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Review

Cite this article: Kumar V, Jha P, Jugulam M, Yadav R, Stahlman PW (2019) Herbicide-Resistant Kochia (*Bassia scoparia*) in North America: A Review. Weed Sci 67:4–15. doi: 10.1017/wsc.2018.72

Received: 2 July 2018 Revised: 15 August 2018 Accepted: 28 August 2018

Associate Editor: Vijay Nandula, USDA-ARS

Key words:

ALS inhibitor; dicamba; glyphosate; integrated weed management; multiple herbicide resistance; PSII inhibitor; weed biology and ecology

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Herbicide-Resistant Kochia (*Bassia scoparia*) in North America: A Review

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Abstract

Kochia [Bassia scoparia (L.) A. J. Scott] is a problematic annual broadleaf weed species in the North American Great Plains. Bassia scoparia inherits unique biological characteristics that contribute to its propensity to evolve herbicide resistance. Evolution of glyphosate resistance in B. scoparia has become a serious threat to the major cropping systems and soil conservation practices in the region. Bassia scoparia populations with resistance to four different herbicide sites of action are a concern for growers. The widespread occurrence of multiple herbicide-resistant (HR) B. scoparia across the North American Great Plains has renewed research efforts to devise integrated weed management strategies beyond herbicide use. In this review, we aim to compile and document the growing body of literature on HR B. scoparia with emphasis on herbicide-resistance evolutionary dynamics, distribution, mechanisms of evolved resistance, agronomic impacts, and current/future weed management technologies. We focused on ecologically based, non-herbicidal strategies such as diverse crop rotations comprising winter cereals and perennial forages, enhanced crop competition, cover crops, harvest weed seed control (HWSC), and tillage to manage HR B. scoparia seedbanks. Remote sensing using hyperspectral imaging and other sensor-based technologies would be valuable for early detection and rapid response and site-specific herbicide resistance management. We propose research priorities based on an improved understanding of the biology, genetic diversity, and plasticity of this weed that will aid in preserving existing herbicide resources and designing sustainable, integrated HR B. scoparia mitigation plans.

Introduction

Kochia [Bassia scoparia (L.) A. J. Scott] is an invasive summer annual native to eastern and central Europe and western Asia (Ball et al. 2000; Friesen et al. 2009). Bassia scoparia is a monoecious diploid (2n = 18) that belongs to the "Chenopodiaceae" family. European immigrants first introduced this species as an ornamental plant to North America in the midto late 1800s (Friesen et al. 2009; Georgia 1914). By 2007, B. scoparia was widespread across several states in the United States and in Canadian provinces (Friesen et al. 2009; Meades et al. 2000; USDA-NRCS 2008). Infestation of B. scoparia is common in cultivated fields, gardens, roadsides, grasslands, ditch banks, pastures, and rangeland (Forcella 1985; Frankton and Mulligan 1987; Friesen et al. 2009).

Bassia scoparia exhibits unique biological characteristics, including C_4 growth habit, low innate seed dormancy (Dille et al. 2017; Friesen et al. 2009; Kumar and Jha 2017), low seed persistence in the soil (\leq 2 yr), early and rapid emergence, and high tolerance to abiotic stresses (Dille et al. 2017; Friesen et al. 2009; Kumar et al. 2018a; Schwinghamer and Van Acker 2008). Bassia scoparia produces protogynous flowers, ensuring a high level of outcrossing and a high genetic diversity within or among populations (Beckie et al. 2016; Mengistu and Messersmith 2002; Stallings et al. 1995).

In recent years, *B. scoparia* has become one of the most problematic weeds in croplands and non-croplands across the region (Eberlein and Fore 1984; Forcella 1985; Heap 2018; Wicks et al. 1994). *Bassia scoparia* at densities of 240 to 520 plants m⁻² reduced spring wheat (*Triticum aestivum* L.) grain yield by up to 60% (Friesen et al. 1991a, 1991b, 1991c). In another study, *B. scoparia* at densities of 14 plants m⁻² reduced wheat grain yield by 10% to 25% (Friesen et al. 1990a, 1990b, 1990c). The presence of *B. scoparia* at wheat harvest not only contaminates wheat grain, but also reduces the harvesting efficiency, because uncontrolled or late-emerging *B. scoparia* plants are normally green at wheat harvest. Furthermore, uncontrolled *B. scoparia* can potentially add more than 100,000 seeds m⁻² to the soil seedbank after wheat harvest (Kumar and Jha 2015d).

Sugar beet (Beta vulgaris L.) is among the least competitive crops to B. scoparia. Even at a low density of 0.2 to 0.5 plants m⁻¹ row, B. scoparia can reduce sugar beet root yields by 18% to 32% (Mesbah et al. 1994; Schweizer 1973). At a B. scoparia density of 3 plants m⁻¹ of row, sugar beet root yield was reduced by 78%. Weatherspoon and Schweizer (1971) reported up to a 95% reduction in sugar beet root yield with a season-long interference of B. scoparia. Season-long interference of B. scoparia at densities of 0.3, 1, 3, and 6 plants m⁻¹ of row reduced common sunflower (Helianthus annuus L.) achene yield by 7%, 10%, 20%, and 27%, respectively (Durgan et al. 1990). Up to 76% yield reductions in sunflower has been reported when B. scoparia plants emerged with sunflower (Lewis and Gulden 2014). Bassia scoparia interference in soybean [Glycine max (L.) Merr.], sorghum [Sorghum bicolor (L.) Moench ssp. bicolor], and corn (Zea mays L.) can reduce grain yields by 30%, 38%, and 40%, respectively (Waite et al. 2013; Wicks et al. 1993, 1994).

The problem is further exacerbated due to the widespread occurrence of B. scoparia populations with evolved resistance to several different herbicide sites of action. Since 1976, when the first case of B. scoparia resistance to atrazine (photosystem II [PSII] inhibitor) was reported, there has been a steady increase in the number of herbicide-resistance cases in B. scoparia (Heap 2018). Increasing reports of herbicide-resistant (HR) B. scoparia have renewed interests of academic weed scientists and industry in an improved understanding of the biology, ecology, and multitactic strategies to manage this weed. Several studies have recently been published on evolution of herbicide resistance and biochemical/physiological mechanisms of evolved resistance, ecological investigations of the life-history traits and fitness, and alternative strategies to manage HR B. scoparia. This article aims to document the current state of knowledge on HR B. scoparia that can serve as a resource for future research and extension needs to manage the problem.

Chronology and Distribution of HR Bassia scoparia

The first case of B. scoparia resistance to atrazine in the United States was documented in 1976 from cornfields in Kansas and along railroads in Idaho and Iowa (Heap 2018). Subsequently, resistance to atrazine was found along railroad rights-of-way from 11 additional states in the United States (Bandeen et al. 1982; Friesen et al. 2009). The first case of B. scoparia resistance to acetolactate synthase (ALS)-inhibiting herbicides was reported from a wheat field in Kansas in 1987, just 5 yr after the commercialization of this herbicide chemistry in wheat (Primiani et al. 1990; Saari et al. 1990). A field survey conducted in 1992 from cropland and non-cropland areas indicated that 46%, 55%, and 45% of B. scoparia samples from Colorado, Idaho, and Montana, respectively, were resistant to ALS inhibitors (Friesen et al. 2009). In Canada, B. scoparia populations resistant to ALS inhibitors were first reported in Manitoba (>10 field sites) and Saskatchewan (>50 field sites) in 1988 and from a wheat field in Alberta in 1989 (Heap 2018; Morrison and Devine 1994). The majority of B. scoparia populations resistant to ALS inhibitors in the Canadian prairies were from semiarid grassland fields (Beckie et al. 2001, 2008; Friesen et al. 2009). In a field survey conducted in southern Manitoba in 2004, 93 out of 112 B. scoparia samples were found resistant to ALS inhibitors (Friesen et al. 2009). Similarly, Beckie et al. (2011) reported ALS inhibitor-resistant B. scoparia in 85% of the fields surveyed in western Canada.

Multiple resistance to PSII and ALS inhibitors was first reported in *B. scoparia* populations along roadsides from Indiana and in wheat/corn from Illinois in 1995 (Chodova and Mikulka 2000; Foes et al. 1999).

The rapid spread of populations with resistance to PSII and ALS inhibitors increased the dependence on the use of auxinic herbicides, primarily dicamba and fluroxypyr, for B. scoparia control in wheat or corn grown in the Great Plains region. However, in 1995, populations resistant to dicamba and/or fluroxypyr were reported from wheat-chemical fallow fields in Montana and North Dakota (Cranston et al. 2001; Nandula and Manthey 2002). Among all HR traits in B. scoparia, the rate of spread of auxinic resistance has been the slowest (Jha et al. 2015a). Since 1995, dicamba-resistant (DR) B. scoparia has been reported from six states in the U.S. Great Plains and in the Mountain West, including Montana, Idaho, North Dakota, Nebraska, Colorado, and Kansas (Heap 2018). The discovery of B. scoparia populations with resistance to dicamba and fluroxypyr is a relatively new event in Canada, with reports from a few wheat production fields in Saskatchewan (H Beckie, personal communication). The auxinic-resistant B. scoparia populations from Canada were also resistant to ALS inhibitors, including thifensulfuron and tribenuron used in wheat (Heap 2018).

After the decline in the price of glyphosate, growers relied heavily on glyphosate for weed control in the fallow phase of winter wheat-fallow or winter wheat-sorghum-fallow rotations across the U.S. Great Plains (Fenster and Wicks 1982; Kumar et al. 2014). On an average, each fallow field received three to four applications of glyphosate per season (spring to summer) before winter wheat planting in the fall. This continuous use of glyphosate had selected B. scoparia populations with evolved resistance to glyphosate. The first confirmation of glyphosate-resistant (GR) B. scoparia was from fallow fields in western Kansas in 2007 (Godar et al. 2015; Heap 2018; Waite et al. 2013). Since then, GR B. scoparia has been confirmed in 10 U.S. states and 3 Canadian provinces (Beckie et al. 2013; Godar et al. 2015; Hall et al. 2014; Kumar et al. 2014; Waite et al. 2013; Wiersma et al. 2015). The majority of these GR populations originated in wheat-fallow systems. However, recent surveys from Montana, Wyoming, Colorado, Nebraska, Idaho, and Oregon indicate the occurrence of GR populations in GR corn-sugar beet rotations (Gaines et al. 2016; Kumar et al. 2018b). In Canada, GR B. scoparia was first documented in 2011 from cereal production fields in southern Alberta (Beckie et al. 2013; Hall et al. 2014). Furthermore, a majority of those GR B. scoparia populations were also resistant to ALS inhibitors (Hall et al. 2014; Kumar et al. 2015).

In Montana, random field surveys for HR B. scoparia conducted from 2013 to 2016 found 45 field sites with GR, 15 with DR, and 10 sites with the presence of GR and DR (multiply resistant) B. scoparia (PJ, unpublished data). More than 95% of those surveyed B. scoparia populations were also resistant to ALS inhibitors (PJ unpublished data). Similarly, multiyear (2011 to 2014) random field surveys conducted in eastern Colorado identified 86 sites with GR, 25 sites with DR, and 29 sites with GR plus DR B. scoparia populations (Westra 2016). Bassia scoparia populations with multiple resistance to glyphosate and dicamba have also been identified in western Kansas (Brachtenbach 2015). More recently, populations with cross-resistance to dicamba and fluroxypyr have been reported from wheat fields in Montana, Nebraska, and Kansas (Jha et al. 2015b; Kumar et al. 2018c; LeClere et al. 2018). Additionally, a B. scoparia population with multiple resistance to glyphosate, ALS inhibitors, PSII inhibitors,

and dicamba has recently been documented from a cornfield in Garden City, KS (Varanasi et al. 2015), indicating the widespread occurrence and severity of the problem.

Level of Herbicide Resistance in Bassia scoparia

Resistance to PSII Inhibitors

The level of resistance to PSII inhibitors was reported in *B. scoparia* accessions from North Dakota and Minnesota. The resistant populations exhibited 16-fold resistance to tebuthiuron and diuron but only up to 4-fold higher resistance to metribuzin compared with a known susceptible accession (Mengistu et al. 2005). However, those populations exhibited a negative cross-resistance and were susceptible to bromoxynil.

Resistance to ALS Inhibitors

Bassia scoparia populations from Kansas were up to 354-fold more resistant to the four sulfonylurea herbicides, namely, chlorsulfuron, metsulfuron, sulfometuron, and thifensulfuron, compared with a susceptible population (Saari et al. 1990). A B. scoparia population from Illinois had 500- to >28,000-fold levels of resistance to atrazine, imazethapyr, thifensulfuron, and chlorsulfuron (Foes et al. 1999). Three populations from Montana exhibited up to a 196-fold resistance to chlorsulfuron and metsulfuron herbicides and were 2- to 6-fold cross-resistant to imazamethabenz, imazethapyr, imazapyr, and imazaquin herbicides (Sivakumaran et al. 1993). Kumar et al. (2015) confirmed B. scoparia populations from Montana with up to 30-fold resistance to a premixture of thifensulfuron + tribenuron + metsulfuron. In a more recent survey from Montana, up to 267fold resistance to thifensulfuron, tribenuron, and metsulfuron were observed in several B. scoparia populations (PJ, unpublished data).

Resistance to Glyphosate

Three *B. scoparia* populations collected from southern Alberta wheat–fallow fields exhibited 4- to 7-fold resistance to glyphosate (Beckie et al. 2013). GR *B. scoparia* from wheat–fallow fields in Montana had 4.6- to 11-fold resistance to glyphosate (Kumar et al. 2014). A population from Sheridan County, NE, had 6- and 15-fold resistance to glyphosate and tribenuron, respectively (Rana and Jhala 2016). GR *B. scoparia* populations collected from Kansas, Colorado, North Dakota, and South Dakota had 3.5- to 13.5-fold resistance to glyphosate (Godar et al. 2015; Wiersma et al. 2015). Similarly, the *B. scoparia* populations collected from sugar beet fields in Idaho and Oregon exhibited 2.0- to 9.6-fold resistance to glyphosate (Kumar et al. 2018b).

Resistance to Synthetic Auxins

An inbred *B. scoparia* line derived from a field population collected in Montana during 1995 had a 4.6-fold resistance to dicamba relative to an inbred susceptible line (Cranston et al. 2001). Three *B. scoparia* populations from Montana identified from wheat fields in 2011 had 1.3- to 6.8-fold and 1.4- to 5.7-fold resistance to dicamba and fluroxypyr, respectively, compared with a susceptible population (Jha et al. 2015b). In Nebraska, *B. scoparia* populations with an 18-fold difference in dicamba resistance between the least and most susceptible populations were found (Crespo et al. 2014). In a recent report,

an inbred DR *B. scoparia* line selected from a field population near Henry, NE, had 38-, 12-, and 13-fold resistance to dicamba, 2,4-D, and fluroxypyr herbicides, respectively (LeClere et al. 2018). Based on the shoot dry weight response (GR_{50} values), 11 populations that were collected from western Kansas had an 8-fold difference in susceptibility to dicamba (Brachtenbach 2015).

Mechanisms of Herbicide Resistance

Resistance to PSII Inhibitors

PSII inhibitors, such as atrazine, bromoxynil, and substituted urea (diuron and tebuthiuron), compete with plastoquinone for binding on the D1 protein in PSII during electron transport, thereby, affecting the production of reducing power (NADPH) and ATP; ultimately, the plant starves to death (Trebst and Draber 1986). Mutations in the psbA gene that encodes D1 protein result in amino acid substitutions conferring resistance to PSII inhibitors. PSII-inhibitor resistance in *B. scoparia* accessions from North Dakota and Minnesota, as a result of a Val-219-Ile substitution in the psbA gene, was found to confer a high resistance to diuron and tebuthiuron and a moderate resistance to metribuzin and atrazine (Mengistu et al. 2005). Conversely, a B. scoparia population from Illinois, was found to show a high level of resistance to atrazine because of a point mutation resulting in a Ser-264-Gly substitution in the psbA gene (Foes et al. 1999). More recently, in a multiple-HR population from Kansas, a high level of resistance to atrazine because of a Ser-264-Gly substitution was also reported (Varanasi et al. 2015). The other amino acid substitutions that are known to confer resistance to PSII inhibitors, such as Val-219-Ser and Ala-251-Val were not found in this population (Varanasi et al. 2015).

Resistance to ALS Inhibitors

The most common mechanism of resistance to ALS inhibitors in plants is due to point mutations spanning five highly conserved domains of the ALS gene (Yu and Powles 2014). Bassia scoparia populations from Kansas exhibited cross-resistance to sulfonylureas, imidazolinones, and sulfonanilides because of reduced sensitivity of the ALS enzyme (Saari et al. 1990). Subsequently, B. scoparia populations from the western Great Plains were found resistant to the ALS inhibitor chlorsulfuron (Guttieri et al. 1995); a point mutation in the ALS gene resulting in a variety of amino acid substitutions conferred resistance in those populations (Guttieri et al. 1995). Later, a B. scoparia population resistant to multiple ALS inhibitors was found in Illinois, and a Trp-570-Leu substitution on the ALS gene was found to confer cross-resistance to ALS inhibitors in this population (Foes et al. 1999). ALS inhibitor-resistant B. scoparia populations from several western provinces in Canada have also been well characterized. It has been reported that amino acid substitutions at the Pro-197, Asp-376, and Trp-574 residues confer resistance (Warwick et al. 2008). This suggests multiple origins of these mutations resulting in the evolution of resistance to ALS inhibitors in B. scoparia populations collected from geographically diverse locations (Warwick et al. 2008). More recently, Pro-197-Thr and Trp-574-Leu substitutions were found to confer high levels of resistance to ALS inhibitors in multiple-HR B. scoparia populations from Kansas (Varanasi et al. 2015).

Resistance to Glyphosate

The first case of field-evolved resistance to glyphosate in B. scoparia was documented in Kansas (Godar et al. 2015). The amplification of the EPSPS gene has been found to confer resistance to glyphosate in all B. scoparia populations that have been tested (Jugulam et al. 2014; Kumar et al. 2015; Wiersma et al. 2015). Furthermore, the EPSPS transcript expression positively correlated with EPSPS copies (Wiersma et al. 2015). Fluorescence in situ hybridization analysis demonstrated that the amplified EPSPS copies are located on two homologous chromosomes, and the EPSPS copies increased with continued glyphosate selection (Jugulam et al. 2014). The continuous variation in EPSPS copies resulting in increased glyphosate resistance suggests that the EPSPS copy number in B. scoparia increases through an adaptive process. Although EPSPS gene amplification appears to be the common mechanism of glyphosate resistance in B. scoparia, it is possible that other mechanisms could confer resistance to this herbicide.

Resistance to Synthetic Auxins

Although the precise mechanism of action of auxinic herbicides is still not completely understood, recent research provides better knowledge about how these herbicides work in plants. Similar to the natural auxin indoleacetic acid (IAA), auxinic herbicides are thought to bind to the transport inhibitor response 1 and/or its homologues, leading to a rapid degradation of Aux/IAA repressors and expression of an auxin-responsive gene (Guilfoyle 2007; Mithila et al. 2011; Tan et al. 2007). Grossmann (2010) suggested that in addition to unregulated auxin response, the auxinic herbicide–sensitive dicots are killed due to the hyperaccumulation of ethylene, ABA, and reactive oxygen species. Any alterations in genes involved in auxinic herbicide signal transduction can potentially contribute to resistance mechanisms in auxinic herbicide–resistant dicot weeds.

The mechanism of auxinic herbicide resistance, specifically dicamba resistance in B. scoparia, has been characterized. It appears that dicamba resistance in B. scoparia can evolve via multiple mechanisms (Cranston et al. 2001; Dyer et al. 2002; Kern et al. 2005; LeClere et al. 2018; Pettinga et al. 2017). It was suggested that reduced uptake, translocation, or increased metabolism of dicamba might not contribute to resistance in B. scoparia (Cranston et al. 2001). However, Dyer et al. (2002) suggested that a mutation in the auxin receptor(s) might affect endogenous auxin binding and alter auxin-mediated responses, such as gravitropism and root growth inhibition. Later, it was found that compared with a dicamba-sensitive population, the DR B. scoparia population had delayed phenotypic response, such as shoot gravitropism, apical dominance, or root growth inhibition in the absence of dicamba (Goss and Dyer 2003). Furthermore, in that DR B. scoparia population, genes involved in cell wall modification (e.g., xyloglucan endotransglycosylase) and a gene/protein with unknown function were found to express differentially compared with a dicamba-sensitive population (Kern et al. 2005). More recently, a transcriptome sequencing study on an inbred DR B. scoparia population from Nebraska has revealed a glycine to asparagine amino acid change within a highly conserved region of an AUX/IAA protein, KsIAA16 (LeClere et al. 2018). Also, a double mutation in the auxin coreceptor gene Aux/IAA was identified, which conferred a low dicamba affinity in the Aux/IAA protein complex, enabling B. scoparia plants to cope with high levels of dicamba in cells (LeClere et al. 2018). In another study using the same DR B. scoparia inbred line as LeClere et al. (2018), there was a 2-fold higher transcription of chalcone synthase (CHS) gene that regulates synthesis of the flavonols quercetin and kaempferol (Pettinga et al. 2017). It has been proposed that greater flavonol synthesis resulting from increased CHS transcription would compete with the intercellular transport of dicamba molecules, which is regulated by the ATP-binding cassette subfamily B membrane transporters, thereby impairing the dicamba translocation in DR B. scoparia plants. Stress-induced (e.g., UV light or pathogen elicitors) transcription of CHS has been found to bestow a higher tolerance to abiotic or biotic stress (Dao et al. 2011). It was also proposed that the restricted auxin translocation with a higher upregulation of CHS might potentially have fitness costs in B. scoparia (Pettinga et al. 2017). Subsequently, LeClere et al. (2018) confirmed that the presence of a dicamba resistance allele contributes to fitness penalty in this population. A previous genetic analysis of this B. scoparia inbred reported that a single gene with a high level of dominance controls dicamba resistance (Preston et al. 2009).

Pollen- and Seed-mediated Gene Flow in Bassia scoparia

Bassia scoparia is a genetically highly diverse species. High levels of both self- and cross-pollination have been shown to occur in this species (Thill et al. 1991), and considerable pollen-mediated gene flow and efficient seed dispersal facilitate both short- and long-distance gene flow (Beckie et al. 2016). A single B. scoparia plant can produce more than 100,000 seeds that can be dispersed long distances via the tumble mechanism, contributing to a rapid gene flow within and among populations (Baker et al. 2010; Beckie et al. 2016; Christoffoleti et al. 1997; Kumar and Jha 2015d). A substantial gene flow contributed to the high genetic diversity within and among B. scoparia populations from Montana, North Dakota, and Minnesota (Dyer et al. 1993a; Mengistu and Messersmith 2002). Pollen-mediated gene flow for the spread of glyphosate resistance and seed-mediated gene flow of ALS-inhibitor resistance have been investigated in Canadian B. scoparia populations (Beckie et al. 2016). The results indicated that the gene transfer from GR to non-GR B. scoparia populations was from 5.3% to 7.5% and decreased significantly at a distance of 96 m. The study also suggested that the direction of wind at the time of pollination significantly influenced the pollen-mediated gene flow in this species (Beckie et al. 2016). On the other hand, seed-mediated gene flow of the ALS-inhibitor resistance varied with the tumbling speed of the mature plant and the distance traveled (Beckie et al. 2016). Gene flow between B. scoparia plants resistant and susceptible to ALS inhibitors was shown to occur at a maximum rate of 13% with a distance of 1.5 m and was substantially reduced (1.4%) at 29 m (Mallory-Smith et al. 1993; Stallings et al. 1995). It was also reported that the pollen-mediated gene flow was 3-fold greater in the Canadian B. scoparia populations (96 m) compared with those from the western United States (26 m) (Beckie et al. 2016; Mallory-Smith et al. 1993; Stallings et al. 1995). Mulugeta et al. (1994) reported that B. scoparia pollen can be deposited at a distance of 150 m from the source. Overall, because of the high frequency of both pollen- and seed-mediated gene flow in B. scoparia, there is a high risk of spread of single, cross-, or multiple-herbicide resistance alleles in this species.

Ecological Perspectives

Seed Germination and Emergence Dynamics

Bassia scoparia seed exhibits zero to very little (<10%) innate dormancy and low persistence (\leq 2 yr) in the soil (Dille et al. 2017). It is often the first weed species to emerge in the spring in the Great Plains region (Schwinghamer and Van Acker 2008; Zorner et al. 1984). Schwinghamer and Van Acker (2008) observed that *B. scoparia* seeds placed at the soil surface had greater seedling emergence compared with those buried at a depth of 10 mm or greater, and no emergence occurred from depths below 80 mm in the soil (Schwinghamer and Van Acker 2008). A more recent study conducted across several states in the U.S. Great Plains found that burial depths of 0 to 10 cm did not influence the seed viability over time; however, seeds buried at depths > 2.5 cm failed to emerge (Dille et al. 2017).

Bassia scoparia emergence initiated at 50 cumulative growingdegree days (GDD T_{base} 0 C) and continued through the summer in the Northern Great Plains (Schwinghamer and Van Acker 2008). At a semiarid site near Akron, CO, a majority of B. scoparia emergence occurred between April 25 and May 9 (Anderson and Nielsen 1996). The average cumulative GDD needed for 10% emergence was 168 across 11 site-years from Garden City, Ness City, Hays, Stockton, and Manhattan in Kansas, while in southern Wyoming and western Nebraska (near Mitchell and Scottsbluff), only 90 cumulative GDD were needed (Dille et al. 2017). In a common garden study conducted in Huntley, MT, B. scoparia populations collected from six different U.S. Great Plains states showed differential emergence patterns (Kumar et al. 2018a). Populations collected from Kansas, Oklahoma, and Montana showed an early onset of emergence. In contrast, a population from New Mexico had a delayed onset of emergence but a more rapid emergence rate, while populations from North Dakota had an extended emergence period. Those populations had two to four emergence peaks between mid-April and mid-July. The researchers concluded that the differential emergence pattern of B. scoparia populations reflects the coexistence of different emergence "biotypes"; hence, there is a need to adopt more location-specific, diversified weed control tactics to manage the weed seedbank (Kumar et al. 2018a).

Very few studies have been conducted to explore the germination and emergence dynamics of HR versus herbicidesusceptible B. scoparia. Populations with resistance to ALS inhibitors (SU herbicides) from Montana had an early and a rapid germination at 4.6 to 13.2 C compared with ALS inhibitor-susceptible populations (Dyer et al. 1993b). The higher germination rate of ALS inhibitor-resistant B. scoparia populations was attributed to higher free levels of branched-chain amino acids (2-fold higher) compared with ALS inhibitor-susceptible populations (Dyer et al. 1993b). Similarly, ALS inhibitor-resistant B. scoparia populations from Kansas and North Dakota had a faster seed germination rate (12 to 70 h earlier) and final cumulative germination (100 to 300 h earlier) than susceptible populations at 8 C (Thompson et al. 1994). These studies indicate that ALS inhibitor-resistant populations will most likely emerge and establish earlier than the susceptible populations, emphasizing the need for early-season weed control to manage the ALS inhibitorresistant B. scoparia.

Seeds of a *B. scoparia* inbred line from Montana with crossresistance to dicamba and fluroxypyr (df-R), had a lower final cumulative germination than the susceptible inbred line (df-S) at a majority of constant (5 to 35 C) and alternating temperatures (5/10 to 25/30 C) (Kumar and Jha 2016). In addition, the df-R inbred line had a delayed onset of germination relative to the df-S inbred line, especially at low temperatures (Kumar and Jha 2016), indicating a higher thermal requirement for germination than the df-S inbred line. This study concluded that the df-R inbred line was relatively more dormant and would potentially be more persistent in the soil seedbank than the df-S line.

Four out of seven GR populations from Montana had a lower cumulative germination and took more time to complete 50% cumulative germination under all constant and alternating temperatures evaluated compared with the glyphosate-susceptible (GS) populations (Kumar and Jha 2017). Those four GR populations also had a delayed germination initiation, particularly at lower temperatures (5 to 10 C constant or 5/10 C alternating). Similarly, GR B. scoparia populations from Kansas had lower total cumulative germination percentages and slower germination rates than GS populations at 15 C (Osipitan and Dille 2017). More recently, Beckie et al. (2018) found that seed burial depth (0 to 10 cm) had no effect on the seed viability of GR populations compared with the GS populations over time, and time to 50% and 90% loss of seed viability averaged 210 and 232 d, respectively. In that study, GR populations were also found to germinate later and had a lower cumulative germination than GS populations (Beckie et al. 2018). These differential germination characteristics of GR versus GS or DR versus DS populations of B. scoparia may indicate coexistence of resistance and avoidance (escaping preseeding treatments) mechanisms. The delayed and reduced germination characteristics of these HR populations may represent options for managing the weed seedbank by altering the PRE soil-residual herbicide timing or tillage timing or by shifting the crop planting dates earlier to enhance crop competitiveness (Beckie et al. 2018; Kumar and Jha 2017).

Growth and Reproduction

A majority of the studies on growth and fecundity characteristics of HR versus susceptible *B. scoparia* populations have been conducted under greenhouse conditions with very limited data from field studies. In a greenhouse study, chlorsulfuron-resistant and chlorsulfuron-susceptible populations from North Dakota or Kansas had similar growth rates and seed production in the absence of competition (Christoffoleti et al. 1997; Thompson et al. 1994). Similarly, in a replacement series experiment, growth characteristics of ALS inhibitor–resistant populations from Alberta and Manitoba with a single point mutation (Trp-574 or Pro-197), did not differ from the susceptible populations (Légère et al. 2013).

Bassia scoparia lines derived (after three generations of recurrent selection) from a single, segregating field population (common genetic background) with cross-resistance to dicamba and fluroxypyr (df-R) had reduced plant height, plant width, primary branches, total leaf area, stem diameter, and shoot dry weight compared with the df-S line in the absence of competition (Kumar and Jha 2016). In this study, the df-R B. scoparia had a 39% reduction in reproductive fitness, and the 1,000-seed weight (1.6 g) was lower compared with the df-S B. scoparia (2.6 g). The replacement series indices further revealed that the df-R was less competitive than the df-S when grown in an intraspecific competition at varying mixture proportions (Kumar and Jha 2016). Similar results have been observed concerning the fitness penalty of a DR inbred line from Nebraska (LeClere et al. 2018). The results imply a possible fitness cost endowed by the auxinic

resistance trait and that the frequency of df-R individuals is likely to decline in the population when the use of auxinic herbicides is interrupted by other weed control methods (Kumar and Jha 2016).

Studies on the growth and reproductive fitness of GR B. scoparia have shown mixed results. In a greenhouse study, Kumar and Jha (2015b) found no differences in growth and fecundity traits between the GR (with 3 to 15 copies of the EPSPS gene) and GS (single copy of the EPSPS gene) B. scoparia populations collected from a wheat-fallow field in Montana. Similarly, GR and GS populations from Kansas did not exhibit any differences in plant height, biomass accumulation, and fecundity characteristics under field conditions (Osipitan and Dille 2017). These studies suggest that GR B. scoparia individuals will most likely persist in field populations even if the growers discontinue glyphosate use. However, in a recent study, Martin et al. (2017) evaluated the fitness costs of EPSPS gene amplification in B. scoparia by comparing susceptible and resistant full siblings from segregating F₂ populations. Some GR B. scoparia plants with high EPSPS gene copy numbers had delayed emergence, delayed flowering, and reductions in viable seed count and seed weight compared with the susceptible plants. Nevertheless, a significant amount of variation in the magnitude of fitness cost was observed among the independent F2 crosses (across genetic backgrounds) (Martin et al. 2017). The authors concluded that B. scoparia with increased EPSPS gene copy number may be at a competitive disadvantage in some genetic backgrounds when glyphosate use is interrupted by other weed control methods.

Management of HR Bassia scoparia

Fallow

Wheat-fallow is a predominant crop rotation in the dryland region of the U.S. Great Plains, primarily due to a limited soil moisture availability (less than 375 mm annual precipitation) for continuous cropping (Peterson and Westfall 2004). In the absence of crop competition, B. scoparia poses a serious problem during the summer fallow (chemical fallow) phase of the rotation, as it depletes soil moisture, and can add a significant amount of seeds $(\geq 250,000 \text{ seeds plant}^{-1})$ to the soil seedbank (Lim et al. 2016). Growers often rely on herbicides for B. scoparia control in chemical fallow fields. Depending on the subsequent crop to be grown, soil-active herbicides including pendimethalin + dimethenamid, pyroxasulfone + pendimethalin, metribuzin, sulfentrazone, flumioxazin, isoxaflutole, and atrazine can be effectively used in the fall or early spring to control B. scoparia resistant to glyphosate, dicamba, and ALS inhibitors (Jha et al. 2015a; Kumar and Jha 2015a; Thompson et al. 2018). Paraquat alone or in combination with linuron, metribuzin, or atrazine, saflufenacil + linuron, and diflufenzopyr + dicamba + 2,4-D can all be effectively used (recommended rate and timing) as POST burndown treatments in chemical fallow for controlling B. scoparia resistant to ALS inhibitors and glyphosate (Kumar and Jha 2015a); however, the options will be very limited with the presence of glyphosate, ALS inhibitors, and dicamba multiply resistant B. scoparia.

Wheat

Bassia scoparia is a poor competitor in a well-established wheat canopy; therefore, it is less challenging to manage in wheat,

especially in winter wheat that attains vigorous growth by the time *B. scoparia* begins to emerge. Although there are very few PRE herbicides registered in wheat, POST herbicides with multiple sites of action, including bromoxynil + fluroxypyr, bromoxynil + pyrasulfotole, or bromoxynil + MCPA at the full labeled rates can provide up to 95% control of GR, ALS inhibitor-resistant, or DR *B. scoparia* (8- to 10-cm tall) in wheat (Kumar and Jha 2015a; Thompson et al. 2018). Kumar and Jha (2015d) reported that paraquat + atrazine, paraquat + linuron, and paraquat + metribuzin applied at the early bloom stage of *B. scoparia* were very effective for late-season control and seed prevention in postharvest wheat stubble.

Corn and Grain Sorghum

There are relatively more options for HR B. scoparia control with PRE soil-residual herbicides compared with POST herbicides in corn. PRE herbicides, including pyroxasulfone + atrazine, dicamba + pendimethalin, pyroxasulfone or dimethenamid-P + pendimethalin, flumioxazin + pyroxasulfone, saflufenacil + dimethenamid-P + pendimethalin, and isoxaflutole, can provide >90% residual control (8 wk after treatment) of B. scoparia populations resistant to ALS inhibitors, dicamba, or glyphosate in corn (Kumar and Jha 2015a; Thompson et al. 2018). These herbicides can be tank mixed with paraguat or saflufenacil to obtain preplant burndown GR B. scoparia control in corn. Among POST herbicide options, dicamba + diflufenzopyr and tembotrione, topramezone, or mesotrione + atrazine would provide effective control of GR and ALS inhibitor-resistant B. scoparia populations in corn (Kumar and Jha 2015a; Thompson et al. 2018; Tonks and Westra 1997). However, B. scoparia resistant to glyphosate, ALS inhibitors, PSII inhibitors, and dicamba will be quite difficult to manage with POST-only herbicide programs, which are limited to 4-hydroxphenylpyruvate dioxygenase (HPPD) inhibitors. Furthermore, atrazine and HPPD inhibitors cannot be used in corn rotated often with sugar beet or dry beans (Phaseolus spp.) (carryover concerns) in the Northern Great Plains.

Soybean

Before evolution of glyphosate resistance, B. scoparia populations resistant to ALS and PSII inhibitors were effectively managed by glyphosate in GR soybean. Evolution of GR B. scoparia in soybean has been reported from four U.S. states (Heap 2018). To manage B. scoparia resistant to ALS inhibitors and glyphosate in soybean, it is crucial to start clean with a preplant burndown herbicide program using saflufenacil, glufosinate, or paraquat (Thompson et al. 2018). To obtain 6 to 8 wk of residual control, PRE herbicides such as pyroxasulfone + flumioxazin, metribuzin, sulfentrazone, saflufenacil + dimethenamid-P + pendimethalin, dimethenamid-P or pyroxasulfone + pendimethalin should be included with the preplant burndown programs (Kumar and Jha 2015c). Among POST herbicides, protoporphyrinogen oxidase (PPO) inhibitors such as acifluorfen, lactofen, and fomesafen can provide 70% to 85% control of glyphosate and ALS inhibitorresistant B. scoparia (Jha et al. 2014; Kumar et al. 2014; Thompson et al. 2018); however, control with PPO inhibitors could be variable depending on B. scoparia size and environmental conditions (PJ, personal observation). Therefore, POST treatments of PPO inhibitor are recommended with the PRE soilresidual herbicides to obtain season-long control of GR and ALS inhibitor-resistant B. scoparia in soybean.

Sugar Beet

Due to the early emergence and high competitive ability of B. scoparia, its control in sugar beet production has always been a challenge (Kniss 2010; Kumar and Jha 2015a). After its commercialization in 2008, GR sugar beet has been rapidly adopted by growers and comprises > 98% of the total sugar beet production in the region (Kniss 2010). In conventional (non-GR) sugar beet, growers had to make three to five herbicide applications in sugar beet that often resulted in unacceptable crop injury (Kniss 2010; Morishita 2018). In addition, non-GR sugar beet required one to three cultivations as well as hand weeding. Among POST herbicide options including triflusulfuron, desmedipham, phenmedipham, and clopyralid, triflusulfuron was the only effective herbicide for B. scoparia control in non-GR sugar beet; nevertheless, this herbicide was rendered ineffective as ALS inhibitorresistant B. scoparia populations became widespread in sugar beet-growing areas of the U.S. Great Plains. Glyphosate provided excellent broad-spectrum weed control, including control of ALS inhibitor-resistant B. scoparia populations. Growers often rely on multiple (two to four) POST glyphosate applications for weed control in GR sugar beet fields (Kniss 2010; Kumar and Jha 2015c; Morishita 2018). This has enhanced selection pressure for evolution of GR weeds in sugar beet, with B. scoparia being the first weed to evolve resistance to glyphosate in sugar beet (Heap 2018). Some of the soil-active herbicides that are labeled in sugar beet, including ethofumesate, dimethenamid-P, EPTC, S-metolachlor, and trifiuralin, are not very effective on *B. scoparia* and cannot be relied upon alone (Morishita 2018). Therefore, the evolution of GR B. scoparia in sugar beet fields in Montana, Wyoming, Colorado, Nebraska, Idaho, and Oregon has raised concerns among growers over the long-term sustainability of sugar beet production (Gaines et al. 2016; Kumar et al. 2018b; Morishita 2018). As GR B. scoparia spreads within sugar beet-growing regions, there will simply not be any herbicide registered for sugar beet that will control this weed. Therefore, diverse ecological strategies need to be urgently implemented in sugar beet-based crop rotations.

Multiple Herbicide-Resistant Trait Technologies

Crop cultivars with "stacked" herbicide resistance traits have recently been commercialized for controlling GR and ALS inhibitor-resistant weeds. Few of those include DR and 2,4-D-resistant weed management system in soybean, corn, or cotton (Gossypium hirsutum L.). The Roundup Ready® 2 Xtend (Monsanto Company, 800 N. Lindbergh Blvd, St. Louis, MI 63167) system provides crop tolerance to POST applications of both glyphosate and dicamba. This technology in soybean will allow the use of dicamba (Xtendimax® [Monsanto Company] or Engenia® [BASF Corporation, 26 Davis Drive, Research Triangle Park, NC 27709], or Fexapan $^{\text{TM}}$ [E. I. du Pont de Nemours and Company, Chestnut Run Plaza, 974 Center Road, Wilmington, DE 19805]) in crop to control GR and PSII and ALS inhibitorresistant weed populations. Several studies have reported excellent control of GR weeds with dicamba alone or in combination with glyphosate (Cahoon et al. 2015; Eubank et al. 2008; Everitt and Keeling 2007; Spaunhorst et al. 2014; Vink et al. 2012). These stacked-trait crops will provide new options with existing herbicides, but will not be the total weed management solution, because B. scoparia has already evolved resistance to dicamba in several states in the U.S. Great Plains (Heap 2018). Furthermore, the utility of dicamba and 2,4-D on large landscapes needs to be

carefully examined because of potential off-target movement of these herbicides via physical or vapor drift, which can potentially cause damage to other sensitive crops and vegetation (Bish and Bradley 2017; Culpepper et al. 2018; Everitt and Keeling 2009; Johnson et al. 2012).

Nonchemical Approaches

Managing HR B. scoparia will require the use of mechanical and ecologically based approaches, such as tillage, increased crop competition, diverse crop rotations, and cover crops to manipulate B. scoparia seedbanks (Ball 1992; Davis et al. 2005; Kumar et al. 2018a). Among all these methods, the selection of improved crop rotations can potentially be the most effective cultural practice for managing B. scoparia seedbanks (Hume et al. 1991; Johnson and Coble 1986; Kumar et al. 2018a). Selecting the most competitive crops such as cereals or corn in the rotation will be crucial in reducing seed inputs of B. scoparia. For instance, a 3-yr field study on the impact of crop canopy on B. scoparia seed reductions found that B. scoparia produced an average of 26,000 seeds plant⁻¹ in fallow compared with only 134 and 104 seeds plant⁻¹ in wheat and corn, respectively (Nyamusamba 2014). The Bassia scoparia seedbank in the top 15cm soil depth declined from 10 to 0 seed m⁻² after 3 yr of continuous corn, whereas 500 and 800 seeds m⁻² were observed after 3 yr of continuous pinto bean (Phaseolus vulgaris L.)/sugar beet -sugar beet-corn rotation, respectively (Ball 1992). Those soil seedbank changes were mainly attributed to the competitive ability of the crop (corn being more competitive than pinto bean or sugar beet) and herbicide use pattern in each cropping sequence (Ball 1992). It is unlikely that crop rotation itself will alter the R:S ratio of the weed seedbank (Davis et al. 2009). However, a well-designed crop rotation comprising winter cereals or perennial forages may provide an opportunity to reduce the overall density of weed seedlings being exposed to a herbicide, thereby delaying or preventing a significant increase in the R:S ratio. A diverse crop rotation could also reduce herbicide selection pressure by stimulating germination when nonchemical control practices can be used, for example, stale seedbed especially in late-planted crops such as dry beans in the irrigated regions of the U.S. Great Plains. These factors could be more important for a weed like B. scoparia with a short-lived seed, where R individuals could be reduced dramatically in just a few years (Jha, Kniss, and Lawrence, unpublished data).

No-till systems favor the germination of small-seeded weeds, including B. scoparia, because under no-till conditions, a majority of weed seeds lies on or near the soil surface where optimum germination conditions prevail (Anderson et al. 1998; Schwinghamer and Van Acker 2008). Bassia scoparia has become the most troublesome weed species in no-till production systems of the Great Plains (Heap 2018). In a 3-yr study, B. scoparia seedbank declined more rapidly after 3 yr of moldboard plowing as compared with chisel plowing (Ball 1992). The more rapid seedbank turnover in no-till versus conventional-till systems may expose a greater proportion of the weed seedbank to herbicides. This interaction with increased herbicide use may result in an increased risk of selection of rare resistance alleles in the weed population under no-till systems (Beckie et al. 2008). In a survey conducted on the risk assessment of herbicide resistance, 21% of the crop area with intensive tillage did not receive any herbicide application, whereas 99% of the crop area with no-tillage received at least one herbicide application. Consequently, the risk of evolution of weed resistance would be higher in no-till than conventional tillage systems (Beckie et al. 2008).

Cover crops suppress weeds by reducing early-season weed densities, growth, and seed production because of direct competition from the living cover crop biomass or from the plant residue after the cover crop is terminated (Al-Khatib et al. 1997; Petrosino et al. 2015; Teasdale et al. 2005). Cover crop residues can trap weed seeds, prevent soil-seed contact required for germination, and provide optimum habitat for increased weed seed predation compared with the bare soil, thereby influencing the persistence of weed seeds in the soil (Cardina and Sparrow 1996; Teasdale et al. 2005). Bassia scoparia density was reduced by 78% to 94% and the biomass was reduced by 98% in fall-planted cover crops, such as Austrian winter pea (Pisum sativum L.), hairy vetch (Vicia villosa Roth), winter triticale (Triticosecale rimpaui C. Yen & J. L. Yang), and mixtures of hairy vetch and winter triticale and of Austrian winter pea and winter triticale compared with the density and biomass in fallow (Petrosino 2010; Petrosino et al. 2015). However, spring-planted cover crops such as lentil (Lens culinaris Medik.), pea, and mixtures of lentil/triticale and pea/triticale did not affect B. scoparia density and biomass compared with fallow plots in the same study (Petrosino et al. 2015). In a greenhouse study, adding white mustard (Sinapis alba L.) plant residue to the soil at 20 g per 400 g air-dried soil reduced B. scoparia emergence by 54% (Al-Khatib et al. 1997). In field experiments, 90% to 99% reductions in early- and lateseason B. scoparia densities were observed with a yellow sweetclover [Melilotus officinalis (L.) Lam.] green manure compared with fallow plots (Blackshaw et al. 2001). This strategy would potentially reduce reliance on herbicide inputs and allow competitive crops to be established before B. scoparia emergence. However, research on quantifying the effect of cover crops on B. scoparia emergence patterns and seedbank dynamics is lacking.

The efficacy and economics of harvest weed seed control (HWSC) technologies (reviewed in Walsh et al. 2013) in managing HR B. scoparia populations need to be evaluated in the North American Great Plains cropping systems. As a nonherbicidal weed management tool, HWSC can be an important component of an integrated weed management program to reduce weed seed inputs and reduce the reliance on herbicides, thereby delaying the evolution of HR weeds (Walsh and Powles 2014). HWSC methods would hold great promise for managing B. scoparia, which can retain 99.8% of the seeds at wheat harvest in the North American Great Plains (Burton et al. 2017). A high level of seed destruction (99.8%) of B. scopariawas obtained using an Harrington Seed Destructor cage mill in barley (Hordeum vulgare L.) chaff (Tidemann et al. 2017). Bassia scoparia has an indeterminate growth habit and plants are immature at the time of cereal harvest (Kumar and Jha 2015a). To maximize the efficiency of HWSC, harvest height should be lower than the current cutting height of \sim 15 to 20 cm to revent regrowth of the portion of the plant that is left behind and that can potentially add ~100,000 seeds m⁻² if not controlled postharvest (Burton et al. 2017; Kumar and Jha 2015a). In addition, the plant can disperse those seeds long distances through the tumbling mechanism in the fall, ensuring rapid movement of resistance alleles (Beckie et al. 2016).

The ideal strategy for mitigating HR *B. scoparia* should embrace a "zero-seed threshold" approach at a cropping-systems level. Therefore, the long-term herbicide-resistance management programs should encourage the use of more diversified crop rotations, tillage, cover crops, and HWSC. The goal should be to identify ecological trends in *B. scoparia* population dynamics as

influenced by multitactic cultural practices, which can be recommended to producers.

Precision Weed Management

In the past few decades, sensor-based technologies have gained wide-scale attention in agriculture. Major advancements in automation include the development of remote-sensing technologies, sophisticated cameras, robots, and unmanned aerial vehicles (UAVs). Site-specific weed management using these automated, sensor-based technologies hold promise. These technological advances can also help in identification of HR weed populations. For instance, GR and GS Palmer amaranth (Amaranthus palmeri S. Watson) populations were distinguished using differences in reflectance across the near-UV, visible, and near-IR spectrum (Reddy et al. 2014). Further work using hyperspectral reflectance properties has shown the ability to differentiate between GS and GR Italian ryegrass [Lolium perenne L. ssp. multiflorum (Lam.) Husnot] populations and between GR and DR B. scoparia from susceptible populations (Lee et al. 2014; Nugent et al. 2018). These optical sensor-based technologies along with automated UAVs have broader implications for widescale field mapping and early detection of HR weed populations, including HR B. scoparia (Nugent et al. 2018).

Light-activated sensor-controlled (LASC) or Weed Seeker® sprayers have shown tremendous success in site-specific weed control and in reducing herbicide costs by 30% to 70% in fallow (Ahrens 1994; Biller 1998; Blackshaw et al. 1998; Jha et al. 2014; Riar et al. 2011). In addition, the LASC sprayer has shown 25% reductions in herbicide cost for selective weed control in cereals and pea compared with a broadcast application (Dammer and Wartenberg 2007). Up to 70% reductions in herbicide use have been achieved with the LASC sprayer compared with conventional broadcast applications in soybean (Hanks and Beck 1998).

Summary and Future Directions

Several factors, including agronomic practices and the unique biological characteristics of B. scoparia, make control of this weed species challenging. Adoption of conservation tillage systems favor rapid emergence of small-seeded weeds like B. scoparia from the soil surface (Dille et al. 2017). Heavy reliance on herbicides in no-till cropping systems, especially chemical fallowbased and frequent use of glyphosate in GR crops, coupled with a high genetic diversity, facilitated evolution of multiple-herbicide resistance in B. scoparia. In addition, B. scoparia was found to evolve resistance to the same chemistry of herbicide via multiple mechanisms (e.g., DR B. scoparia). This may warrant diversified tactics for managing this troublesome weed. Our research on DR B. scoparia indicates that intensive cropping and weed management practices favor the shift in the population to late-emerging weed cohorts and a common selection of herbicideresistance and avoidance mechanisms (Kumar and Jha 2016, 2017). There is a research gap in understanding the impact of ecologically based weed management strategies on the seedbank dynamics of B. scoparia. In this context, long-term field studies in Montana, Wyoming, and Nebraska are underway to develop a bioeconomic model to understand the effect of diverse cultural and mechanical strategies on mitigating HR *B. scoparia* seedbanks. In another study across the three-state region, a hydrothermal time model will be developed to predict regional B. scoparia emergence patterns and to test the impact of non-herbicide

management strategies (cover crops, stale seedbed, and improved crop rotations) that have a high likelihood of decreasing *B. scoparia* seedbanks, thereby reducing reliance on herbicides.

The genetic plasticity and epigenetic adaptability of *B. scoparia* in response to climate change and biotic or abiotic stresses imposed by crop management practices need to be investigated. Whole-genome sequencing of B. scoparia will help in elucidating the molecular and genetic basis of stress adaptability of this species, including rapid evolution of resistance to multiple herbicides (T Gaines, personal communication). New, stacked herbicide-tolerant crop technologies may aid in managing HR B. scoparia in the short term. However, with the presence of B. scoparia populations with resistance to four herbicide sites of action, there is an urgent need to develop ecological weed management strategies at a cropping-system level based on an improved understanding of the biology, plasticity, and genetic diversity of this weed. Modeling the effectiveness of multitactic weed management strategies at different spatial scales (landscape levels) to delay or preclude herbicide resistance in B. scoparia will aid in attaining cooperative management goals.

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Acknowledgments. This work was jointly supported by the USDA National Institute of Food and Agriculture (Hatch Projects MON00658 and KS534) and USDA Western SARE (Project No. EW16-029, Montana State University Subaward No. 150893-00001-207). This publication is contribution no. 18-621-J from the Kansas Agricultural Experiment Station, Manhattan, KS. No conflicts of interest have been declared.

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