



Herbicide resistance gene flow in weeds: Under-estimated and under-appreciated



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ABSTRACT

Interest in the magnitude and consequences of intra- and inter-specific herbicide resistance gene flow, particularly that mediated by pollen, increased in the mid-1990s with the introduction of herbicide-resistant (HR) transgenic crops. During that time, less attention was paid to the movement of HR alleles via pollen or seed among weed populations. Incidence of HR weeds in a region is often attributed to independent evolution through herbicide selection; the role or contribution of HR allele movement via pollen, seeds and/or vegetative propagules is often under-estimated and under-appreciated. Once a new HR weed biotype has been confirmed in a jurisdiction, how often have we been surprised at its rapid areawide expansion? In genotypic studies of HR weed populations, the contribution of gene flow to incidence of resistance is frequently similar or greater than that of independent evolution. Simulation models have consistently predicted that frequent widespread applications of highly effective herbicides (e.g., acetolactate synthase inhibitors, glyphosate) provide connective high-fitness habitats across the landscape, which facilitate a rapid increase in the frequency and movement of an HR trait within and among populations. Such habitats, characterized by minimal heterogeneity but high selection intensity due to frequent herbicide 'on' vs. 'off' exposure periods, strongly favour the fitness of HR propagules at great disadvantage of herbicide-susceptible individuals. The unanticipated speed of areawide expansion of some HR weed biotypes has spurred numerous calls over the past decade for a collective community or regional response to mitigate this unhindered spread of HR alleles. The best mitigation strategy is minimizing weed population abundance and seed bank replenishment in fields and adjacent ruderal areas. This goal is difficult, but necessary for preserving the remaining public good and common pool resource of herbicide susceptibility.

1. Introduction

Gene flow is an integral element in the evolutionary biology of plant species. Gene flow promotes genetic variability, allows gene migration, and can enable more rapid evolutionary dynamics (Ehrlich and Raven, 1969; Mallory-Smith et al., 2015). Defined as the movement of genes by gametes, diasporas, or individuals from one location to another (Golenburg, 1986), gene flow in plants can occur through the dispersal of pollen, seeds, and/or vegetative propagules. In highly self-pollinated species, gene flow occurs mainly by seed dispersal, whereas pollen movement may potentially contribute more to gene flow in highly outcrossing species (Darmency, 1996).

In the past, gene flow was not generally investigated within agricultural ecosystems. With the introduction of herbicide-resistant (HR) transgenic crops in North America in 1996, there was renewed interest

in quantifying intraspecific pollen-mediated gene flow (PMGF) from glyphosate (GR)- or glufosinate-resistant cultivars of crops such as *Brassica napus* L. (oilseed rape or canola) to conventional (non-HR) cultivars. Understanding and addressing PMGF was central to coexistence measures implemented in various jurisdictions (Beckie and Hall, 2015). Additionally, the potential for PMGF from genetically-engineered HR crops to wild or weedy relatives was important in environmental risk assessments. Before and during that time, less attention was paid to the movement of HR alleles via pollen or seed within and among weed populations of the same species. From an agronomic perspective, a weed population constitutes individuals of a weedy species present within a field, the largest spatial scale where management practices and selection pressures are relatively homogeneous (Délye et al., 2010).

Gene flow by pollen or seed dispersal from HR weed populations

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can introduce HR alleles into previously herbicide-susceptible (HS) populations (Jasieniuk et al., 1996; Busi et al., 2011). Although long-distance (kilometer-scale) HR weed gene movement occurs less frequently and at lower levels than short-distance (sub-kilometer or meter-scale) dispersal, it can provide a ‘beachhead’ for subsequent rapid range expansion, akin to that of invasive alien weeds. Rates of gene flow even in highly self-pollinated species are generally greater than rates of mutation (typically 1 in 10^5 to 10^6 gametes per locus per generation; Crow, 1983). The time required for resistance to appear is greatly reduced when gene flow introduces alleles from an HR population than when alleles must evolve *de novo* from mutation (Jasieniuk et al., 1996). Therefore, gene flow can contribute to potentially rapid spread of resistance within and among weed populations.

The extent of PMGF is determined by a number of biological, environmental, and management factors and their interactions, such as mating system of the plant, type of vector (wind or insect), pollen viability and longevity, synchrony of flowering or pollen production, wind speed and direction, temperature, humidity, and area and plant density of donor and receptor populations; at a landscape or regional scale, additional factors influencing pollen flow are topography, vegetation, and number, shape and spatial arrangement of pollen donor and receptor populations (Beckie and Hall, 2008). Frequency of HR gene flow (percentage outcrossing) typically declines exponentially with increasing distance from the pollen source (Table 1). The maximum distance of PMGF is usually underestimated and not known with certainty, as it depends upon the sample size tested and limits of detection. The maximum distance measured often equates with the limit of a study area.

It is challenging to mitigate the spread of herbicide resistance via pollen, particularly when resistance is usually endowed by a single dominant or semidominant nuclear gene (Richter and Powles, 1993). Levels of PMGF in weed species are correlated with viable pollen longevity. For example, pollen viability of *Bassia scoparia* (L.) A. J. Scott [synonym: *Kochia scoparia* (L.) Schrad.] (kochia) is about 10% after 2 days (Friesen et al., 2009), whereas pollen of *Amaranthus tuberculatus* L. (waterhemp) is nonviable after 2 h (Liu et al., 2012). Whereas crops are usually planted within a short time period across an agroecoregion, weed populations of a species can exhibit widely varying phenological stages (*i.e.*, cohorts) due to staggered emergence over the growing

season within a field and across the landscape. This phenological heterogeneity may adversely affect rates of cross-fertilization among weed populations if there is poor synchrony of flowering or pollen production. High temperatures (*e.g.*, > 30 C) and low humidity (*e.g.*, < 30%) may also reduce potential longevity of viable pollen. Conversely, frequent moderate or gusty winds from the same direction during pollination will increase the potential magnitude and distance of PMGF (Beckie et al., 2016). Similarly, PMGF among weed populations will be greater for abundant species found in a high percentage of fields (and area within a field) in a region compared with rare species with a similar outcrossing rate. Furthermore, PMGF among weed populations is greater in fallow fields or bareground ruderal (non-cropped disturbed) areas than cropped fields due to the crop canopy acting as a physical barrier to pollen movement (Murray et al., 2002).

Seed dispersal has the potential to impact HR gene movement on a much larger scale than pollen flow (Fig. 1). Whereas PMGF is important in short distance HR gene dispersal (Bagavathiannan and Norsworthy, 2014), the majority of gene flow in weed populations at long distances is probably due to seed movement (Jasieniuk et al., 1996; Diggle and Neve, 2001). Nevertheless, long-distance pollen movement of HR alleles in allogamous wind-pollinated weed species (often grasses) has been reported (Busi et al., 2008; Délye et al., 2010). Wind dispersal of weed species having light-weight seeds, such as members of the Asteraceae, *Lactuca serriola* L. (prickly lettuce) and *Conyza canadensis* L. Cronq. (horseweed or Canada fleabane), can spread herbicide resistance rapidly and widely (Thill and Mallory-Smith, 1997; Shields et al., 2006; Okada et al., 2013). However, movement of HR seed among fields or regionally via equipment (especially combine harvesters), manure, commercial seed stocks, feed, crop residues/plant by-products, or irrigation water can be greater (100 s of kilometers) than natural seed dispersal as documented in a number of studies (*e.g.*, Stephenson et al., 1990; Eberlein et al., 1992; Anderson et al., 1996; Norsworthy et al., 2009; Aper et al., 2012; Tafoya-Razo et al., 2017). Many weed species have no specialized features or mechanisms for natural seed dispersal and therefore rely upon anthropogenic (human-mediated) modes of spread (Benvenuti, 2007).

When examining HR gene (seed, pollen, vegetative propagule) movement within and among weed populations, what is the relative importance of, and factors or conditions that promote high rates of gene

Table 1

Examples of empirical studies on wind-vectored pollen flow of herbicide resistance (HR) alleles in weed populations (*: denotes high risk; A = adjacent; ED₅₀, ED₉₀: denotes predicted distance for 50 and 90% reduction in outcrossing frequency, respectively).

Weed	HR marker	Outcrossing	Distance	Distance measured	ED ₅₀	ED ₉₀	Reference
		(%)	(m)	(m)	(m)		
<i>Amaranthus palmeri</i> S. Watson*	Glyphosate	55	A				Sosnoskie et al. (2012)
		20	300	300	–	–	
<i>Amaranthus tuberculatus</i> L.*	Glyphosate	0.46	A				Sarangi et al. (2017)
		0.07	50	50	1.3	39.4	
<i>Ambrosia trifida</i> L.	Glyphosate	0.5	A				Ganie and Jhala (2017)
		0.04	50	50	2.0	33.1	
<i>Avena fatua</i> L.	ACCcase inhibitor	5.2	A				Murray et al. (2002)
		0.09	0.6	0.6	–	–	
<i>Bassia scoparia</i> L. Schrad.*	ALS inhibitor	13.1	A				Stallings et al. (1995b)
		1.4	29.0	29	–	–	
		6.4	A				Beckie et al. (2016)
		0.25	96	96	3.3	13.9	
<i>Echinochloa crus-galli</i> (L.) Beauv.	Auxin	12.5	A				Bagavathiannan and Norsworthy (2014)
		0.01	50	50	0.2	0.9	
<i>Helianthus annuus</i> L.	ALS inhibitor	20	5.5				Marshall et al. (2001)
		0.7	30	30	–	–	
<i>Hordeum leporinum</i> Link.	Paraquat	0.06-0.15	0.12	0.12	–	–	Hidayat et al. (2006)
<i>Lolium perenne</i> ssp. <i>multiflorum</i> *	ACCcase inhibitor	1.0	6.8				Maxwell (1992)
<i>Lolium rigidum</i> Gaud.*	ACCcase inhibitor	–	10				Hawthorn-Jackson et al. (2003)
	ALS inhibitor	–	3,000	3,000	–	–	Busi et al. (2008)
		7.1	A				Loureiro et al. (2016)
		2.5	25	25	16.7	–	
<i>Setaria faberi</i> Herrm.	ACCcase inhibitor	0.24-0.73	0.36	0.36	–	–	Volenberg and Stoltenberg (2002)

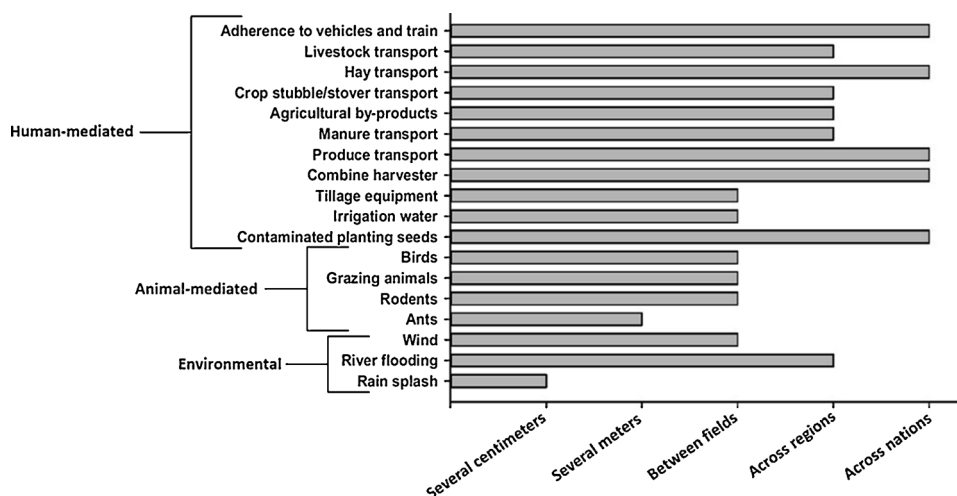


Fig. 1. Potential distances of seed-mediated spread of herbicide resistance (adapted from Bagavathiannan et al., 2016).

flow vs. long-distance gene flow? Clearly, high rates of HR weed gene flow are spatially and temporally restricted, and typically measured within field borders (Jasieniuk et al., 1996). It is facilitated in weed species that have efficient gene dissemination and high incidence of HR alleles in abundant populations that occur in a high percentage of fields in an agroecoregion. Characteristics of species with efficient HR gene dispersal would include wind-pollinated, high longevity of viable pollen, and high fecundity with seeds adapted for natural dispersal (e.g., seed shatter before crop maturity, small light-weight seeds easily dispersed by wind, specialized seed dispersal structures such as pappus) or via anthropogenic vectors (e.g., difficult-to-remove contaminant in crop seed or feed; within-field spread by tillage or harvest equipment) (Darmency, 1996; Lewellyn and Allen, 2006; Benvenuti, 2007). As described previously, long-distance movement of HR weed seeds is generally more probable and prevalent (particularly anthropogenic vectors) than that of PMGF of HR alleles. Whereas PMGF declines exponentially with increasing distance from the pollen donor, seed dispersal patterns are often stochastic and less predictable (Dauer et al., 2007). However, abundant HR weed populations across a region in sufficiently close proximity to each other can act as a bridge, enabling relatively low-level, long-distance PMGF of HR alleles (Busi et al., 2008).

Incidence of HR weeds in a region is often attributed to independent evolution; the role or contribution of HR allele movement via pollen, seeds and/or vegetative propagules is often under-estimated and under-appreciated (Davis and Frisvold, 2017). Once a new HR weed biotype has been confirmed in a county or municipality, how often have we been surprised at how fast the biotype is suspected or confirmed at multiple sites within that county/municipality, adjacent counties/municipalities, or adjacent states or provinces over a few months or years? In genotypic studies of HR weed populations, the contribution of gene flow to incidence of resistance is frequently similar or greater than that of independent evolution (e.g., Délye et al., 2010; Küpper et al., 2018; Martin et al., 2018; Molin et al., 2018). Simulation models have consistently predicted that even with low rates of gene flow, frequent and widespread applications of highly effective herbicides (e.g., acetolactate synthase (ALS) inhibitors, glyphosate) provide connective high-fitness habitats across the landscape that facilitate a rapid increase in the frequency and movement of an HR trait within and among populations (Brûlé-Babel et al., 2006; Dauer et al., 2009). Such habitats, characterized by minimal heterogeneity but high selection intensity due to frequent herbicide 'on' vs. 'off' exposure periods, strongly favour the fitness of HR propagules at great disadvantage of HS individuals (Gressel and Segel, 1982).

Direct evidence of long-distance HR gene (seed and pollen)

movement is becoming more obtainable and available with continuing advances in molecular weed science, with the increasing focus and development of weed genomics to study the evolution of herbicide resistance (Basu et al., 2004; Ravet et al., 2018). Four epidemiological studies (among others) in different regions of the world eloquently quantified long-distance HR gene flow using HR molecular markers. Across an 8,800-km² (880,000 ha) area of Côte d'Or, France, extensive, recurrent HR gene (acetyl-CoA carboxylase or ACCase marker) movement attributed to pollen flow in the allogamous wind-pollinated grass, *Alopecurus myosuroides* Huds. (blackgrass), was measured over a 4-year period to a maximum distance of 9 km (Délye et al., 2010). *A. myosuroides* populations in organic fields surveyed within the region had a high frequency (75% of plants) of ACCase-inhibitor resistance due to massive PMGF. Using 10 microsatellite loci, long distance (up to 9.6 km) PMGF in *Beta vulgaris* L. (weedy beet) in a 60 km² (6000 ha) area of France was documented; a significant proportion of mating events over a growing season occurred between individuals located several kilometers apart (Fénart et al., 2007). Across a 360 km² (36,000 ha) region of South Australia, ALS gene movement via wind-blown seeds of *L. serriola* between 1999 and 2004 was documented up to 43 km (Lu et al., 2007). In that study, many unsprayed roadside populations were ALS inhibitor-resistant, due to seed dispersal from crop fields or spillage during grain transportation. In north-western Mexico, movement of ACCase inhibitor-resistant *Avena fatua* L. (wild oat) was measured up to 1000 km using ACCase and microsatellite markers; this regional movement was attributed to contaminated wheat seedlots (Tafoya-Razo et al., 2016). Given the results of the genotypic studies involving natural dispersal of HR alleles, it should not be surprising how far and how fast HR alleles can move via anthropogenic vectors, such as contaminated seed or feed.

In the following section, we outline three case studies of weed species that have demonstrated great propensity for HR gene flow: *B. scoparia* in western North America, *Amaranthus palmeri* S. Watson (Palmer amaranth) in the United States (U.S.), and *Lolium rigidum* Gaud. (annual or rigid ryegrass) in Australia. These three species share three common features: (1) a top troublesome and economically damaging weed in their respective jurisdictions; (2) high incidence of multiple resistance in populations; and (3) rapid expansion of resistance incidence across jurisdictions in a short period of time.

2. Case studies

2.1. *Bassia scoparia*

Bassia scoparia is a C₄ annual weed native to Eurasia and introduced

to the Americas in the mid- to late 1800s as an ornamental plant (reviewed in Friesen et al., 2009). This species is an abundant and troublesome weed in cropping systems and ruderal areas in arid regions of western North America, and has expanded northward in the Northern Great Plains of Canada as well as southward in the High Plains of Texas, U.S. during the past 50 years (Forcella, 1985; Beckie et al., 2002). The competitiveness and persistence of *B. scoparia* in cropland and ruderal areas are attributed to its ability to germinate at cool soil temperatures and emerge early in the growing season, grow rapidly, tolerate heat, drought, and salinity, exert allelopathic effects on neighbouring species, and evolve resistance to multiple herbicide sites of action (SOA) (Friesen et al., 2009).

Herbicidal control of *B. scoparia* has been compromised by the widespread evolution of multiple herbicide resistance in this species, which directly promoted its persistence and spread. Since the mid-2000s, most populations are resistant to ALS inhibitors, as confirmed by surveys and random testing (Varanasi et al., 2015; Beckie et al., 2019a). Thus, areawide incidence of herbicide resistance in this species has progressed rapidly within 20 years since first reported in the late 1980s (Heap, 2019).

Occurrence of resistance to glyphosate or synthetic auxin herbicides in *B. scoparia* populations across the western Great Plains has similarly increased rapidly over the past decade. Glyphosate-resistant *B. scoparia* was first reported in Kansas, U.S. in 2007, and is now listed as occurring in 11 U.S. states and three Canadian provinces (Heap, 2019). In Canada, GR *B. scoparia* was first confirmed in three close-proximity chemical fallow fields in one Alberta county in 2011 (Beckie et al., 2013). A random survey of 309 *B. scoparia* populations across southern Alberta (80,000 km²) the following year found that 5% of populations in three counties were resistant to glyphosate, but none to dicamba, an auxinic herbicide (Hall et al., 2014). Five years later, a second random survey of 305 *B. scoparia* populations in the same region found that 50% of populations in 15 counties were resistant to glyphosate and 18% to dicamba (nine counties) (Beckie et al., 2019a). Moreover, 10% of the populations in the 2017 survey were resistant to herbicides of three different SOA: ALS inhibitors, glycine, and synthetic auxins. Therefore, the effectiveness of glyphosate to control the species has been compromised and we will soon lose another major herbicide SOA, the synthetic auxins. There are no remaining in-crop herbicide options to control triple-HR *B. scoparia* in mustard (*Brassica juncea* L. or *Sinapis alba* L.), field pea (*Pisum sativum* L.), or lentil (*Lens culinaris* Medik.) crops.

Inter-population gene flow of HR alleles is directly responsible for the rapid areawide expansion of HR *B. scoparia*. Although populations have been found to have higher than expected levels of homozygosity (Martin et al., 2018), this wind-pollinated species shows moderate levels of PMGF (Table 1). Rate of PMGF from GR to non-GR *B. scoparia* was 0.25% at 96 m, the farthest distance tested in the study; efficient seed dispersal (tumbling mechanism) (Fig. 2) aids both short- and long-distance spread of this species (Beckie et al., 2016). The tumbling mechanism is an efficient and effective adaptation for the dispersal of HR weed seeds by wind over long distances (Stallings et al., 1995a, b). With an average *B. scoparia* plant with tumbleweed architecture containing 100,000 viable, non-dormant seeds and able to traverse a kilometer in ca. 5 min dropping 90% of its seeds (Beckie et al., 2016), the potential for rapid mass seed dispersal across a region is enormous. We have learned through experience that once herbicide resistance (e.g., ALS inhibitor) evolves in a field population of *B. scoparia*, the regional spread of HR alleles via both seed and pollen is extremely rapid. In a regional study conducted across western Canada spanning 1000 km, it was concluded that GR *B. scoparia* populations with high or low enolpyruvylshikimate-3-phosphate synthase (EPSPS) copy number showed little genetic differentiation (no correlation between genetic and geographic distance, i.e., high connectivity) and maintained similar genetic diversity as a result of high rates of gene flow (Fig. 3; Martin et al., 2018). The authors have concluded that any HR alleles will be

able to spread quickly throughout all populations and that the spread of these alleles appears unlikely to reduce genetic variation. The tremendous magnitude of recurrent, unrelenting gene flow of HR alleles will result in frequent, widespread multiple-HR trait stacking in individuals and populations. Moreover, a warming climate is expected to promote population abundance and range expansion and further exacerbate the problem in agricultural systems (Beckie et al., 2002).

The weakness in the life cycle of *B. scoparia* is its short seed bank longevity (< 1 year), which can be exploited to reduce population abundance (Beckie et al., 2018). However, this exploitation is conditional upon mitigating HR seed immigration into fields and seed bank replenishment from weed escapes. Glyphosate-resistant *B. scoparia* has a detectable fitness penalty, manifested by delayed germination, emergence and flowering, as well as reduced competitiveness and fecundity (Martin et al., 2017; Beckie et al., 2018). Therefore, crop seeding and preemergence herbicide application dates may be altered to preferentially control this biotype. With wind-vectored pollination and high level HR gene flow, reintroducing herbicide susceptibility in the landscape using individuals with altered CRISPR-Cas9 gene drive (reviewed in Neve, 2018) for susceptibility may also spread easily and quickly through populations. This potential future strategy may be particularly effective if the selection pressure for resistance evolution has been significantly reduced because control with most herbicides is ineffective.

2.2. *Amaranthus palmeri*

Amaranthus palmeri is a C₄ summer annual forb native to the Sonoran Desert region of northern Mexico and southwestern U.S. (reviewed in Ward et al., 2013). In just over 20 years, it has become the most widespread and troublesome weed in the southern U.S. This species is now found throughout the continental U.S., except in some northern states (e.g., Washington State, Maine; USDA, 2018). Similar to *B. scoparia*, its abundance, persistence, and spread have been aided by its efficient gene dissemination, rapid growth rate, high fecundity, genetic diversity, ability to tolerate adverse environmental conditions, and propensity for evolving herbicide resistance. Moreover, a warming climate is similarly expected to expand its range northward and exacerbate the challenges of managing this species (Kistner and Hatfield, 2018).

The rise of *A. palmeri* as a major, economically-important weed is relatively recent. By 1995, it was ranked as the most troublesome weed of cotton (*Gossypium hirsutum* L.) in North and South Carolina, U.S.; by 2009, it was ranked as the most troublesome cotton weed in the southern U.S., and among the most troublesome weeds of soybean (*Glycine max* L. Merr.) and maize (*Zea mays* L.) (Webster and Nichols, 2012). Since the evolution of GR biotypes beginning in 2004 in Georgia, U.S. (Culpepper et al., 2006), control of this species has become much more expensive and difficult.

As a dioecious species, *A. palmeri* is an obligate outcrosser (Franssen et al., 2001). It is wind-pollinated, with male plants producing copious amounts of pollen. A PMGF study showed high levels of outcrossing (20%) at 300 m (Sosnoskie et al., 2012; Table 1). Therefore, the contribution of PMGF to HR gene flow in this species is greater than that of *B. scoparia*.

Female plants are prolific seed producers, even when late-emerging or grown under competition (Ward et al., 2013). Under crop competition, seed return levels ranging from < 100,000 to 500,000 m⁻² have been recorded (e.g., Jha et al., 2008). Seeds of *A. palmeri* are small (1 to 2 mm), primarily gravity-dispersed, but can also be spread naturally by water, birds (e.g., ducks) and mammals. The small seed size facilitates movement by strong winds over long distances. For example, a hurricane introduced millions of *A. palmeri* seeds into a previously uninfested area in South Texas, U.S. (Menges, 1987). Substantial anthropogenic movement of weed seeds occur via agricultural machinery and use of contaminated amendments such as compost, manure or gin trash

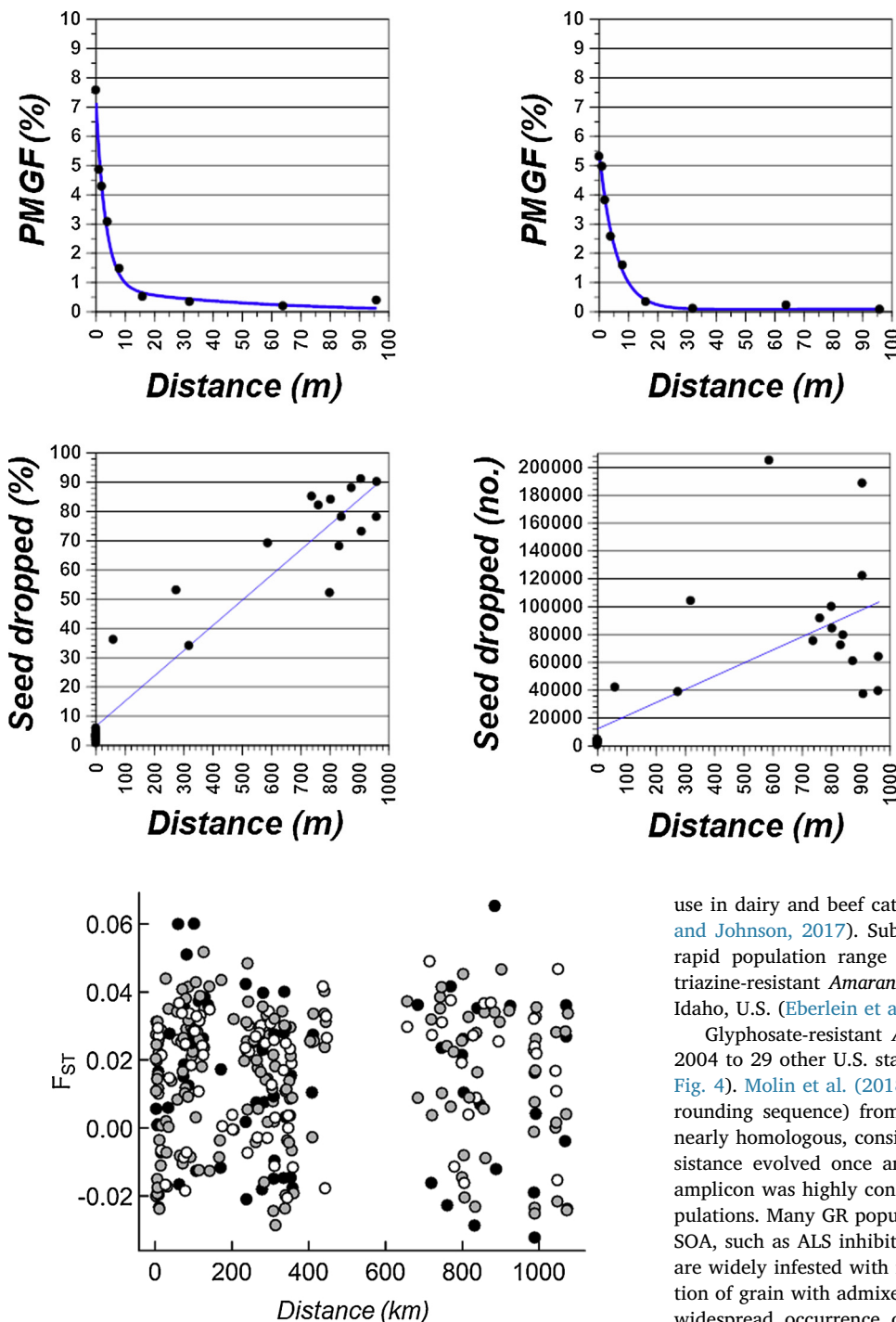


Fig. 2. Pollen-mediated gene flow (PMGF) (% outcrossing) from glyphosate-resistant (GR) *Bassia scoparia* pollen donor to varying distances of non-GR receptor plants at a field site at Saskatoon, Saskatchewan, Canada in 2014 (top left) and 2015 (top right). *B. scoparia* tumbleweed seed dropped, expressed as a percentage (bottom left) or number (bottom right) with increasing distance, at a field site at Lethbridge, Alberta, Canada (adapted from Beckie et al., 2016).

Fig. 3. Lack of correlation between geographic distance and pairwise F_{ST} (measure of genetic differentiation) among 26 populations of *Bassia scoparia* populations in western Canada (Mantel test; $r^2 = -0.02$; $p = 0.57$). Pairings between low enolpyruvylshikimate-3-phosphate synthase (EPSPS) populations are shown in white, pairs between high EPSPS populations are shown in black, and pairs between low and high EPSPS populations are shown in grey.

(e.g., Norsworthy et al., 2009; Bagavathiannan et al., 2016). In 2016, unintentional contamination in some native seed mixes purchased by growers participating in conservation programs helped increase range expansion of this species significantly (Haines et al., 2017). Additionally, *A. palmeri* seed moved from the southern to northern U.S. states (e.g., Michigan) via harvesting equipment as well as a contaminant in hay and cotton seed and hulls purchased from the south for

use in dairy and beef cattle rations (Norsworthy et al., 2012; Jeschke and Johnson, 2017). Subsequent spreading of cattle manure allowed rapid population range expansion, similar to that documented for triazine-resistant *Amaranthus powellii* S. Watson (Powell amaranth) in Idaho, U.S. (Eberlein et al., 1992).

Glyphosate-resistant *A. palmeri* has now spread from Georgia in 2004 to 29 other U.S. states, up to the Canadian border (Heap, 2019; Fig. 4). Molin et al. (2018) found that EPSPS cassettes (gene plus surrounding sequence) from distant GR populations of *A. palmeri* were nearly homologous, consistent with the hypothesis that glyphosate resistance evolved once and then rapidly spread across the U.S. The amplicon was highly conserved among the investigated *A. palmeri* populations. Many GR populations are resistant to herbicides of different SOA, such as ALS inhibitors (Heap, 2019). Even roadside populations are widely infested with multiple-resistant biotypes due to transportation of grain with admixed weed seeds. For example, surveys revealed widespread occurrence of multiple resistance (glyphosate plus pyriithiobac, an ALS inhibitor) in roadside *A. palmeri* populations in eastern Arkansas, U.S. (Bagavathiannan and Norsworthy, 2016). These ruderal populations in roadside habitats serve as conduits for further inter-population spread of HR alleles. The introduction of HR *A. palmeri* into Argentina in 2012 and Brazil in 2015 highlights the global impact of seed-mediated gene movement (Carvalho et al., 2015; Berger et al., 2016; Küpper et al., 2017). As with *B. scoparia*, the rapid increase in occurrence of multiple-HR populations has substantially restricted herbicide options in some major crops such as cotton and soybean.

Managing the soil seed bank by preventing replenishment from weed escapes is a promising strategy for reducing population abundance. The potential efficacy of harvest weed seed control (HWSC) of *A. palmeri* is excellent (Norsworthy et al., 2016), as most seeds (99%) are retained at soybean crop maturity and can be collected by the combine harvester (Schwartz et al., 2016). Although not as short-lived in the soil

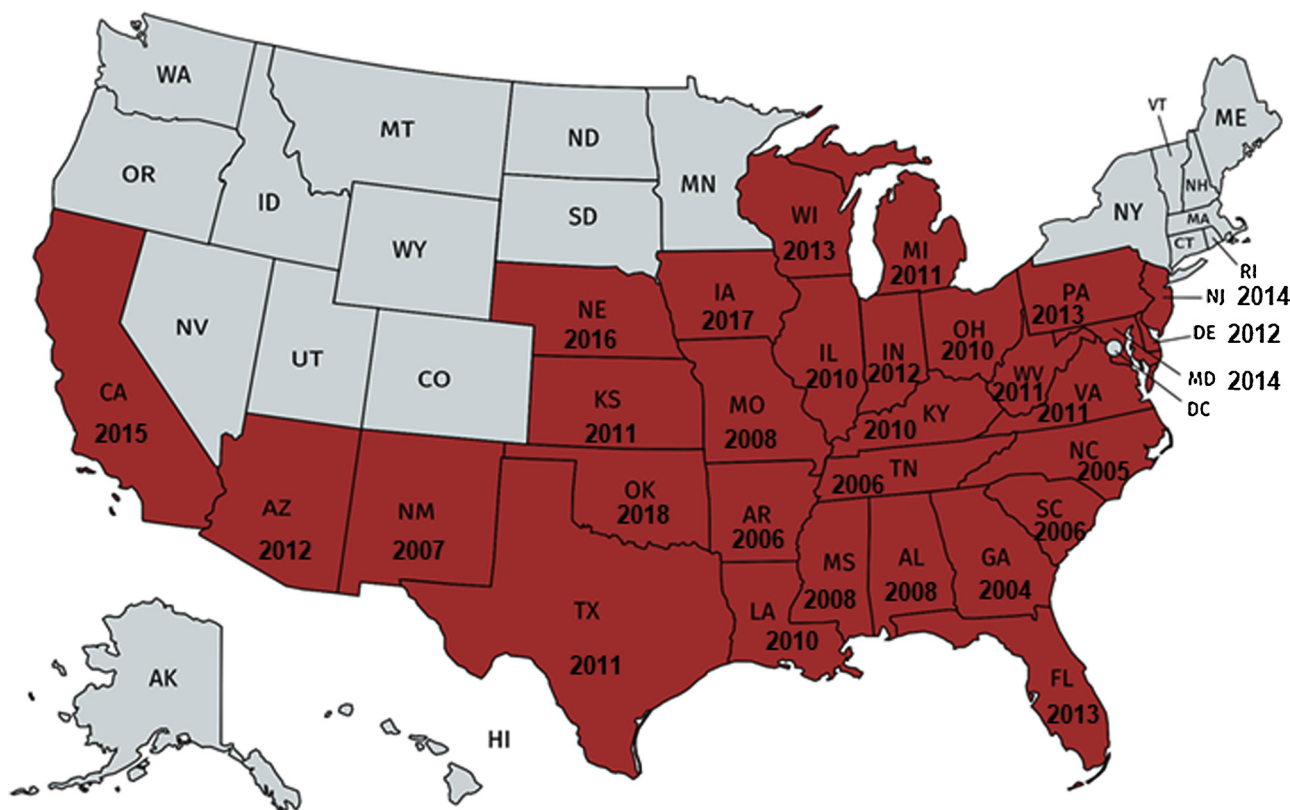


Fig. 5; Busi et al., 2008). As noted previously, recurrent long-distance PMGF is probable in allogamous, wind-pollinated grass weed species.

In another study in Western Australia, Busi et al. (2011) confirmed that gene flow could cause a substantial increase in the frequency of HR genes of *L. rigidum* plants infesting commercial organic fields located at considerable distance (up to 2.5 km) from neighbouring conventional fields. In both studies, an extensive source of HR alleles (i.e., multiplicative effect of frequency of HR alleles and weed population abundance) promoted long distance gene flow over time. Both studies concluded that the population dynamics of weed resistance evolution caused by gene flow vs. independent herbicide selection are complex, and depend upon several factors such as weed population demography, relative size of donor and receptor plant populations, and spatial heterogeneity (Neve et al., 2014).

As with a number of other HR weeds, regional or national anthropogenic HR *L. rigidum* weed seed movement via contaminated crop seed or livestock feed is a recurring problem (Michael et al., 2010). Moreover, internationally-traded grain commodities such as wheat (*Triticum aestivum* L.) can be contaminated with HR weeds, including *L. rigidum* (Shimono et al., 2010). Thus, in addition to pervasive independent evolution at the field level, the high levels of gene flow via pollen and seed can quickly spread new HR alleles across a shire (administrative district), to neighbouring shires, to neighbouring states, even other countries, as previously described for cross-border movement of *A. palmeri* and *B. scoparia*. In Australia, spread of HR alleles from one farm to another was viewed as relatively unimportant because of widespread perception of independent, concurrent evolution through herbicide selection occurring on neighbouring farms, which are amongst the largest in the world (Pannell et al., 2016). However, those authors cautioned that the potential contribution of inter-farm GR gene flow to the areawide spread of GR weed populations will likely be greater than that of previous HR alleles due to the widespread and frequent use of glyphosate in fields and adjacent ruderal areas (high-fitness habitats as described previously).

The dual nature of *L. rigidum*, an obligate allogamous and competitive crop weed species as well as a valuable forage pasture, has led researchers to investigate strategies to exploit PMGF to reduce the impact (frequency) of HR alleles or undesirable evolved traits. For example, it was shown that PMGF in admixtures of tetraploid and diploid varieties of HS *Lolium* had the potential to reduce the frequency of herbicide resistance (Ferris, 2007) by producing triploid seeds with markedly reduced germination (Griffiths et al., 1971). Research is warranted to improve the success rate of reciprocal pollination between diploid and tetraploid varieties, which remains a major hurdle for this strategy to be adopted under field conditions. Preliminary work on pollination between early- and late-flowering *L. rigidum* plants shows that F₁ hybrids possess intermediate phenotypes, and suggests exploitation of PMGF to avoid potential 'creeping' resistance to HWSC at harvest (R. Busi, unpublished data). Studies are also investigating the potential for CRISPR-Cas9-based gene drive systems for reversing HR *L. rigidum* populations to their original condition of wild-types (H. Han, personal communication).

As recommended for *B. scoparia* and *A. palmeri*, mitigation of gene flow in *L. rigidum* requires attention to reducing HR weed population abundance in fields through diverse management practices, such as effective preemergence herbicides, competitive crops, glyphosate or paraquat application during weed seed development (crop/spray topping), and HWSC. Because weed seed retention at harvest time is high, HWSC practices are very effective. Annual usage of HWSC in Western Australian farms from 2002 to 2011 resulted in *L. rigidum* plant densities declining from an average of 35 plants m⁻² to 0.5 m⁻², a level that was consistently maintained (Walsh et al., 2013). Similar to *B. scoparia* and *A. palmeri*, populations in ruderal areas also need to be controlled before flowering to mitigate seed bank return and HR gene flow across the landscape.

3. Conclusions and future outlook

As the incidence of weed resistance increases in a region, HR allele movement along with independent evolution through herbicide selection will increasingly influence such occurrences. The difficulty or complexity in determining the relative contribution of independent evolution vs. gene flow in the rapid regional expansion of HR weeds, such as *A. palmeri*, reinforces the need for research in evolutionary biology and ecology to achieve effective weed management (Neve et al., 2014). In hindsight, despite the difficulty of mitigating gene flow among weed populations, implementation of timely, rigorous containment or biosecurity measures at the earliest stages of evolution ('invasion') of highly mobile GR or multiple-HR weed biotypes may have slowed their rate of areawide expansion. Their categorization as noxious weeds, even though HR plants are visually indistinguishable from HS plants, would have elevated the urgency and rigour of mitigation measures.

Despite widespread multiple resistance in many weed species with efficient gene dissemination, adherence to weed sanitation (hygiene) practices to mitigate cross-border HR gene dispersal is critical to prolonging the efficacy of current and future herbicides. Weed sanitation, which includes HWSC, are included in the top best management practices for HR weed management (Norsworthy et al., 2012; Beckie and Harker, 2017). A number of studies have shown that management practices that limit the spread of HR alleles can slow the occurrence of herbicide resistance. For example, growers with the greatest adoption of weed sanitation practices were less likely to have HR weeds on their farm than those with low adoption (Légère et al., 2000). In general, diverse integrated management practices that keep weed population densities low in cropland will help mitigate gene flow of HR alleles. In particular, a weed-competitive crop significantly reduces HR gene flow in weed populations (Murray et al., 2002).

Across Australian grain-growing regions, HR gene proliferation and spread in *L. rigidum* have been successfully managed and profitable crop production sustained by a concerted, long-term focus on minimizing weed seed set and seed bank densities (Pannell et al., 2016; Walsh et al., 2013, 2018). A recent study conducted across Western Australian farms (average farm size ca. 4000 ha) demonstrated that hand-weeding *Raphanus raphanistrum* L. (wild radish) escapes at low population densities to stop seed set was economically cost-effective (P. Newman, unpublished data).

In the weed science community over the past decade, there have been a chorus of calls for a coordinated community or regional response to combat HR allele mobility (i.e., areawide pest management) to avoid the 'tragedy of the commons' (Llewellyn and Allen, 2006; Busi et al., 2008; Dauer et al., 2009; Sosnoskie et al., 2012; Okada et al., 2013; Délye et al., 2016; Sarangi et al., 2017; Evans et al., 2018; Bagavathiannan et al., 2019, among others). Thus, we are indeed slowly starting to appreciate and comprehend the magnitude and consequence of HR gene flow in those weed species that are capable of efficient short- and long-distance dispersal by both seed (natural and anthropogenic vectors) and pollen. As outlined above, *B. scoparia*, *A. palmeri*, and *L. rigidum* are three important species with such capability.

There are numerous socio-economic challenges to achieving the goal of reducing inter-field and inter-farm weed mobility, as outlined in Norsworthy et al. (2012) and others. Perhaps the biggest challenge is controlling weed populations in ruderal areas throughout the agricultural landscape, because they are likely not the responsibility of the grower or land manager. For example, the collective failure to control widespread and abundant HR *B. scoparia* populations across the western Great Plains is largely because the problem is so daunting given the vast infestation area, coordination logistics are complex because of the numerous stakeholders involved, and there are no regulations or financial incentives for action. As consistently observed worldwide, management of HR weed populations is reactive, not proactive (Beckie, 2006). When there are limited herbicides left to control populations of multiple-HR

weed species, as is now becoming the reality with *B. scoparia*, *A. palmeri*, and *L. rigidum*, the appeal of a coordinated community or regional response will likely become stronger because of changed economic circumstances. Abundance and spread of mobile HR weeds, such as described herein, would decline if they were prioritized for control (similar to noxious-class weeds) by local and state/provincial governments in field margins, roadsides, ditches, railway rights-of-way, and other ruderal areas by mowing or other methods.

Greater awareness through enhanced educational and extension efforts and greater adoption through private- and public-sector financial incentives should be among the current and future priorities for sustainable management of mobile HR weeds. Coexistence measures for transgenic crops implemented over the past 20 years in many jurisdictions globally have successfully limited transgene dispersal (Beckie and Hall, 2015), showing that it is possible to similarly restrict HR gene movement in weed populations. Some of these proven public- and private-sector coexistence measures can and should be adapted and utilized to mitigate HR gene movement in weeds.

With input and support of relevant stakeholders – growers, land managers, county or municipal administrators, weed inspectors, agronomists, consultants, agrichemical industry representatives, weed extension specialists, etc. – and careful planning, effective cooperative management principles and structures can be implemented with demonstrable success to mitigate HR allele spread (Ervin and Frisvold, 2016; Bagavathiannan et al., 2019). Using *A. tuberculatus* as a case study, demographic modeling predicted that herbicide resistance evolution and spread markedly slowed with collective vs. individual weed management efforts (Evans et al., 2018). Government resources and incentives are needed to encourage and support community efforts in the management of HR weeds with high gene flow potential (e.g., cover crops, weed sanitation), similar to those offered for environmental protection (Beckie et al., 2019b).

Areawide HR weed management is challenging but possible. For example, a successful ‘Zero Tolerance’ program for *A. palmeri* in the southern U.S., which was initially established as a pilot project in two counties in Arkansas, involves collective efforts by growers, crop consultants, county agents, extension personnel, and policy-makers (Barber et al., 2015). All participation is voluntary and no regulations are imposed, but university personnel monitor the areas routinely and encourage compliance. The program has led to a rapid decline in *A. palmeri* population abundance within the first few years of implementation (Smith et al., 2015; Grant, 2017). Many row-crop growers across the southern U.S. eradicate *A. palmeri* escapes by hand-weeding, the cost of which declines after successive years because of reduced seed bank size (Smith et al., 2015; Lindsay et al., 2017). Ruderal populations are also managed in the program. Although this recommended zero-tolerance strategy for management of GR *A. palmeri* may have been implemented too late to reduce inter-farm GR allele spread in the southern U.S., it lays the foundation for mitigation of landscape mobility of this trait in other regions or future HR genes when new herbicide SOAs are introduced.

Solutions to address these public good or common pool resource issues or challenges often involve a subset of design principles (Ostrom, 1990). Using herbicide susceptibility as a case study, it was concluded that the most relevant and important design principle was clearly identifying and engaging the stakeholders (contributors) and to a lesser extent, defining the boundaries of the HS weed resource (usually a jurisdictional boundary); additional design principles relevant to addressing this issue were contributors having strong working relationships or shared values, agreeing to a shared goal, and pooling resources to support weakest links (Bagavathiannan et al., 2019). The Zero Tolerance program described above exhibit these design principles. Overall, collective actions were facilitated by workshops and field tours where stakeholders became aware of *A. palmeri* HR gene mobility and economic impact, committed to population management across the landscape, and viewed and shared results after successive growing

seasons (Bagavathiannan et al., 2019). Participants attending HR weed management workshops held across the U.S. in 2016 and 2017 stressed the need for effective communication and coordination among community stakeholders (Schroeder et al., 2018).

Strategies, tactics, and practices for areawide management of HR weeds that have high mobility across the landscape can be informed by lessons learned from government-led programs for watershed management or areawide control of invasive and noxious weeds or insects (Ervin and Frisvold, 2016). For example, there is a long history (since the mid-1970s) of successful areawide programs in the U.S. to control insect pests in agronomic crops, such as boll weevil (*Anthonomus grandis*), pink bollworm (*Pectinophora gossypiella*), corn rootworm (*Diabrotica* spp.), and codling moth (*Cydia pomonella*). Program features included pest scouting, target dates for field operations, and recommended control measures. Community-wide actions reduced pest distribution, abundance, and insecticide use, while increasing crop yields and quality (Chu et al., 1996; Calkins and Faust, 2003; Chandler, 2003). Of greater relevance to areawide HR weed management than specific practices were the development of formal frameworks, structures, networks, and federal/state governmental technical and financial support to encourage high participatory, collaborative areawide pest control (detailed in Ervin and Frisvold, 2016). These programs were often initiated because of the increasing adverse economic impact of these insect pests on crop yield and quality as well as pesticide resistance (Chandler, 2003).

The weed HR gene mobility challenge needs to be accepted before it can be addressed. With current and future loss of herbicides to control the three mobile weed species detailed herein and others exhibiting widespread resistance in global agronomic crops, we believe the changing agronomic and economic conditions will increasingly favour areawide HR weed management programs. Public policy-makers typically prioritize problems that cause significant immediate economic or environmental harm or are a threat to the public good. Highly-mobile HR weeds need to be considered as an economic and environmental threat to sustainable agroecosystems and food security at a regional or national level. Increasing focus of biosecurity measures to mitigate cross-border (domestic or international) movement of undesirable pests (weeds, insects, pathogens) (Anonymous, 2019) must consider HR weed propagules. Presence of HR weed seeds in imported grain shipments have the potential to become a non-tariff international trade barrier.

However, justification for a community or regional response to mitigate HR weed mobility first requires science-based evidence. Areawide programs for HR weed management need to be economically cost-effective for implementation to be feasible. Therefore, economic studies are of greatest priority to estimate the costs and benefits of any areawide control program (Gill et al., 2018), using case studies as described previously. Economic studies need to incorporate the development and validation of bioeconomic models, using scenarios comparing individual and collective HR weed management. For example, model simulations over a 20-year period found that collective actions to manage the highly mobile weed biotype, GR *C. canadensis*, in U.S. corn/soybean cropping systems optimized profits for individual growers after only the second year (Livingston et al., 2016). Studies have shown that access to information on forecast economic benefits (e.g., reduction in populations and crop losses) vs. costs, as well as incentives to act on that information, are primary factors influencing the participation of growers or land managers in areawide weed management programs (Coutts et al., 2013). Collective actions are also more likely if recommended pest management practices are not too complex and relatively easy to integrate with existing farming systems (Keenan and Burgener, 2008).

Internationally, catalyzing transdisciplinary research is urgently needed with the ultimate goal of building a scientific framework that utilizes dynamic integrated socio-environmental (coupled human-natural) systems to understand and manage HR weeds with high mobility. Such an approach integrates biological and social science with

experiential knowledge from industry and government to innovate cross-sector/cross-scale collective approaches for HR weed management (Ervin et al., 2019). Key activities would include establishing the environmental and social science foundations for HR weed management, assuring congruence of environmental processes with social capacity and institutions (e.g., matching scale of social networks with that of ecological and biophysical components), and identifying and evaluating private and public governance systems that best incentivize human behaviours to sustain herbicide susceptibility, which includes monitoring, compliance, and adaptive management functions (D. Ervin and S. Graham, personal communications). This proposed approach has many challenges in design and implementation, but also potentially transformative for areawide HR weed management.

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