PMGF between neighboring giant ragweed populations resistant to ALS inhibitors or glyphosate may have resulted in multiple HR populations (Regnier et al. 2016). Harre et al. (2017) reported that in Indiana, 43 of 53 giant ragweed populations were GR where five and 16 populations displayed rapid-response or nonrapid-response phenotypes, respectively; 22 populations had both rapid-response and nonrapid-response phenotypes. Therefore, it is possible that PMGF between rapid-response and nonrapid-response GR giant ragweed biotypes have integrated two mechanisms of glyphosate resistance into a single biotype.

Interspecific Hybridization and Gene Flow in Ambrosia species

Common ragweed (*Ambrosia artemisiifolia* L.; $2n = 36$) is a closely related species of giant ragweed. These two species require somewhat similar climatic conditions and grow in common habitats but display some phenological differences such as plant height and leaf shape (Figure 3). They have overlapping flowering times and possess commonalities in their floral biology and breeding systems, both are monoecious and wind pollinated (Bassett and Crompton 1975). Interspecific gene flow between giant ragweed and common ragweed is possible, although it is rare in nature (Vincent and Cappadocia 1987; Vincent et al. 1988). Vincent and Cappadocia (1987) reported that common ragweed × giant ragweed hybrids were easily produced, compared with giant ragweed × common ragweed, due to the postzygotic barrier of interspecific incompatibility in the latter crosses that required embryo rescue to produce viable hybrids. Common ragweed has evolved resistance to several herbicide SOAs including ALS, EPSPS, PS II, and protoporphyrinogen oxidase (PPO)-inhibiting herbicides. Multiple HR biotypes include resistance to ALS + EPSPS, ALS + PPO, and ALS + EPSPS + PPO inhibitors (Heap 2020a). Consequently, common ragweed and giant ragweed growing in proximity in the same habitat create the potential for interspecific hybridization and possible transfer of herbicide-resistance alleles.

Figure 3. Coexistence of *Ambrosia* species, common ragweed and giant ragweed, growing at the same height in a soybean field. Interspecific gene transfer is possible between the species.

Horseweed

Horseweed, also known as marestail, Canada fleabane, and Canadian horseweed, is a forb commonly found in meadows, farmland, orchards (Ford et al. 2014; Shrestha et al. 2008), and agronomic crops (Bhowmik and Bekech 1993; Chahal and Jhala 2019). The plant has one to several erect stems and can reach a height of 1 to 2 m (Huang et al. 2015; Regehr and Bazzaz 1979). Horseweed inflorescences, also known as capitula (a capitulum is a collection of 16 to 22 individual flowers, both ray and disc flowers), are numerous and have very small heads, 2 to 4 mm tall and 2 to 4 mm wide (Ford et al. 2014). In addition to competing with agronomic crops for resources and reducing yields, horseweed is a problematic weed in no-till crop production systems because of the small, wind-dispersed seeds that cannot germinate from soil depths much greater than approximately 3 mm and evolution of resistance to several herbicide chemistries (Davis and Johnson 2008; Huang et al. 2015; VanGessel 2001; Weaver 2001). It can emerge throughout the year, except in winter months when temperature is not favorable (Ford et al. 2014); however, early fall or spring are the seasons when the majority of horseweed emerge, depending on location, moisture, and weather (Buhler and Owen 1997; Holm et al. 1997; Nandula et al. 2006; Regehr and Bazzaz 1979).

Reproductive Biology of Horseweed

Horseweed is a monoecious species with perfect flowers (Shields et al. 2006), and when the capitula are closed, self-pollination can occur (Huang et al. 2015). After the flowers are fully opened, horseweed releases pollen, largely influenced by its biological characteristics, ambient meteorological conditions, and geographic location (Huang et al. 2015; Ye et al. 2016). As a result, pollen

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production during the flowering season fluctuates day to day and year to year (Aboulaich et al. 2013). Horseweed pollen is lightweight and has a low settling speed (i.e., the downward-motion speed of a pollen particle in still air) and primarily carried by wind (Aylor 2002), although insect pollination has not been ruled out, because insects visit horseweed flower (Davis et al. 2010). The settling speed of horseweed pollen is 0.019 m s^{-1}; their density is 1,218 kg m^{-3} (Wang et al. 2017). Horseweed pollen diameter ranges from 16 to 22 μm (Huang et al. 2015). The diameter may vary during the flight, because of dehydration (Aylor 2003), which affects the settling velocity of pollen (up to 30%) when moving in the air (Chamecki et al. 2011). After approximately 10 to 12 d of flowering, the seeds start to mature (Huang et al. 2015). A single plant can produce a substantial number of seeds, which subsequently become windborne with the aid of a pappus (Bhowmik and Bekech 1993; Weaver 2001).

Huang et al. (2015) in Illinois and Ye et al. (2016) in Tennessee reported that the total number of pollen grains generated from horseweed was 2.3 to 5.1 × 10^6 $plant^{-1}$ during a pollination season. Diurnal pollen release started around 9 AM and the peak release was around 1:30 PM; little pollen was released after 7 PM. Approximately 79% of pollen was released between 9 AM and 7 PM (Huang et al. 2015; Ye et al. 2016). Seasonal pollen releases were multimodal (i.e., had multiple peaks) and lasted about approximately 60 d (Huang et al. 2015; Ye et al. 2016). A seasonal release pattern of horseweed pollen in a field study concluded that most pollen was deposited close to the source (Huang et al. 2015). At 25 m from the source, the pollen deposition rate (pollen grains m^{-2}) decreased to 18% of that at the horseweed source (148 m by 160 m source with a density of 9.5 plants m^{-2}). Because the pollen size was small and the settling speed was slow (1.7 cm s^{-1}), the pollen was lifted 80 to 100 m in the air in field experiments. Thus, pollen can be transported long distances. Smisek et al. (1998) found that an average of 96% of florets were self-pollinated and that the adjacent GR and susceptible horseweed plants had a PMGF of 4%. Within a population, PMGF was reported to range from 1.2% to 14.5% (Loux et al. 2006).

Herbicide Resistance in Horseweed

The first reported case of herbicide resistance in horseweed was to paraquat in Japan in 1980 (Matsunaka and Ito 1991). As of early 2020, there were 19 HR horseweed biotypes (Heap 2020a). GR horseweed population was confirmed in Delaware in the United States in 2001 (VanGessel 2001). Multiple HR horseweed biotypes, particularly those resistant to glyphosate and ALS inhibitors, have been confirmed and are widespread in corn-soybean cropping systems in the United States (Chahal and Jhala 2019; Davis et al. 2009; Heap 2020a).

PMGF from HR to Susceptible Horseweed

A field study conducted in Tennessee provided information about the release rate, release pattern, and pollen dispersal pattern of GR horseweed (Ye et al. 2016). Huang et al. (2015) conducted a field study in Illinois to measure horseweed pollen production, dispersal, and deposition, coupled with atmospheric data to reveal the release pattern and the factors that affect pollen release and dispersal. Wang et al. (2017) modeled the pollen dispersal on the basis of a Lagrangian statistical model. Like other weed species, pollen dispersal of horseweed is affected by many factors, including wind speed, atmospheric stability, size of the pollen source, pollen release rate, and presence of buffer plants. It has been estimated that a single horseweed plant can produce approximately 200,000 seeds (Smisek 1995; Wang et al. 2017; Weaver 2001) with a 4% outcrossing rate (Huang et al. 2015; Smisek et al. 1998). Results revealed that one horseweed plant might be sufficient to spread glyphosate-resistance alleles through pollen movement (Wang et al. 2017). Because of the rapid evolution of herbicide resistance in horseweed biotypes, the introgression to herbicide-susceptible plants might have happened relatively quickly (Chapman and Abbott 2010; Okada et al. 2015); however, little information is available concerning various stages of PMGF and introgression (Okada et al. 2015; Yuan et al. 2010).

Interspecific Hybridization and Gene Flow in Erigeron *Species*

Adaptive introgression of herbicide resistance from horseweed to closely related species can result from interspecific hybridization (Gaines et al. 2012; Okada et al. 2013; 2015). With the aid of microsatellite markers, evidence was obtained of interspecific hybridization between horseweed and a polypoid *Erigeron* species (syn. *Conyza* sp.), hairy fleabane [*C. bonariensis* (L.) Cronq.] (Okada et al. 2013). However, it remains uncertain whether interspecific hybridization and introgression have occurred in nature between horseweed and hairy fleabane (Okada et al. 2015). Nevertheless, in the study of alleles between the two species, the low genetic structure and high value of genetic identity indicated there were exchanged alleles between hairy fleabane and horseweed. This provides additional evidence of the existence of PMGF between *Erigeron* species (Soares et al. 2015).

Kochia

Kochia is a C_4 annual, dicot weed native to Eurasia that is widespread in Europe and parts of temperate Asia, including China and Japan (Jalas and Suominen 1980; Shu 2003). Kochia is also widely naturalized in Africa and South America (Holm et al. 1997). The plant was introduced into the Americas from Eurasia in the mid to late 1800s as an ornamental plant (Friesen et al. 2009). The competitiveness and persistence of kochia in cropland and ruderal (i.e., noncropped, disturbed) areas are aided by its ability to germinate at cool soil temperatures and emerge early in the growing season, grow rapidly, tolerate environmental stresses (e.g., heat, drought, salinity), and evolve resistance to multiple herbicide SOAs (Friesen et al. 2009). In North America, kochia has expanded northward in the Northern Great Plains of Canada (to 53°N) as well as southward in the High Plains of Texas (to 33°N) over the past 50 yr (Beckie et al. 2002; Forcella 1985).

Reproductive Biology of Kochia

Kochia is self-compatible with moderate outcrossing; it produces protogynous flowers in which the stigmas emerge before anther development (Guttieri et al. 1995; Stallings et al. 1995; Thompson et al 1994). The stigmas usually emerge 1 wk before pollen is shed, are receptive to foreign pollen during that time, and deteriorate before anther dehiscence, thereby preventing self-pollination within the same flower. Pollen grains are spheroidal (20 to 40 μm diam) with a granular surface (Stallings et al. 1995). Pollen viability after dehiscence declines to approximately 30% after 1 d and 10% after 2 d under environmental conditions typically present during the pollination period: mid-day temperatures of 23 to 28 C and relative humidity of not more than 30% (Mulugeta et al. 1992; Stallings et al. 1995). Wind is the primary pollination vector, although bees (Colletidae and Halictidae) can

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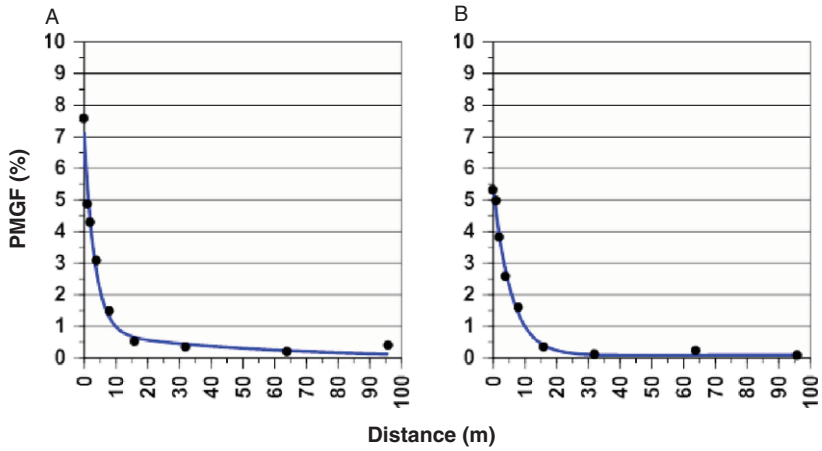

Figure 4. Pollen-mediated gene flow (PMGF) from a glyphosate-resistant kochia pollen source to varying distances of glyphosate-susceptible receptor plants at a field site at Saskatchewan, Canada, in (A) 2014 and (B) 2015. (Adapted from Beckie et al. 2016)

contribute to PMGF in kochia (Blackwell and Powell 1981). Adult plants produce large amounts of pollen for extended periods (Mulugeta 1991), approximately 1 mo (Beckie et al. 2016).

Herbicide-Resistance in Kochia

The PS-II inhibitor (triazine)-resistant kochia populations were discovered in Kansas and along railroads in Idaho and Iowa in 1976 in the United States (Heap 2020a). In 1987, the first kochia biotype resistant to ALS-inhibiting herbicides was confirmed in a wheat field in Kansas, only 5 yr after introduction of these herbicides (Primiani et al. 1990; Saari et al. 1990). In Canada, ALS inhibitor–resistant kochia was first reported in 1988 in Manitoba and Saskatchewan (Morrison and Devine 1994). Since the mid 2000s, most kochia populations are resistant to ALS inhibitors (Beckie et al. 2019b; Varanasi et al. 2015). Thus, area-wide incidence of ALS-inhibitor resistance in this species has progressed rapidly within 20 yr since first reported in the late 1980s (Heap 2020a). Kochia populations with multiple herbicide resistance (namely to PS II and ALS inhibitors) were first reported in biotypes from Illinois and Indiana in 1995 (Foes et al. 1999). The only reported case outside of North America is ALS inhibitor–resistant kochia from the Czech Republic (Chodova and Mikulka 2000; Holá et al. 2004).

Kochia populations resistant to auxinic herbicides were first discovered in 1995 in Montana and North Dakota (Nandula and Manthey 2002). To date, auxin-resistant biotypes have been reported in corn, wheat, or fallow fields in six states in the United States and two Canadian provinces (Beckie et al. 2019b; Kumar et al. 2019a). GR kochia was first reported in Kansas in 2007 and now occurs in 10 states in the United States and three Canadian provinces (Beckie et al. 2013, 2019b; Hall et al. 2014). The mechanism of glyphosate resistance in kochia is increased copy number and expression of the EPSPS enzyme, which is inhibited by glyphosate in susceptible plants (Wiersma et al. 2015). The EPSPS copy number correlates with level of glyphosate resistance, with four or more copies required for resistance to glyphosate when applied at labelled rates (Godar et al. 2015; Varanasi et al. 2015). Inheritance of increased copy number follows a single-locus Mendelian pattern, because the gene copies are in a tandem array on a single chromosome (Jugulam et al. 2014). Therefore, PMGF may contribute to an increase in EPSPS copy number and, therefore, levels of resistance to glyphosate. In Manitoba, where kochia is much less abundant, the incidence of glyphosate resistance in kochia increased from two fields (less than 1% of sites surveyed) in 2013 (Beckie et al. 2015) to 59% of fields in 2018 (Geddes et al. 2019). In the 2017 Alberta survey, 18% of kochia populations from nine counties were resistant to dicamba (Beckie et al. 2019b) compared with none in 2012 (Hall et al. 2014). Moreover, 10% of the populations in the 2017 survey were triple resistant to ALS inhibitors, glyphosate, and synthetic auxins. In surveys conducted in Colorado, 14% of fields in 2012, 15% in 2013, and 20% in 2014 had populations resistant to both glyphosate and dicamba (Westra et al. 2019).

PMGF from HR to Susceptible Kochia

The PMGF in kochia contributes to short-distance (less than 1 km) propagule dispersal. Studies in the western United States using ALS-inhibitor resistance as a marker have indicated that kochia is primarily self-pollinated, although moderate outcrossing can occur. The PMGF between ALS inhibitor–resistant (donor) and susceptible (receptor) plants occurred at a maximum rate of 13% at a distance of 1.5 m and declined to 1.4% at 29 m, the farthest distance sampled (Mallory-Smith et al. 1993; Stallings et al. 1995). In another PMGF study, 4% of progeny of susceptible plants transplanted within an ALS inhibitor–resistant kochia field population were resistant (Mulugeta et al. 1992).

Although western Canadian kochia populations have greater than expected levels of homozygosity (Martin et al. 2018), moderate levels of PMGF in the species were confirmed. Using glyphosate resistance as a marker, PMGF from resistant to susceptible plants averaged 6.4% at 0-m distance and exponentially declined to 0.25% at 96 m (farthest distance sampled; Figure 4) (Beckie et al. 2016). The predicted distance for 50% and 90% reduction in PMGF was at 3.3 m and 13.9 m, respectively. However, PMGF was markedly influenced by prevailing wind direction during the pollination period (over 1 mo), with a maximum PMGF of 17% downwind. The PMGF study in the United States was conducted in a spring barley (*Hordeum vulgare* L.) field (Stallings et al. 1995), whereas the Canadian study was conducted in a fallow field (Beckie et al. 2016) that favored PMGF because of lack of potential crop-pollen competition or the crop canopy acting as a wind break. Nevertheless, PMGF in kochia, using different herbicide resistance

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Figure 5. Palmer amaranth. (left) Anthers and (right) female flowers.

markers under cropped and noncropped conditions, were relatively similar in both studies.

Interspecific Hybridization and Gene Flow in Kochia

Interspecific hybridization has not been reported in kochia. Both green molly [*Bassia americana* S. Watson) A.J. Scott] and rusty molly [*B. californica* S. Watson) A.J. Scott] are native perennial subshrubs, whereas forage kochia [*B. prostrata* (L.) A.J. Scott] is a recently naturalized species found in the western United States (Mosyakin 2003). No hybrids were obtained in artificial crosses between *B. americana* × *B. scoparia* (female × male) and *B. prostrata* × *B. scoparia* (female × male) (Lee et al. 2005).

Palmer Amaranth

Palmer amaranth is an annual, broadleaf species native to the deserts of the southwestern United States and northwestern Mexico, where the leaves and seeds of the species historically served as a food source for indigenous people (Ehleringer 1983; Moerman 1998; Sauer 1957, 1967). Palmer amaranth has since migrated east- and northward across the North American continent, where it has become one of the most problematic weeds in corn, cotton (*Gossypium hirsutum* L.), and soybean, among other crops (Webster and Nichols 2012); the species can now be found in parts of Africa, Europe, and South America, where its presence is associated with agricultural activities (Kistner and Hatfield 2018; Runquist et al. 2019). Although Palmer amaranth's range expansion, to date, has largely been driven by human-mediated dispersal events (e.g., contaminated seed, movement on equipment), models predict that climate change will help facilitate its spread into other geographic regions (Kistner and Hatfield 2018; Runquist et al. 2019).

Palmer amaranth is characterized as being erect, tall (1 to 2 m or taller), and frequently branched with elliptical to obovate, hairless leaves arranged in an alternate pattern around the stem (Mosyakin and Robertson 2008). Plants may appear poinsettia-like when viewed from above, although considerable plasticity in form and structure has been observed (Bravo et al. 2017). Petioles are often longer than the leaf blades, which may display a white or purple chevron on the upper side (Mosyakin and Robertson 2008). Palmer amaranth has a high photosynthetic rate (81 μmol m^{-2} s^{-1}) compared with other C_4 plants; this allows Palmer amaranth to quickly accumulate significant amounts of biomass, which results in growth rates of more than 5 cm day^{-1} under optimal growing conditions (Ehleringer 1983; Horak and Loughlin 2000). Keeley et al. (1987), MacRae et al. (2013), and Sellers et al. (2003) reported that thousands to hundreds of thousands of seed could be produced by individual female Palmer amaranth plants depending on emergence time and the intensity of competitive interactions.

Reproductive Biology of Palmer Amaranth

Palmer amaranth is dioecious; male (pistillate) and female (staminate) flowers are produced on separate plants (Figure 5A and 5B) in long, terminal inflorescences (Figure 6) that may be either solitary or branched and may droop with age (Mosyakin and Robertson 2008). On the basis of flowering morphology, *Amaranthus* species are placed in two subgenera: *Amaranthus* and *Acnidia* (Sauer 1957). Palmer amaranth and waterhemp belong to the subgenus *Acnida* (L.) Aellen ex K. R. Robertson (Borsch 1998). Male inflorescences can be distinguished from the female flower spikes by touch; male flowers lack the sharp, stiff bracts that subtend female flowers and thus feel softer (Mosyakin and Robertson 2008). Flowering in Palmer amaranth usually starts in summer and continues into fall, although it may also occur during the spring and winter in the southernmost part of the species' native range (Mosyakin and Robertson 2008). Keeley et al. (1987) demonstrated that Palmer amaranth flowering responses are influenced by day length; shorter days hasten flowering, which, in turn, reduces plant size and seed set.

Male Palmer amaranth plants can produce substantial amounts of wind-dispersed pollen grains that are spherical and covered in surface pores (Borsch 1998; Franssen et al. 2001a; Tsukada 1967; Walkington 1960). Mean pollen-grain diameter is reported to range from 20 to 31 μm depending on pollen collection timing (i.e., from unopened or opened anthers) and visualization or size determination methodology (i.e., using electron or light microscopy or an electronic particle sizer) (Durham 1946; Franssen et al. 2001a; Sosnoskie et al. 2009; Vaissière and Vinson 1994). One significant result from Franssen et al. (2001a) is the observation that pollen size and morphology differed with respect to reproductive biology, with the notable exception of Palmer amaranth, which was more like the monoecious amaranths in appearance (both size and pore density). Sosnoskie et al. (2009) estimated the mean density of fully hydrated Palmer amaranth pollen grains to be 1,218 kg m^{-3}. Using Stokes's law, the estimated settling

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Figure 6. Palmer amaranth inflorescence. (Left) male plants and (right) female plants.

velocity for individual Palmer amaranth pollen grains ranged from 0.015 to 0.05 m s^{-1}. Results from laboratory studies conducted using a settling chamber showed that most Palmer amaranth pollen grains fell at a rate of 0.05 m s^{-1}. The difference between the theoretical and observed estimates of settling velocity was suggested to be a function of changes in pollen density and shape, due to desiccation postanthesis, as well as the presence of pollen clusters, which may affect the movement of nearby solitary grains (Sosnoskie et al. 2009).

Herbicide Resistance in Palmer Amaranth

As of 2020, there were 65 reported cases of Palmer amaranth with resistance to herbicides across eight SOAs (ALS, microtubule, PS II, EPSPS, PPO, long-chain fatty acid, 4-hydroxyphenylpyruvate dioxygenase inhibitors, and synthetic auxins) in Argentina, Brazil, Israel, and the United States (Heap 2020a). The first incidence of herbicide resistance in Palmer amaranth was to trifluralin and other dinitroanilines confirmed in 1989 in South Carolina (Gossett et al. 1992). The first GR Palmer amaranth was confirmed in Georgia (Culpepper et al. 2006). The most recent documented occurrence was to 2,4-D, with potential cross-resistance to other auxin herbicides in Kansas (Heap 2020a). There have been 18 confirmed cases of multiple herbicide resistance in Palmer amaranth, the majority ($n = 16$) of which are to two SOAs (Heap 2020a). Reports have documented multiple resistance to four herbicide SOAs in Kansas (ALS, EPSPS, and PS II inhibitors, and synthetic auxins) (Kumar et al. 2019b) and to five SOAs in Arkansas (ALS, EPSPS, long-chain fatty acid, microtubule, and PS-II inhibitors) (Heap 2020a).

PMGF from HR to Susceptible Palmer Amaranth

Field experiments were conducted in cotton and soybean fields in Georgia to evaluate PMGF from GR to susceptible Palmer amaranth using a source and receptor experimental design for 2 yr (Sosnoskie et al. 2012). The site was a 30-ha field planted alternately to cotton and soybean with a 0.01-ha center block planted to a GR Palmer amaranth biotype. Glyphosate-susceptible Palmer amaranth plants were planted at distances between 1 and 300 m from the edge of the GR source in the four cardinal and four ordinal directions to account for daily variability in wind flow patterns during peak pollination hours. Across all distances, the mean percentage of GR progeny ranged from 18% to 80%, with a trend toward fewer resistant offspring at the farthest distance from the source. The proportion of resistant individuals at each distance from the GR pollen source was greater in this trial compared with a similar study conducted in Nebraska in waterhemp, a closely related species of Palmer amaranth (Sarangi et al. 2017). It is unknown if apomixis (i.e., asexual seed formation) may have affected seed set and observed resistance patterns (Ribeiro et al. 2014; Trucco et al. 2007).

Waterhemp

Waterhemp is a summer annual, competitive broadleaf weed native to the Great Plains of North America (Liu et al. 2012). It is the most abundant and widely distributed weed, particularly in corn-soybean production systems, in the Midwestern United States (Jhala et al. 2017a; Prince et al. 2012). The interference of waterhemp in corn-soybean cropping systems reduces grain yield and quality, depending on density, as well as hindering harvest (Steckel 2007). Waterhemp was first reported in Oklahoma in 1830 (Sauer 1957) and has since expanded from a rare wetland weed to an economically important weed in several agronomic crops in the Midwestern agriculture landscape (Trucco et al. 2009). The widespread occurrence and invasion of waterhemp are due to its ability to adapt and survive in a wide range of climatic conditions, including the ability to survive and produce seeds under water-stressed conditions (Sarangi et al. 2016).

Reproductive Biology of Waterhemp

Waterhemp is a dioecious species with male and female inflorescences present on separate plants (Figure 7A and 7B). Pollen grains of waterhemp are spherical and very small (18.5 µm diam) with golf ball–like aperture arrangement (Franssen et al. 2001a). Franssen et al. (2001a) reported that pollen grains of waterhemp had more apertures on the visible surface compared with monoecious *Amaranthus* species. Flowers of waterhemp are contained on long, slender inflorescences (Figure 7A and 7B). The lower pollen settling velocity of waterhemp (0.0185 to 0.021 m s^{-1}) compared with major wind-pollinated crops such as corn (Costea et al. 2005) help pollen grains travel longer distances under pollen competition (Raynor et al. 1972).

Herbicide Resistance in Waterhemp

The widespread occurrence of waterhemp in the midwestern United States is partly due to its rapid evolution of resistance to many herbicide SOAs in the past two decades. GR waterhemp in the United States was first reported in Missouri in 2006 (Legleiter and Bradley 2008) and has now been confirmed in 22 states (Heap 2020b) and in Ontario, Canada (Schryver et al. 2017). In addition, waterhemp biotypes resistant to ALS inhibitors (Horak and Peterson 1995; Sarangi et al. 2015), PS-II inhibitors (Anderson et al. 1996), PPO inhibitors (Sarangi et al. 2019; Shoup et al. 2003), 4-hydroxyphenylpyruvate dioxygenase inhibitors (Hausman et al. 2011; Oliveira et al. 2017), and 2,4-D (Bernards et al. 2012) have been confirmed. Multiple HR biotypes have been identified, including glyphosate, ALS-, and PPO-

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Figure 7. Waterhemp inflorescences of (A) male and (B) female plants.

inhibitor resistance in Nebraska (Sarangi et al. 2019), atrazine, glyphosate, ALS-, and PPO-inhibitor resistance in Illinois (Bell et al. 2013), and a six-way SOA-resistant biotype (2,4-D, atrazine, chlorimuron, glyphosate, fomesafen, and mesotrione) in Missouri (Shergill et al. 2018).

PMGF from HR to Susceptible Waterhemp

The dioecy and wind-pollinated nature of waterhemp are believed to promote the rapid spread of herbicide-resistance alleles in an agricultural landscape via pollen migration. Liu et al. (2012) conducted greenhouse and field experiments to determine pollen biology and dispersal dynamics in waterhemp and revealed that waterhemp pollen can remain viable up to 120 h and pollen dispersal declined exponentially with distance, with most pollen fertilizing recipient plants within 50 m; however, a rare gene-flow event was observed at 800 m. A multiyear field study was conducted in Nebraska to evaluate PMGF from GR to susceptible waterhemp and role of wind direction (Sarangi et al. 2017). More than 130,000 waterhemp plants were screened and 26,199 plants were confirmed GR. The PMGF declined by 50% at less than 3 m from the pollen source. The greatest gene flow ranged from 54% to 38% at 0.1-m distance from the pollen source during both years of the study, with gene flow decreasing with increasing distance; however, 5% to 9% gene flow was detected at the farthest distance of 50 m (Sarangi et al. 2017). Mallory-Smith et al. (2015) outlined procedures for conducting a PMGF study and noted that the phenotypic screening of herbicide resistance can be considered an excellent marker, though it should be supplemented with a molecular marker to confirm the resultant hybrid. Therefore, *EPSPS* gene copy-number analysis was conducted and it was determined that the mechanism of glyphosate resistance was gene amplification in the GR waterhemp parent used in this study, with the mean relative copy number of 5.3 (Sarangi et al. 2017). The researchers concluded that *EPSPS* gene amplification is heritable in waterhemp and can be transferred via pollen.

Interspecific Hybridization and Gene Flow in Amaranthus *species*

Amaranthus is one of the largest groups of weed species native to the Americas, with approximately 60 species present, and additional 25 species are present globally (Sauer 1957). Herbicide-resistance alleles can transfer via pollen and successful hybridization occurs between *Amaranthus* species, although, the numbers of successful crosses are typically low. For example, Wetzel et al. (1999) documented the transfer of ALS-inhibitor resistance between Palmer amaranth and waterhemp, although only 15 potential hybrids resulted from 10 000 pollination events. Franssen et al. (2001b) reported 35 confirmed hybrid plants from 44 000 seeds generated by crossing 11 female ALS inhibitor–sensitive waterhemp plants with male ALS inhibitor–resistant Palmer amaranth. Oliveira et al. (2018) conducted field experiments in Nebraska to determine interspecific and intraspecific transfer of metabolism-based mesotrione resistance in dioecious *Amaranthus* species. Results showed that 0.1% hybridization between waterhemp and Palmer amaranth occurred under field conditions. Gaines et al. (2012) described the results of a study examining transfer of glyphosate resistance from Palmer amaranth pollen donor to green amaranth (*A. hybridus* L.), Powell amaranth (*A. powellii* S. Watson), redroot pigweed (*A. retro*flexus L.), spiny amaranth (*A. spinosus* L.), and waterhemp under field and greenhouse conditions. Hybridization was observed between Palmer amaranth and green amaranth (less than0.01% in the field), Palmer amaranth and waterhemp (0.2% in the field), and Palmer amaranth and spiny amaranth (less than 0.01% to 0.4% in the field; 1.4% in the greenhouse). Nandula et al. (2014) reported that spiny amaranth resistant to glyphosate had a portion of *EPSPS* amplicon derived from resistant Palmer amaranth, suggesting a naturally occurring hybridization event between the species. The transfer of resistance traits between Palmer amaranth and spiny amaranth is likely because they have the same chromosome number ($2n = 34$), similar genome size, and produce comparably sized pollen (Franssen et al. 2001b; Rayburn et al. 2005).

Summary and Research Needs

The widespread occurrence of HR weeds has increased interest in the mechanisms of resistance-allele movement at the landscape level. Seed movement is the greatest contributor of HR allele dispersal; however, PMGF also contributes to HR allele movement, but little attention is usually given to this phenomenon. Reviewing the PMGF literature on common lambsquarters, giant ragweed, horseweed, kochia, Palmer amaranth, and waterhemp confirms that transfer of HR alleles is possible under field conditions and it is not a rare event. The potential for PMGF depends on many factors, including plant reproductive biology. Dioecious species such as Palmer amaranth and waterhemp are obligate-outcrossing, wind-pollinated species, which increases the potential for PMGF and subsequent transfer of resistance alleles compared with monoecious species. There is widespread GR Palmer amaranth in the southern region and GR waterhemp in the midwestern region of the United States, partially attributed to PMGF. In contrast, common lambsquarters has a high degree of self-pollination, which reduces the potential for PMGF. Even though there is

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relatively low-level PMGF in common lambsquarters, it still may be sufficient to facilitate long-term persistence of resistance allele in a population. Consequently, PMGF may still constitute an important mechanism of resistance-allele transfer in this species, which lacks a natural seed dispersal mechanism.

The species with efficient seed dispersal mechanisms such as horseweed, a monoecious species, has lightweight seeds that become windborne with the aid of pappus; thus, seeds are the primary contributor in transferring resistance alleles among populations compared with PMGF. Kochia populations resistant to glyphosate and synthetic auxins have increased rapidly over the past decade across the western Great Plains. Rapid range expansion of kochia across North America has been facilitated by efficient propagule (both seed and pollen) dispersal. Natural seed dispersal (via tumbling mechanism) aids both short- and long-distance spread of this species. The tumbleweed architecture is an efficient and effective adaptation for the dispersal of susceptible or HR weed seeds over long distances. Similarly, interpopulation PMGF of herbicide-resistance alleles has contributed to rapid area-wide expansion of HR kochia since the late 1980s.

To better quantify the spatial and temporal dynamics of PMGF and transfer of herbicide-resistance alleles, more information is needed about the reproductive biology of economically important HR weeds, including research on the longevity of pollen under different climatic conditions as well as flowering phenology and synchronicity with other compatible species (intra- and interspecific) across latitudes. Multiple HR weeds are of greatest concern for growers, scientists, and regulators. More research is needed on how PMGF transfers multiple HR alleles at a landscape level, particularly in dioecious species. On the basis of computer modeling, it has been estimated that climate change is likely to support the expansion of weed species into new geographic regions; therefore, more research is needed on how climate change may affect PMGF and introgression of herbicide-resistance alleles within and between compatible species.

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