

Palmer amaranth (*Amaranthus palmeri*) adaptation to US Midwest agroecosystems

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2 ABSTRACT

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Keywords: Evolution Flowering Management Pigweed Weed

INTRODUCTION

Palmer amaranth (*Amaranthus palmeri* S. Watson) is currently ranked as one of the most economically detrimental weed species to cropping systems in the United States (ADD CITATION; WSSA Survey Perhaps). Unmanaged Palmer amaranth plants compete for water, light, and nutrients, which can drastically impact crop yields (Berger et al., 2015). For example, Palmer amaranth has been documented to reduce up to 91%, 68%, and 54% corn (Massinga et al., 2001), soybean (Klingaman and Oliver, 1994), and cotton (Morgan et al., 2001) yields, respectively. Moreover, Palmer amaranth has shown a remarkable capacity to evolve resistance to herbicides. To date, Palmer amaranth has evolved resistance to eight herbicide sites of action (Heap, 2021), increasing the weed management complexity (Lindsay et al., 2017). Thus, Palmer amaranth poses an economical and environmental risk to sustainable agriculture.

Palmer amaranth is a fast growing summer annual forb indigenous to the Sonoran Desert (Sauer, 1957). The species would eventually emerge as a threat to US agriculture in the 1990s. Palmer amaranth weediness is likely a result of human-assisted selection in combination with plant biology. Farm mechanization, adoption of conservation agriculture (e.g., no-till), and reliance on herbicides for weed management are the main human-mediated selection of Palmer amaranth into cropping systems (Ward et al., 2013). On the other hand, Palmer amaranth is a prolific seed producer with a C4 photosynthetic apparatus (Wang et al., 1992). With a dioecy nature, Palmer amaranth male and female plants are obligate outcrosser species, increasing the chances of exchanging adaptive traits among plants (Oliveira et al., 2018). Also, Palmer amaranth small seed size (e.g, 1 mm) tend to thrive in no-tillage systems (Price et al., 2011), and spread across locations through farm equipment (Sauer, 1972), manure (Hartzler and Anderson, 2016), animals (Farmer et al.,

26 2017). The dispersal capacity of Palmer amaranth makes the species one of the most successful cases of
27 weed adaptation to current cropping systems.

28 Light and temperature are likely the main environment requirements for Palmer amaranth successful
29 grow and development (CITATION). Palmer amaranth is reported with an extended germination period
30 (Jha et al., 2010). Germination of Palmer amaranth is triggered by 18 C soil temperature (Keeley et al.,
31 1987), and optimal germination and biomass production occur at 35/30 C day and night temperatures (Guo
32 and Al-Khatib, 2003). In addition, Palmer amaranth establishment is human-mediated by tillage timings
33 and preemergence-applied herbicides (Chahal et al., 2021), which can result in weed germination shifts
34 (Sbatella and Wilson, 2010). Water has not shown to limit Palmer amaranth fitness. Under continuous
35 water stress, Palmer amaranth survived and produced at least 14000 seeds plant-1 (Chahal et al., 2018).
36 Seeds from Palmer amaranth growing with limited water conditions were heavier, less dormant, and
37 prompt for germination (Matzrafi et al., 2021). Growing conditions and management practices also
38 influence Palmer amaranth sex dimorphism and flowering pattern (Korres et al., 2017; Rumpa et al.,
39 2019). Therefore, Palmer amaranth has shown plasticity to evolve and adapt under selection pressure.
40 The continuous global temperature warming is likely impact agriculture and promote niches for Palmer
41 amaranth invasion/adaptation into new habitats. Currently, it is estimated that the greatest climatic risk
42 of Palmer amaranth establishment are agronomic crops in Australia and Sub-Saharan Africa (Kistner and
43 Hatfield, 2018). Temperature is a key factor limiting Palmer amaranth expansion to cooler geographies
44 (Briscoe Runquist et al., 2019); however, under future climate change Palmer amaranth is likely to expand
45 northward into Canada and Northern Europe (Kistner and Hatfield, 2018; Briscoe Runquist et al., 2019).

46 Palmer amaranth is already found in agronomic crops of South America (Larran et al., 2017; Küpper
47 et al., 2017) and Southern Europe (Milani et al., 2021). In the United States, Palmer amaranth is well
48 established in the Cotton Belt (Garetson et al., 2019; Bagavathiannan and Norsworthy, 2016) in the southern
49 United States but its range is expanding northward. For example, herbicide resistant Palmer amaranth
50 is widespread in Nebraska (Oliveira et al., 2021). There are some reported cases of Palmer amaranth in
51 Michigan (Kohrt et al., 2017) and Connecticut (Aulakh et al., 2021). Also, it is estimated that Palmer
52 amaranth can cause high damage to soybean fields in Illinois (Davis et al., 2015), which is concerning
53 as soybean along with corn make most of US Midwest agronomic hectares. In Iowa, a study showed
54 that Palmer amaranth is still not well adapted compared to waterhemp (*Amaranthus tuberculatus*) (Baker,
55 2021). Invasion and successful eradication of Palmer amaranth is documented in Minnesota (Yu et al.,
56 2021). Palmer amaranth infestations have not been detected in Canada; however, Palmer amaranth seeds
57 were detected in sweet potato slips in the country (Page et al., 2021). Palmer amaranth is still not as
58 well adapted and established to Northern as it is in the Southern North America. Therefore, its range of
59 expansion into new habitats is increasing. It seems fated the need to manage Palmer amaranth in agronomic
60 crops throughout multiple environments in the near future. Strategies on Palmer amaranth management
61 should encompass the agroecosystem level but not only attempts to eradicate the weed. Most tactics to
62 manage Palmer amaranth are based on technology fixes (Scott, 2011), which are short-term (e.g., herbicide
63 and/or tillage) rather than long-term weed management. Palmer amaranth management should be built on
64 minimizing the species ability to adapt, grow and develop into agroecosystems.

65 In the southeastern US, early growing Palmer amaranth is well known to have a higher impact on cotton
66 yields compared to late established plants (MacRae et al., 2013). In the northern states, Palmer amaranth
67 impact on the agroecosystem is recent. Studies investigating Palmer amaranth in those locations are limited
68 due to the plant classification as noxious weed species in some northern states (Yu et al., 2021). Nonetheless,
69 the continuous Palmer amaranth dispersal and potential establishment across the northern United States is

70 concerning and warrants investigations on species morphology in such environments. Understanding Palmer
 71 amaranth biology and growing strategies under different agroecosystems can enhance our knowledge on
 72 species adaptation and management practices. It can also aid in designing proactive and ecological tactics
 73 to limit the species range expansion, reduce its negative impact, and developing resilient and sustainable
 74 farming systems (MacLaren et al., 2020). Therefore, the objective of this study was to investigate the
 75 flowering pattern, gender, biomass production, and height of Palmer amaranth cohorts growing under corn,
 76 soybean and bareground across five locations in the United States Midwest.

MATERIAL AND METHODS

77 Plant material and growing conditions

78 A Palmer amaranth accession (Per1) from Perkins County, Nebraska, with no reported herbicide resistance
 79 according to Oliveira et al. (2021) was selected for this study. Three weeks prior to the onset of the field
 80 experiments, seeds were planted in plastic trays containing potting-mix. Emerged seedlings (1 cm) were
 81 transplanted into 200 cm⁻³ plastic pots (a plant pot-1). Palmer amaranth seedlings were supplied with
 82 adequate water and kept under greenhouse conditions at Arlington, Clay Center, Lincoln, and Macomb;
 83 and kept outdoors in Grant until the 2-3 leaf stage (5 to 8 cm height) when they were transported to the
 84 field.

85 Field study

86 The experiment was conducted in 2018 and 2019 under field conditions at five locations: Arlington,
 87 WI (43°18'N, 89°29'W), Clay Center, NE ('N, 'W), Grant, NE ('N, 'W), Lincoln, NE ('N, 'W)), and
 88 Macomb, IL ('N, 'W)).

89 Fields were conventionally tilled prior to crop planting. Corn hybrid and soybean varieties were planted
 90 in 76-cm row spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using
 91 Daymet weather data from June through September across the five locations in 2018 and 2019 (Correndo
 92 et al., 2021) (Figure 1)

Table 1. Field study attributes

Attributes	Arlington, WI	Clay Center, NE	Grant, NE	Lincoln, NE	Macomb, IL
Bareground					
Corn	Weed control	glyphosate	saflufenacil + imazethapyr + pyroxasulfone		
	Hybrid		DKC60-67		
	Seeding rate		86487		
	Weed control	glyphosate / S-metolachor	S-metolachlor + trazine + mesotrione, + bicyclopyrone		
	Stage 1 cohort	V2-3			
	Stage 2 cohort	V6-7			
Soybean	Variety	DSR-1950	AG21X8		
	Seeding rate	296400	321237		
	Stage 1 cohort	V1-2			
	Stage 2 cohort	V5-6			
	Weed control	glyphosate / S-metolachor	saflufenacil + imazethapyr + pyroxasulfone		
Planting day		May 10 to 20	May 10 to 14		
Soil	Type		Crete Silt Loam		
	Ratio (sand-clay-silt)		58-25-6.5		
	pH	6.6	6.5		
	Organic matter (%)		3		

93 The field experimental units were three adjacent 9.1 m wide (12 rows at 76.2 cm row spacing) by 10.7
 94 m long. The experimental design were arranged in factorial design with three crops, two transplanting

95 times simulating two cohorts, repeated across five locations. Each experimental unit was planted with
96 corn, soybean, or kept under bareground. The two transplanting timings were June 1 (first cohort) and
97 July 1 (second cohort). Palmer amaranth seedlings (potting mix + two seedlings) were transplanted (6 cm
98 deep and 8 cm wide). Forty-eight plants were equidistantly placed (0.76 m apart) between rows within
99 each crop (Figure 2). After a week, one plant was eliminated and one was kept, resulting in 24 plants per
100 experimental unit and transplanting time (Figure 2). When needed, Palmer amaranth plants were supplied
101 with water during the first week after transplanting.

102 After transplanting, Palmer amaranth flowering was monitored until the end of the study. When a plant
103 flowered, the day was recorded, plant sex was identified (male or female), plant height was measured from
104 soil surface to the top of plant. Also, aboveground plant biomass was harvest near soil surface and oven
105 dried at 65 C until reaching constant weight before weighing (g plant-1 was recorded).

106 Plants had to be harvested at flowering because Palmer amaranth is neither endemic in Wisconsin nor in
107 Illinois. In our study, all locations follow the methodology of plant harvest at flowering initiation, except in
108 Grant, NE. In this location, all Palmer amaranth plants were harvest at once on July 06, 2018 and 2019
109 (first cohort), and on August 17, 2018 and on July 31, 2019 (second cohort).

110 Statistical analyses

111 The statistical analyses were performed using R statistical software version 4.0.1.

112 Analyses of Palmer amaranth height and biomass were performed with a linear mixed model using *lmer*
113 function from “lme4” package (Bates et al., 2015). Plant height and biomass were log transformed to meet
114 model assumption of normality. In the model, crop (bareground, corn, soybean) was the fixed effect and
115 year nested with location the random effects. Analysis of variance was performed with *anova* function
116 from “car” package (Fox and Weisberg, 2018). Marginal means and compact letter display were estimated
117 with *emmeans* and *cld* from packages “emmeans” and “multcomp” (Hothorn et al., 2008).

118 The cumulative Palmer amaranth flowering estimation was determined using an asymmetrical three
119 parameter log logistic Weibull model of the drc package (Ritz et al., 2015).

$$Y(x) = 0 + (d - 0)\exp(-\exp(b(\log(x) - e)))$$

120 In this model, Y is the Palmer amaranth cumulative flowering, d is the upper limit (set to 100), and e is
121 the XXX, and x day of year (doy).

122 The doy for 10, 50, and 90% Palmer amaranth cumulative flowering were determined using the *ED*
123 function of drc package. Also, the 10, 50, and 90% Palmer amaranth cumulative flowering were compared
124 among crops and cohorts using the *EDcomp* function of drc package. The *EDcomp* function compares the
125 ratio of cumulative flowering using t-statistics, where P-value < 0.05 indicates that we fail to reject the null
126 hypothesis.

127 Palmer amaranth sex was fitted to a binary logistic regression (Bangdiwala, 2018). Binary logistic
128 regression is used for predicting binary classes, such as the probability of a plant being female in a
129 dioecious species. Prior to the analysis, all missing values were removed from the dataset. Also, data from
130 Grant was not used in this analysis due to the uniform plant harvesting at that location. The complete
131 dataset was splitted into 80% train and 20% test data. The 80% train is used for the model training and the
132 20% test is used for checking how the model generalized on unseen dataset. With 80% dataset, a binary
133 response variable, male (0) and female (1), was fitted to a generalized linear model (*glm* function) including

134 day of year harvest, height, weight, crop and month as independent variables. The model family was
135 binomial with a logit function. The model fit was assessed through pseudo R-squared values (McFadden,
136 Cox and Snell, Cragg and Uhler) and likelihood ratio using *nagelkerke* function (“rcompanion” package).
137 The marginal effects computation was performed with Average Marginal Effects at every observed value of
138 x and average across the results (AMEs) (Leeper, 2017) using *margins* function from “margins” package.
139 The rest 20% dataset was predicted using *predict* function with a cutoff estimation for male or female using
140 *performance* function. The model quality prediction from the classification algorithm was measured with
141 precision (*precision* function), recall (*recall* function) and F1 score (*f_meas* function) using the “yardstick”
142 package. The precision determines the accuracy of positive predictions (female plants), recall determines
143 the fraction of positives that were correctly identified, and F1 score is a weighted harmonic mean of
144 precision and recall with the best score of 1 and the worst score of 0. F1 score conveys the balance between
145 the precision and the recall.

RESULTS

146 Palmer amaranth height and biomass

147 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants
148 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3 g,
149 and 16.3 g plant-1 in bareground, soybean and corn, respectively. Plants from the second cohort produced
150 62.6 g plant in bareground, followed by 6.3 g plant in soybean, and 1.4 g plant in corn.

151 Palmer amaranth height was more uniform across cohort timings, except when growing in corn (figure
152 3B). Palmer amaranth plants from the first cohort were on average 69.2 cm tall in bareground, which
153 was not different from the 70.7 cm tall plants from the second cohort timing ($P = 0.74$). In addition, no
154 difference in Palmer amaranth height (69.3 cm) was detected from first cohort plants in soybean to first and
155 second cohort plants in bareground ($P > 0.75$). Palmer amaranth plants from the second cohort were nearly
156 10 cm lower compared to the first cohort in soybeans ($P = 0.04$). The tallest (first cohort) and smallest
157 (second cohort) Palmer amaranth plants were found in corn. Palmer amaranth reached 85.2 and 38.2 cm
158 tall, respectively.

159 Palmer amaranth cumulative flowering

160 Palmer amaranth plants from the first cohort growing in corn resulted in a longer flowering window
161 compared to plants growing in bareground and soybean (Figure 4A). The 10% cumulative Palmer amaranth
162 flowering in soybean, bareground and corn occurred at the end of June. Palmer amaranth reached 10%
163 flowering in soybean, bareground and corn at doy 180, 180.9 and 181.7, respectively. The 50% Palmer
164 amaranth cumulative flowering occurred in July. Palmer amaranth reached 50% flowering in bareground,
165 soybean and corn at doy 193.4, 194.8, and 206.6, respectively. Similar trend was observed at 90%
166 Palmer amaranth cumulative flowering. Palmer amaranth reached 90% flowering at doy 252.6 in corn
167 (early September), which was 38 and 32 days after reaching 90% flowering in bareground and soybean,
168 respectively.

169 Palmer amaranth cumulative flowering at the second cohort ranged from mid July to mid September
170 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to
171 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at
172 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at
173 doy 210.9, which was 6 days prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering,
174 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; P

175 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean
 176 (260.5; $P = 0.66$).

177 Palmer amaranth gender

178 The model fit was 0.23, 0.32, 0.40 using pseudo R-squared test from McFadden, Cox and Snell, and
 179 Cragg and Uhler, respectively. The likelihood ratio test showed a p-value of < 0.00 . The average marginal
 180 effects showed that Palmer amaranth growing in corn resulted in 14.8% less females plants (Table 2).
 181 Moreover, increasing a unit doy increases the probability of having a female plant by 0.4% (Table 2 and
 182 Figure4A). Similar trend is observed for weight as well as height, whereas the probability of being female
 183 increase by 0.2% (Figure 4B) and 0.1% (Figure 4C) when a unit of weight (g) and height (cm) increases,
 184 respectively.

Table 2. Average marginal means of gender logistic model. Factor pararemter values (e.g. crop) is shown related to soybean.

Term	AME	SE	Lower	Upper	Z-score	P-value
crop_bareground	-0.048	0.054	-0.154	0.059	-0.876	0.381
crop_corn	-0.148	0.052	-0.250	-0.046	-2.842	0.004
doyh	0.004	0.001	0.003	0.006	4.959	0.000
height	0.002	0.001	0.001	0.003	2.953	0.003
weight	0.001	0.000	0.000	0.001	2.179	0.029

^a Average Marginal Effects. ^b Standard Error.

185 The model accuracy evaluation accuracy in the 20% test dataset was 0.62 with a cutoff value for female
 186 and male plants of 0.43. The model classification showed a precision of 0.64, recall of 0.66, and a F means
 187 score of 0.65. In addition, the area under the curve was 0.64.

DISCUSSION

188 Our study showed that Palmer amaranth biomass, height, flowering pattern and gender varied within
 189 agroecosystems and cohort timings. In general, first cohort of Palmer amaranth plants were heavier and
 190 taller when compared to the second cohort. At first cohort, resources (e.g., soil nutrients) and conditions
 191 (e.g., light) were more timely available for the species. High biomass and taller Palmer amaranth plants are
 192 likely a weed strategy to compete for light in between crop rows in absence of canopy. In such conditions,
 193 Palmer amaranth showed an extraordinary plasticity to adapt upon the agroecosystem. This is evident
 194 when comparing Palmer amaranth canopy shape, and its extended flowering pattern when growing into
 195 corn compared to soybean. The Palmer amaranth competition strategy was to mimic the crop grow and
 196 development (Figure 6). These results suggests that Palmer amaranth can fast evolve life-history traits to
 197 adapt into cropping systems and cultural practices, which was also showed in a study varying nitrogen
 198 fertilization (Bravo et al., 2018). Our results highlight the Palmer amaranth as a threat to field crops as
 199 breeding more competitive crop varieties is likely to select more competitive biotypes (Bravo et al., 2017).

200 Palmer amaranth grow and development in second cohort was limited due to the crop competitive ability
 201 at advanced development stages. Palmer amaranth was transplanted when corn canopy was nearly closed,
 202 which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was
 203 lower compared to its first cohort. Under crop canopy (e.g., second cohort), Palmer amaranth flowering
 204 window was near to similar in corn and soybean. Palmer amaranth growing without crop competition

produced the highest amounts of biomass and less extended flowering window. The Palmer amaranth strategy in bareground was to invest biomass in growing plant width and height. Nonetheless, Palmer amaranth produced 21% less biomass in second cohort compared to first cohort timing. In a bareground study, early emerged Palmer amaranth without competition was 50% taller than late emerged plants (Webster and Grey, 2015). These results suggest that crop competition is not the only factor limiting late Palmer amaranth establishment. The limited growth of Palmer amaranth at second cohort is likely a reduced plant response to day length, light availability and thermal units (e.g., growing degree days). It is hypothesize that reduced day length contributed to smaller plants at second cohort as well as shorter flowering period. A study in North Carolina and Illinois predicted that less than 10% Palmer amaranth seedlings emergence occurred after June (Piskackova et al., 2021). In addition, Palmer amaranth negative impact on soybean (Korres et al., 2020) and cotton (Webster and Grey, 2015) yields was higher when plants were established near to crop planting.

Seed production was not evaluated due to plant harvest at initiation of flowering. Nonetheless, it is well documented a strong positive correlation between Palmer amaranth biomass and seed production (Schwartz et al., 2016; Spaunhorst et al., 2018). In our study, Palmer amaranth growing at first cohort accumulated an overall 36% more biomass when compared to second cohort. Therefore, Palmer amaranth plants growing in the second cohort is likely to produce less seeds regardless the cropping system. Our observation is consistent with the findings that first Palmer amaranth cohort produced 50% more seeds per plant than Palmer amaranth plants established six weeks later in bareground (Webster and Grey, 2015). Still, seed production at second cohort is likely to replenish the soil seedbank. Seed production and deposition in the seedbank is also a key factor for species perpetuation (Menges, 1987). Palmer amaranth can produce hundred thousands seeds per plant (Schwartz et al., 2016; Keeley et al., 1987), and stay viable buried in the seedbank for at least 36 months (Sosnoskie et al., 2013). Therefore, preventing Palmer amaranth seed production or/and seed migration to its non-native habitat is an essential strategy to minimize weed impact into agroecosystem (Davis et al., 2015).

An ecological approach to reduce seed production in Palmer amaranth is understanding its flowering pattern. Our study suggests that Palmer amaranth flowering pattern was slightly influenced by cropping systems and cohort timings. Palmer amaranth growing in bareground and corn resulted in the overall shortest and longest flowering pattern, respectively. When growing in soybean, Palmer amaranth flowering pattern was similar to bareground at first cohort but similar to corn at second cohort timing. Plant flowering initiation is complex and depends on biological and ecological factors (Lang, 1965). We hypothesize that when growing in high competition (e.g., second cohort), Palmer amaranth plants tend to initiate flowering early, as well as having an extended flowering pattern. Early flower initiation is plant strategy when growing in stress conditions. For example, when growing under water stress, early flowering in Palmer amaranth resulted in a mismatch between female and male plants by seven days (Mesgaran et al., 2021). A mismatch in Palmer amaranth male and female flowering period can minimize plant outcross, and thus reduce plant seed production. Sex dimorphism manipulation is considered a potential ecological pest control (McFarlane et al., 2018; Schliekelman et al., 2005).

The mechanisms of sex-determination in plant species is intriguing and arouse the curiosity of many scientists, including Charles Darwin (Darwin, 1888). In our study, the gender model performance was decent (AIC 0.64) considering the plant flowering biology. A 1:1 male and female sex ratio is a general evolutionary stable strategy for plant species perpetuation (Fisher, 1930). However, a slight deviation from 1:1 sex ratio might occur in some dioecious species. For example, the dioecious *Halophila stipulacea* is a female-biased plant in its native habitat, but the naturalized *H. stipulacea* have a 1:1 ratio (Nguyen et

249 al., 2018). Naturalized of *H. stipulacea* reduced female-male ratio to expand into its non-native habitat
250 (Nguyen et al., 2018). Also, biotic and/or abiotic stress can influence plant sex determination. Palmer
251 amaranth male-to-female ratio was greater under high plant densities (Korres and Norsworthy, 2017) and
252 after herbicide application (Rumpa et al., 2019). Our model estimated that late flowering, heavier and
253 taller Palmer amaranth plants deviated from 1:1 ratio in favor to female plants. It was reported that female
254 Palmer amaranth plants invested more in height, stem and biomass while male invested more in leaf area
255 and leaf dry weight under nutrient deficiency (Korres et al., 2017). Our model also estimated more female
256 plants in soybean and bareground compared to corn, which might linked to plant competition strategy
257 in each agroecosystem. Our results showed the influence of life-history and ecological traits on sexual
258 dimorphism in Palmer amaranth. Sexual dimorphism is documented in other dioecious species (Barrett and
259 Hough, 2013). For example, stronger female plant competition and greater male tolerance to herbivory was
260 reported in *Spinacia oleracea* (Pérez-Llorca and Sánchez Vilas, 2019). Research on candidate genes for
261 sex determination in *Amaranthus* species are currently underway but it is far to complete (Montgomery et
262 al., 2021, 2019). Further studies are also needed to understand the ecological basis of Palmer amaranth
263 flowering, including the plant behavior under climate change.

264 Our study demonstrated the short-term Palmer amaranth plasticity to grow and develop into cropping-
265 systems. Is likely that Palmer amaranth range will continue to expanding to new geographies. Therefore,
266 preventive management is a priority to minimizing Palmer amaranth dispersal. Reactive management
267 should focus on early-season management programs, which would have a large negative effect on Palmer
268 amaranth growth and development. Tactics that promote early-season crop advantage against Palmer
269 amaranth, including early crop planting, crop rotation (Oliveira et al., 2021), plant width, preemergence
270 applied herbicide (Sanctis et al., 2021), and crop residue (e.g. cover crops) would minimize the negative
271 impact of Palmer amaranth in agroecosystems. The aggressiveness and differential Palmer amaranth
272 adaptation to agroecosystem is striking and require national efforts to minimize the species impact on
273 economy and sustainability.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

274 Flower manipulation is a promising ecological Palmer amaranth but it is not well understood.

275 The authors declare that the research was conducted in the absence of any commercial or financial
276 relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

277 RW and MO: designed the experiments; AJ, CP, MB, MO, and SS: conducted the experiments; MO:
278 analyzed the data and wrote the manuscript; AJ, CP, MB, MO, SS, and RW: conceptualized the research.
279 All authors reviewed the manuscript.

ACKNOWLEDGMENTS

280 Funding: This work received no specific grant from any funding agency, commercial, or not-for-profit
281 sectors

1 SUPPLEMENTAL DATA

282 Supplementary Material should be uploaded separately on submission, if there are Supplementary Figures,
283 please include the caption in the same file as the figure. LaTeX Supplementary Material templates can be
284 found in the Frontiers LaTeX folder

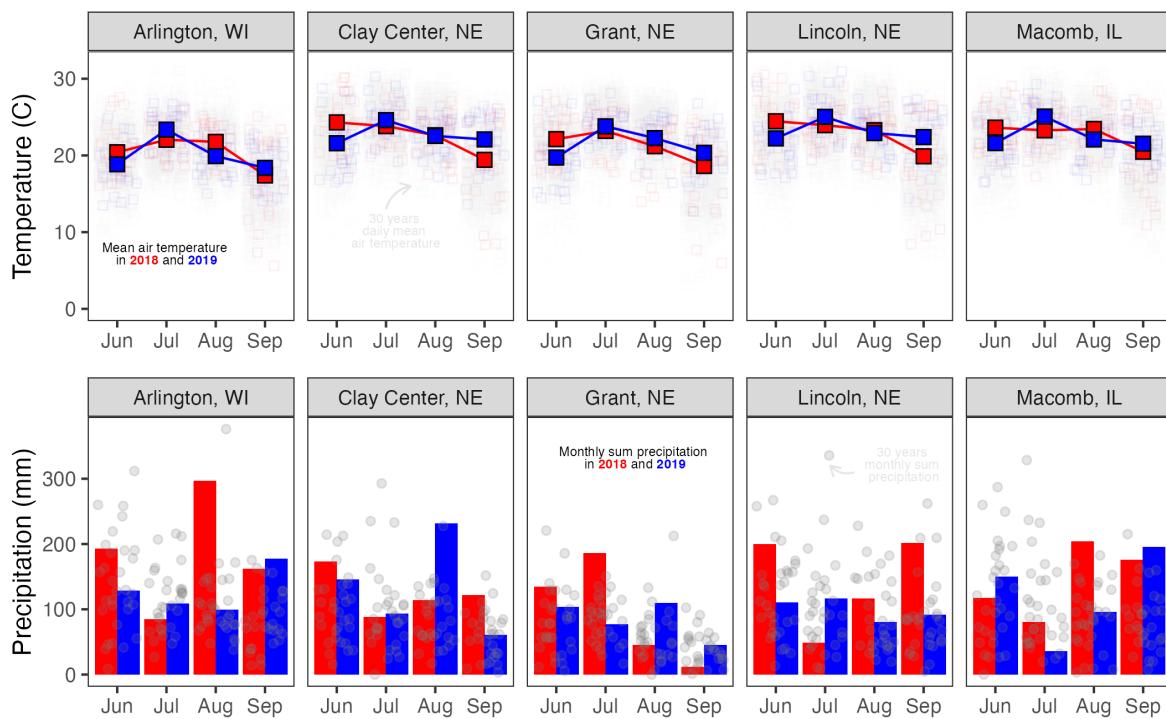


Figure 1. Mean average temperature (C) and monthly sum precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE and Macomb, IL

2 REFERENCES

285 A reference list should be automatically created here. However it won't. Pandoc will place the list of
 286 references at the end of the document instead. There are no convenient solution for now to force Pandoc to
 287 do otherwise. The easiest way to get around this problem is to edit the LaTeX file created by Pandoc before
 288 compiling it again using the traditional LaTeX commands.

FIGURES

- 289 Aulakh, J. S., Chahal, P. S., Kumar, V., Price, A. J., and Guillard, K. (2021). Multiple herbicide-resistant
 290 Palmer amaranth (*Amaranthus palmeri*) in Connecticut: Confirmation and response to POST herbicides.
 291 *Weed Technology* 35, 457–463. doi:10.1017/wet.2021.6.
- 292 Bagavathiannan, M. V., and Norsworthy, J. K. (2016). Multiple-Herbicide Resistance Is Widespread in
 293 Roadside Palmer Amaranth Populations. *PLOS ONE* 11, e0148748. doi:10.1371/journal.pone.0148748.
- 294 Baker, R. (2021). Comparative analysis of Palmer amaranth (*Amaranthus palmeri*) and waterhemp (*A.
 295 Tuberculatus*) in Iowa. doi:10.31274/etd-20210609-11.
- 296 Bangdiwala, S. I. (2018). Regression: Binary logistic. *International Journal of Injury Control and Safety
 297 Promotion* 25, 336–338. doi:10.1080/17457300.2018.1486503.
- 298 Barrett, S. C. H., and Hough, J. (2013). Sexual dimorphism in flowering plants. *Journal of Experimental
 299 Botany* 64, 67–82. doi:10.1093/jxb/ers308.
- 300 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using
 301 Lme4. *Journal of Statistical Software* 67, 1–48. doi:10.18637/jss.v067.i01.

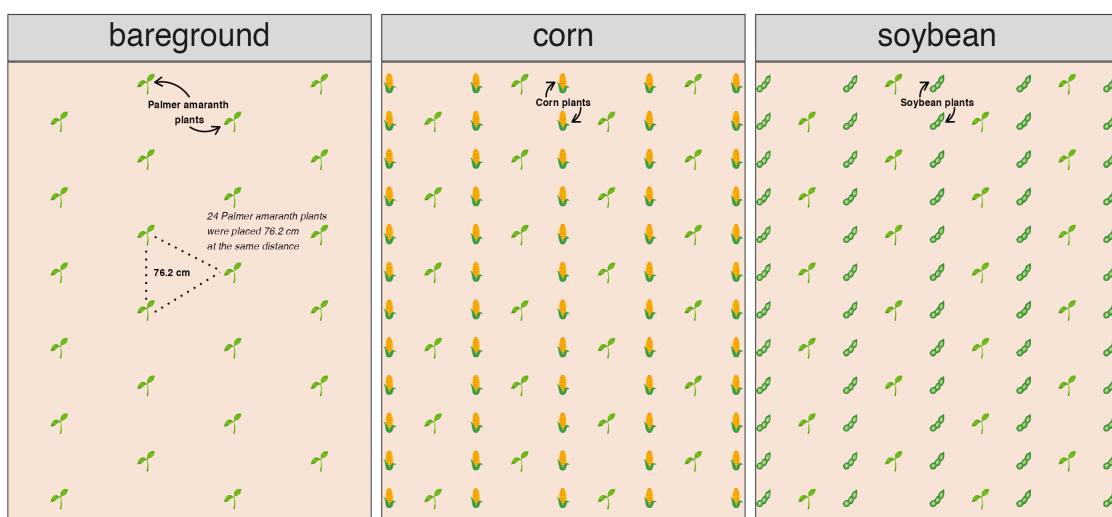


Figure 2. Palmer amaranth adaptation study layout of a transplanting time. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each crop

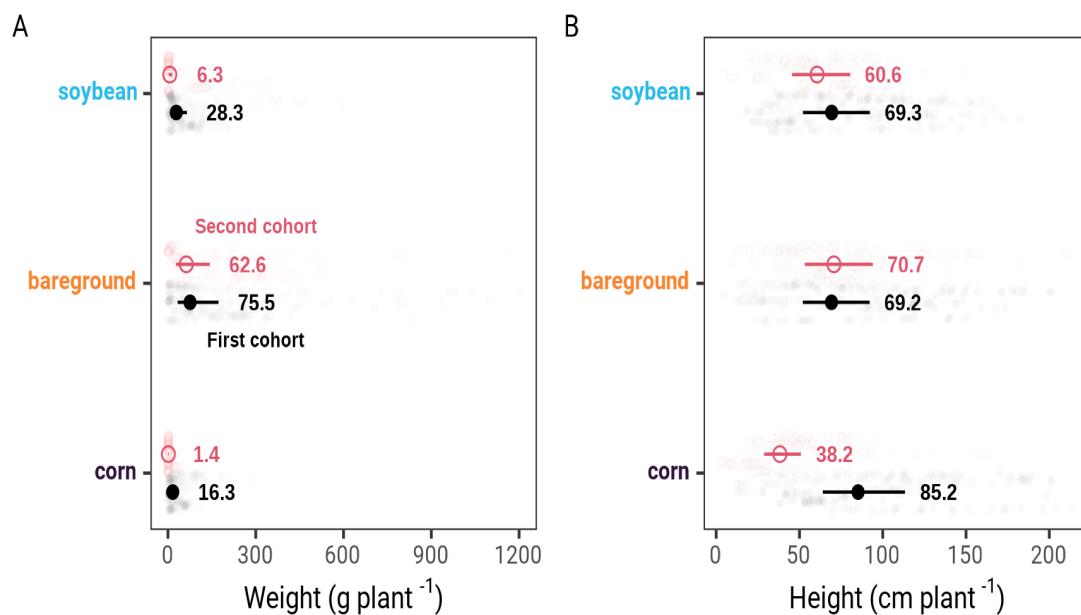


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

302 Berger, S. T., Ferrell, J. A., Rowland, D. L., and Webster, T. M. (2015). Palmer Amaranth (*Amaranthus*
303 *palmeri*) Competition for Water in Cotton. *Weed Science* 63, 928–935. doi:10.1614/WS-D-15-00062.1.

304 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2017). Differentiation of
305 Life-History Traits among Palmer Amaranth Populations (*Amaranthus palmeri*) and Its Relation to
306 Cropping Systems and Glyphosate Sensitivity. *Weed Science* 65, 339–349. doi:10.1017/wsc.2017.14.

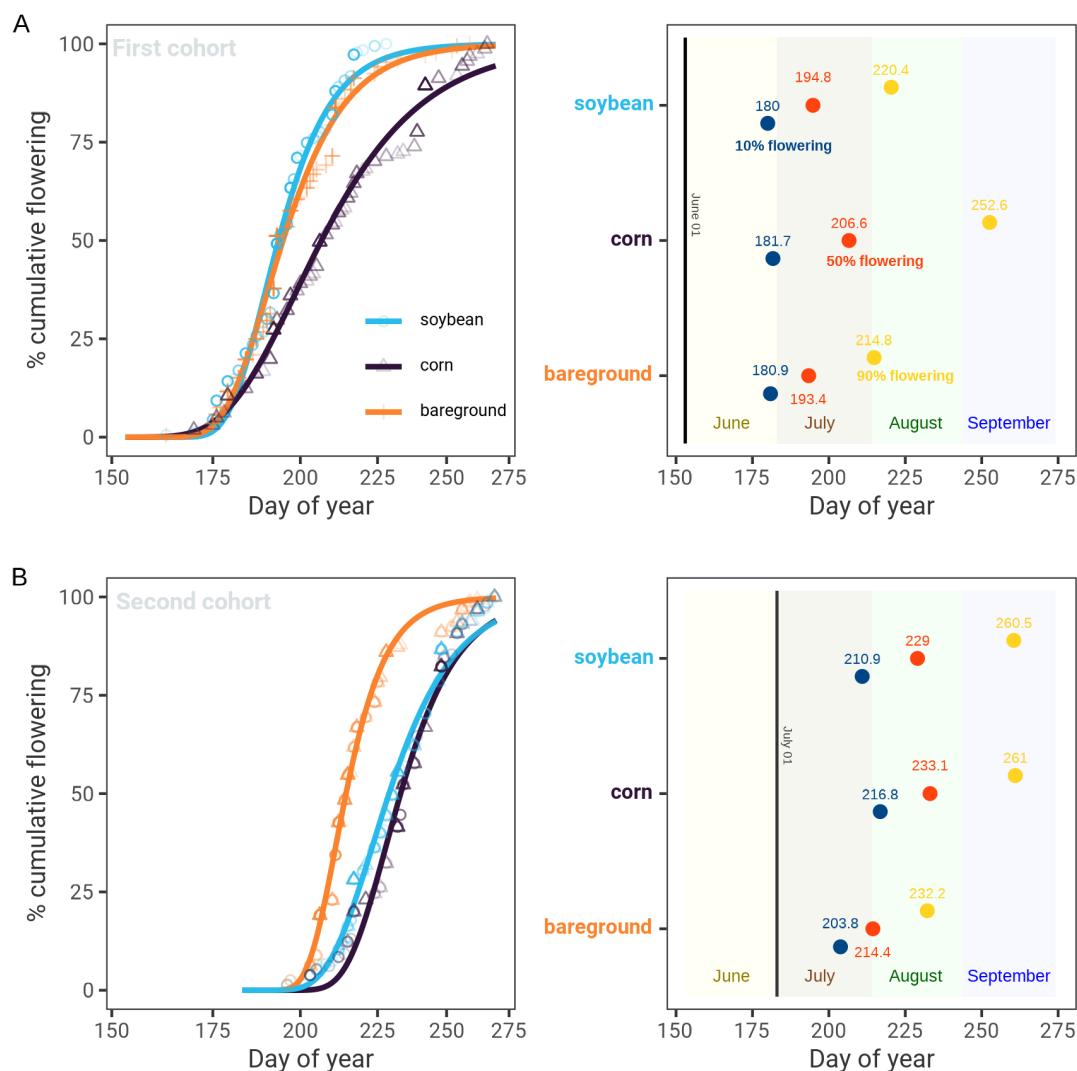


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

307 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2018). Evolutionary Adaptations
 308 of Palmer Amaranth (*Amaranthus palmeri*) to Nitrogen Fertilization and Crop Rotation History Affect
 309 Morphology and Nutrient-Use Efficiency. *Weed Science* 66, 180–189. doi:10.1017/wsc.2017.73.

310 Briscoe Runquist, R. D., Lake, T., Tiffin, P., and Moeller, D. A. (2019). Species distribution models
 311 throughout the invasion history of Palmer amaranth predict regions at risk of future invasion and reveal
 312 challenges with modeling rapidly shifting geographic ranges. *Sci Rep* 9, 2426. doi:10.1038/s41598-
 313 018-38054-9.

314 Chahal, P. S., Barnes, E. R., and Jhala, A. J. (2021). Emergence pattern of Palmer amaranth (*Amaranthus*
 315 *palmeri*) influenced by tillage timings and residual herbicides. *Weed Technology* 35, 433–439.
 316 doi:10.1017/wet.2020.136.

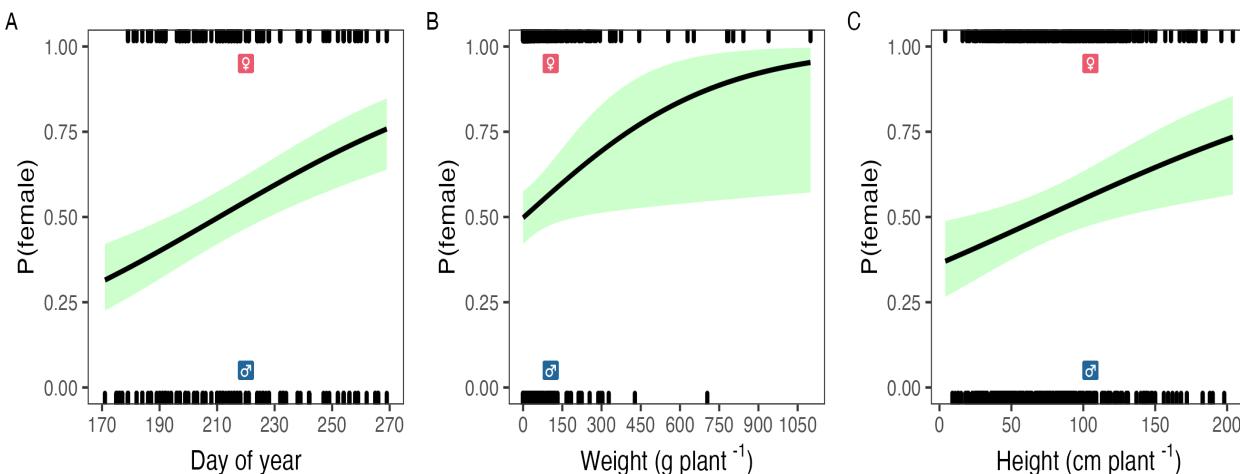


Figure 5. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)



Figure 6. MCO (180 cm) holding harvested Palmer amaranth plants at 40 days after first transplant (1st cohort, A) and 33 days after second transplant (2nd cohort, B). From left to right, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin

- 317 Chahal, P. S., Irmak, S., Jugulam, M., and Jhala, A. J. (2018). Evaluating Effect of Degree of Water Stress
 318 on Growth and Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors.
 319 *Weed Science* 66, 738–745. doi:10.1017/wsc.2018.47.
- 320 Correndo, A. A., Moro Rosso, L. H., and Ciampitti, I. A. (2021). Retrieving and processing agro-
 321 meteorological data from API-client sources using R software. *BMC Research Notes* 14, 205.
 322 doi:10.1186/s13104-021-05622-8.

- 323 Darwin, C. (1888). *The Different Forms of Flowers on Plants of the Same Species*. J. Murray Available at:
324 <http://books.google.com?id=7uMEAAAAYAAJ>.
- 325 Davis, A. S., Schutte, B. J., Hager, A. G., and Young, B. G. (2015). Palmer Amaranth (*Amaranthus palmeri*)
326 Damage Niche in Illinois Soybean Is Seed Limited. *Weed Science* 63, 658–668. doi:10.1614/WS-D-14-
327 00177.1.
- 328 Farmer, J. A., Webb, E. B., Pierce, R. A., and Bradley, K. W. (2017). Evaluating the potential for weed seed
329 dispersal based on waterfowl consumption and seed viability. *Pest Management Science* 73, 2592–2603.
330 doi:10.1002/ps.4710.
- 331 Fisher, R. A. (1930). The genetical theory of natural selection. *Eugen Rev* 22, 127–130. Available at:
332 <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2984947/> [Accessed August 12,
333 2021].
- 334 Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications Available at:
335 <http://books.google.com?id=uPNrDwAAQBAJ>.
- 336 Garetson, R., Singh, V., Singh, S., Dotray, P., and Bagavathiannan, M. (2019). Distribution of herbicide-
337 resistant Palmer amaranth (*Amaranthus palmeri*) in row crop production systems in Texas. *Weed
338 Technology* 33, 355–365. doi:10.1017/wet.2019.14.
- 339 Guo, P., and Al-Khatib, K. (2003). Temperature effects on germination and growth of redroot pigweed
340 (*Amaranthus retroflexus*), Palmer amaranth (*A. Palmeri*), and common waterhemp (*A. rudis*). *Weed
341 Science* 51, 869–875. doi:10.1614/P2002-127.
- 342 Hartzler, B., and Anderson, M. (2016). Palmer amaranth: It's here, now what? 10.
- 343 Heap, I. (2021). Internation Herbicide-Resistant Weed Database. Available at: <http://www.weedscience.org/Home.aspx> [Accessed July 26, 2021].
- 344 Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models.
345 *Biometrical Journal* 50, 346–363. doi:10.1002/bimj.200810425.
- 346 Jha, P., Norsworthy, J. K., Riley, M. B., and Bridges, W. (2010). Annual Changes in Temperature and Light
347 Requirements for Germination of Palmer Amaranth (*Amaranthus palmeri*) Seeds Retrieved from Soil.
348 *Weed Science* 58, 426–432. doi:10.1614/WS-D-09-00038.1.
- 349 Keeley, P. E., Carter, C. H., and Thullen, R. J. (1987). Influence of Planting Date on Growth of Palmer
350 Amaranth (*Amaranthus palmeri*). *Weed Science* 35, 199–204. doi:10.1017/S0043174500079054.
- 351 Kistner, E. J., and Hatfield, J. L. (2018). Potential Geographic Distribution of Palmer
352 Amaranth under Current and Future Climates. *Agricultural & Environmental Letters* 3, 170044.
353 doi:10.2134/ael2017.12.0044.
- 354 Klingaman, T. E., and Oliver, L. R. (1994). Palmer Amaranth (*Amaranthus palmeri*) Interference in
355 Soybeans (*Glycine max*). *Weed Science* 42, 523–527. doi:10.1017/S0043174500076888.
- 356 Kohrt, J. R., Sprague, C. L., Nadakuduti, S. S., and Douches, D. (2017). Confirmation of a Three-Way
357 (Glyphosate, ALS, and Atrazine) Herbicide-Resistant Population of Palmer Amaranth (*Amaranthus
358 palmeri*) in Michigan. *Weed Science* 65, 327–338. doi:10.1017/wsc.2017.2.
- 359 Korres, N. E., and Norsworthy, J. K. (2017). Palmer Amaranth (*Amaranthus palmeri*) Demographic and
360 Biological Characteristics in Wide-Row Soybean. *Weed Science* 65, 491–503. doi:10.1017/wsc.2017.12.

- 362 Korres, N. E., Norsworthy, J. K., FitzSimons, T., Roberts, T. L., and Oosterhuis, D. M. (2017). Differential
363 Response of Palmer Amaranth (*Amaranthus palmeri*) Gender to Abiotic Stress. *Weed Science* 65,
364 213–227. doi:10.1017/wsc.2016.34.
- 365 Korres, N. E., Norsworthy, J. K., Mauromoustakos, A., and Williams, M. M. (2020). Soybean density and
366 Palmer amaranth (*Amaranthus palmeri*) establishment time: Effects on weed biology, crop yield, and
367 economic returns. *Weed Science* 68, 467–475. doi:10.1017/wsc.2020.41.
- 368 Küpper, A., Borgato, E. A., Patterson, E. L., Netto, A. G., Nicolai, M., Carvalho, S. J. P. de, Nissen, S.
369 J., Gaines, T. A., and Christoffoleti, P. J. (2017). Multiple Resistance to Glyphosate and Acetolactate
370 Synthase Inhibitors in Palmer Amaranth (*Amaranthus palmeri*) Identified in Brazil. *Weed Science* 65,
371 317–326. doi:10.1017/wsc.2017.1.
- 372 Lang, A. (1965). “Physiology of flower initiation,” in *Differenzierung und Entwicklung / Differentiation
373 and Development* Handbuch der Pflanzenphysiologie / Encyclopedia of Plant Physiology., ed. A. Lang
374 (Berlin, Heidelberg: Springer), 1380–1536. doi:10.1007/978-3-642-50088-6_39.
- 375 Larran, A. S., Palmieri, V. E., Perotti, V. E., Lieber, L., Tuesca, D., and Permingeat, H. R. (2017). Target-site
376 resistance to acetolactate synthase (ALS)-inhibiting herbicides in *Amaranthus palmeri* from Argentina.
377 *Pest Management Science* 73, 2578–2584. doi:10.1002/ps.4662.
- 378 Leeper, T. J. (2017). Interpreting Regression Results using Average Marginal Effects with R’s margins. 31.
- 379 Lindsay, K., Popp, M., Norsworthy, J., Bagavathiannan, M., Powles, S., and Lacoste, M. (2017). PAM:
380 Decision Support for Long-Term Palmer Amaranth (*Amaranthus palmeri*) Control. *Weed Technology*
381 31, 915–927. doi:10.1017/wet.2017.69.
- 382 MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., and Dehnen-Schmutz, K. (2020). An ecological
383 future for weed science to sustain crop production and the environment. A review. *Agron. Sustain. Dev.*
384 40, 24. doi:10.1007/s13593-020-00631-6.
- 385 MacRae, A. W., Webster, T. M., Sosnoskie, L. M., Culpepper, A. S., and Kichler, J. M. (2013). Cotton
386 Yield Loss Potential in Response to Length of Palmer Amaranth (*Amaranthus palmeri*) Interference.
387 17, 6.
- 388 Massinga, R. A., Currie, R. S., Horak, M. J., and Boyer, J. (2001). Interference of Palmer amaranth in corn.
389 *Weed Science* 49, 202–208. doi:10.1614/0043-1745(2001)049[0202:IOPAIC]2.0.CO;2.
- 390 Matzrafi, M., Osipitan, O. A., Ohadi, S., and Mesgaran, M. B. (2021). Under pressure: Maternal effects
391 promote drought tolerance in progeny seed of Palmer amaranth (*Amaranthus palmeri*). *Weed Science*
392 69, 31–38. doi:10.1017/wsc.2020.75.
- 393 McFarlane, G. R., Whitelaw, C. B. A., and Lillico, S. G. (2018). CRISPR-Based Gene Drives for Pest
394 Control. *Trends in Biotechnology* 36, 130–133. doi:10.1016/j.tibtech.2017.10.001.
- 395 Menges, R. M. (1987). Weed Seed Population Dynamics during Six Years of Weed Management Systems
396 in Crop Rotations on Irrigated Soil. *Weed Science* 35, 328–332. Available at: <http://www.jstor.org/stable/4044593>.
- 398 Mesgaran, M. B., Matzrafi, M., and Ohadi, S. (2021). Sex dimorphism in dioecious Palmer amaranth
399 (*Amaranthus palmeri*) in response to water stress. *Planta* 254, 17. doi:10.1007/s00425-021-03664-7.

- 400 Milani, A., Panozzo, S., Farinati, S., Iamonico, D., Sattin, M., Loddo, D., and Scarabel, L. (2021). Recent
401 Discovery of Amaranthus palmeri S. Watson in Italy: Characterization of ALS-Resistant Populations
402 and Sensitivity to Alternative Herbicides. *Sustainability* 13, 7003. doi:10.3390/su13137003.
- 403 Montgomery, J. S., Giacomini, D. A., Weigel, D., and Tranel, P. J. (2021). Male-specific Y-chromosomal
404 regions in waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *New*
405 *Phylogist* 229, 3522–3533. doi:10.1111/nph.17108.
- 406 Montgomery, J. S., Sadeque, A., Giacomini, D. A., Brown, P. J., and Tranel, P. J. (2019). Sex-specific
407 markers for waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *Weed*
408 *Science* 67, 412–418. doi:10.1017/wsc.2019.27.
- 409 Morgan, G. D., Baumann, P. A., and Chandler, J. M. (2001). Competitive Impact of Palmer Amaranth
410 (*Amaranthus palmeri*) on Cotton (*Gossypium hirsutum*) Development and Yield. *Weed Technology* 15,
411 408–412. doi:10.1614/0890-037X(2001)015[0408:CIOPAA]2.0.CO;2.
- 412 Nguyen, H. M., Kleitou, P., Kletou, D., Sapir, Y., and Winters, G. (2018). Differences in flowering sex
413 ratios between native and invasive populations of the seagrass *Halophila stipulacea*. *Botanica Marina*
414 61, 337–342. doi:10.1515/bot-2018-0015.
- 415 Oliveira, M. C., Gaines, T. A., Patterson, E. L., Jhala, A. J., Irmak, S., Amundsen, K., and Knezevic, S.
416 Z. (2018). Interspecific and intraspecific transference of metabolism-based mesotrione resistance in
417 dioecious weedy *Amaranthus*. *The Plant Journal* 96, 1051–1063. doi:10.1111/tpj.14089.
- 418 Oliveira, M. C., Giacomini, D. A., Arsenijevic, N., Vieira, G., Tranel, P. J., and Werle, R. (2021).
419 Distribution and validation of genotypic and phenotypic glyphosate and PPO-inhibitor resistance in
420 Palmer amaranth (*Amaranthus palmeri*) from southwestern Nebraska. *Weed Technology* 35, 65–76.
421 doi:10.1017/wet.2020.74.
- 422 Page, E. R., Nurse, R. E., Meloche, S., Bosveld, K., Grainger, C., Obeid, K., Filotas, M., Simard, M.-J., and
423 Laforest, M. (2021). Import of Palmer amaranth (*Amaranthus palmeri* S. Wats.) Seed with sweet potato
424 (*Ipomea batatas* (L.) Lam) slips. *Can. J. Plant Sci.*, CJPS-2020-0321. doi:10.1139/CJPS-2020-0321.
- 425 Pérez-Llorca, M., and Sánchez Vilas, J. (2019). Sexual dimorphism in response to herbivory and
426 competition in the dioecious herb *Spinacia oleracea*. *Plant Ecol* 220, 57–68. doi:10.1007/s11258-
427 018-0902-7.
- 428 Piskackova, T. A. R., Reberg-Horton, S. C., Richardson, R. J., Jennings, K. M., Franca, L., Young, B. G.,
429 and Leon, R. G. (2021). Windows of action for controlling palmer amaranth (*Amaranthus palmeri*)
430 using emergence and phenology models. *Weed Research* 61, 188–198. doi:10.1111/wre.12470.
- 431 Price, A. J., Balkcom, K. S., Culpepper, S. A., Kelton, J. A., Nichols, R. L., and Schomberg, H. (2011).
432 Glyphosate-resistant Palmer amaranth: A threat to conservation tillage. *Journal of Soil and Water*
433 *Conservation* 66, 265–275. doi:10.2489/jswc.66.4.265.
- 434 Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. (2015). Dose-Response Analysis Using R. *PLOS ONE*
435 10, e0146021. doi:10.1371/journal.pone.0146021.
- 436 Rumpa, M. M., Krausz, R. F., Gibson, D. J., and Gage, K. L. (2019). Effect of PPO-Inhibiting Herbicides
437 on the Growth and Sex Ratio of a Dioecious Weed Species *Amaranthus palmeri* (Palmer Amaranth).
438 *Agronomy* 9, 275. doi:10.3390/agronomy9060275.

- 439 Sanctis, J. H. S. de, Barnes, E. R., Knezevic, S. Z., Kumar, V., and Jhala, A. J. (2021). Residual herbicides
440 affect critical time of Palmer amaranth removal in soybean. *Agronomy Journal* 113, 1920–1933.
441 doi:10.1002/agj2.20615.
- 442 Sauer, J. (1957). Recent Migration and Evolution of the Dioecious Amaranths. *Evolution* 11, 11–31.
443 doi:10.2307/2405808.
- 444 Sauer, J. D. (1972). The dioecious amaranths: A new species name and major range extensions. *Madroño*
445 21, 426–434. Available at: <http://www.jstor.org/stable/41423815>.
- 446 Sbatella, G. M., and Wilson, R. G. (2010). Isoxaflutole Shifts Kochia (Kochia scoparia) Populations in
447 Continuous Corn. *Weed Technology* 24, 392–396. doi:10.1614/WT-D-09-00023.1.
- 448 Schliekelman, P., Ellner, S., and Gould, F. (2005). Pest Control by Genetic Manipulation of Sex Ratio.
449 *Journal of Economic Entomology* 98, 18–34. doi:10.1093/jee/98.1.18.
- 450 Schwartz, L. M., Norsworthy, J. K., Young, B. G., Bradley, K. W., Kruger, G. R., Davis, V. M., Steckel,
451 L. E., and Walsh, M. J. (2016). Tall Waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth
452 (*Amaranthus palmeri*) Seed Production and Retention at Soybean Maturity. *Weed Technology* 30,
453 284–290. doi:10.1614/WT-D-15-00130.1.
- 454 Scott, D. (2011). The Technological Fix Criticisms and the Agricultural Biotechnology Debate. *J Agric
455 Environ Ethics* 24, 207–226. doi:10.1007/s10806-010-9253-7.
- 456 Sosnoskie, L. M., Webster, T. M., and Culpepper, A. S. (2013). Glyphosate Resistance Does Not
457 Affect Palmer Amaranth (*Amaranthus palmeri*) Seedbank Longevity. *Weed Science* 61, 283–288.
458 doi:10.1614/WS-D-12-00111.1.
- 459 Spaunhorst, D. J., Devkota, P., Johnson, W. G., Smeda, R. J., Meyer, C. J., and Norsworthy, J. K. (2018).
460 Phenology of Five Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and
461 Arkansas. *Weed Science* 66, 457–469. doi:10.1017/wsc.2018.12.
- 462 Wang, J. L., Klessig, D. F., and Berry, J. O. (1992). Regulation of C4 Gene Expression in Developing
463 Amaranth Leaves. *The Plant Cell* 4, 173–184. doi:10.1105/tpc.4.2.173.
- 464 Ward, S. M., Webster, T. M., and Steckel, L. E. (2013). Palmer Amaranth (*Amaranthus palmeri*): A Review.
465 *Weed Technology* 27, 12–27. doi:10.1614/WT-D-12-00113.1.
- 466 Webster, T. M., and Grey, T. L. (2015). Glyphosate-Resistant Palmer Amaranth (*Amaranthus palmeri*)
467 Morphology, Growth, and Seed Production in Georgia. *Weed Science* 63, 264–272. doi:10.1614/WS-D-
468 14-00051.1.
- 469 Yu, E., Blair, S., Hardel, M., Chandler, M., Thiede, D., Cortilet, A., Gunsolus, J., and Becker, R. (2021).
470 Timeline of Palmer amaranth (*Amaranthus palmeri*) invasion and eradication in Minnesota. *Weed
471 Technology*, 1–31. doi:10.1017/wet.2021.32.