

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

Maxwel C. Oliveira<sup>1</sup>, Amit J. Jhala<sup>2</sup>, Mark L. Bernards<sup>3</sup>, Chris Proctor<sup>2</sup>,  
Strahinja Stepanovic<sup>2</sup>, Rodrigo Werle<sup>1\*</sup>

<sup>1</sup> Department of Agronomy, University of Wisconsin-Madison, Madison, Wisconsin, United States

<sup>2</sup> Department of Agronomy and Horticulture, University of Nebraska-Lincoln, Lincoln, Nebraska, United States

<sup>3</sup> School of Agriculture, Western Illinois University, Macomb, Illinois, United States

Correspondence\*:

Rodrigo Werle

rwerle@uwisc.edu

## 2 ABSTRACT

3 Palmer amaranth (*Amaranthus palmeri* S. Watson) is one of the most troublesome agronomic  
4 weed species in the United States. Palmer amaranth is prevalent in the Southern Great Plains and  
5 Southeastern United States, and its range is expanding northward through natural dispersal and  
6 human intervention. Palmer amaranth dispersal warrants studies assessing species adaptation  
7 into new geographies. A study was conducted to investigate morphology, flowering and gender  
8 from cohorts of Palmer amaranth growing under corn, soybean, and bareground across five  
9 locations in the US Midwest. Results demonstrated that the first cohort of Palmer amaranth,  
10 established in June, produced 42% more biomass than plants from the second cohort (established  
11 in July). The first Palmer amaranth cohort produced 75.5 g plant<sup>-1</sup> in bareground, 28.3 g plant<sup>-1</sup> in  
12 soybean and 16.3 g plant<sup>-1</sup> in corn, whereas the second Palmer amaranth cohort produced 62.6,  
13 6.3, and 1.4 g plant<sup>-1</sup> in bareground, soybean and corn, respectively. Palmer amaranth height  
14 was most impacted when growing in corn, and averaged 85.2 cm tall in the first cohort, and  
15 38.2 cm tall in the second cohort in corn. Moreover, Palmer amaranth flowering window shifted  
16 according to crop and cohort timings. Palmer amaranth growing in intense competition, such as  
17 under low light in corn, resulted in the longest flowering window. Palmer amaranth gender was  
18 slightly influenced by day of year, weight and height. We documented a high degree of plasticity in  
19 Palmer amaranth, which will presumably favor its adaptation and expansion in cropping systems  
20 north of its current range. Therefore, preventing Palmer amaranth dispersal into new habitats is  
21 the most effective management strategy.

22 **Keywords:** Evolution, Flowering, Management, Pigweed, Weed

## INTRODUCTION

23 Palmer amaranth (*Amaranthus palmeri* S. Watson) is currently ranked as one of the most economically  
24 detrimental weed species to cropping systems in the United States (Van Wychen, 2020). Unmanaged  
25 Palmer amaranth plants compete for water, light, and nutrients, which can drastically impact crop yields  
26 (Berger et al., 2015). For example, Palmer amaranth has been documented to reduce up to 91%, 68%, and

27 54% corn (Massinga et al., 2001), soybean (Klingaman and Oliver, 1994), and cotton (Morgan et al., 2001)  
28 yields, respectively. Moreover, Palmer amaranth has shown a remarkable capacity to evolve resistance  
29 to herbicides. To date, Palmer amaranth has evolved resistance to eight herbicide sites of action (Heap,  
30 2021), increasing the weed management complexity (Lindsay et al., 2017) and posing an economical and  
31 ecological risk to row-crop agriculture.

32 Palmer amaranth as a problem weed is a function of both inherent adaptations and selected management  
33 practices. Palmer amaranth is a fast growing summer annual forb indigenous to the Sonoran Desert (Sauer,  
34 1957). It became a serious problem weed in US agriculture in the 1990s (Ward et al., 2013). Palmer  
35 amaranth weediness is likely a result of human-assisted selection combined with plant biology. Farm  
36 mechanization, adoption of conservation agriculture (e.g., no-till), and intensive use of herbicides for weed  
37 management are the main human-mediated selections of Palmer amaranth in cropping systems (Ward et  
38 al., 2013). Palmer amaranth is a prolific seed producer with a C4 photosynthetic apparatus (Wang et al.,  
39 1992). With dioecious nature, Palmer amaranth male and female plants are obligate outcrossers, increasing  
40 the chances of exchanging adaptive traits among plants (Jhala et al., 2021; Oliveira et al., 2018). Also,  
41 Palmer amaranth's small seeds (e.g., 1 mm) tend to thrive in no-tillage systems (Price et al., 2011), and  
42 spread across locations through farm equipment (Sauer, 1972), seed mixes (Hartzler and Anderson, 2016),  
43 wildlife (Farmer et al., 2017), etc., making it one of the most successful examples of weed adaptation to  
44 current cropping systems.

45 Palmer amaranth's plasticity allows it to respond successfully to environmental changes. Palmer amaranth  
46 demonstrates a high degree of plasticity to light, temperature, water availability, and human management  
47 (Jha et al., 2010). Palmer amaranth has an extended germination period of up to \_\_\_\_ (Ward et al., 2013).  
48 Germination of Palmer amaranth was triggered by 18 C soil temperature at 5 cm depth (Keeley et al., 1987),  
49 and optimal germination and biomass production occurred at 35/30 C day and night temperatures (Guo and  
50 Al-Khatib, 2003). Palmer amaranth emergence can be influenced by tillage and the use of preemergence  
51 herbicides (Chahal et al., 2021), and may result in weed germination shifts within a population, as  
52 documented in *Bassia scoparia* (Sbatella and Wilson, 2010). In an experiment where Palmer amaranth was  
53 subjected to continuous water stress, it survived and produced at least 14000 seeds plant<sup>-1</sup> (Chahal et al.,  
54 2018). Seeds from Palmer amaranth growing with limited water conditions were heavier, less dormant,  
55 and prompt for germination (Matzrafi et al., 2021). Growing conditions and management practices also  
56 influence Palmer amaranth sex dimorphism and flowering pattern (Korres et al., 2017; Rumpa et al., 2019).

57 Palmer amaranth's current global range includes agronomic cropland in Italy (Milani et al., 2021), soybean  
58 producing regions of Brazil and Argentina (Larran et al., 2017; Küpper et al., 2017), and the Cotton Belt  
59 (Garetson et al., 2019; Bagavathiannan and Norsworthy, 2016) and southern Great Plains of the United  
60 States (Kumar et al. (2020), Crespo et al. (2016)]. However, its range appears to be expanding steadily, and  
61 in some cases rapidly, in the U.S. For example, in states with large Palmer amaranth infestations its range is  
62 gradually pushing north as it displaces other weeds in agronomic row crops (R Werle, personal observation),  
63 aided by wildlife (Farmer et al., 2017) and agricultural machinery. But there are other examples where it  
64 has suddenly become a problem weed hundreds of miles away from known infestations. New infestations in  
65 Michigan, Indiana and North Dakota appear to have resulted from Palmer amaranth contaminated livestock  
66 feed. New infestations in Iowa and Minnesota were associated with planting contaminated pollinator habitat  
67 seed (Yu et al., 2021). Palmer amaranth infestations have not been detected in Canada, but Palmer amaranth  
68 seeds were found in sweet potato slips imported into the country (Page et al., 2021). Global warming will  
69 create new opportunities for Palmer amaranth invasion. Although agronomic crops in warm environments  
70 like Australia and Sub-Saharan Africa are currently at greatest risk for Palmer amaranth invasion, warming

71 temperatures will reduce barriers that may have limited Palmer amaranths spread into cooler climates like  
72 Canada and Northern Europe (Kistner and Hatfield, 2018; Briscoe Runquist et al., 2019).

73 There are many areas in the U.S. Corn Belt (North Central States) where Palmer amaranth is not yet  
74 established, and its potential adaptability is untested. Nonetheless, the rapid expansion of Palmer amaranth  
75 across the Northern U.S. is concerning and warrants investigations on its adaptability. We do know that  
76 Palmer amaranth caused yield loss in Illinois soybean fields (Davis et al., 2015), but an Iowa study showed  
77 that Palmer amaranth was not as well adapted as waterhemp (*Amaranthus tuberculatus*) to conditions in that  
78 geography (Baker, 2021). We also know that Palmer amaranth plants that establish shortly after row-crop  
79 planting have a much greater impact on crop yield than plants that emerge after the crop has produced  
80 several leaves (MacRae et al., 2013). Understanding Palmer amaranth morphology and development under  
81 different agroecosystems and across a wide geography can enhance our knowledge of its adaptability, and  
82 may also aid in designing effective tactics to limit its range expansion and minimize its negative effects on  
83 row crops. The objective of this study was to investigate the flowering pattern, gender, biomass production,  
84 and height of Palmer amaranth cohorts growing in corn, soybean and bareground environments across five  
85 locations in the North Central United States.

## MATERIAL AND METHODS

### Plant material and growing conditions

86 A Palmer amaranth accession (Kei3) from Perkins County, Nebraska with no glyphosate resistance was  
87 selected for this study (Oliveira et al., 2021). Three weeks prior to the establishment of each cohort, seeds  
88 were planted in plastic trays containing potting-mix. Emerged seedlings (1 cm) were transplanted into 200  
89  $\text{cm}^{-3}$  plastic pots (a plant pot $^{-1}$ ). Palmer amaranth seedlings were supplied with adequate water and kept  
90 under greenhouse conditions at the University of Wisconsin-Madison, University of Nebraska-Lincoln, and  
91 Western Illinois University; and kept outdoors at the Perkins extension office in Grant, NE until the 2-3  
92 leaf stage (5 to 8 cm height) when they were transported to the field.  
93

### Field study

94 The experiment was conducted in 2018 and 2019 under field conditions at five locations: Arlington, WI  
95 (43°18'N, 89°29'W), Clay Center, NE (40.57'N, 9814'W), Grant, NE (40.85'N, -101.70'W), Lincoln, NE  
96 (41.16'N, 96.42'W), and Macomb, IL (XXX'N, XXX'W).

97 Fields were conventionally tilled prior to crop planting. Corn and soybean were planted in 76-cm row  
98 spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using Daymet  
99 weather data from June through September across the five locations in 2018 and 2019 (Correndo et al.,  
100 2021) (Figure 1).

101 The field experimental units were three adjacent 9.1 m wide (12 rows at 76.2 cm row spacing) by 10.7 m  
102 long. The experimental design were arranged in factorial design with three crops, two transplanting times  
103 simulating two cohorts, repeated across five locations. Each field experimental unit was planted with corn,  
104 soybean, or maintained as bareground. The two transplant timings were June 1 (first cohort) and July 1  
105 (second cohort). Palmer amaranth seedlings (potting mix + two seedlings) were transplanted (6 cm deep  
106 and 8 cm wide). Forty-eight plants were equidistantly placed (0.76 m apart) between rows within each  
107 crop. After a week, one plant was eliminated and one was kept, resulting in 24 plants per experimental unit  
108 and transplanting time (Figure 2). When needed, Palmer amaranth plants were supplied with water during  
109 the first week after transplanting to assure seedling survival.

**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	NK0142 3120-EZ1	DKC60-67		
	Seeding rate	88956	86487		
	Weed control	glyphosate / S-metolachlor	S-metolachlor + trazine + mesotrione, + bicyclopyrone		
	Stage at 1 cohort	V2-3			
	Stage at 2 cohort	V6-7			
	Planting day	April 30, 2018 / May 5, 2019	May 10, 2018/19		
	Fertilization	N (46-0-0) at 157 kg ha <sup>-1</sup>			
Soybean	Variety	DSR-1950	AG21X8		
	Seeding rate	296400	321237		
	Weed control	glyphosate / S-metolachlor	saflufenacil + imazethapyr + pyroxasulfone		
	Stage at 1 cohort	V1-2			
	Stage at 2 cohort	V5-6			
	Planting day	May 5, 2018 / May 10, 2009	May 14, 2018/19		
Soil	Type	Plano-silt-loam	Crete Silt Loam		
	Ratio (sand-clay-silt)	10-64-26	17-58-25		
	pH	6.6	6.5		
	Organic matter (%)	3.5	3		

<sup>a</sup> glyphoste, 840 g ae ha; <sup>b</sup> S-metolachlor, 1324 g ai ha; <sup>c</sup> S-metolachlor + trazine + mesotrione, + bicyclopyrone, 2409 g ai ha; <sup>d</sup> saflufenacil + imazethapyr + pyroxasulfone, 215 g ai ha

111 After transplanting, Palmer amaranth flowering was monitored until the end of the study. When a plant  
 112 flowered, the day was recorded, plant gender was identified (male or female), plant height was measured  
 113 from soil surface to the top of plant. Also, aboveground plant, and all aboveground plant organs were  
 114 harvested, then oven dried at 65 C until a constant weight was reached, and dry biomass (g plant<sup>-1</sup>) was  
 115 recorded. Plants were harvested at flowering because Palmer amaranth infestations do not occur at the  
 116 Wisconsin or Illinois research locations. In our study, all locations followed the methodology of plant  
 117 harvest at flowering initiation, except in Grant, NE. At the Grant, NE, location, all plants from the first  
 118 cohort were harvested on July 6, 2018 or July 6, 2019, and all plants from the second cohort were harvested  
 119 on August 17, 2018 or July 31, 2019, regardless of flowering status.

## 120 Statistical analyses

121 The statistical analyses were performed using R statistical software version 4.0.1 (Team, 2021).

122 Analyses of Palmer amaranth height and biomass were performed with a linear mixed model using *lmer*  
 123 function from “lme4” package (Bates et al., 2015). Plant height and biomass were log transformed to meet  
 124 model assumption of normality. In the model, crop (bareground, corn, soybean) and cohort time (first and  
 125 second) were the fixed effects and year nested with location were the random effects. Analysis of variance  
 126 at  $\alpha$  0.05 was performed with *anova* function from “car” package (Fox and Weisberg, 2018). Marginal  
 127 means and compact letter display were estimated with *emmeans* and *cld* from packages “emmeans” (Lenth  
 128 et al., 2021) and “multcomp” (Hothorn et al., 2008), respectively.

129 Palmer amaranth cumulative flowering estimation was determined across all locations, except Grant,  
 130 NE. Cumulative flowering estimation was determined using an asymmetrical three parameter log logistic  
 131 Weibull model of the drc package (Ritz et al., 2015):

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

132 In this model,  $Y$  is the cumulative flowering,  $d$  is the upper limit (set to 100), and  $e$  is the inflection point,  
 133 and  $x$  is the day of year (doy).

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

138 A binary logistic regression was fitted to Palmer amaranth gender. Binary logistic regression is used for  
139 predicting binary classes (Bangdiwala, 2018), such as the probability of a plant being female in a dioecious  
140 species. Prior to the analysis, missing values were removed from the dataset (including all data from the  
141 Grant location). The resulting dataset was split into 80% train and 20% test data. The 80% train is used  
142 for model training and the 20% test is used for checking model performance on unseen dataset. Using the  
143 80% train data, a generalized linear model (base R *glm* function) was fitted to binary response variable, the  
144 probability of being female (0 to male and 1 to female). The independent variables were harvest day of year,  
145 height, weight, and crop (without interaction). The model family was binomial with a logit function. The  
146 model fit was assessed through pseudo R-squared values (McFadden, Cox and Snell, Cragg and Uhler) and  
147 likelihood ratio using *nagelkerke* function from “rcompanion” package (Mangiafico, 2021). The marginal  
148 effects computation was performed with Average Marginal Effects (AMEs) at every observed value of x  
149 and averaged across the results (Leeper, 2017) using *margins* function from “margins” package (Leeper et  
150 al., 2021). The 20% test data was predicted using the *predict* function with a cutoff estimation for male or  
151 female using *performance* function from ROCR package (Sing et al., 2005). The model quality prediction  
152 from the classification algorithm was measured with precision (*precision* function), recall (*recall* function)  
153 and F1-score (*f\_meas* function) using the “yardstick” package (Kuhn et al., 2021). The precision determines  
154 the accuracy of positive predictions (female plants), recall determines the fraction of positives that were  
155 correctly identified, and F1-score is a weighted harmonic mean of precision and recall with the best score  
156 of 1 and the worst score of 0 (Raoniar, 2021). F1-score conveys the balance between the precision and the  
157 recall (Yacoub and Axman, 2020). The area under the receiver operating curve (AUC-ROC) was also  
158 estimated with performance function using the true positive and false positive rates. The higher the AUC,  
159 better the model is at distinguishing between female and male Palmer amaranth.

## RESULTS

### 160 Palmer amaranth height and biomass

161 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants  
162 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3,  
163 and 16.3 g plant<sup>-1</sup> in bareground, soybean and corn, respectively. Plants from the second cohort produced  
164 62.6 g plant<sup>-1</sup> in bareground, followed by 6.3 g plant<sup>-1</sup> in soybean, and 1.4 g plant<sup>-1</sup> in corn.

165 Palmer amaranth height was less affected by cohort timing than was weight, with the exception of plants  
166 growing in corn (Figure 3B). Plants from the first cohort were on average 69.2 cm tall in bareground, which  
167 was not different from the 70.7 cm tall plants from the second cohort timing (P = 0.74). In addition, no  
168 difference in Palmer amaranth height (69.3 cm) was detected from first cohort plants in soybean to first and  
169 second cohort plants in bareground (P > 0.75). Palmer amaranth plants from the second cohort were nearly  
170 10 cm shorter compared to the first cohort in soybeans (P = 0.04). The tallest (85.2 cm, first cohort) and  
171 shortest (38.2 cm, second cohort) plants were observed in corn.

### 172 Palmer amaranth cumulative flowering

173 The initiation and duration of Palmer amaranth flowering was strongly influenced by cohort and  
174 surrounding vegetation (Figure 4A, 4B). In the first cohort, floral initiation (10% flowering) occurred near  
175 the end of June for all three treatments, at day 180, 180.9, and 181.7 for soybean, bareground, and corn,

176 respectively. In the second cohort, floral initiation occurred earlier on plants growing in the bareground than  
 177 plants growing in soybean or corn (doy 203.8 versus doy 210.9 or 216.8, respectively). Palmer amaranth  
 178 growing in the bareground had the shortest duration of floral initiation (measured as the difference between  
 179 10% and 90% cumulative flowering) in both the first (34 days) and second (28 days) cohorts. Palmer  
 180 amaranth growing in soybean had a shorter duration of flowering than corn in the first cohort (40 days vs  
 181 71 days), but a longer duration in the second cohort (50 vs 44 days).

182 Palmer amaranth cumulative flowering in the second cohort ranged from mid July to mid September  
 183 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to  
 184 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at  
 185 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at  
 186 doy 210.9, which was 6 days prior to corn ( $P$ -value = 0.00). Similar trend was observed at 50% flowering,  
 187 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9;  $P$   
 188 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean  
 189 (260.5;  $P$  = 0.66).

### 190 Palmer amaranth gender

191 The model goodness of fit was 0.23, 0.32, 0.40 using pseudo R-squared test from McFadden, Cox and  
 192 Snell, and Cragg and Uhler, respectively. The likelihood ratio test showed a p-value of < 0.00. The average  
 193 marginal effects showed that Palmer amaranth growing in corn resulted in 14.8% fewer females plants  
 194 (Table 2). Moreover, increasing a cumulative flowering unit doy increases the probability of having a  
 195 female plant by 0.4% (Table 2 and Figure 5A). A similar trend was observed for weight (Figure 5B) and  
 196 height (Figure 5C), where the probability of being female increased 0.1% and 0.2% for each unit increase  
 197 of weight (g) and height (cm), respectively (Table 2).

198 \begin{table}[\!h]

199 \caption{Average marginal effects of Palmer amaranth gender logistic model. Factor pararamter values  
 200 (crop\_corn and 'crop\_bareground) are calculated relative to soybean.}

201

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

<sup>a</sup> Average Marginal Effects. <sup>b</sup> Standard Error.

202 \end{table}

203 The model accuracy evaluation accuracy in the 20% test dataset was 0.62 with a cutoff value for female and male plants of 0.43.  
 204 The model classification showed a precision of 0.64, recall of 0.66, and a F1-score of 0.65. In addition, the AUC was 0.64.

## DISCUSSION

205 Our study confirmed that Palmer amaranth is well adapted to growing throughout the Midwestern United States, and is simply  
 206 limited in its range by seed dispersal (Davis et al. 2015). We also confirmed Palmer amaranth's extraordinary plasticity to adapt  
 207 to different agroecosystems. For example, Palmer amaranth mimicked crop architecture in competing for light (Figure 6), where  
 208 plants growing in corn allocated resources to height, while plants growing in bareground allocated resources to numerous

209 branches. Plants growing in the absence of a crop produced the greatest biomass, responding to a greater abundance of light,  
210 nutrient and water resources (Figure 3A, 3B). These results support the argument that Palmer amaranth can quickly evolve  
211 life-history traits to adapt to different cultural practices, similar to observations in a Palmer amaranth response to nitrogen study  
212 (Bravo et al., 2018). Our results highlight Palmer amaranth as a threat to field crops as breeding more competitive crop varieties  
213 is likely to select more competitive weed biotypes (Bravo et al., 2017).

214 Palmer amaranth growth and development in second cohort was limited due to the crop competitive ability at advanced  
215 development stages. Plants were transplanted at greater crop height and width, which reduced Palmer amaranth competitiveness.  
216 As a result, Palmer amaranth height and biomass was lower compared to its first cohort. Moreover, Palmer amaranth growing  
217 without crop competition produced the highest amounts of biomass. The Palmer amaranth strategy in bareground was to invest  
218 biomass in growing plant width and height. Nonetheless, Palmer amaranth produced 17% less biomass in second cohort  
219 compared to first cohort timing. In a bareground study, early emerged Palmer amaranth without competition was 50% taller than  
220 late emerged plants (Webster and Grey, 2015). These results suggest that crop competition is not the only factor limiting late  
221 Palmer amaranth establishment. The limited growth of Palmer amaranth at second cohort is likely a reduced plant response to  
222 day length, light availability and thermal units (e.g, growing degree days). The *Amaranthus* species are sensitive to photoperiod  
223 (Wu and Owen, 2014). It is hypothesize that reduced day length or red/far-red effect contributed to smaller plants at second  
224 cohort regardless the crop. A study in North Carolina and Illinois predicted that less than 10% Palmer amaranth seedlings  
225 emergence occurred after June (Piskackova et al., 2021). In addition, Palmer amaranth negative impact on soybean (Korres et al.,  
226 2020) and cotton (Webster and Grey, 2015) yields was higher when plants were established near to crop planting. Therefore,  
227 early management is a key strategy to minimize the damaging impact of Palmer amaranth to US Midwest cropping systems.

228 Seed production was not evaluated due to plant harvest at initiation of flowering. Nonetheless, it is well documented a strong  
229 positive correlation between Palmer amaranth biomass and seed production (Schwartz et al., 2016; Spaunhorst et al., 2018). In  
230 our study, plants growing from the first cohort accumulated 42% more biomass when compared to the second cohort. Therefore,  
231 Palmer amaranth plants growing in the second cohort is likely to produce less seeds regardless the crop. Our observation is  
232 consistent with the findings that the first Palmer amaranth cohort produced 50% more seeds per plant than Palmer amaranth  
233 plants established six weeks later in bareground (Webster and Grey, 2015). Still, seed production at the second cohort will  
234 replenish the soil seedbank. Seed production and deposition in the seedbank is also a key factor for species perpetuation  
235 (Menges, 1987). Palmer amaranth can produce a hundred thousands seeds per plant (Schwartz et al., 2016; Keeley et al., 1987),  
236 which can stay viable in the soil seedbank for at least 36 months (Sosnoskie et al., 2013). Therefore, preventing Palmer  
237 amaranth seed production or/and seed migration to non-native habitats is an essential strategy to minimize the species impact in  
238 agroecosystems (Davis et al., 2015).

239 Floral initiation depends on the complex interaction between a plant's genetic makeup and environmental conditions (Lang,  
240 1965). We observed a significant disruption in flowering caused by surrounding vegetation and cohort timing. Although all three  
241 treatments began flowering at the same time in the first cohort (about doy 180), it took much less time for the bareground  
242 treatment to reach 90% flowering (34 days versus 40 for soybean and 71 for corn). The lack of competition (and stress) in the  
243 bareground resulted in plants that flowered earlier, and were they not harvested, would have had longer reproductive periods,  
244 thereby producing more seed. Similarly, in the second cohort, the window for all plants to initiate flowering was much shorter  
245 for the bareground (28 days) compared to Palmer amaranth in soybean (50 days) or corn (44 days). Significantly, plants in the  
246 bareground treatment flowered one week earlier than soybean, and almost two weeks earlier than corn, again allowing for  
247 greater seed production per plant had they not been harvested at initial flowering. In some cases, early flowering may confer an  
248 evolutionary advantage, provided the plant has an indeterminate habit and flowering does not restrict plant growth. In an Iowa  
249 study, Palmer amaranth initiated flowering two weeks prior to waterhemp (Baker, 2021), and this characteristic may partially  
250 explain why Palmer amaranth can displace waterhemp where both occur in the same agronomic field. In other cases, however,  
251 early flower initiation may be a response to stressful conditions as a plant attempts to reproduce before running out of resources.  
252 In a dioecious species like Palmer amaranth, exerting stress on plants to manipulate flowering may be beneficial in limiting seed

253 production (McFarlane et al., 2018; Schliekelman et al., 2005). For example, when growing under water stress, there was a  
254 seven days flowering mismatch between male and female plants (Mesgaran et al., 2021), which can minimize plant outcrossing,  
255 reduce seed production and the exchange of resistant alleles (Jhala et al., 2021). In our study we observed

256 An ecological approach to reduce Palmer amaranth seed production is understanding plant biology, including flowering pattern.  
257 Our study suggests that Palmer amaranth flowering was slightly influenced by crops and cohort timings. Palmer amaranth  
258 growing in bareground and corn resulted in the overall shortest and longest flowering window, respectively. The shortest  
259 flowering window of second cohorts of Palmer amaranth growing in bareground highlighted the impact of photoperiod on  
260 flowering. When growing in soybean, Palmer amaranth flowering window was similar to bareground for the first cohort but  
261 similar to corn at second cohort timing. Plant flowering initiation is complex and depends on the complex interaction between  
262 genetic makeup and the environmental conditions (Lang, 1965). We hypothesize that when growing in high competition (e.g.,  
263 second cohort), Palmer amaranth plants tend to initiate flowering early, as well as having an extended flowering window. A  
264 study has shown that Palmer amaranth initiated flowering two weeks prior to the native waterhemp in Iowa (Baker, 2021). Early  
265 flower initiation could also be a plant strategy when growing in stressful conditions. For example, when growing under water  
266 stress, early flowering in Palmer amaranth resulted in a mismatch between female and male plants by seven days (Mesgaran et  
267 al., 2021). A mismatch in Palmer amaranth male and female flowering period can minimize plant outcrossing, reducing plant  
268 seed production and/or exchange of resistant alleles (Jhala et al., 2021). Sex dimorphism manipulation is considered a potential  
269 ecological pest control strategy (McFarlane et al., 2018; Schliekelman et al., 2005).

270 The mechanisms of gender-determination in plant species is intriguing and has aroused the curiosity of many scientists, including  
271 Charles Darwin (Darwin, 1888). In our study, the gender model performance was decent (AUC 0.64) considering the biology of  
272 plant flowering. A 1:1 male and female sex ratio is generally an evolutionarily stable strategy for plant species perpetuation  
273 (Fisher, 1930). However, a slight deviation from 1:1 sex ratio occurs in some dioecious species. For example, the dioecious  
274 *Halophila stipulacea* is a female-biased plant in its native habitat, but the naturalized *H. stipulacea* has a 1:1 ratio (Nguyen et al.,  
275 2018). Naturalization of *H. stipulacea* reduced female-male ratio to expand into its non-native habitat (Nguyen et al., 2018).  
276 Also, biotic and/or abiotic stress can influence plant gender determination. Palmer amaranth male-to-female ratio was greater  
277 under high plant densities (Korres and Norsworthy, 2017) and after herbicide application (Rumpa et al., 2019). We observed  
278 sexual dimorphism in Palmer amaranth in response to surrounding vegetation and plant morphological attributes. Our model  
279 estimated that late flowering, heavier and taller Palmer amaranth plants slightly deviated from 1:1 ratio in favor of female plants.  
280 It was reported that female Palmer amaranth plants invested more in height, stem and biomass while male plants invested more  
281 in leaf area and leaf dry weight under nutrient deficiency (Korres et al., 2017). We observed more female plants in soybean and  
282 bareground compared to corn. Palmer amaranth plants in the corn were more stressed by interspecific competition as evidenced  
283 by less biomass and a lower weight:height ratio. Sexual dimorphism is documented in other dioecious species (Barrett and  
284 Hough, 2013). For example, stronger female plant competition and greater male tolerance to herbivory was reported in *Spinacia*  
285 *oleracea* (Pérez-Llorca and Sánchez Vilas, 2019). Research on candidate genes for sex determination in *Amaranthus* species are  
286 currently underway but is far from complete (Montgomery et al., 2021, 2019). Further studies are also needed to understand the  
287 ecological basis of Palmer amaranth flowering, including plant behavior under climate change.

288 Our study demonstrated that Palmer amaranth is adapted to grow on arable land throughout the Midwestern U.S. Palmer  
289 amaranth's range will continue to expand if current cropping practices are continued. As waterhemp and Palmer amaranth begin  
290 to share the same habitat, it will increase weed management complexity. Preventing Palmer amaranth seed dispersal must be a  
291 priority. Regional collaboration is necessary to slow the spread of this aggressive and adaptable weed. Where Palmer amaranth  
292 occurs, management tactics should focus on limiting Palmer amaranth establishment until row crops can shade late-emerging  
293 plants. Increasing the diversity of crops in rotation, varying row crop planting date, narrowing row width, and increasing residue  
294 cover through the use of cover crops are all tactics that can minimize the growth and seed production of Palmer amaranth, and  
295 improve the sustainability of Midwestern cropping systems.

## DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

## DATA ACCESSIBILITY

298 The data and scripts used to analyse the data presented in this work can be found at Zenodo (Oliveira, 2021).

## AUTHOR CONTRIBUTIONS

299 RW and MO: designed the experiments; AJ, CP, MB, MO, and SS: conducted the experiments; MO: analyzed the data; MO:  
300 wrote the manuscript and all authors revised; AJ, CP, MB, MO, SS, and RW: conceptualized the research. All authors reviewed  
301 the manuscript.

## ACKNOWLEDGMENTS

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

## REFERENCES

- 303 Bagavathiannan, M. V., and Norsworthy, J. K. (2016). Multiple-Herbicide Resistance Is Widespread in Roadside Palmer  
304 Amaranth Populations. *PLOS ONE* 11, e0148748. doi:10.1371/journal.pone.0148748.
- 305 Baker, R. (2021). Comparative analysis of Palmer amaranth (*Amaranthus palmeri*) and waterhemp (*A. Tuberculatus*) in Iowa.  
306 doi:10.31274/etd-20210609-11.
- 307 Bangdiwala, S. I. (2018). Regression: Binary logistic. *International Journal of Injury Control and Safety Promotion* 25,  
308 336–338. doi:10.1080/17457300.2018.1486503.
- 309 Barrett, S. C. H., and Hough, J. (2013). Sexual dimorphism in flowering plants. *Journal of Experimental Botany* 64, 67–82.  
310 doi:10.1093/jxb/ers308.
- 311 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using Lme4. *Journal of  
312 Statistical Software* 67, 1–48. doi:10.18637/jss.v067.i01.
- 313 Berger, S. T., Ferrell, J. A., Rowland, D. L., and Webster, T. M. (2015). Palmer Amaranth (*Amaranthus palmeri*) Competition  
314 for Water in Cotton. *Weed Science* 63, 928–935. doi:10.1614/WS-D-15-00062.1.
- 315 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2017). Differentiation of Life-History Traits among  
316 Palmer Amaranth Populations (*Amaranthus palmeri*) and Its Relation to Cropping Systems and Glyphosate Sensitivity.  
317 *Weed Science* 65, 339–349. doi:10.1017/wsc.2017.14.
- 318 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2018). Evolutionary Adaptations of Palmer Amaranth  
319 (*Amaranthus palmeri*) to Nitrogen Fertilization and Crop Rotation History Affect Morphology and Nutrient-Use Efficiency.  
320 *Weed Science* 66, 180–189. doi:10.1017/wsc.2017.73.
- 321 Briscoe Runquist, R. D., Lake, T., Tiffin, P., and Moeller, D. A. (2019). Species distribution models throughout the invasion  
322 history of Palmer amaranth predict regions at risk of future invasion and reveal challenges with modeling rapidly shifting  
323 geographic ranges. *Sci Rep* 9, 2426. doi:10.1038/s41598-018-38054-9.
- 324 Chahal, P. S., Barnes, E. R., and Jhala, A. J. (2021). Emergence pattern of Palmer amaranth (*Amaranthus palmeri*) influenced by  
325 tillage timings and residual herbicides. *Weed Technology* 35, 433–439. doi:10.1017/wet.2020.136.

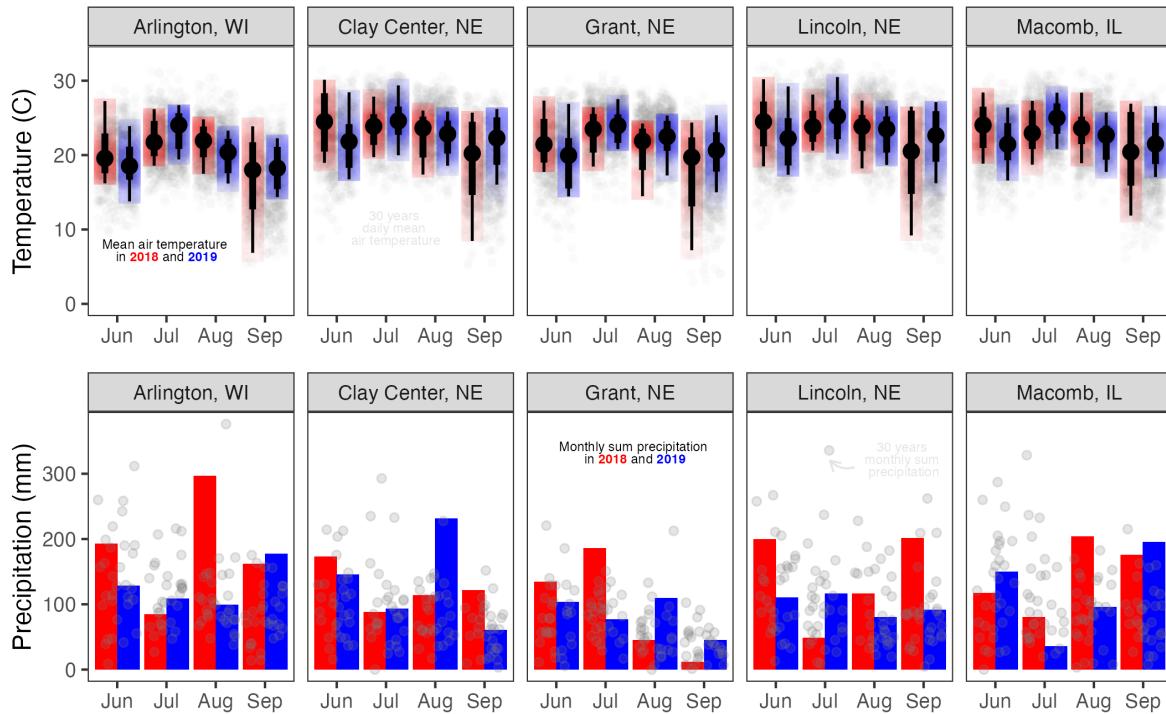
- 326 Chahal, P. S., Irmak, S., Jugulam, M., and Jhala, A. J. (2018). Evaluating Effect of Degree of Water Stress on Growth and  
327 Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors. *Weed Science* 66, 738–745.  
328 doi:10.1017/wsc.2018.47.
- 329 Correndo, A. A., Moro Rosso, L. H., and Ciampitti, I. A. (2021). Retrieving and processing agro-meteorological data from  
330 API-client sources using R software. *BMC Research Notes* 14, 205. doi:10.1186/s13104-021-05622-8.
- 331 Crespo, R. J., Wingeier, A. B., Borman, C. J., and Bernards, M. L. (2016). Baseline Sensitivity of Nebraska Waterhemp and  
332 Palmer Amaranth to Dicamba and 2,4-D. *Agronomy Journal* 108, 1649–1655. doi:10.2134/agronj2015.0465.
- 333 Darwin, C. (1888). *The Different Forms of Flowers on Plants of the Same Species*. J. Murray Available at:  
334 <http://books.google.com?id=7uMEAAAAYAAJ>.
- 335 Davis, A. S., Schutte, B. J., Hager, A. G., and Young, B. G. (2015). Palmer Amaranth (*Amaranthus palmeri*) Damage Niche in  
336 Illinois Soybean Is Seed Limited. *Weed Science* 63, 658–668. doi:10.1614/WS-D-14-00177.1.
- 337 Farmer, J. A., Webb, E. B., Pierce, R. A., and Bradley, K. W. (2017). Evaluating the potential for weed seed dispersal based on  
338 waterfowl consumption and seed viability. *Pest Management Science* 73, 2592–2603. doi:10.1002/ps.4710.
- 339 Fisher, R. A. (1930). The genetical theory of natural selection. *Eugen Rev* 22, 127–130. Available at:  
340 <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2984947/> [Accessed August 12, 2021].
- 341 Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications Available at:  
342 <http://books.google.com?id=uPNrDwAAQBAJ>.
- 343 Garetson, R., Singh, V., Singh, S., Dotray, P., and Bagavathiannan, M. (2019). Distribution of herbicide-resistant Palmer  
344 amaranth (*Amaranthus palmeri*) in row crop production systems in Texas. *Weed Technology* 33, 355–365.  
345 doi:10.1017/wet.2019.14.
- 346 Guo, P., and Al-Khatib, K. (2003). Temperature effects on germination and growth of redroot pigweed (*Amaranthus retroflexus*),  
347 Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*). *Weed Science* 51, 869–875. doi:10.1614/P2002-127.
- 348 Hartzler, B., and Anderson, M. (2016). Palmer amaranth: It's here, now what? 10.
- 349 Heap, I. (2021). Internation Herbicide-Resistant Weed Database. Available at:  
350 <http://www.weedscience.org/Home.aspx> [Accessed July 26, 2021].
- 351 Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal* 50,  
352 346–363. doi:10.1002/bimj.200810425.
- 353 Jha, P., Norsworthy, J. K., Riley, M. B., and Bridges, W. (2010). Annual Changes in Temperature and Light Requirements for  
354 Germination of Palmer Amaranth (*Amaranthus palmeri*) Seeds Retrieved from Soil. *Weed Science* 58, 426–432.  
355 doi:10.1614/WS-D-09-00038.1.
- 356 Jhala, A. J., Norsworthy, J. K., Ganie, Z. A., Sosnoskie, L. M., Beckie, H. J., Mallory-Smith, C. A., Liu, J., Wei, W., Wang, J.,  
357 and Stoltenberg, D. E. (2021). Pollen-mediated gene flow and transfer of resistance alleles from herbicide-resistant  
358 broadleaf weeds. *Weed Technology* 35, 173–187. doi:10.1017/wet.2020.101.
- 359 Keeley, P. E., Carter, C. H., and Thullen, R. J. (1987). Influence of Planting Date on Growth of Palmer Amaranth (*Amaranthus*  
360 *palmeri*). *Weed Science* 35, 199–204. doi:10.1017/S0043174500079054.
- 361 Kistner, E. J., and Hatfield, J. L. (2018). Potential Geographic Distribution of Palmer Amaranth under Current and Future  
362 Climates. *Agricultural & Environmental Letters* 3, 170044. doi:10.2134/ael2017.12.0044.
- 363 Klingaman, T. E., and Oliver, L. R. (1994). Palmer Amaranth (*Amaranthus palmeri*) Interference in Soybeans (*Glycine max*).  
364 *Weed Science* 42, 523–527. doi:10.1017/S0043174500076888.

- 365 Korres, N. E., and Norsworthy, J. K. (2017). Palmer Amaranth (*Amaranthus palmeri*) Demographic and Biological  
366 Characteristics in Wide-Row Soybean. *Weed Science* 65, 491–503. doi:10.1017/wsc.2017.12.
- 367 Korres, N. E., Norsworthy, J. K., FitzSimons, T., Roberts, T. L., and Oosterhuis, D. M. (2017). Differential Response of Palmer  
368 Amaranth (*Amaranthus palmeri*) Gender to Abiotic Stress. *Weed Science* 65, 213–227. doi:10.1017/wsc.2016.34.
- 369 Korres, N. E., Norsworthy, J. K., Mauromoustakos, A., and Williams, M. M. (2020). Soybean density and Palmer amaranth  
370 (*Amaranthus palmeri*) establishment time: Effects on weed biology, crop yield, and economic returns. *Weed Science* 68,  
371 467–475. doi:10.1017/wsc.2020.41.
- 372 Kuhn, M., Vaughan, D., and RStudio (2021). *Yardstick: Tidy Characterizations of Model Performance*. Available at:  
373 <https://CRAN.R-project.org/package=yardstick> [Accessed August 24, 2021].
- 374 Kumar, V., Liu, R., and Stahlman, P. W. (2020). Differential sensitivity of Kansas Palmer amaranth populations to multiple  
375 herbicides. *Agronomy Journal* 112, 2152–2163. doi:10.1002/agj2.20178.
- 376 Küpper, A., Borgato, E. A., Patterson, E. L., Netto, A. G., Nicolai, M., Carvalho, S. J. P. de, Nissen, S. J., Gaines, T. A., and  
377 Christoffoleti, P. J. (2017). Multiple Resistance to Glyphosate and Acetolactate Synthase Inhibitors in Palmer Amaranth  
378 (*Amaranthus palmeri*) Identified in Brazil. *Weed Science* 65, 317–326. doi:10.1017/wsc.2017.1.
- 379 Lang, A. (1965). “Physiology of flower initiation,” in *Differenzierung und Entwicklung / Differentiation and Development*  
380 Handbuch der Pflanzenphysiologie / Encyclopedia of Plant Physiology, ed. A. Lang (Berlin, Heidelberg: Springer),  
381 1380–1536. doi:10.1007/978-3-642-50088-6\_39.
- 382 Larran, A. S., Palmieri, V. E., Perotti, V. E., Lieber, L., Tuesca, D., and Permingeat, H. R. (2017). Target-site resistance to  
383 acetolactate synthase (ALS)-inhibiting herbicides in *Amaranthus palmeri* from Argentina. *Pest Management Science* 73,  
384 2578–2584. doi:10.1002/ps.4662.
- 385 Leeper, T. J. (2017). Interpreting Regression Results using Average Marginal Effects with R’s margins. 31.
- 386 Leeper, T. J., Arnold, J., Arel-Bundock, V., and Long, J. A. (2021). *Margins: Marginal Effects for Model Objects*. Available at:  
387 <https://CRAN.R-project.org/package=margins> [Accessed August 24, 2021].
- 388 Lenth, R. V., Buerkner, P., Herve, M., Love, J., Riebl, H., and Singmann, H. (2021). *Emmeans: Estimated Marginal Means, aka*  
389 *Least-Squares Means*. Available at: <https://CRAN.R-project.org/package=emmeans> [Accessed August 24,  
390 2021].
- 391 Lindsay, K., Popp, M., Norsworthy, J., Bagavathiannan, M., Powles, S., and Lacoste, M. (2017). PAM: Decision Support for  
392 Long-Term Palmer Amaranth (*Amaranthus palmeri*) Control. *Weed Technology* 31, 915–927. doi:10.1017/wet.2017.69.
- 393 MacRae, A. W., Webster, T. M., Sosnoskie, L. M., Culpepper, A. S., and Kichler, J. M. (2013). Cotton Yield Loss Potential in  
394 Response to Length of Palmer Amaranth (*Amaranthus palmeri*) Interference. 17, 6.
- 395 Mangiafico, S. (2021). *Rcompanion: Functions to Support Extension Education Program Evaluation*. Available at:  
396 <https://CRAN.R-project.org/package=rcompanion> [Accessed August 24, 2021].
- 397 Massinga, R. A., Currie, R. S., Horak, M. J., and Boyer, J. (2001). Interference of Palmer amaranth in corn. *Weed Science* 49,  
398 202–208. doi:10.1614/0043-1745(2001)049[0202:IOPAIC]2.0.CO;2.
- 399 Matzrafi, M., Osipitan, O. A., Ohadi, S., and Mesgaran, M. B. (2021). Under pressure: Maternal effects promote drought  
400 tolerance in progeny seed of Palmer amaranth (*Amaranthus palmeri*). *Weed Science* 69, 31–38. doi:10.1017/wsc.2020.75.
- 401 McFarlane, G. R., Whitelaw, C. B. A., and Lillico, S. G. (2018). CRISPR-Based Gene Drives for Pest Control. *Trends in*  
402 *Biotechnology* 36, 130–133. doi:10.1016/j.tibtech.2017.10.001.

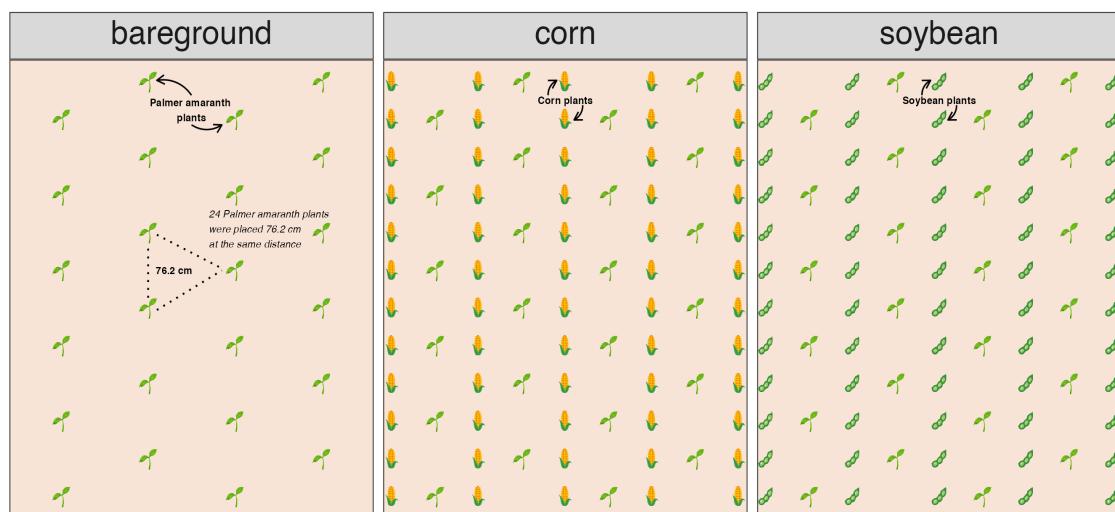
- 403 Menges, R. M. (1987). Weed Seed Population Dynamics during Six Years of Weed Management Systems in Crop Rotations on  
404 Irrigated Soil. *Weed Science* 35, 328–332. Available at: <http://www.jstor.org/stable/4044593>.
- 405 Mesgaran, M. B., Matzrafi, M., and Ohadi, S. (2021). Sex dimorphism in dioecious Palmer amaranth (*Amaranthus palmeri*) in  
406 response to water stress. *Planta* 254, 17. doi:10.1007/s00425-021-03664-7.
- 407 Milani, A., Panozzo, S., Farinati, S., Iamonic, D., Sattin, M., Loddo, D., and Scarabel, L. (2021). Recent Discovery of  
408 *Amaranthus palmeri* S. Watson in Italy: Characterization of ALS-Resistant Populations and Sensitivity to Alternative  
409 Herbicides. *Sustainability* 13, 7003. doi:10.3390/su13137003.
- 410 Montgomery, J. S., Giacomini, D. A., Weigel, D., and Tranel, P. J. (2021). Male-specific Y-chromosomal regions in waterhemp  
411 (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *New Phytologist* 229, 3522–3533.  
412 doi:10.1111/nph.17108.
- 413 Montgomery, J. S., Sadeque, A., Giacomini, D. A., Brown, P. J., and Tranel, P. J. (2019). Sex-specific markers for waterhemp  
414 (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *Weed Science* 67, 412–418.  
415 doi:10.1017/wsc.2019.27.
- 416 Morgan, G. D., Baumann, P. A., and Chandler, J. M. (2001). Competitive Impact of Palmer Amaranth (*Amaranthus palmeri*) on  
417 Cotton (*Gossypium hirsutum*) Development and Yield. *Weed Technology* 15, 408–412.  
418 doi:10.1614/0890-037X(2001)015[0408:CIOPAA]2.0.CO;2.
- 419 Nguyen, H. M., Kleitou, P., Kletou, D., Sapir, Y., and Winters, G. (2018). Differences in flowering sex ratios between native and  
420 invasive populations of the seagrass *Halophila stipulacea*. *Botanica Marina* 61, 337–342. doi:10.1515/bot-2018-0015.
- 421 Oliveira, M. C. (2021). *Maxwelco/palmer\_adaptation*. Zenodo Available at:  
422 <https://doi.org/10.5281/zenodo.5236831>.
- 423 Oliveira, M. C., Gaines, T. A., Patterson, E. L., Jhala, A. J., Irmak, S., Amundsen, K., and Knezevic, S. Z. (2018). Interspecific  
424 and intraspecific transference of metabolism-based mesotrione resistance in dioecious weedy *Amaranthus*. *The Plant  
425 Journal* 96, 1051–1063. doi:10.1111/tpj.14089.
- 426 Oliveira, M. C., Giacomini, D. A., Arsenijevic, N., Vieira, G., Tranel, P. J., and Werle, R. (2021). Distribution and validation of  
427 genotypic and phenotypic glyphosate and PPO-inhibitor resistance in Palmer amaranth (*Amaranthus palmeri*) from  
428 southwestern Nebraska. *Weed Technology* 35, 65–76. doi:10.1017/wet.2020.74.
- 429 Page, E. R., Nurse, R. E., Meloche, S., Bosveld, K., Grainger, C., Obeid, K., Filotas, M., Simard, M.-J., and Laforest, M. (2021).  
430 Import of Palmer amaranth (*Amaranthus palmeri* S. Wats.) Seed with sweet potato (*Ipomea batatas* (L.) Lam) slips. *Can. J.  
431 Plant Sci.*, CJPS-2020-0321. doi:10.1139/CJPS-2020-0321.
- 432 Pérez-Llorca, M., and Sánchez Vilas, J. (2019). Sexual dimorphism in response to herbivory and competition in the dioecious  
433 herb *Spinacia oleracea*. *Plant Ecol* 220, 57–68. doi:10.1007/s11258-018-0902-7.
- 434 Piskackova, T. A. R., Reberg-Horton, S. C., Richardson, R. J., Jennings, K. M., Franca, L., Young, B. G., and Leon, R. G.  
435 (2021). Windows of action for controlling palmer amaranth (*Amaranthus palmeri*) using emergence and phenology models.  
436 *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). Glyphosate-resistant  
438 Palmer amaranth: A threat to conservation tillage. *Journal of Soil and Water Conservation* 66, 265–275.  
439 doi:10.2489/jswc.66.4.265.
- 440 Raoniar, R. (2021). Modelling Binary Logistic Regression Using R (research-oriented modelling and interpretation). Available  
441 at: <https://bit.ly/3BhucN3> [Accessed August 11, 2021].

- 442 Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. (2015). Dose-Response Analysis Using R. *PLOS ONE* 10, e0146021.  
443 doi:10.1371/journal.pone.0146021.
- 444 Rumpa, M. M., Krausz, R. F., Gibson, D. J., and Gage, K. L. (2019). Effect of PPO-Inhibiting Herbicides on the Growth and  
445 Sex Ratio of a Dioecious Weed Species *Amaranthus palmeri* (Palmer Amaranth). *Agronomy* 9, 275.  
446 doi:10.3390/agronomy9060275.
- 447 Sauer, J. (1957). Recent Migration and Evolution of the Dioecious Amaranths. *Evolution* 11, 11–31. doi:10.2307/2405808.
- 448 Sauer, J. D. (1972). The dioecious amaranths: A new species name and major range extensions. *Madroño* 21, 426–434.  
449 Available at: <http://www.jstor.org/stable/41423815>.
- 450 Sbatella, G. M., and Wilson, R. G. (2010). Isoxaflutole Shifts Kochia (*Kochia scoparia*) Populations in Continuous Corn. *Weed  
451 Technology* 24, 392–396. doi:10.1614/WT-D-09-00023.1.
- 452 Schliekelman, P., Ellner, S., and Gould, F. (2005). Pest Control by Genetic Manipulation of Sex Ratio. *Journal of Economic  
453 Entomology* 98, 18–34. doi:10.1093/jee/98.1.18.
- 454 Schwartz, L. M., Norsworthy, J. K., Young, B. G., Bradley, K. W., Kruger, G. R., Davis, V. M., Steckel, L. E., and Walsh, M. J.  
455 (2016). Tall Waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*) Seed Production and  
456 Retention at Soybean Maturity. *Weed Technology* 30, 284–290. doi:10.1614/WT-D-15-00130.1.
- 457 Sing, T., Sander, O., Beerenwinkel, N., and Lengauer, T. (2005). ROCR: Visualizing classifier performance in R. *Bioinformatics*  
458 21, 3940–3941. doi:10.1093/bioinformatics/bti623.
- 459 Sosnoskie, L. M., Webster, T. M., and Culpepper, A. S. (2013). Glyphosate Resistance Does Not Affect Palmer Amaranth  
460 (*Amaranthus palmeri*) Seedbank Longevity. *Weed Science* 61, 283–288. doi:10.1614/WS-D-12-00111.1.
- 461 Spaunhorst, D. J., Devkota, P., Johnson, W. G., Smeda, R. J., Meyer, C. J., and Norsworthy, J. K. (2018). Phenology of Five  
462 Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and Arkansas. *Weed Science* 66, 457–469.  
463 doi:10.1017/wsc.2018.12.
- 464 Team, R. C. (2021). *R: The R Project for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing  
465 Available at: <https://www.r-project.org/> [Accessed August 24, 2021].
- 466 Van Wychen, L. (2020). 2020 Survey of the most common and troublesome weeds in grass crops, pasture, and turf in the United  
467 States and Canada. Available at:  
468 [https://wssa.net/wp-content/uploads/2020-Weed-Survey\\_grass-crops.xlsx](https://wssa.net/wp-content/uploads/2020-Weed-Survey_grass-crops.xlsx).
- 469 Wang, J. L., Klessig, D. F., and Berry, J. O. (1992). Regulation of C4 Gene Expression in Developing Amaranth Leaves. *The  
470 Plant Cell* 4, 173–184. doi:10.1105/tpc.4.2.173.
- 471 Ward, S. M., Webster, T. M., and Steckel, L. E. (2013). Palmer Amaranth (*Amaranthus palmeri*): A Review. *Weed Technology*  
472 27, 12–27. doi:10.1614/WT-D-12-00113.1.
- 473 Webster, T. M., and Grey, T. L. (2015). Glyphosate-Resistant Palmer Amaranth (*Amaranthus palmeri*) Morphology, Growth, and  
474 Seed Production in Georgia. *Weed Science* 63, 264–272. doi:10.1614/WS-D-14-00051.1.
- 475 Wu, C., and Owen, M. D. K. (2014). When Is the Best Time to Emerge: Reproductive Phenology and Success of Natural  
476 Common Waterhemp (*Amaranthus rudis*) Cohorts in the Midwest United States? *Weed Science* 62, 107–117. Available at:  
477 <http://www.jstor.org/stable/43700638>.
- 478 Yacoub, R., and Axman, D. (2020). Probabilistic Extension of Precision, Recall, and F1 Score for More Thorough Evaluation  
479 of Classification Models. in *Proceedings of the First Workshop on Evaluation and Comparison of NLP Systems* (Online:  
480 Association for Computational Linguistics), 79–91. doi:10.18653/v1/2020.eval4nlp-1.9.

- 481 Yu, E., Blair, S., Hardel, M., Chandler, M., Thiede, D., Cortilet, A., Gunsolus, J., and Becker, R. (2021). Timeline of Palmer  
482 amaranth (*Amaranthus palmeri*) invasion and eradication in Minnesota. *Weed Technology*, 1–31. doi:10.1017/wet.2021.32.

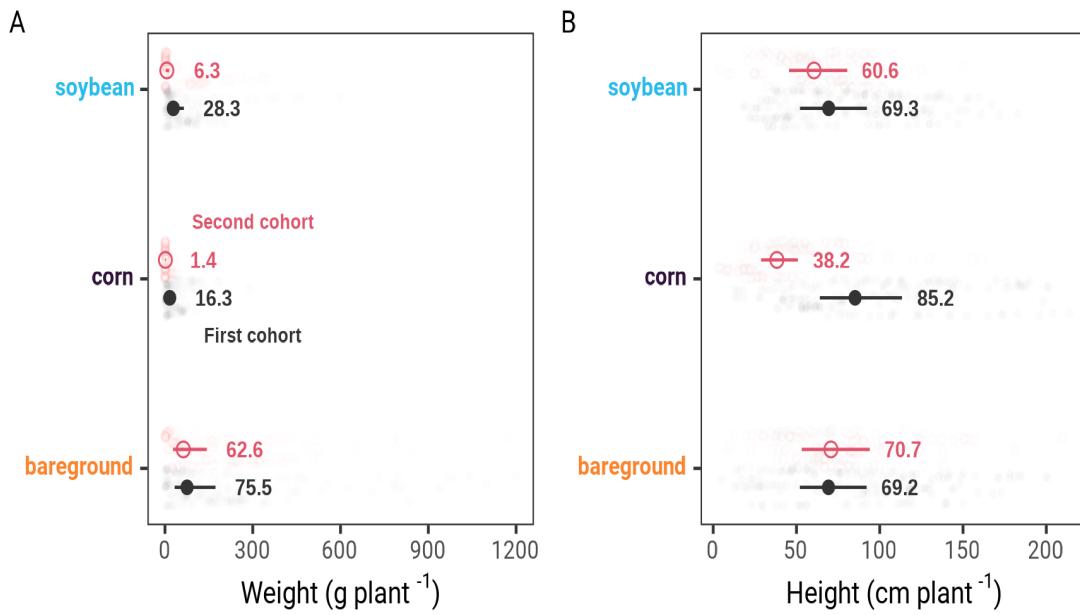


**Figure 1.** Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE and Macomb, IL

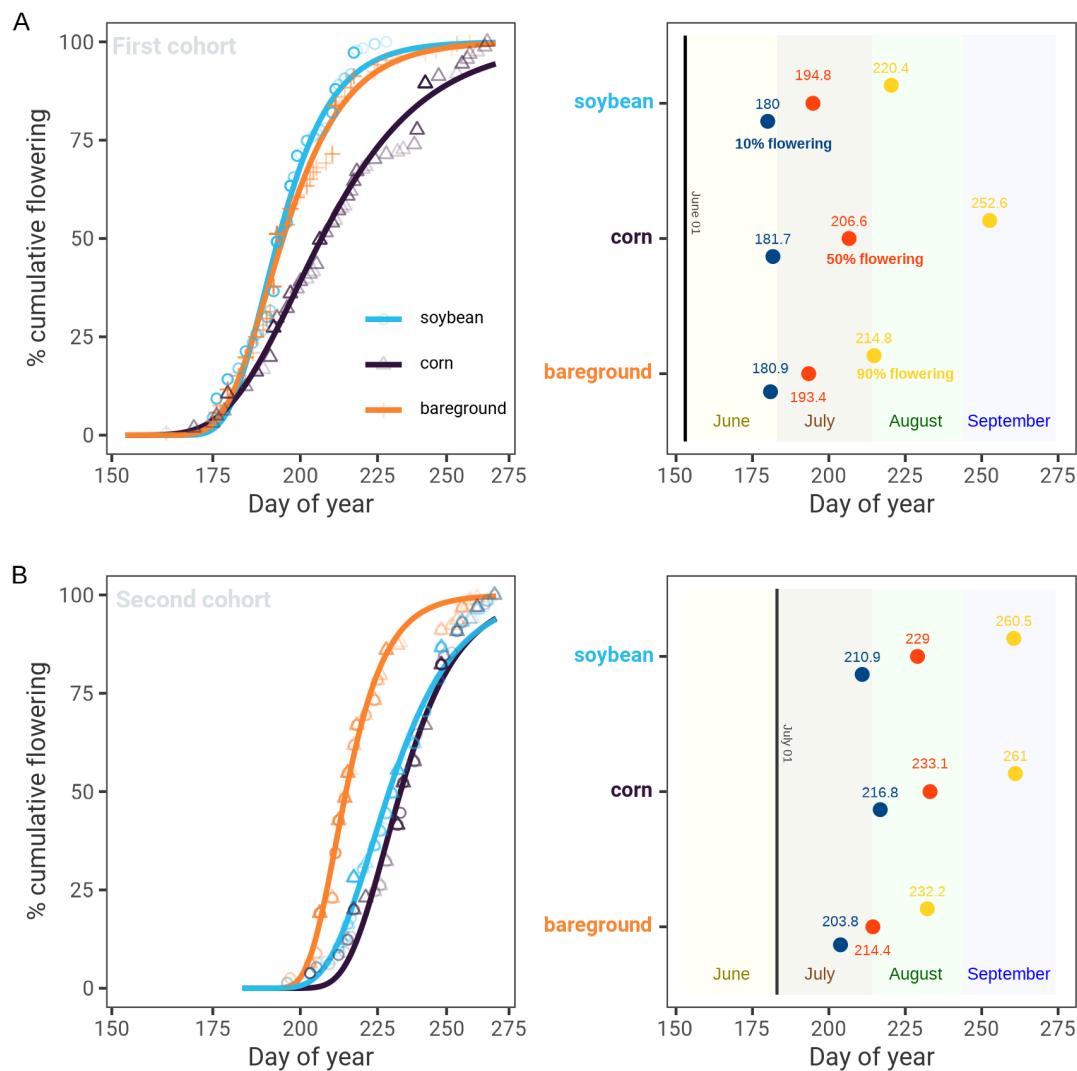


**Figure 2.** Palmer amaranth adaptation study layout of a plant cohort timing in bareground, corn, and soybean. Twenty-four Palmer amaranth plants were placed 76.2 cm apart in each field experimental unit

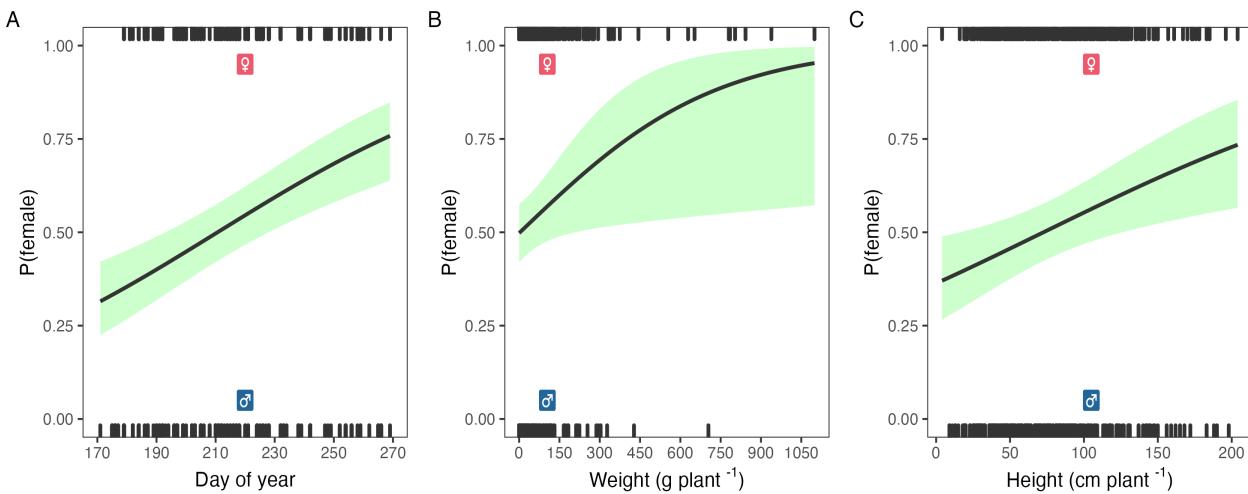
## FIGURES



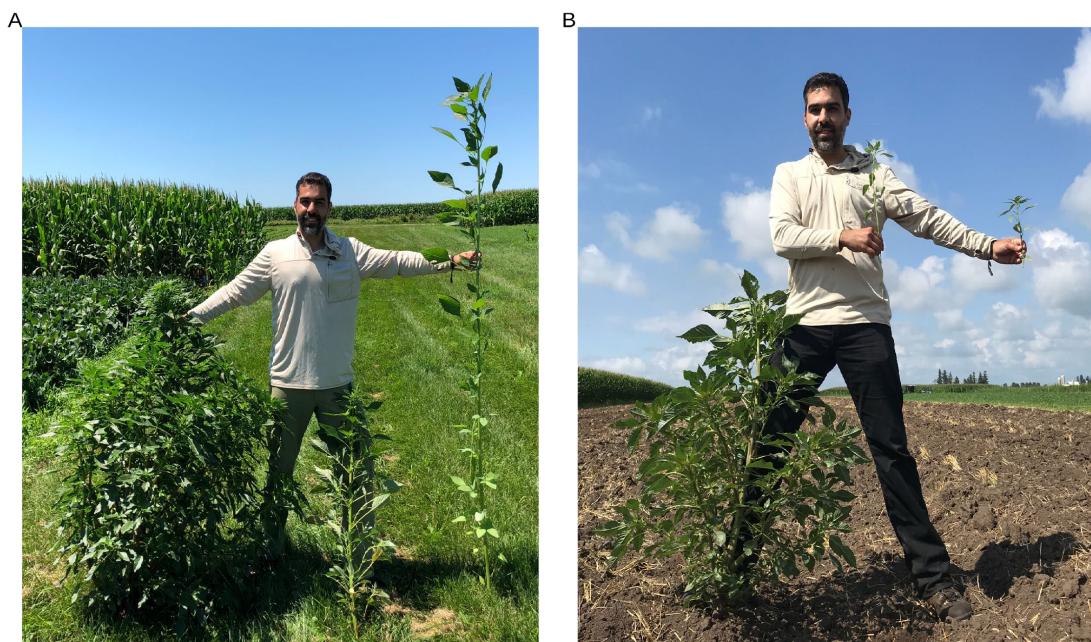
**Figure 3.** Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL



**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 cohort transplanting time (B) nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL



**Figure 5.** The probability (P) of being female Palmer amaranth by day of year (A), weight (B), and height (C). Black line represents the model estimation and shaded green the confidence intervals



**Figure 6.** MCO (180 cm) holds harvested Palmer amaranth plants at 40 days after first cohort transplanting (A) and 33 days after second cohort transplanting (B) time. From left to right in each image, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin