

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

Maxwel C Oliveira¹, Amit J Jhala², Mark Bernards³, Chris Proctor², Strahinja Stepanovic², Rodrigo Werle^{1*}

¹ Department of Agronomy, University of Wisconsin-Madison, Madison, Wisconsin, United States

² Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, Nebraska, United States

³ Department of Agronomy, Western Illinois University, Macomb, Illinois, United States

Correspondence*:

Rodrigo Werle

rwerle@uwisc.edu

2 ABSTRACT

Abstract length and content varies depending on article type. Refer to <http://www.frontiersin.org/about/AuthorGuidelines> for abstract requirement and length according to article type.

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 (Van Wychen, 2020). 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 the main environment requirements for Palmer amaranth successful grow and
29 development (Jha et al., 2010). Palmer amaranth is reported with an extended germination period (Ward et
30 al., 2013). Germination of Palmer amaranth was triggered by 18 C soil temperature at 5 cm depth (Keeley et
31 al., 1987), and optimal germination and biomass production occurred at 35/30 C day and night temperatures
32 (Guo and Al-Khatib, 2003). In addition, Palmer amaranth establishment is human-mediated by tillage
33 timings and preemergence-applied herbicides (Chahal et al., 2021), which can result in weed germination
34 shifts (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 prompt
37 for germination (Matzrafi et al., 2021). Growing conditions and management practices also influence
38 Palmer amaranth sex dimorphism and flowering pattern (Korres et al., 2017; Rumpa et al., 2019). Therefore,
39 Palmer amaranth has shown plasticity to evolve and fast adapt under selection pressure. Palmer amaranth
40 invasion/adaptation into new habitats is likely to increase with the global temperature warming. Currently,
41 it is estimated that the greatest climatic risk of Palmer amaranth establishment are agronomic crops in
42 Australia and Sub-Saharan Africa (Kistner and Hatfield, 2018). Temperature is a key factor limiting Palmer
43 amaranth expansion to cooler geographies (Briscoe Runquist et al., 2019); however, under future climate
44 change Palmer amaranth is likely to expand northward into Canada and Northern Europe (Kistner and
45 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 the University of Wisconsin-Madison, University
 83 of Nebraska-Lincoln, and Western Illinois University; and kept outdoors in the Perkins extension office at
 84 Grant, NE until the 2-3 leaf stage (5 to 8 cm height) when they were transported to the 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 Palmer amaranth flowering timing was estimated as cumulative flowering across all location. Dataset
119 was nested but id did not include Grant, NE. Palmer amaranth cumulative flowering estimation was
120 determined using an asymmetrical three parameter log logistic Weibull model of the drc package (Ritz et
121 al., 2015).

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

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

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

129 Palmer amaranth sex was fitted to a binary logistic regression (Bangdiwala, 2018). Binary logistic
130 regression is used for predicting binary classes, such as the probability of a plant being female in a
131 dioecious species. Prior to the analysis, all missing values were removed from the dataset. Also, data from
132 Grant was not used in this analysis due to the uniform plant harvesting at that location. The complete dataset
133 was splitted into 80% train and 20% test data. The 80% train is used for the model training and the 20% test

is used for checking how the model generalized on unseen dataset. With 80% dataset, a binary response variable, male (0) and female (1), was fitted to a generalized linear model (*glm* function) including day of year harvest, height, weight, crop and month as independent variables (without interaction). The model family was binomial with a logit function. The model fit was assessed through pseudo R-squared values (McFadden, Cox and Snell, Cragg and Uhler) and likelihood ratio using *nagelkerke* function (“rcompanion” package). The marginal effects computation was performed with Average Marginal Effects (AMEs) at every observed value of x and average across the results (Leeper, 2017) using *margins* function from “margins” package. The rest 20% dataset was predicted using *predict* function with a cutoff estimation for male or female using *performance* function. The model quality prediction from the classification algorithm was measured with precision (*precision* function), recall (*recall* function) and F1-score (*f_meas* function) using the “yardstick” package. The precision determines the accuracy of positive predictions (female plants), recall determines the fraction of positives that were correctly identified, and F1-score is a weighted harmonic mean of precision and recall with the best score of 1 and the worst score of 0. F1-score conveys the balance between the precision and the recall (Yacoub and Axman, 2020).

RESULTS

148 Palmer amaranth height and biomass

149 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants
150 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3 g,
151 and 16.3 g plant-1 in bareground, soybean and corn, respectively. Plants from the second cohort produced
152 62.6 g plant in bareground, followed by 6.3 g plant in soybean, and 1.4 g plant in corn.

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

161 Palmer amaranth cumulative flowering

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

171 Palmer amaranth cumulative flowering at the second cohort ranged from mid July to mid September
172 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to
173 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at
174 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at

175 doy 210.9, which was 6 days prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering,
 176 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; P
 177 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean
 178 (260.5; P = 0.66).

179 Palmer amaranth gender

180 The model fit was 0.23, 0.32, 0.40 using pseudo R-squared test from McFadden, Cox and Snell, and
 181 Cragg and Uhler, respectively. The likelihood ratio test showed a p-value of < 0.00. The average marginal
 182 effects showed that Palmer amaranth growing in corn resulted in 14.8% less females plants (Table 2).
 183 Moreover, increasing a unit doy increases the probability of having a female plant by 0.4% (Table 2 and
 184 Figure4A). Similar trend is observed for weight as well as height, whereas the probability of being female
 185 increase by 0.2% (Figure 4B) and 0.1% (Figure 4C) when a unit of weight (g) and height (cm) increases,
 186 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.

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

DISCUSSION

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

202 Palmer amaranth grow and development in second cohort was limited due to the crop competitive ability
 203 at advanced development stages. Palmer amaranth was transplanted when corn canopy was nearly closed,
 204 which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was

lower compared to its first cohort. Under crop canopy (e.g., second cohort), Palmer amaranth flowering 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 window. Our study suggests that Palmer amaranth flowering was slightly influenced by cropping systems and cohort timings. Palmer amaranth growing in bareground and corn resulted in the overall shortest and longest flowering window, respectively. When growing in soybean, Palmer amaranth flowering window 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 window. 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 and exchange of resistant alleles (Jhala et al., 2021). 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 biology of plant flowering. 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

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

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

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

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

AUTHOR CONTRIBUTIONS

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

ACKNOWLEDGMENTS

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

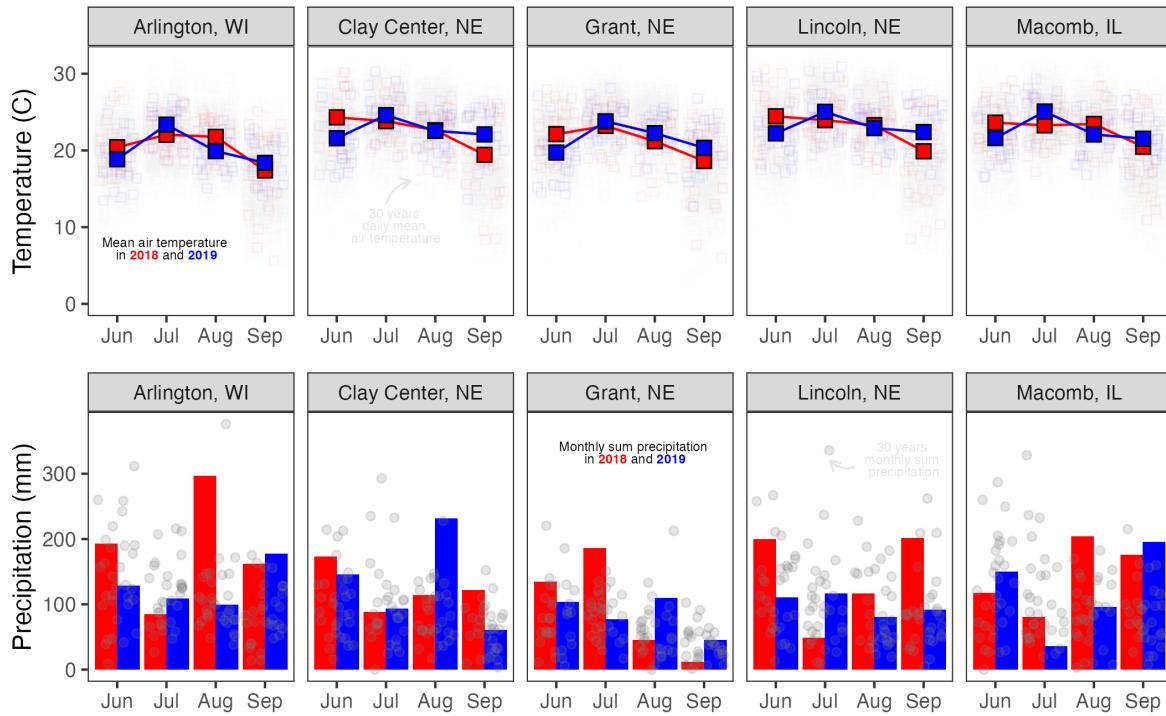


Figure 1. Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE and Macomb, IL

1 SUPPLEMENTAL DATA

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

2 REFERENCES

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

FIGURES

291 Aulakh, J. S., Chahal, P. S., Kumar, V., Price, A. J., and Guillard, K. (2021). Multiple herbicide-resistant
 292 Palmer amaranth (*Amaranthus palmeri*) in Connecticut: Confirmation and response to POST herbicides.
 293 *Weed Technology* 35, 457–463. doi:10.1017/wet.2021.6.

294 Bagavathiannan, M. V., and Norsworthy, J. K. (2016). Multiple-Herbicide Resistance Is Widespread in
 295 Roadside Palmer Amaranth Populations. *PLOS ONE* 11, e0148748. doi:10.1371/journal.pone.0148748.

296 Baker, R. (2021). Comparative analysis of Palmer amaranth (*Amaranthus palmeri*) and waterhemp (*A.
 297 Tuberculatus*) in Iowa. doi:10.31274/etd-20210609-11.

298 Bangdiwala, S. I. (2018). Regression: Binary logistic. *International Journal of Injury Control and Safety
 299 Promotion* 25, 336–338. doi:10.1080/17457300.2018.1486503.

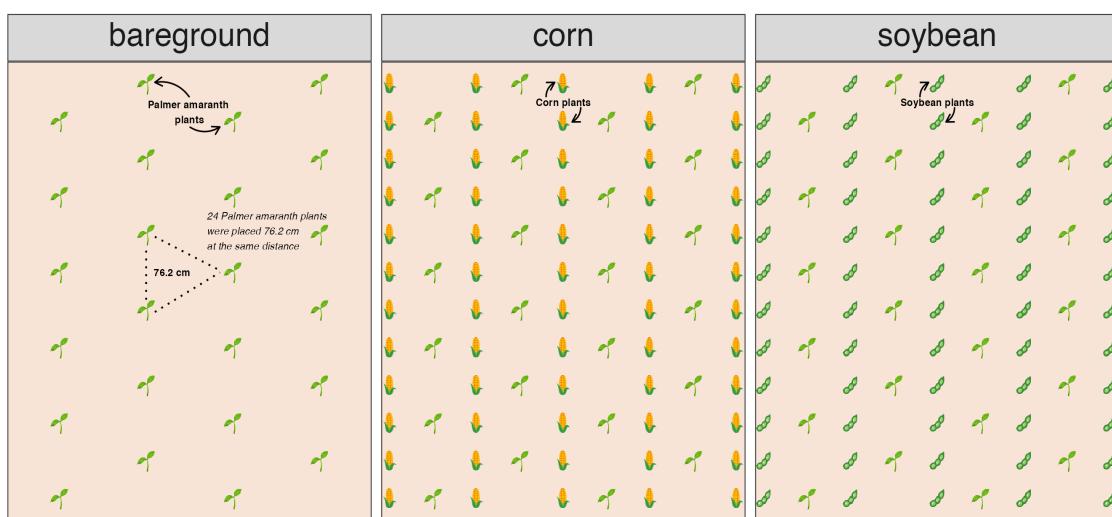


Figure 2. Palmer amaranth adaptation study layout of a plant cohort timing. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each experimental unit

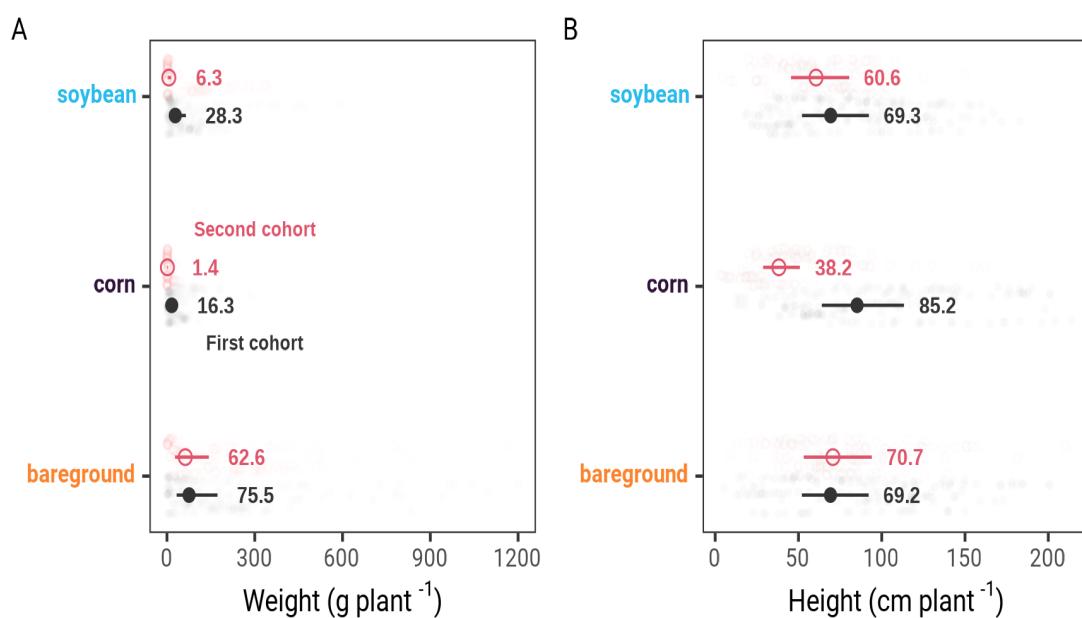


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

- 300 301 Barrett, S. C. H., and Hough, J. (2013). Sexual dimorphism in flowering plants. *Journal of Experimental Botany* 64, 67–82. doi:10.1093/jxb/ers308.
- 302 303 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using Lme4. *Journal of Statistical Software* 67, 1–48. doi:10.18637/jss.v067.i01.
- 304 305 Berger, S. T., Ferrell, J. A., Rowland, D. L., and Webster, T. M. (2015). Palmer Amaranth (*Amaranthus palmeri*) Competition for Water in Cotton. *Weed Science* 63, 928–935. doi:10.1614/WS-D-15-00062.1.

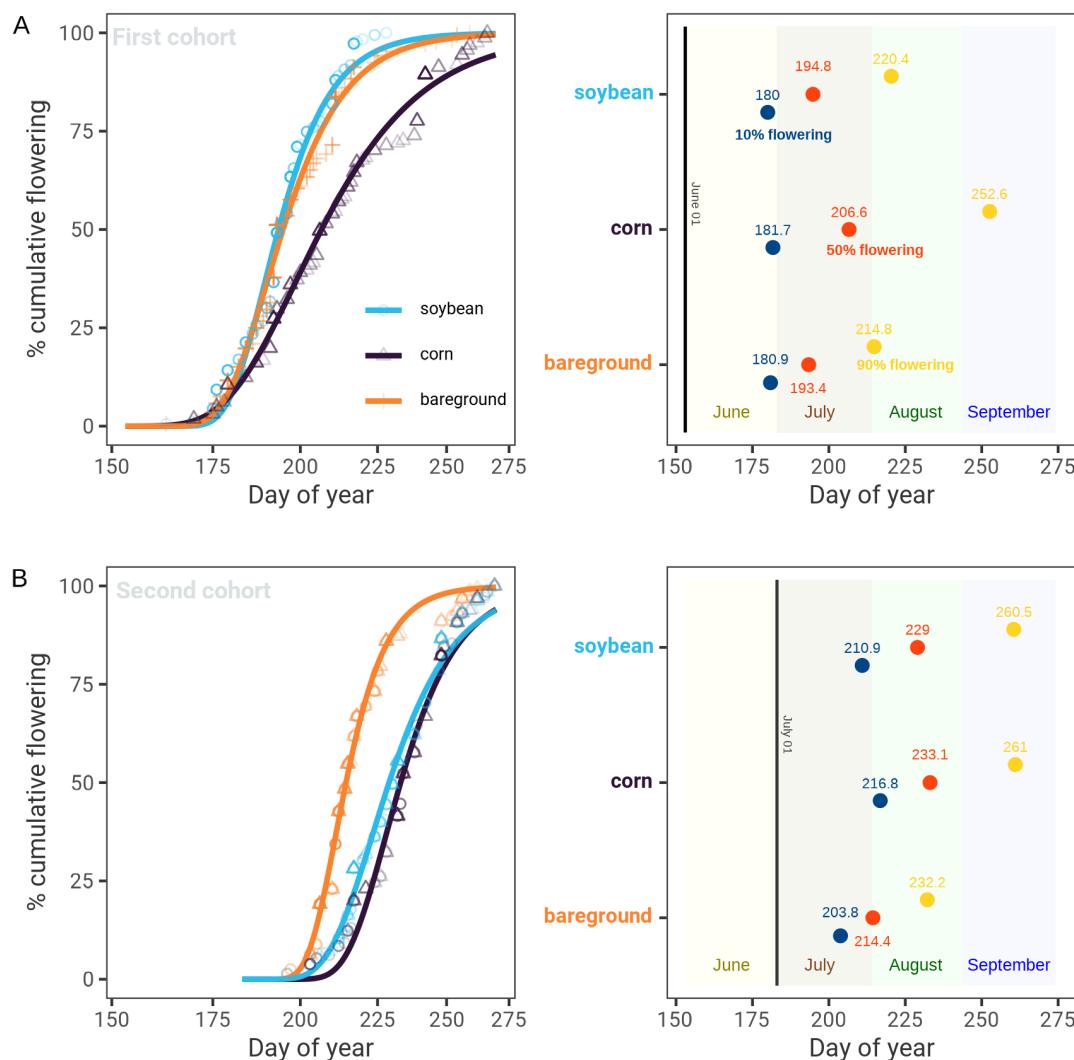


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

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

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

312 Briscoe Runquist, R. D., Lake, T., Tiffin, P., and Moeller, D. A. (2019). Species distribution models
 313 throughout the invasion history of Palmer amaranth predict regions at risk of future invasion and reveal
 314 challenges with modeling rapidly shifting geographic ranges. *Sci Rep* 9, 2426. doi:10.1038/s41598-
 315 018-38054-9.

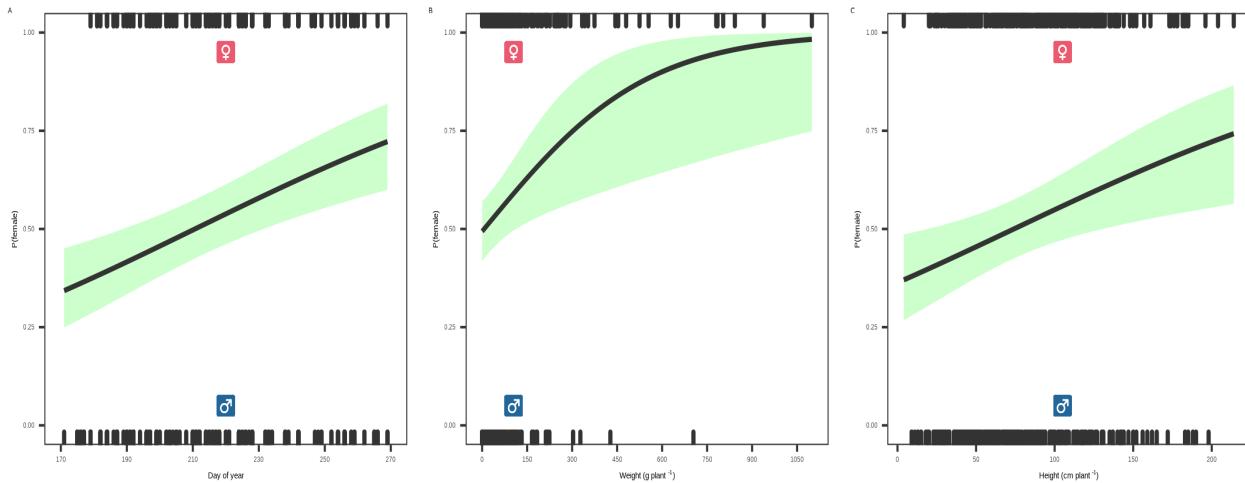


Figure 5. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)



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

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

319 Chahal, P. S., Irmak, S., Jugulam, M., and Jhala, A. J. (2018). Evaluating Effect of Degree of Water Stress
320 on Growth and Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors.
321 *Weed Science* 66, 738–745. doi:10.1017/wsc.2018.47.

- 322 Correndo, A. A., Moro Rosso, L. H., and Ciampitti, I. A. (2021). Retrieving and processing agro-
323 meteorological data from API-client sources using R software. *BMC Research Notes* 14, 205.
324 doi:10.1186/s13104-021-05622-8.
- 325 Darwin, C. (1888). *The Different Forms of Flowers on Plants of the Same Species*. J. Murray Available at:
326 <http://books.google.com?id=7uMEAAAAYAAJ>.
- 327 Davis, A. S., Schutte, B. J., Hager, A. G., and Young, B. G. (2015). Palmer Amaranth (*Amaranthus palmeri*)
328 Damage Niche in Illinois Soybean Is Seed Limited. *Weed Science* 63, 658–668. doi:10.1614/WS-D-14-
329 00177.1.
- 330 Farmer, J. A., Webb, E. B., Pierce, R. A., and Bradley, K. W. (2017). Evaluating the potential for weed seed
331 dispersal based on waterfowl consumption and seed viability. *Pest Management Science* 73, 2592–2603.
332 doi:10.1002/ps.4710.
- 333 Fisher, R. A. (1930). The genetical theory of natural selection. *Eugen Rev* 22, 127–130. Available at:
334 <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2984947/> [Accessed August 12,
335 2021].
- 336 Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications Available at:
337 <http://books.google.com?id=uPNrDwAAQBAJ>.
- 338 Garetson, R., Singh, V., Singh, S., Dotray, P., and Bagavathiannan, M. (2019). Distribution of herbicide-
339 resistant Palmer amaranth (*Amaranthus palmeri*) in row crop production systems in Texas. *Weed
340 Technology* 33, 355–365. doi:10.1017/wet.2019.14.
- 341 Guo, P., and Al-Khatib, K. (2003). Temperature effects on germination and growth of redroot pigweed
342 (*Amaranthus retroflexus*), Palmer amaranth (*A. Palmeri*), and common waterhemp (*A. rudis*). *Weed
343 Science* 51, 869–875. doi:10.1614/P2002-127.
- 344 Hartzler, B., and Anderson, M. (2016). Palmer amaranth: It's here, now what? 10.
- 345 Heap, I. (2021). Internation Herbicide-Resistant Weed Database. Available at: <http://www.weedscience.org/Home.aspx> [Accessed July 26, 2021].
- 347 Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models.
348 *Biometrical Journal* 50, 346–363. doi:10.1002/bimj.200810425.
- 349 Jha, P., Norsworthy, J. K., Riley, M. B., and Bridges, W. (2010). Annual Changes in Temperature and Light
350 Requirements for Germination of Palmer Amaranth (*Amaranthus palmeri*) Seeds Retrieved from Soil.
351 *Weed Science* 58, 426–432. doi:10.1614/WS-D-09-00038.1.
- 352 Jhala, A. J., Norsworthy, J. K., Ganie, Z. A., Sosnoskie, L. M., Beckie, H. J., Mallory-Smith, C.
353 A., Liu, J., Wei, W., Wang, J., and Stoltenberg, D. E. (2021). Pollen-mediated gene flow and
354 transfer of resistance alleles from herbicide-resistant broadleaf weeds. *Weed Technology* 35, 173–187.
355 doi:10.1017/wet.2020.101.
- 356 Keeley, P. E., Carter, C. H., and Thullen, R. J. (1987). Influence of Planting Date on Growth of Palmer
357 Amaranth (*Amaranthus palmeri*). *Weed Science* 35, 199–204. doi:10.1017/S0043174500079054.
- 358 Kistner, E. J., and Hatfield, J. L. (2018). Potential Geographic Distribution of Palmer
359 Amaranth under Current and Future Climates. *Agricultural & Environmental Letters* 3, 170044.
360 doi:10.2134/ael2017.12.0044.

- 361 Klingaman, T. E., and Oliver, L. R. (1994). Palmer Amaranth (*Amaranthus palmeri*) Interference in
362 Soybeans (*Glycine max*). *Weed Science* 42, 523–527. doi:10.1017/S0043174500076888.
- 363 Kohrt, J. R., Sprague, C. L., Nadakuduti, S. S., and Douches, D. (2017). Confirmation of a Three-Way
364 (Glyphosate, ALS, and Atrazine) Herbicide-Resistant Population of Palmer Amaranth (*Amaranthus*
365 *palmeri*) in Michigan. *Weed Science* 65, 327–338. doi:10.1017/wsc.2017.2.
- 366 Korres, N. E., and Norsworthy, J. K. (2017). Palmer Amaranth (*Amaranthus palmeri*) Demographic and
367 Biological Characteristics in Wide-Row Soybean. *Weed Science* 65, 491–503. doi:10.1017/wsc.2017.12.
- 368 Korres, N. E., Norsworthy, J. K., FitzSimons, T., Roberts, T. L., and Oosterhuis, D. M. (2017). Differential
369 Response of Palmer Amaranth (*Amaranthus palmeri*) Gender to Abiotic Stress. *Weed Science* 65,
370 213–227. doi:10.1017/wsc.2016.34.
- 371 Korres, N. E., Norsworthy, J. K., Mauromoustakos, A., and Williams, M. M. (2020). Soybean density and
372 Palmer amaranth (*Amaranthus palmeri*) establishment time: Effects on weed biology, crop yield, and
373 economic returns. *Weed Science* 68, 467–475. doi:10.1017/wsc.2020.41.
- 374 Küpper, A., Borgato, E. A., Patterson, E. L., Netto, A. G., Nicolai, M., Carvalho, S. J. P. de, Nissen, S.
375 J., Gaines, T. A., and Christoffoleti, P. J. (2017). Multiple Resistance to Glyphosate and Acetolactate
376 Synthase Inhibitors in Palmer Amaranth (*Amaranthus palmeri*) Identified in Brazil. *Weed Science* 65,
377 317–326. doi:10.1017/wsc.2017.1.
- 378 Lang, A. (1965). “Physiology of flower initiation,” in *Differenzierung und Entwicklung / Differentiation*
379 and *Development* Handbuch der Pflanzenphysiologie / Encyclopedia of Plant Physiology, ed. A. Lang
380 (Berlin, Heidelberg: Springer), 1380–1536. doi:10.1007/978-3-642-50088-6_39.
- 381 Larran, A. S., Palmieri, V. E., Perotti, V. E., Lieber, L., Tuesca, D., and Permingeat, H. R. (2017). Target-site
382 resistance to acetolactate synthase (ALS)-inhibiting herbicides in *Amaranthus palmeri* from Argentina.
383 *Pest Management Science* 73, 2578–2584. doi:10.1002/ps.4662.
- 384 Leeper, T. J. (2017). Interpreting Regression Results using Average Marginal Effects with R’s margins. 31.
- 385 Lindsay, K., Popp, M., Norsworthy, J., Bagavathiannan, M., Powles, S., and Lacoste, M. (2017). PAM:
386 Decision Support for Long-Term Palmer Amaranth (*Amaranthus palmeri*) Control. *Weed Technology*
387 31, 915–927. doi:10.1017/wet.2017.69.
- 388 MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., and Dehnen-Schmutz, K. (2020). An ecological
389 future for weed science to sustain crop production and the environment. A review. *Agron. Sustain. Dev.*
390 40, 24. doi:10.1007/s13593-020-00631-6.
- 391 MacRae, A. W., Webster, T. M., Sosnoskie, L. M., Culpepper, A. S., and Kichler, J. M. (2013). Cotton
392 Yield Loss Potential in Response to Length of Palmer Amaranth (*Amaranthus palmeri*) Interference.
393 17, 6.
- 394 Massinga, R. A., Currie, R. S., Horak, M. J., and Boyer, J. (2001). Interference of Palmer amaranth in corn.
395 *Weed Science* 49, 202–208. doi:10.1614/0043-1745(2001)049[0202:IOPAIC]2.0.CO;2.
- 396 Matzrafi, M., Osipitan, O. A., Ohadi, S., and Mesgaran, M. B. (2021). Under pressure: Maternal effects
397 promote drought tolerance in progeny seed of Palmer amaranth (*Amaranthus palmeri*). *Weed Science*
398 69, 31–38. doi:10.1017/wsc.2020.75.
- 399 McFarlane, G. R., Whitelaw, C. B. A., and Lillico, S. G. (2018). CRISPR-Based Gene Drives for Pest
400 Control. *Trends in Biotechnology* 36, 130–133. doi:10.1016/j.tibtech.2017.10.001.

- 401 Menges, R. M. (1987). Weed Seed Population Dynamics during Six Years of Weed Management Systems
402 in Crop Rotations on Irrigated Soil. *Weed Science* 35, 328–332. Available at: <http://www.jstor.org/stable/4044593>.
- 404 Mesgaran, M. B., Matzrafi, M., and Ohadi, S. (2021). Sex dimorphism in dioecious Palmer amaranth
405 (Amaranthus palmeri) in response to water stress. *Planta* 254, 17. doi:10.1007/s00425-021-03664-7.
- 406 Milani, A., Panizzo, S., Farinati, S., Iamonico, D., Sattin, M., Loddo, D., and Scarabel, L. (2021). Recent
407 Discovery of Amaranthus palmeri S. Watson in Italy: Characterization of ALS-Resistant Populations
408 and Sensitivity to Alternative Herbicides. *Sustainability* 13, 7003. doi:10.3390/su13137003.
- 409 Montgomery, J. S., Giacomini, D. A., Weigel, D., and Tranel, P. J. (2021). Male-specific Y-chromosomal
410 regions in waterhemp (Amaranthus tuberculatus) and Palmer amaranth (Amaranthus palmeri). *New*
411 *Phylogist* 229, 3522–3533. doi:10.1111/nph.17108.
- 412 Montgomery, J. S., Sadeque, A., Giacomini, D. A., Brown, P. J., and Tranel, P. J. (2019). Sex-specific
413 markers for waterhemp (Amaranthus tuberculatus) and Palmer amaranth (Amaranthus palmeri). *Weed*
414 *Science* 67, 412–418. doi:10.1017/wsc.2019.27.
- 415 Morgan, G. D., Baumann, P. A., and Chandler, J. M. (2001). Competitive Impact of Palmer Amaranth
416 (Amaranthus palmeri) on Cotton (*Gossypium hirsutum*) Development and Yield. *Weed Technology* 15,
417 408–412. doi:10.1614/0890-037X(2001)015[0408:CIOPAA]2.0.CO;2.
- 418 Nguyen, H. M., Kleitou, P., Kletou, D., Sapir, Y., and Winters, G. (2018). Differences in flowering sex
419 ratios between native and invasive populations of the seagrass *Halophila stipulacea*. *Botanica Marina*
420 61, 337–342. doi:10.1515/bot-2018-0015.
- 421 Oliveira, M. C., Gaines, T. A., Patterson, E. L., Jhala, A. J., Irmak, S., Amundsen, K., and Knezevic, S.
422 Z. (2018). Interspecific and intraspecific transference of metabolism-based mesotrione resistance in
423 dioecious weedy Amaranthus. *The Plant Journal* 96, 1051–1063. doi:10.1111/tpj.14089.
- 424 Oliveira, M. C., Giacomini, D. A., Arsenijevic, N., Vieira, G., Tranel, P. J., and Werle, R. (2021).
425 Distribution and validation of genotypic and phenotypic glyphosate and PPO-inhibitor resistance in
426 Palmer amaranth (Amaranthus palmeri) from southwestern Nebraska. *Weed Technology* 35, 65–76.
427 doi:10.1017/wet.2020.74.
- 428 Page, E. R., Nurse, R. E., Meloche, S., Bosveld, K., Grainger, C., Obeid, K., Filotas, M., Simard, M.-J., and
429 Laforest, M. (2021). Import of Palmer amaranth (Amaranthus palmeri S. Wats.) Seed with sweet potato
430 (*Ipomea batatas* (L.) Lam) slips. *Can. J. Plant Sci.*, CJPS-2020-0321. doi:10.1139/CJPS-2020-0321.
- 431 Pérez-Llorca, M., and Sánchez Vilas, J. (2019). Sexual dimorphism in response to herbivory and
432 competition in the dioecious herb *Spinacia oleracea*. *Plant Ecol* 220, 57–68. doi:10.1007/s11258-
433 018-0902-7.
- 434 Piskackova, T. A. R., Reberg-Horton, S. C., Richardson, R. J., Jennings, K. M., Franca, L., Young, B. G.,
435 and Leon, R. G. (2021). Windows of action for controlling palmer amaranth (Amaranthus palmeri)
436 using emergence and phenology models. *Weed Research* 61, 188–198. doi:10.1111/wre.12470.
- 437 Price, A. J., Balkcom, K. S., Culpepper, S. A., Kelton, J. A., Nichols, R. L., and Schomberg, H. (2011).
438 Glyphosate-resistant Palmer amaranth: A threat to conservation tillage. *Journal of Soil and Water*
439 *Conservation* 66, 265–275. doi:10.2489/jswc.66.4.265.

- 440 Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. (2015). Dose-Response Analysis Using R. *PLOS ONE*
441 10, e0146021. doi:10.1371/journal.pone.0146021.
- 442 Rumpa, M. M., Krausz, R. F., Gibson, D. J., and Gage, K. L. (2019). Effect of PPO-Inhibiting Herbicides
443 on the Growth and Sex Ratio of a Dioecious Weed Species *Amaranthus palmeri* (Palmer Amaranth).
444 *Agronomy* 9, 275. doi:10.3390/agronomy9060275.
- 445 Sanctis, J. H. S. de, Barnes, E. R., Knezevic, S. Z., Kumar, V., and Jhala, A. J. (2021). Residual herbicides
446 affect critical time of Palmer amaranth removal in soybean. *Agronomy Journal* 113, 1920–1933.
447 doi:10.1002/agj2.20615.
- 448 Sauer, J. (1957). Recent Migration and Evolution of the Dioecious Amaranths. *Evolution* 11, 11–31.
449 doi:10.2307/2405808.
- 450 Sauer, J. D. (1972). The dioecious amaranths: A new species name and major range extensions. *Madroño*
451 21, 426–434. Available at: <http://www.jstor.org/stable/41423815>.
- 452 Sbatella, G. M., and Wilson, R. G. (2010). Isoxaflutole Shifts Kochia (*Kochia scoparia*) Populations in
453 Continuous Corn. *Weed Technology* 24, 392–396. doi:10.1614/WT-D-09-00023.1.
- 454 Schliekelman, P., Ellner, S., and Gould, F. (2005). Pest Control by Genetic Manipulation of Sex Ratio.
455 *Journal of Economic Entomology* 98, 18–34. doi:10.1093/jee/98.1.18.
- 456 Schwartz, L. M., Norsworthy, J. K., Young, B. G., Bradley, K. W., Kruger, G. R., Davis, V. M., Steckel,
457 L. E., and Walsh, M. J. (2016). Tall Waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth
458 (*Amaranthus palmeri*) Seed Production and Retention at Soybean Maturity. *Weed Technology* 30,
459 284–290. doi:10.1614/WT-D-15-00130.1.
- 460 Scott, D. (2011). The Technological Fix Criticisms and the Agricultural Biotechnology Debate. *J Agric
461 Environ Ethics* 24, 207–226. doi:10.1007/s10806-010-9253-7.
- 462 Sosnoskie, L. M., Webster, T. M., and Culpepper, A. S. (2013). Glyphosate Resistance Does Not
463 Affect Palmer Amaranth (*Amaranthus palmeri*) Seedbank Longevity. *Weed Science* 61, 283–288.
464 doi:10.1614/WS-D-12-00111.1.
- 465 Spaunhorst, D. J., Devkota, P., Johnson, W. G., Smeda, R. J., Meyer, C. J., and Norsworthy, J. K. (2018).
466 Phenology of Five Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and
467 Arkansas. *Weed Science* 66, 457–469. doi:10.1017/wsc.2018.12.
- 468 Van Wychen, L. (2020). 2020 Survey of the most common and troublesome weeds in grass crops, pasture,
469 and turf in the United States and Canada. Available at: [https://wssa.net/wp-content/
470 uploads/2020-Weed-Survey_grass-crops.xlsx](https://wssa.net/wp-content/uploads/2020-Weed-Survey_grass-crops.xlsx).
- 471 Wang, J. L., Klessig, D. F., and Berry, J. O. (1992). Regulation of C4 Gene Expression in Developing
472 Amaranth Leaves. *The Plant Cell* 4, 173–184. doi:10.1105/tpc.4.2.173.
- 473 Ward, S. M., Webster, T. M., and Steckel, L. E. (2013). Palmer Amaranth (*Amaranthus palmeri*): A Review.
474 *Weed Technology* 27, 12–27. doi:10.1614/WT-D-12-00113.1.
- 475 Webster, T. M., and Grey, T. L. (2015). Glyphosate-Resistant Palmer Amaranth (*Amaranthus palmeri*)
476 Morphology, Growth, and Seed Production in Georgia. *Weed Science* 63, 264–272. doi:10.1614/WS-D-
477 14-00051.1.

- 478 Yacoubi, R., and Axman, D. (2020). Probabilistic Extension of Precision, Recall, and F1 Score for
479 More Thorough Evaluation of Classification Models. in *Proceedings of the First Workshop on*
480 *Evaluation and Comparison of NLP Systems* (Online: Association for Computational Linguistics),
481 79–91. doi:10.18653/v1/2020.eval4nlp-1.9.
- 482 Yu, E., Blair, S., Hardel, M., Chandler, M., Thiede, D., Cortilet, A., Gunsolus, J., and Becker, R. (2021).
483 Timeline of Palmer amaranth (*Amaranthus palmeri*) invasion and eradication in Minnesota. *Weed*
484 *Technology*, 1–31. doi:10.1017/wet.2021.32.