

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

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## 2 ABSTRACT

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

Keywords: Evolution, Flowering, Weed management, Pigweed

## 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

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 throughout the growing season  
48 (Ward et al., 2013). Germination of Palmer amaranth was triggered by 18 C soil temperature at 5 cm  
49 depth (Keeley et al., 1987), and optimal germination and biomass production occurred at 35/30 C day and  
50 night temperatures (Guo and Al-Khatib, 2003). Palmer amaranth emergence can be influenced by tillage  
51 and the use of preemergence herbicides (Chahal et al., 2021), and may result in weed germination shifts  
52 within a population, as documented in *Bassia scoparia* (Sbatella and Wilson, 2010). In an experiment  
53 where Palmer amaranth was subjected to continuous water stress, it survived and produced at least 14000  
54 seeds plant<sup>-1</sup> (Chahal et al., 2018). Seeds from Palmer amaranth growing with limited water conditions  
55 were heavier, less dormant, and prompt for germination (Matzrafi et al., 2021). Growing conditions and  
56 management practices also influence Palmer amaranth sex dimorphism and flowering pattern (Korres et al.,  
57 2017; Rumpa et al., 2019).

58 Palmer amaranth's current global range includes agronomic cropland in Italy (Milani et al., 2021),  
59 soybean producing regions of Brazil and Argentina (Larran et al., 2017; Küpper et al., 2017), and the  
60 Cotton Belt (Garetson et al., 2019; Bagavathiannan and Norsworthy, 2016) and southern Great Plains  
61 of the United States Crespo et al. (2016). However, its range appears to be expanding steadily, and in  
62 some cases rapidly, in the U.S. For example, in states with large Palmer amaranth infestations its range is  
63 gradually pushing north as it displaces other weeds in agronomic row crops (R Werle, personal observation),  
64 aided by wildlife (Farmer et al., 2017) and agricultural machinery (Ward et al., 2013). But there are other  
65 examples where it has suddenly become a problem weed hundreds of miles away from known infestations.  
66 New infestations in Michigan, Indiana and North Dakota appear to have resulted from Palmer amaranth  
67 contaminated livestock feed. New infestations in Iowa and Minnesota were associated with planting  
68 contaminated pollinator habitat seed (Yu et al., 2021). Palmer amaranth infestations have not been detected  
69 in Canada, but Palmer amaranth seeds were found in sweet potato slips imported into the country (Page  
70 et al., 2021). Global warming will create new opportunities for Palmer amaranth invasion. Although

71 agronomic crops in warm environments like Australia and Sub-Saharan Africa are currently at greatest risk  
72 for Palmer amaranth invasion, warming temperatures will reduce barriers that may have limited Palmer  
73 amaranths spread into cooler climates like Canada and Northern Europe (Kistner and Hatfield, 2018;  
74 Briscoe Runquist et al., 2019).

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

## MATERIAL AND METHODS

### 88 Plant material and growing conditions

89 A Palmer amaranth accession (Kei3) from Perkins County, Nebraska susceptible to glyphosate was  
90 selected for this study (Oliveira et al., 2021). Three weeks prior to the establishment of each cohort, seeds  
91 were planted in plastic trays containing potting-mix. Emerged seedlings (1 cm) were transplanted into 200  
92  $\text{cm}^{-3}$  plastic pots (one plant  $\text{pot}^{-1}$ ). Palmer amaranth seedlings were supplied with adequate water and kept  
93 under greenhouse conditions at the University of Wisconsin-Madison, University of Nebraska-Lincoln, and  
94 Western Illinois University; and kept outdoors at the Perkins Extension office in Grant, NE until the 2-3  
95 leaf stage (5 to 8 cm height) when they were transported to the field.

### 96 Field study

97 The experiment was conducted in 2018 and 2019 under field conditions at five locations: Arlington, WI  
98 ( $43^{\circ}18'N$ ,  $89^{\circ}29'W$ ), Clay Center, NE ( $40.57'N$ ,  $9814'W$ ), Grant, NE ( $40.85'N$ ,  $-101.70'W$ ), Lincoln, NE  
99 ( $41.16'N$ ,  $96.42'W$ ), and Macomb, IL ( $40.49'N$ ,  $-90.69'W$ ).

100 Fields were conventionally tilled prior to crop planting. Corn and soybean were planted in 76-cm row  
101 spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using Daymet  
102 weather data from June through September across the five locations in 2018 and 2019 (Correndo et al.,  
103 2021) (Figure 1).

104 The field experimental units were three adjacent 9.1 m wide (12 rows at 76.2 cm row spacing) by 10.7 m  
105 long. The experimental design were arranged in factorial design with three crops, two transplanting times  
106 simulating two cohorts, repeated across five locations. Each field experimental unit was planted with corn,  
107 soybean, or maintained as bareground. The two transplant timings were June 1 (first cohort) and July 1  
108 (second cohort). Palmer amaranth seedlings (potting mix + two seedlings) were transplanted (6 cm deep  
109 and 8 cm wide). Forty-eight plants were equidistantly placed (0.76 m apart) between rows within each  
110 crop. After a week, one plant was eliminated and one was kept, resulting in 24 plants per experimental unit  
111 and transplanting time (Figure 2). When needed, Palmer amaranth plants were supplied with water during  
112 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

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

## 122 Statistical analyses

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

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

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

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

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

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

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

## RESULTS

### 162 Palmer amaranth height and biomass

163 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants  
164 growing in soybean and corn (Figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3,  
165 and 16.3 g plant<sup>-1</sup> in bareground, soybean and corn, respectively. Plants from the second cohort produced  
166 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.

167 Palmer amaranth height was less affected by cohort timing than was weight, with the exception of plants  
168 growing in corn (Figure 3B). Plants from the first cohort were on average 69.2 cm tall in bareground, which  
169 was not different from the 70.7 cm tall plants from the second cohort timing (P = 0.74). In addition, no  
170 difference in Palmer amaranth height (69.3 cm) was detected from first cohort plants in soybean to first and  
171 second cohort plants in bareground (P > 0.75). Palmer amaranth plants from the second cohort were nearly  
172 10 cm shorter compared to the first cohort in soybeans (P = 0.04). The tallest (85.2 cm, first cohort) and  
173 shortest (38.2 cm, second cohort) plants were observed in corn.

### 174 Palmer amaranth cumulative flowering

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

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

184 Palmer amaranth cumulative flowering in the second cohort occurred from mid July to mid September  
 185 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to  
 186 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at  
 187 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at  
 188 doy 210.9, which was 6 days prior to corn ( $P$ -value = 0.00). Similar trend was observed at 50% flowering,  
 189 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9;  $P$   
 190 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean  
 191 (260.5;  $P$  = 0.66).

## 192 Palmer amaranth gender

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

200 \begin{table}[\!h]

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

203

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.

204 \end{table}

205 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.  
 206 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

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

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

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

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

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

255 (Baker, 2021), and this characteristic may partially explain why waterhemp can displace Palmer amaranth in Iowa, where  
256 Palmer amaranth is not well adapted. In a dioecious species like Palmer amaranth, exerting stress on plants to manipulate  
257 flowering may be beneficial in limiting seed production (McFarlane et al., 2018; Schliekelman et al., 2005). For example, when  
258 growing under water stress, there was a seven days flowering mismatch between male and female plants (Mesgaran et al., 2021),  
259 which can minimize plant outcrossing, reduce seed production and the exchange of resistant alleles (Jhala et al., 2021).

260 The mechanisms of gender-determination in plant species is intriguing and has aroused the curiosity of many scientists, including  
261 Charles Darwin (Darwin, 1888). In our study, the gender model performance was decent (AUC 0.64) considering the biology of  
262 plant flowering. A 1:1 male and female sex ratio is a general and evolutionarily stable strategy for plant species perpetuation  
263 (Fisher, 1930). However, a slight deviation from 1:1 sex ratio occurs in some dioecious species. For example, the dioecious  
264 *Halophila stipulacea* is a female-biased plant in its native habitat, but the naturalized *H. stipulacea* has a 1:1 ratio (Nguyen et al.,  
265 2018). Naturalization of *H. stipulacea* reduced female-male ratio to expand into its non-native habitat (Nguyen et al., 2018).  
266 Also, biotic and/or abiotic stress can influence plant gender determination. Palmer amaranth male-to-female ratio was greater  
267 under high plant densities (Korres and Norsworthy, 2017) and after herbicide application (Rumpa et al., 2019). We observed  
268 sexual dimorphism in Palmer amaranth in response to surrounding vegetation and plant morphological attributes. Our model  
269 estimated that late flowering, heavier and taller Palmer amaranth plants slightly deviated from 1:1 ratio in favor of female plants.  
270 It was reported that female Palmer amaranth plants invested more in height, stem and biomass while male plants invested more  
271 in leaf area and leaf dry weight under nutrient deficiency (Korres et al., 2017). We observed more female plants in soybean and  
272 bareground compared to corn. Palmer amaranth plants in the corn were more stressed by interspecific competition as evidenced  
273 by less biomass and a lower weight:height ratio. Sexual dimorphism is documented in other dioecious species (Barrett and  
274 Hough, 2013). For example, stronger female plant competition and greater male tolerance to herbivory was reported in *Spinacia*  
275 *oleracea* (Pérez-Llorca and Sánchez Vilas, 2019). Research on candidate genes for sex determination in *Amaranthus* species are  
276 currently underway but is far from complete (Montgomery et al., 2021, 2019). Further studies are also needed to understand the  
277 ecological basis of Palmer amaranth flowering, including plant behavior under climate change.

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

## DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

## DATA ACCESSIBILITY

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

## AUTHOR CONTRIBUTIONS

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

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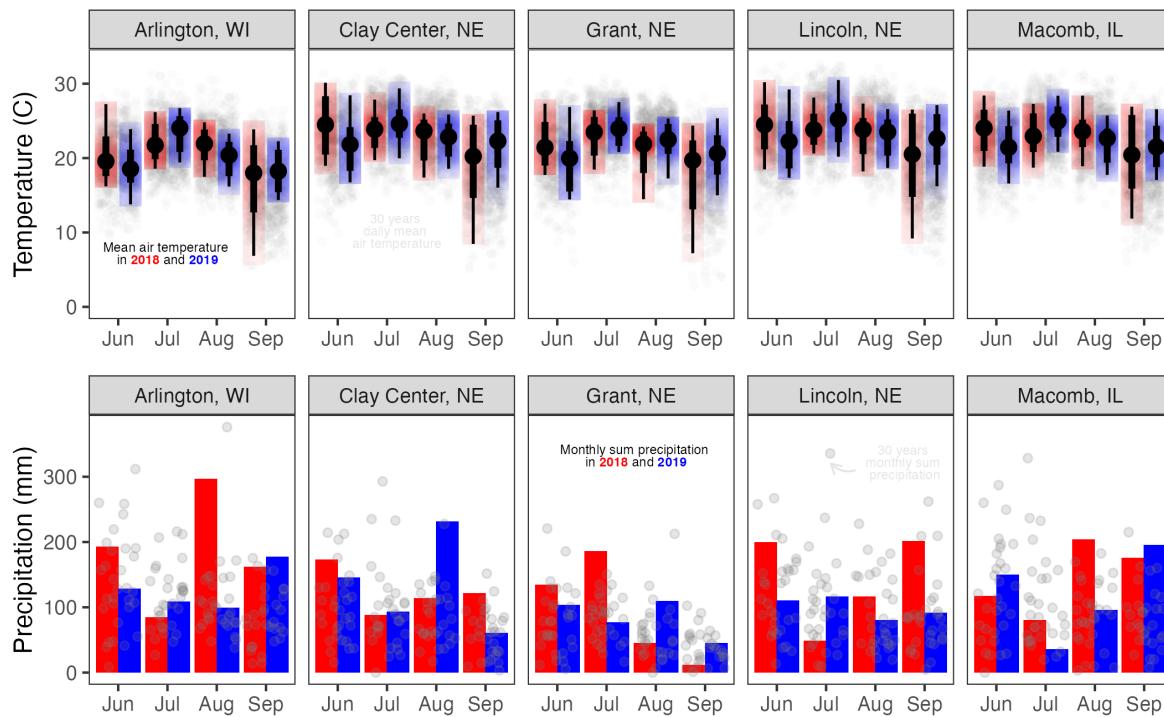
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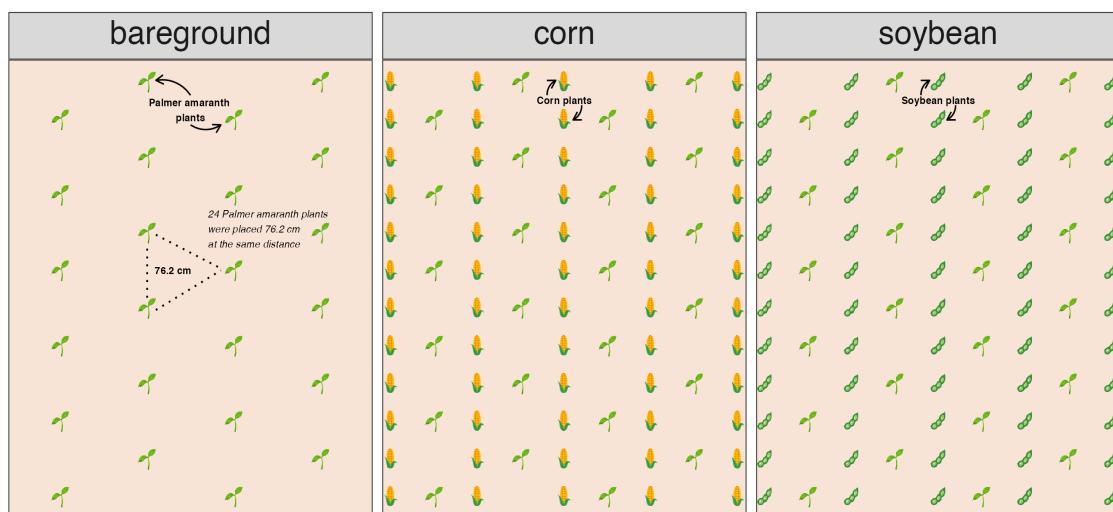
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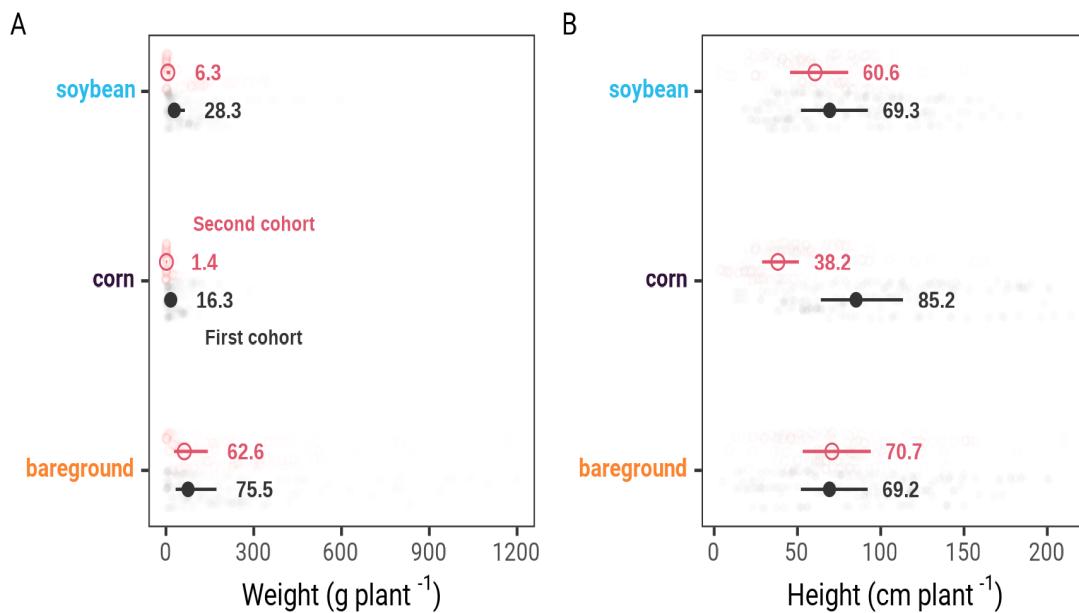


**Figure 1.** Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL.

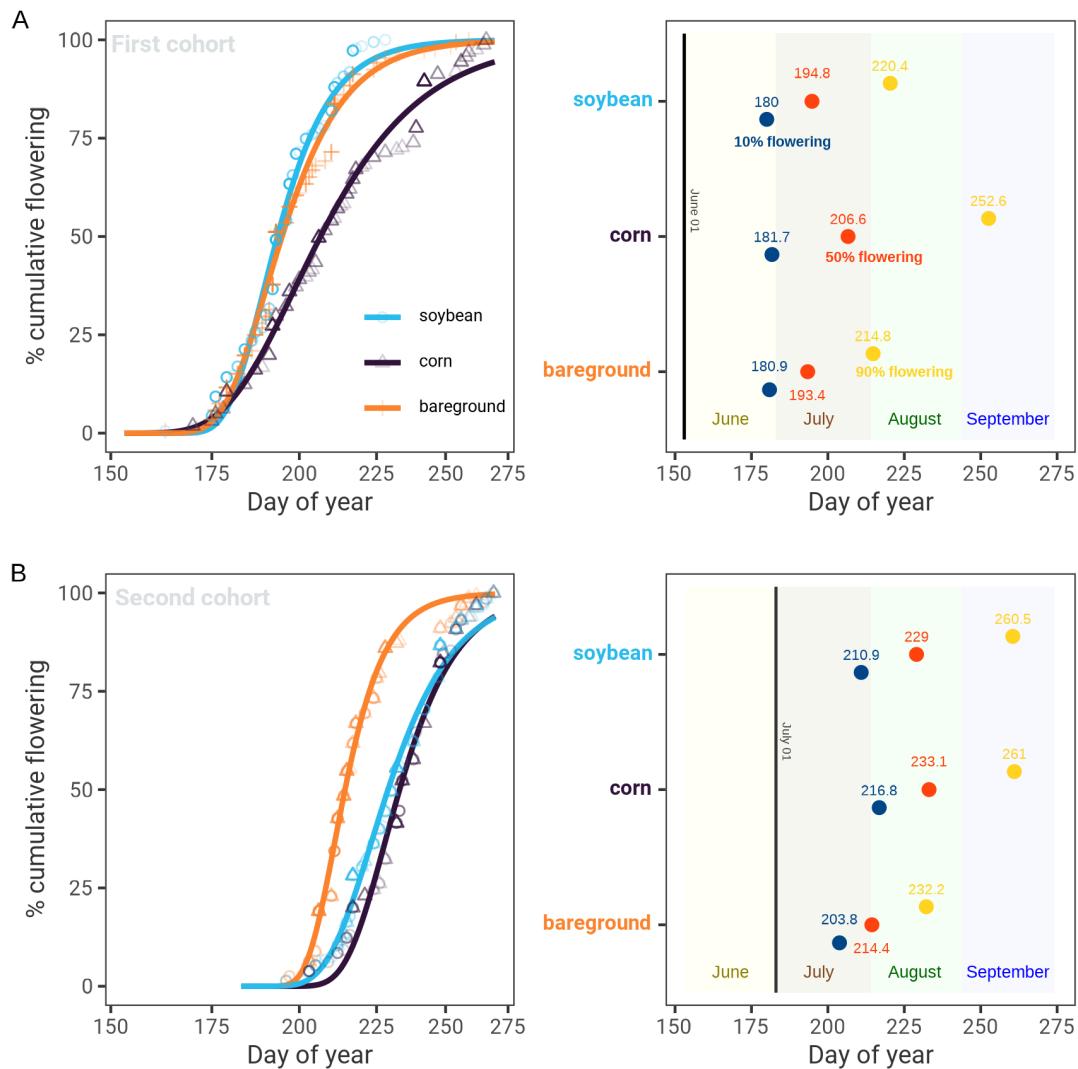


**Figure 2.** Palmer amaranth adaptation study layout of a plant cohort timing in bareground, corn, and soybean. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each field experimental unit.

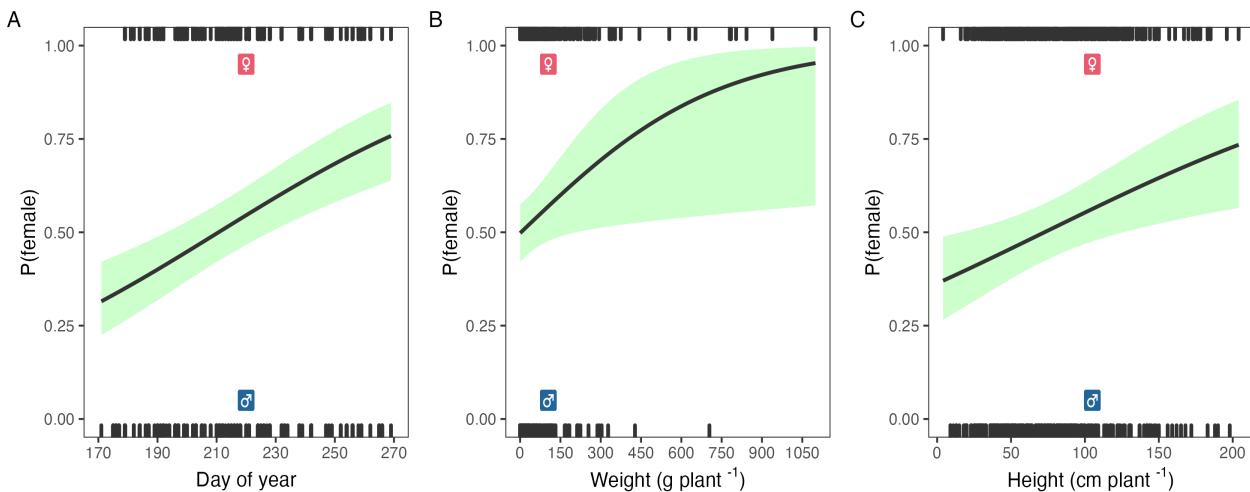
## FIGURES



**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.