Kochia (*Bassia Scoparia*) Growth and Fecundity As Influenced By Crop Competition and Weed Density

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Abstract

Kochia [*Bassia scoparia* (L.) A. J. Scott] represents one the most troublesome weeds in crop production systems in the North American Great Plains. The development of herbicide-resistant *B. scoparia* populations further exacerbated this problem. More ecologically driven approaches to its control are necessary. This study examined the competitive effects of four crops (sugar beet, soybean, barley, and corn) in combination with *B. scoparia* densities (3, 13, 24, 47, 94, and 188 plants m⁻²) on *B. scoparia* development and seed production across 2 years. Corn and barley had the greatest impact on *B. scoparia* growth and fecundity. *B. scoparia* biomass was 87 and 82% lower and seed production was 98 and 96% lower ($p < 0.001$) in corn and barley, respectively, relative to fallow. Corn had greatest effect in reducing *B. scoparia* biomass and seed production. Barley had greatest effect in delaying *B. scoparia* flowering which occurred 113 days after *B. scoparia* emergence ($p < 0.001$). Soybean and sugar beet had the least effect reducing *B. scoparia* biomass by 70 and 65% and seed production by 84 and 80% ($p < 0.001$), respectively, relative to fallow. Increasing *B. scoparia* densities resulted in reductions in *B. scoparia* width, number of primary branches, biomass plant⁻¹, and seeds plant⁻¹ but increased *B. scoparia* height, biomass m⁻², and seeds m⁻² ($p < 0.001$) under all cropping treatments except corn. Barley represents the greatest opportunity to impact *B. scoparia* through reduced fecundity and delayed flowering, with the latter providing a window of opportunity for post-harvest control. The effects observed here were isolated from differences in herbicide practices that are associated with each of these crops, differences that have a dramatic effect on *B. scoparia* in their own right.

Introduction

Kochia [*Bassia scoparia* (L.) A. J. Scott] is an herb originally from Europe and Asia that was introduced into the United States as an ornamental in the 1800s¹⁻³. Today, *B. scoparia* is an invasive summer annual weed species found widespread across the Continental US and Canadian provinces where it thrives in prairies, roadsides, pastures, wastelands, cultivated fields, floodplains, and riparian habitats^{2,4-8}. Its high rate of spread makes *B. scoparia* one of the most serious weeds in the northwest region⁶. *B. scoparia* affects the yields of oats (*Avena sativa* L.), wheat (*Triticum aestivum* L.), sugar beet (*Beta vulgaris* L.), sunflower (*Helianthus annuus* L.), corn (*Zea mays* L.), soybeans [*Glycine max* (L.) Merr.], and sorghum [*Sorghum bicolor* (L.) Moench]⁹⁻¹⁷. It also ranks among the top six most troublesome weeds of canola (*Brassica napus* L.), corn, alfalfa (*Medicago sativa* L.), sugar beet, spring grains, and pulse crops¹⁸⁻¹⁹.

The unique features and competitive nature of *B. scoparia* have made it problematic in diverse cropping systems. A monoecious diploid ($2n = 18$) with C4 carbon fixation, *B. scoparia* exhibits protogynous flowering that forces high levels of outcrossing and promotes high genetic diversity within and among populations²⁰⁻²². Among the reasons for its widespread distribution and its troublesome nature, are its ability to rapidly emerge early in the growing season, low seed dormancy, high environmental stress tolerance, high seed production, and the tumble mechanism for effective seed dispersal across long

distances^{2,6,16,23-28}. While its small seeds cannot emerge from more than 80 mm of soil cover and won't persist in the soil for more than 2 years²⁶, *B. scoparia* is strongly nitrogen responsive and capable of flourishing under many different tillage and crop rotation systems²⁹⁻³². Moreover, *B. scoparia* populations rapidly shift from early-emerging to late-emerging cohorts in response to early-season chemical control tactics that rapidly select for biotypes with elevated levels of seed dormancy and higher thermal requirements for seed germination³³.

Increased herbicide use, due in part to the decline in herbicide prices, has led to the development of field-evolved herbicide-resistant *B. scoparia* populations that pose great challenges for their control and management^{24,29,33-36}. Herbicide-resistant *B. scoparia* is now widespread in the Great Plains, Pacific Northwest, Rocky Mountains, and Midwestern USA²⁴. These herbicide-resistances include resistance to acetolactate synthase (ALS) inhibitors, synthetic auxins, photosystem II (PSII) inhibitors, and 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) inhibitors^{24,37}. To make matters worse, several states have *B. scoparia* populations confirmed resistant to multiple herbicide sites of action, among of these are *B. scoparia* populations from Illinois with resistance to both PSII and ALS inhibitors, and more recent *B. scoparia* populations from Kansas with resistances to glyphosate, ALS inhibitors, PSII inhibitors, and dicamba^{38,39}. Even more troubling, some of these herbicide resistances have been shown to neither reduce the vegetative growth nor affect the reproductive success of the herbicide-resistant population in the absence of herbicide selection⁹⁵. This suggests that herbicide resistant phenotypes of *B. scoparia* will likely persist in fields long after herbicide use has ceased^{40,41,95}.

The great challenge for the continued control and management of herbicide-resistant *B. scoparia* will be the development of diverse approaches to weed management that reduce the reliance on chemical weed control. Mechanical and ecological approaches such as tillage, increased crop competition, cover crops, and diverse and improved crop rotations hold great potential for decreasing *B. scoparia* seedbanks and managing *B. scoparia* herbicide resistance^{37,40,42-44}. Growing interests in ecological approaches to weed management that can be integrated into current herbicide weed control programs has become a renewed frontier in integrated weed management. One ecological approach is to take advantage of the natural competitive abilities of crops including their ability to tolerate weed competition (tolerance) thus maintaining yields while reducing weed fitness (suppression)^{45,46}. A strong suppressive crop can reduce weed seed production, which can have positive long-term effect on weed seed banks^{47,48}. For instance, the early biomass production in wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) is one of the two traits responsible for significant suppression of perennial ryegrass (*Lolium perenne* L.) and volunteer oil rapeseed (*Brassica napus* L.)^{49,50}. For *B. scoparia*, seed production was reduced in corn and wheat plots relative to a fallow control⁵¹. In comparison to other crops, corn has been shown to reduce *B. scoparia* seed banks compared to dry beans (*Phaseolus vulgaris* L.) and to a rotation of sugar beet – sugar beet–corn⁴². For the latter, differences were suggested to be due to differing herbicide use for each crop in the cropping sequence and the more competitive nature of corn crop⁴². At this time, it is unclear the relative contribution of each of these factors on *B. scoparia* control. There is currently little

information on the interactions between *B. scoparia* density and crop competition on *B. scoparia* growth and development. This study aims to address this deficiency as well as assess the relative competitiveness of viable rotational crops for *B. scoparia* management in Montana. Our objective is to determine the impact of corn, barley, soybean, and sugar beet and varying *B. scoparia* densities have on overall *B. scoparia* growth and fecundity. An effective integrated weed management strategy relies on accurate description of biological characteristics and prediction of ecological behaviors of weeds in agricultural situations^{52,53}. As part of a diversified and ecological approach to weed control and management, taking advantage of competitive crops could be a viable approach to reduce herbicide-resistant *B. scoparia* seedbanks.

Results

In both trial years, *B. scoparia* emergence was 2-4 days earlier than crop emergence. Neither crop nor *B. scoparia* density affected 1000-seed weight ($p=0.214$ and $p=0.061$, respectively), seed viability ($p=0.878$ and $p=0.056$, respectively), and radicle length ($p=0.216$ and $p=0.858$, respectively).

Presence of a crop had a profound effect on *B. scoparia* growth and development compared to its absence (fallow) [Figure 1]. Among the main effects, the crop treatment affected the width, number of primary branches, biomass plant⁻¹, biomass m⁻², seeds plant⁻¹, seeds m⁻², height, and days to flowering (all $p<0.001$) as shown in Table 1. Averaged across *B. scoparia* densities, the crop treatments decreased the *B. scoparia* final width, height, number of primary branches, biomass plant⁻¹, biomass m⁻², seeds plant⁻¹, and seeds m⁻² compared to fallow treatment (Table 2). Corn and barley were the most suppressive on *B. scoparia* growth and fecundity. Soybean and sugar beet reduced *B. scoparia* growth and fecundity compared to fallow treatment but the effects were not as dramatic as compared to the effects of barley or corn (Table 2, Figure 3, Figure 4). *B. scoparia* width was narrowest in barley and corn at 0.26 and 0.37 m, respectively, followed in ascending order by *B. scoparia* in sugar beet and soybean at 0.53 and 0.60 m, respectively (Table 2). *B. scoparia* was widest at 0.76 m in fallow plots. *B. scoparia* in barley had the least number of primary branches at 25.7, followed in ascending order by *B. scoparia* in sugar beet, corn, and soybean at 44.9, 49.9, and 50.3 primary branches, respectively (Table 2). For fallow, *B. scoparia* had 53.3 primary branches (HSD=2.1). *B. scoparia* biomass plant⁻¹ was least in corn and barley at 77 g and 107 g, respectively, followed in ascending order by *B. scoparia* biomass plant⁻¹ in soybean and sugar beet at 177 g, and 212 g, respectively, and was greatest in fallow at 600 g (Table 2). Thus, *B. scoparia* biomass plant⁻¹ was reduced by 87, 82, 70, and 65% in corn, barley, soybean, and sugar beet, respectively, when compared to the fallow treatment. The same trend was observed with respect to biomass m⁻². *B. scoparia* in corn and barley had the lowest biomasses m⁻² at 2,363 g, and 3,254 g, respectively, followed in ascending order by *B. scoparia* biomasses in soybean and sugar beet at 5,375 g, and 6,430 g m⁻², respectively, and was greatest in fallow at 18,211 g m⁻² (Table 2), which translate to 87, 82, 70, and 65% less biomass m⁻² in corn, barley, soybean, and sugar beet, respectively. Seed production plant⁻¹ was lowest in corn and barley at 5,227 and 9,392 seeds plant⁻¹, respectively, followed in ascending order by *B. scoparia* in soybean and sugar beet at 38,029 and 45,904 seeds plant⁻¹,

respectively, and was greatest in fallow at 231,979 seeds plant⁻¹. *B. scoparia* seed production plant⁻¹ in corn, barley, soybean, and sugar beet was 98, 96, 84 and 80% less, respectively, compared to the seeds plant⁻¹ in fallow (Table 2). Seed production m⁻² were lowest for *B. scoparia* in corn and barley at 158,498 and 284,788 seeds m⁻², respectively, followed in ascending order by *B. scoparia* in soybean and sugar beet at 1,153,256 and 1,391,927 seeds m⁻², respectively, and was highest in fallow at 7,034,239 seeds m⁻² (Table 2). *B. scoparia* seeds m⁻² was reduced by 98, 96, 84, and 80% in corn, barley, soybean, and sugar beet, respectively, compared to *B. scoparia* in fallow. Among the different crops, there were additional differential effects. Crop treatment affected the number of days for *B. scoparia* to reach 50% flowering ($p<0.001$, Figure 2B) with barley having the greatest effect. Time to 50% flowering was shortest in sugar beet and soybean at 66.2 and 66.8 days, respectively, took longer in corn and fallow at 81.4 and 102.2 days, respectively, and was greatest in barley at 113.4 days (HSD=2.67). *B. scoparia* was tallest in fallow at 1.66 m followed in descending order by *B. scoparia* in corn (1.64 m), soybean (1.44 m), sugar beet (1.40 m), and was shortest in barley at 0.69 m (HSD=0.0178) [Figure 2A]. Crop treatment and *B. scoparia* density affected final height (both with $p<0.001$, Figure 2A, Figure 2C) but no interaction was observed between the two factors ($p=0.261$).

Table 1

Results of split-plot analysis of variance test showing *F* statistics and *P* values for eight response variables across six *Bassia scoparia* densities in four crops (sugar beet, soybean, barley, corn) and fallow combined over two years.

Response Variable	Independent variable					
	Crop		<i>B. scoparia</i> density		Interaction	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Width	941.3	<0.001	408.3	<0.001	10.2	<0.001
Primary branches	590.3	<0.001	136.2	<0.001	4.02	<0.001
Biomass plant ⁻¹	702.9	<0.001	271.8	<0.001	4.1	<0.001
Biomass m ⁻²	702.9	<0.001	799.4	<0.001	4.1	<0.001
Seeds plant ⁻¹	4418	<0.001	822.6	<0.001	32.0	<0.001
Seeds m ⁻²	4418	<0.001	1004	<0.001	32.0	<0.001
Height	999.6	<0.001	56.95	<0.001	1.20	0.261
Days to flowering	1293.3	<0.001	0.12	0.988	0.11	1.000

Table 2

Growth and fecundity of *Bassia scoparia* in four crops (sugar beet, soybean, barley, corn) and fallow averaged across two years when grown near Huntley, MT. Where analyses were conducted with transformed values (*log e*), transformed means and HSD values are presented in italics. In these instances, non-italicized means are reverse transformed values. Means followed by the same letter within a response variable are not significantly different at Tukey-Kramer's HSD ($\alpha = 0.05$).

Crop	Final width	Primary branches	Biomass plant ⁻¹	Biomass m ⁻²	Seeds plant ⁻¹	Seeds m ⁻²
	m	no. plant ⁻¹	g	g	no.	no.
Fallow	0.76	53.3a	600	18,211	231,979	7,034,239
	-0.3a		6.4a	9.8a	12.4a	15.8a
Sugar beet	0.53	44.9c	212	6,430	45,904	1,391,927
	-0.6b		5.4b	8.8b	10.7b	14.1b
Soybean	0.60	50.3b	177	5,375	38,029	1,153,256
	-0.5c		5.2c	8.6c	10.5c	14.0c
Barley	0.26	25.7d	107	3,254	9,392	284,788
	-1.3e		4.7d	8.1d	9.1d	12.6d
Corn	0.37	49.9b	77	2,363	5,227	158,498
	-1.0d		4.4e	7.8e	8.6e	12.0e
HSD _{$\alpha = 0.05$}	<i>0.06</i>	2.20	<i>0.13</i>	<i>0.13</i>	<i>0.10</i>	<i>0.10</i>

B. scoparia's response to increasing *B. scoparia* densities were complex. *B. scoparia* density affected *B. scoparia* width, height, primary branches, biomass plant⁻¹, biomass m⁻², seeds plant⁻¹, and seeds m⁻² (all $p < 0.001$) but not days to flowering ($p = 0.98$) [Table 1]. Averaged across crop treatments, the increasing *B. scoparia* densities (3, 13, 24, 47, 94, and 188 plants m⁻²) resulted in decreasing *B. scoparia* final width (0.72, 0.59, 0.50, 0.44, 0.38, and 0.31 m, respectively), decreasing number of primary branches (54, 48, 45, 43, 40, and 37, respectively, with HSD=2.4), decreasing biomass plant⁻¹ (414, 260, 198, 149, 111, and 97 g), and decreasing seeds plant⁻¹ (75, 51, 34, 24, 16, and 11 x 1000 seeds, respectively) but also resulted in increasing *B. scoparia* height (1.23, 1.28, 1.35, 1.39, 1.43, and 1.5 m, respectively, HSD=0.018), increasing biomass m⁻² (1.24, 3.37, 4.75, 6.99, 10.3, and 18.2 kg, respectively), and increasing seeds m⁻² (0.244, 0.667, 0.824, 1.126, 1.514, and 2.122 x 10⁶ seeds, respectively) [Table 3]. *B. scoparia* biomass plant⁻¹ decreased by as much as 77% when *B. scoparia* density increased from 3 to 188 plants m⁻². However, *B. scoparia* biomass m⁻² increased 14-fold when *B. scoparia* density increased from 3 to 188 plants m⁻². The increase in *B. scoparia* density from 3 to 188 plants per m² reduced seeds plant⁻¹ by 85% but increased overall seed production m⁻² 9-fold.

Table 3

Mean growth and fecundity characteristics of *Bassia scoparia* as influenced by six weed densities (3, 13, 24, 47, 94, and 188 plants m⁻²) averaged across two years when grown near Huntley, MT. Where analyses were conducted with transformed values (*log e*), transformed means and HSD values are presented in italics. In these instances, non-italicized means are reverse transformed values. Means followed by the same letter within a response variable are not significantly different at Tukey-Kramer's HSD ($\alpha = 0.05$).

<i>B. scoparia</i> density	Final width	Primary branches	Biomass plant ⁻¹	Biomass m ⁻²	Seeds plant ⁻¹	Seeds m ⁻²
plants m ⁻²	m	no. plant ⁻¹	g	g	no.	no.
3	0.72	54.2a	414	1,243	74,787	224,381
	-0.3a		6.0a	7.1f	11.2a	12.3f
13	0.59	48.2b	260	3,377	51,380	667,904
	-0.5b		5.6b	8.1e	10.8b	13.4e
24	0.50	45.5c	198	4,752	34,362	824,638
	-0.7c		5.3c	8.5d	10.4c	13.6d
47	0.44	43.0d	149	6,989	23,961	1,126,133
	-0.8d		5.0d	8.9c	10.1d	13.9c
94	0.38	40.5e	111	10,388	16,115	1,514,809
	-1.0e		4.7e	9.2b	9.7e	14.2b
188	0.31	37.5f	97	18,241	11,238	2,112,748
	-1.2f		4.6f	9.8a	9.3f	14.6a
HSD _{$\alpha = 0.05$}	<i>0.07</i>	2.44	<i>0.14</i>	<i>0.14</i>	<i>0.12</i>	<i>0.12</i>

Significant interactions were observed between crop and *B. scoparia* density for final width, final number of primary branches, biomass plant⁻¹, biomass m⁻², seeds plant⁻¹, and seeds m⁻² (all $p < 0.001$) [Table 1, Figure 3, and Figure 4]. However, most significant differences were only observed between fallow and crop treatments rather than among crops except for the seeds plant⁻¹ and seeds m⁻² response variables. In both instances, density effects were limited for barley and corn crops (Figure 4A and 4B). In terms of seed production plant⁻¹ in each crop treatment, the increased *B. scoparia* density showed a decreasing trend (Figure 4A). In fallow, there were 609,138 seeds plant⁻¹ at the lowest density of 3 plants m⁻² but started to be reduced at density of 24 plants m⁻² density with 255,148 seeds plant⁻¹. In sugar beet, there were 143,889 seeds plant⁻¹ at 3 plants m⁻² density but significant reduction started at 13 plants m⁻² density with 66,890 seeds plant⁻¹. In soybean, there were 84,770 seeds plant⁻¹ at lowest density, but a significant reduction started at 13 plants m⁻² density with 63,634 seeds plant⁻¹. In barley, there were 15,195 seeds plant⁻¹ at the lowest density but started to be reduced at 94 plants m⁻² density with 7,074 seeds plant⁻¹. In corn, seeds per plant was 20,729 at lowest density but started to be reduced at density of 13 plants

m^{-2} density with 14,056 seeds plant^{-1} (Figure 4A). In terms of *B. scoparia* seed production per area, the increased *B. scoparia* density showed an increasing trend in seeds m^{-2} from each crop treatment (Figure 4B). In all crop treatments, seed production per area started to be increased starting at 13 plants per m^2 . At the lowest density, seed production was 1,827,391 seeds m^{-2} in fallow, 431,663 seeds m^{-2} in sugar beet, 254,308 seeds m^{-2} in soybean, 45,583 seeds m^{-2} in barley, and 62,187 seeds m^{-2} in corn. At 13 plants m^{-2} density, seed production per area increased to 5,903,170 seeds m^{-2} in fallow, 869,523 seeds m^{-2} in sugar beet, 827,199 seeds m^{-2} in soybean, 171,305 seeds m^{-2} in barley, and 182,736 seeds m^{-2} in corn. In corn, the further increase in *B. scoparia* density from 13 to 188 plants m^{-2} did not increase seed production m^{-2} (from 182,736 to 196,339 seeds m^{-2}) (Figure 4B). Neither crop nor *B. scoparia* density affected 1000-seed weight ($p=0.214$ and $p=0.061$, respectively), seed viability ($p=0.878$ and $p=0.056$, respectively) and radicle length ($p=0.216$ and $p=0.858$, respectively) [Data not shown].

As a general rule, *B. scoparia* grew taller and produced less seeds plant^{-1} as densities increased (Table 3, Figure 2, and Figure 4). This observation was similar to previous work⁴⁰. In our study, seed production plant^{-1} started to be affected at a density of 13 and 24 plants m^{-2} (Table 3 and Figure 4). This occurred regardless of crop treatment indicating that weed to weed competition became significant at this point in these crop canopies. With that said, it is important to emphasize that even though *B. scoparia* seeds plant^{-1} were decreased as the result of increased *B. scoparia* densities, the total biomass, and total seeds produced per unit area (m^2) were greatly increased by the higher *B. scoparia* densities (Table 3, Figure 3, and Figure 4). This indicates that high densities allowed *B. scoparia* plants to better capture and exploit available resources. Interestingly, the patterns of *B. scoparia* seed production observed in fallow, soybean, and sugar beet were less pronounced in corn and barley plots, which may be an indication that crop on weed competition in these crops was a greater factor on *B. scoparia* performance than weed to weed competition regardless of *B. scoparia* densities.

Discussion

Corn had the greatest negative effect on *B. scoparia* biomass and *B. scoparia* seed production. Even though *B. scoparia* plants were tallest in corn compared to other crops, they were thinner stemmed, and had fewer secondary branches, and leaves, resulting in lower biomass and seed production (Table 2, Figure 3, and Figure 4). This dramatic change in *B. scoparia*'s architecture is likely due to its struggle for light interception within the corn canopy. Under irrigated and high fertilizer production system, corn rapidly accumulates biomass and height, thus, light becomes the primary source of competition for weeds⁵⁷. Increases in total canopy leaf area index, height, rate of canopy closure and height at which the leaf area occurs have all been associated with improved tolerance and suppressive ability of corn relative to weeds⁵⁸⁻⁶⁰. In particular, corn's relative growth rate and specific leaf area strongly correlated with relative competitiveness among corn cultivars⁶¹. This was demonstrated in sweet corn, where the dense canopy and rapid growth of the hybrid variety Rocker was found to contribute to season long performance of sub-rates of the herbicide sethoxydim against *Panicum miliaceum* (L.) fecundity⁶².

Barley suppression of *B. scoparia* growth and fecundity was second only to corn. Barley had the greatest effect in reducing *B. scoparia* height, width, number of primary branches, and in increasing the number of days for *B. scoparia* to reach flowering (Figure 1, Figure 2B, and Figure 3). Barley was harvestable prior to *B. scoparia* flowering, which suggest that planting barley provides a significant window of opportunity for preventing *B. scoparia* reproduction through post-harvest herbicide burndown applications, or targeted tillage. In barley, the primary branches and leaves of *B. scoparia* were only formed in the upper half of the *B. scoparia* plants. This was likely due to the dense barley canopy that prevented light from reaching the under canopy as barley rapidly achieved row closure. Despite early season competition, enough resources and time remained after barley senescence for *B. scoparia* to recover and significantly reproduce if allowed. This enabled *B. scoparia* to produce more secondary and tertiary branches producing a bushier appearance post-barley senescence and resulted in a significant gain of late season plant biomass and production of seeds. In wheat, it was found that uncontrolled and late emerging *B. scoparia* plants contribute in excess of 100,000 seed m⁻² when left to set seed post-harvest⁶³. In our trials, *B. scoparia* seed production, post barley senescence, was in excess of 200,000 seed m⁻². As a general rule, barley develops faster and senesces earlier than spring wheat. In addition to these differences, we observed a significant reduction in the number of *B. scoparia* plants surviving at the end of the season in the high *B. scoparia* density, barley plots (data not shown). This reduction in survival was not observed in any other crop treatments and demonstrates just how extreme the early season competition barley applied to *B. scoparia* populations. Tremendous effects of barley on *B. scoparia* occurred despite barley being a relatively short crop among our cropping treatments. This suggests that parameters other than crop height are important contributors to the competitive ability of barley. Over the years, many different studies have shown the competitiveness of barley against weeds including *B. scoparia*. Growth parameters such as tillering capacity, leaf angle, early season vigor and time to maturity are crop traits previously associated with competitiveness of cereal crops including barley⁶⁴⁻⁷¹. Lemerle and colleagues highlighted vigorous early growth, root competitiveness and allelopathy as significant contributors to the competitiveness of barley and wheat cultivars against weeds⁷². Others studies have shown that even though tall wheat cultivars are more competitive against weeds than the short, amongst the most competitive are several short wheat cultivars as well⁷³⁻⁷⁶. In another study that compared competitiveness among cereals, spring barley and winter cereals were found most effective in reducing the density and biomass (per unit area) of dicot and monocot weed species, with spring barley being most effective in suppressing dicot weeds and the winter cereals being most effective in suppressing monocot weeds⁷⁵. Replacement-series pot experiments conducted in the greenhouse have previously shown that cool temperatures in combination with shade adversely affected *B. scoparia* competitiveness⁷⁷. This was attributed to the high energy cost of the C₄ pathway in *B. scoparia* as compared to the C₃ pathway in cereals⁷⁸. Another study showed that under warm, dry, shady conditions, *B. scoparia* has higher dark respiratory CO₂ losses, lower net photosynthetic rates, and lower water use efficiency as compared to wheat or barley⁷⁷. Light interception by a leafy, cold-tolerant crop grown early in the season such as barley appears particularly effective in suppressing *B. scoparia* establishment and development⁷⁷.

Unlike corn and barley, *B. scoparia* would outgrow soybean and sugar beet. *B. scoparia* in soybean produced less biomass and seeds (both per plant and per unit area) than in sugar beet suggesting that soybean is more competitive than sugar beet. Many different studies have shown that soybean is not very competitive against weeds. One study has shown that soybean is not very competitive at the early growth stages and soybean cultivars vary in their competitive abilities against different weeds with as much as 45% difference in weed biomass observed among soybean cultivar treatments^{52,79,80}. Another study showed that variation in soybean canopy width, height, area, and volume have no consistent relationship with soybean competitiveness against weeds^{81,82}. Instead, competitiveness was found to be associated with the increased vegetative growth of late-maturing soybean cultivars⁸². To improve weed suppression by soybeans, recommendations that increase the rate of row closure have been suggested including decreasing soybean row width, and increasing planting density^{83,84}. Lastly, sugar beet had the least effect on *B. scoparia* as compared to all other crops in this study. *B. scoparia* biomass and seed production were greatest in sugar beet, which was second only to fallow (Figure 3 and Figure 4). Like soybean, many studies have shown that sugar beet is poor competitor against weeds. Due to its low-stature and rosette growth habit, sugar beet has been shown susceptible to competition from *B. scoparia* with significant reductions in yield reported even at low *B. scoparia* densities⁸⁵⁻⁹¹. In the past, sugar beet's sensitivity to weed competition and the many different herbicides available for weed control have led to a complex weed management program that involved mechanical weeding and several herbicide modes of action⁹². Despite the complexity, these herbicide regimens were only 32% effective against *B. scoparia*, which is lower than those used in corn (99%), soybean (96%), winter wheat (93%) or fallow (97%)⁸⁶. Glyphosate-resistant sugar beets dramatically changed the weed management landscape for this crop^{85,86}. Unfortunately, glyphosate-resistant *B. scoparia* populations have evolved in several sugar beet growing regions and multi-pronged strategies for managing these populations are critically needed^{24,85,86,95}.

This study eliminated herbicide effects from those associated with cropping choice. This was particularly important as herbicide options are an especially powerful contributor to *B. scoparia* control, particularly in corn and barley^{44,86}. Our study demonstrated the heightened competitiveness of corn and barley relative to other cropping systems that is independent of herbicide treatment. In addition, nitrogen rates were limited to high (corn and soybeans) and low rates (barley and sugar beets). As quickly becomes apparent while observing the response data, *B. scoparia* responses were independent of nitrogen rate. The other common cultural practices associated with each crop species were accommodated by the trial design. Cultural practices (i. e., cultivar choice, irrigation, planting date, seeding rate, row spacing, fertilizer rate) were admittedly confounded with the crop's competitive effects on the weed's overall performance and they may have had a significantly affected outcomes for *B. scoparia* growth and fecundity.

For our trials, *B. scoparia* was harvested on a single day independent of crop harvest. This disjunction may misrepresent the differences in control different cropping systems offer, particularly barley where crop harvest occurred prior to weed flowering. This may be relevant not only for a particular crop but for crop usage as well i.e., hay barley and silage corn. Recently, pulses (i.e., pea, lentil, and chickpea) and oil

crops (i.e., camelina, canola) have gained popularity within Montana due to increased demand for plant-based protein for food and feed, and for biofuels. How these crops relate to each other and to the crops used in this study would be of considerable interest especially given their relative sensitivity to herbicides.

In conclusion, corn and barley were the most *B. scoparia* suppressive crops. Corn's effects on *B. scoparia* were primarily on biomass, height, and seed production. These effects were likely due to corn's dense, tall canopy that effectively shaded the *B. scoparia* stand. The most dramatic effect barley had on *B. scoparia* was in delaying flowering until after barley senescence. This may present an opportunity to virtually eliminate *B. scoparia* seed production if post-senescence weed control practices are applied in a timely manner. If not properly handled however, enough time and resources are available post barley senescence for *B. scoparia* to recover and produce a significant amount of weed seeds in the remainder of the cropping season. Regardless of post-harvest treatment, *B. scoparia* seed production under barley was still significantly reduced relatively with soybean and sugar beet. Barley's effects on *B. scoparia* likely relate to its ability to rapidly grow and achieve row closure under cool conditions. Soybean and sugar beet were not particularly competitive with *B. scoparia*. Between them, soybean was the better. Techniques to enhance crop competition include choosing competitive cultivars, narrowing rows, increasing plant population, and orienting rows from east to west⁹⁶. Given the advent of glyphosate-resistant *B. scoparia* in sugar beet cropping systems and the particular sensitivity of sugar beets to weedy competition, *B. scoparia* control in sugar beet is a particularly a troublesome issue. With no alternative herbicide option that is effective for its control, *B. scoparia* will greatly influence key weed management decisions in sugar beet farms especially when conservation tillage systems (i.e., strip tillage, no-till) are adopted. Additionally, *B. scoparia* possess biological traits (i.e., high genetic diversity, highly outcrossing, short life cycle, efficient seed dispersal mechanism) that will likely enable it to persist and evolve resistance to a new herbicide site of action (SOA) if introduced as added trait in sugar beet (i.e., stacking dicamba resistance to glyphosate-resistant sugar beet to control glyphosate-resistant *B. scoparia* field populations). There is no guarantee that a new SOA will be used/misused with limited intensity and coverage to control resistant weed populations, thus selection pressure towards resistance to multiple SOAs is expected to be high and the utility of the added herbicide trait will be at risk of being lost to resistance. Gaines et al. argued that if the manner of herbicide use remains unchanged, the rate of evolution for multiple herbicide resistance will eventually exceed the rate of new herbicide discovery, and herbicide options available for weed control in certain crops will be much limited in the future even as new SOAs are discovered⁹⁷. An example is the water hemp [*Amaranthus tuberculatus* (Moq.) J. D. Sauer] population collected from a continuous soybean field reported resistant to six SOAs⁹⁸ which extremely limited herbicide options available for its control. Thus, the importance of integrated weed management approaches in conjunction with other methods (i.e., depleting soil seedbank, maximizing cropping systems diversity, effective monitoring and rapid diagnosis for emerging resistance) to combat herbicide resistance have been greatly emphasized since a new SOA will not solve the issue⁹⁷. In the future, long rotations away from sugar beet and towards crops (and herbicides) that are more suppressive will likely play an important role in *B. scoparia* management for sugar beet production.

In a time when the advance of herbicide-resistant *B. scoparia* populations is rapid and widespread⁹⁹, and as herbicide options will increasingly be limited with time⁹⁷, taking advantage of the competitive abilities of crops is not only a robust and effective strategy for short-term weed control but also holds great value in the long-term reduction of *B. scoparia* soil seedbank through reduced weed seed rain⁹⁶. Additionally, this strategy is simple, inexpensive, and compatible with the mechanized crop production systems in the US Great Plains. Its integration with other weed management strategies such as use of suppressive cultivars, use of cover crops, modifying row width spacing, increasing planting density, and use of harvest weed seed control (HWSC) systems^{48,93,94}, could potentially be even more effective in the long-term reduction of *B. scoparia* soil seedbank. In the future, studies that determine effects of competitive crops and enhanced crop competition on the life history traits of herbicide-resistant *B. scoparia* are needed to better understand dynamic weed-crop interactions within a cropping environment and to provide better field recommendations. The results of this study are only one part of the answer in addressing the ever-evolving *B. scoparia* weed problem.

Methods

Plant Material. Mature seeds from an herbicide-susceptible *B. scoparia* accession collected from a nearby field at Montana State University Southern Agricultural Research Center (MSU-SARC) near Huntley, MT, were used in this study. The *B. scoparia* accession was obtained with permission from the local research station and complied with the relevant institutional, national, and international guidelines and legislation. The crop seeds were obtained from a local seed distributor (Northern Seed, 1400 Minnesota Ave, Billings, MT 59101). The crop varieties used were DKC36-30RIB (DEKALB®, Monsanto Technology LLC, 800 N. Lindbergh Boulevard, St. Louis, MO 63167) for corn, DKB008-81 (DEKALB®, Monsanto Technology LLC 800 N. Lindbergh Boulevard, St. Louis, MO 63167) for soybean, BetaShield BTS39RR8N RP (BetaSeed, Inc. 5746 50TH Ave S., Moorhead, MN, 56560) for sugar beet and Moravian 115 (MillerCoors, LLC, 311 10th Street, Golden, CO, 80401) for barley.

Field Establishment and Experimental Design. The study was conducted at Montana State University – Southern Agricultural Research Station (MSU-SARC) in Huntley, between early to mid-April of 2015 and 2016. The trials used split plots deployed within a randomized complete block design with four replications. Whole plots were the cropping treatments, while sub-plots were the six *B. scoparia* density treatments randomly placed within each whole plot.

Treatments. The whole-plot crop treatments were sugar beet, soybean, barley, corn, and fallow (bare ground). The crop treatments were randomly assigned within each block. Corn was seeded at a rate of 101,800 seeds ha⁻¹ with rows spaced at 76 cm. Soybean was seeded at a rate of 432,400 seeds ha⁻¹ with rows spaced at 15 cm. Sugar beet was seeded at 123,500 seeds ha⁻¹ with rows spaced at 61 cm. Barley was seeded at 2,100,300 seeds ha⁻¹ with rows spaced at 19 cm. The whole-plot were 6 m by 4.5 m and spaced 4.5 m from neighboring whole-plots. The sub-plot treatments were the increasing *B. scoparia* densities of 1, 5, 9, 18, 36 and 72 plants per 0.36 m² (0.6 x 0.6 m) or equivalent to 3, 13, 24, 47,

94 and 188 plants m^{-2} . The six *B. scoparia* density treatments were randomly spaced within each whole plot. Each subplot was 0.6 m by 0.6 m and were spaced 0.6 m from each other. The sub-plot treatments were arranged in a zigzag pattern within the middle rows of each plot. A thin wooden board (same dimensions as the sub-plot) with holes equally spaced from each other was used as a sowing guide for *B. scoparia* densities. To ensure at least one *B. scoparia* seedling emerged per hole, 10 to 20 *B. scoparia* seeds were hand sown through the appropriate holes of the wooden board based on their density treatment. Sowing of *B. scoparia* occurred immediately following crop seeding to simulate emergence in a freshly prepared field. *B. scoparia* seedlings were thinned down to respective *B. scoparia* density treatments one week after *B. scoparia* emergence. In 2015, barley emerged on April 17th, sugar beet on May 18th, soybean on May 26th, and corn on May 21st, and in these crops *B. scoparia* emerged on April 13th, May 16th, May 21st, and May 16th, respectively, while *B. scoparia* in the fallow treatment emerged on April 13th. In 2016, barley emerged on April 20th, sugar beet on May 25th, soybean on May 23rd, and corn on May 18th, and in these crops *B. scoparia* emerged on April 17th, May 20th, May 21st, and May 16th, respectively, while *B. scoparia* in the fallow treatment emerged on April 20th. In the fallow treatment, *B. scoparia* seeds were sown on the same day as *B. scoparia* seed sowing date in the barley crop. Seed germination was stimulated by either rainfall or irrigation within a week after crop planting and *B. scoparia* seed sowing. Irrigation was applied as needed throughout the duration of the study. To keep whole-plots free of extra *B. scoparia* plants and other weed species, herbicides were applied at field use rates in-crop as needed. Glyphosate (Roundup PowerMax®, Monsanto Company, 800 North Lindberg Ave., St. Louis, MO) was applied at $1.36 \text{ kg ae ha}^{-1}$ in fallow, soybean, and sugar beet canopy treatments. Dicamba (Clarity®, BASF, Research Triangle Park, NC) was applied at 280 g ae ha^{-1} in the corn canopy treatments and a premix of bromoxynil and pyrasulfotole (Huskie®, Bayer Crop Science, Research Triangle Park, NC 27709) was applied at 0.229 and $0.040 \text{ kg ai ha}^{-1}$ respectively, in the barley crop treatments. Plastic boxes were used to cover the sub-plots prior to herbicide applications to protect the *B. scoparia* density treatments. Hand-weeding inside the sub-plots was completed as needed to maintain *B. scoparia* density treatments and to keep sub-plots free of other weed species and extra *B. scoparia* plants. Prior to crop planting, the experimental area was chisel-plowed to incorporate spring barley stubble from the previous year and early weed flushes (at least two) were over-sprayed with glyphosate (Roundup PowerMax®, Monsanto Company, 800 North Lindberg Ave., St. Louis, MO) at $1.36 \text{ kg ae ha}^{-1}$ as a burndown to establish a clean field. Nitrogen fertilizer (46-0-0) was incorporated in the soil at 91 kg N ha^{-1} in corn and soybean plots, and at 46 kg N ha^{-1} in sugar beet and barley plots prior to crop planting. Crop seeds were planted and mature *B. scoparia* seeds from the herbicide-susceptible *B. scoparia* accession were sown within 3 days after crop seeding.

***B. scoparia* growth and fecundity.** *B. scoparia* plant height, canopy, and number of branches were measured for three representative *B. scoparia* plants from each experimental plot at the maximum vegetative stage to determine *B. scoparia* growth. Dates of when the *B. scoparia* plants from each treatment were first observed to undergo flower initiation, flowering, and seed set were recorded. *B. scoparia* reproduction data on *B. scoparia* days-to-flower initiation, days-to-flowering, and days-to-seed set were determined by the number of days (starting from *B. scoparia* emergence) it took for 50% of the

B. scoparia plants in each experimental plot to first form reproductive structures, protruded inflorescence and shed pollens, and produced mature dark brown seeds, respectively. *B. scoparia* seed production was determined by harvesting three representative mature *B. scoparia* plants from each experimental plot. Seeds from the mature *B. scoparia* plants were separated and cleaned. All the seeds from the three harvested *B. scoparia* plants were mixed thoroughly, pooled and total weight of seeds were recorded. From the seed pool, 1000 seeds were counted, and the weight was recorded. The process was repeated three times. The total weight of the pooled seeds was divided by its average 1000-seed weight multiplied by a thousand to determine the total number of seeds from the three *B. scoparia* plants. The total number of seeds was divided by three to determine *B. scoparia* seeds plant⁻¹.

B. scoparia seed viability and seedling vigor. Seed viability test was done at the MSU-SARC physiology laboratory in 2015 and 2016. A total of 125 seeds from each treatment were tested for viability and seedling vigor. Twenty-five seeds were placed in between two layers of filter papers (Whatman®, Grade 2, Sigma-Aldrich Inc., St. Louis, MO 63178, USA) inside 10-cm diameter petri dishes (Sigma-Aldrich, Sigma-Aldrich Inc., St. Louis, MO 63178, USA) The seeds were soaked with 10ml of double distilled water. *B. scoparia* seed germination does not require light thus, petri dishes were wrapped in aluminum foil to maintain moisture within each plate and then the plates were placed in an incubator (VMR International, Sheldon Manufacturing Inc., Cornelius, OR 97113, USA) at 25°C for optimum *B. scoparia* seed germination^{54,55}. Radicle length of three randomly selected seedlings from each petri dish was measured 24 h after incubation. Germinated seedlings were counted daily for 15 days and then terminated. Ungerminated seeds were tested for viability using a 1% w/v tetrazolium chloride solution³³. Seeds were considered germinated when the radicles emerged, and the tip of the radicle uncoiled⁵⁶. Seed viability was calculated as the percentage of germinated seeds and seeds that were positive in the tetrazolium chloride test. The petri dish experiment was conducted in a randomized complete block with five replications using the shelves inside the incubator as blocks.

Data analyses. Data were subjected to *type 3 split plot analysis of variance test* ($\alpha = 0.05$) combined over trial years following the *procmixed* procedure in SAS (Statistical Analysis Systems®, version 9.2, SAS Institute Inc., SAS Campus Drive, Cary, NC 27513-2414) to test the significance of trial year, treatment, replication, and interaction. The trial year, treatment, and interaction were considered fixed effects. Replication, trial year*replication, and treatment*replication were considered random effects. All observations were transformed to their natural logarithm (*log e*) values before being subjected to analysis of variance test except for observations taken for days to flowering, height, and number of primary branches. Data assumptions for normality of residuals and homogeneity of variance were met when tested with shapiro-wilk and levene's test, respectively, following the *procunivariate* procedure in SAS. Means were separated using Tukey-Kramer's HSD ($\alpha = 0.05$) test. Results from the two trial years were not significantly different across the response variables. Given the trends within the data being consistent across trial years, the results from two trials were combined for simplicity of presentation.

Declarations

Data availability

Data for the current study will be made available by the corresponding author upon request.

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Author contributions

C.L. conducted the experiments. A.D. provided the analysis tools. C.L. and A.D. analyzed the data. C.L. and A.D. wrote and reviewed the manuscript. P.J. conceived, designed, and contributed the reagents/materials for the experiments.

Competing interests

The authors declare no competing interests.

Additional information

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Figures

Figure 1

Plant canopies displaying *Bassia scoparia* growth in fallow (A), sugar beet (B), soybean (C), barley (D), and corn (E) when grown near Huntley, MT in 2015 (left column) and in 2016 (right column).

Figure 2

Mean final height (A) and days to flowering (B) of *Bassia scoparia* as influenced by five cropping treatments (fallow, sugar beet, soybean, barley, corn), and mean height (C) of *Bassia scoparia* as influenced by six weed densities (3, 13, 24, 47, 94, 188 plants m⁻²) averaged over two years when grown near Huntley, MT. Means (bars ± standard errors) with the same letter are not significantly different at Tukey-Kramer's HSD ($\alpha = 0.05$).

Figure 3

Mean biomass plant⁻¹ (A), biomass m⁻² (B), number of primary branches (C), and width (D) of *Bassia scoparia* as influenced by five cropping treatments (fallow, sugar beet, soybean, barley, corn) and six weed densities (3, 13, 24, 47, 94, 188 plants m⁻²) over two years when grown near Huntley, MT. Transformed values ($\log e$) were used to compare means and the means reverse transformed. Means

(bars $\pm$ standard errors) with the same letter within a cropping treatment are not significantly different at Tukey-Kramer's HSD ($\alpha = 0.05$).

Figure 4

Mean seeds plant⁻¹ (A) and seeds m⁻² (B) of *Bassia scoparia* as influenced by five cropping treatments (fallow, sugar beet, soybean, barley, corn) and six weed densities (3, 13, 24, 47, 94, 188 plants m⁻²) over

two years when grown near Huntley, MT. Transformed values ($\log e$) were used to compare means and the means reverse transformed. Means (bars $\pm$ standard errors) with the same letter within a cropping treatment are not significantly different at Tukey-Kramer's HSD ($\alpha = 0.05$).