

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 weed species in the United States. Palmer amaranth is endemic in the Southern United States but its range is expanding northward. Palmer amaranth dispersal warrants studies assessing species adaptation into new geographies. A study was conducted to investigate morphology, flowering and sex dimorphism from cohorts of Palmer amaranth growing under corn, soybean, and bareground across five locations of United States Midwest. In general, results demonstrated that first cohort of Palmer amaranth, established in June, produced 42% more biomass than plants from second cohort (established in July). At first cohort, Palmer amaranth produced 75.5 g plant⁻¹ in bareground, 28.3 g plant⁻¹ in soybean and 16.3 g plant⁻¹ in corn, whereas Palmer amaranth produced 62.6, 6.3, and 1.4 g plant⁻¹ at second cohort in bareground, soybean and corn, respectively. The plant height was more impacted by Palmer amaranth growing in corn. Palmer amaranth plants averaged 85.2 cm tall in the first cohort but 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. Also, Palmer amaranth sex dimorphism was slightly influenced by day of year, weight and height. The model estimated that probability of being a female plant increase as biomass and height increases. Our results showed the fast adaptation and plasticity of Palmer amaranth to grow and adapt to cropping systems. Palmer amaranth is likely to continue its expansion northward. Therefore, preventing plant dispersal into new habitat is the most effective management strategy. Reactive management to reduce Palmer amaranth impact on cropping systems should encompass diversity of tactics that minimize the species ability establish into cropping systems, including crop rotation (not only corn and soybean), early/late crop planting, row spacing, and cover crops. Our results also shed a light on sex dimorphism as a future Palmer amaranth ecological management.

Keywords: Evolution Flowering Management Pigweed Weed

INTRODUCTION

28 Palmer amaranth (*Amaranthus palmeri* S. Watson) is currently ranked as one of the most economically
29 detrimental weed species to cropping systems in the United States (Van Wychen, 2020). Unmanaged
30 Palmer amaranth plants compete for water, light, and nutrients, which can drastically impact crop yields
31 (Berger et al., 2015). For example, Palmer amaranth has been documented to reduce up to 91%, 68%, and
32 54% corn (Massinga et al., 2001), soybean (Klingaman and Oliver, 1994), and cotton (Morgan et al., 2001)
33 yields, respectively. Moreover, Palmer amaranth has shown a remarkable capacity to evolve resistance
34 to herbicides. To date, Palmer amaranth has evolved resistance to eight herbicide sites of action (Heap,
35 2021), increasing the weed management complexity (Lindsay et al., 2017). Thus, Palmer amaranth poses
36 an economical and environmental risk to sustainable agriculture.

37 Palmer amaranth is a fast growing summer annual forb indigenous to the Sonoran Desert (Sauer, 1957).
38 The species would eventually emerge as a threat to US agriculture in the 1990s. Palmer amaranth weediness
39 is likely a result of human-assisted selection in combination with plant biology. Farm mechanization,
40 adoption of conservation agriculture (e.g., no-till), and reliance on herbicides for weed management are
41 the main human-mediated selection of Palmer amaranth into cropping systems (Ward et al., 2013). On
42 the other hand, Palmer amaranth is a prolific seed producer with a C4 photosynthetic apparatus (Wang et
43 al., 1992). With a dioecy nature, Palmer amaranth male and female plants are obligate outcrosser species,
44 increasing the chances of exchanging adaptive traits among plants (Jhala et al., 2021; Oliveira et al., 2018).
45 Also, Palmer amaranth small seed size (e.g., 1 mm) tend to thrive in no-tillage systems (Price et al., 2011),
46 and spread across locations through farm equipment (Sauer, 1972), manure (Hartzler and Anderson, 2016),
47 animals (Farmer et al., 2017). The dispersal capacity of Palmer amaranth makes the species one of the most
48 successful cases of weed adaptation to current cropping systems.

49 Light and temperature are the main environment requirements for Palmer amaranth successful growth
50 and development (Jha et al., 2010). Palmer amaranth is reported with an extended germination period
51 (Ward et al., 2013). Germination of Palmer amaranth was triggered by 18 C soil temperature at 5 cm depth
52 (Keeley et al., 1987), and optimal germination and biomass production occurred at 35/30 C day and night
53 temperatures (Guo and Al-Khatib, 2003). In addition, Palmer amaranth establishment is human-mediated
54 by tillage timings and preemergence-applied herbicides (Chahal et al., 2021), which can result in weed
55 germination shifts (Sbatella and Wilson, 2010). Water has not shown to limit Palmer amaranth fitness.
56 Under continuous water stress, Palmer amaranth survived and produced at least 14000 seeds plant⁻¹
57 (Chahal et al., 2018). Seeds from Palmer amaranth growing with limited water conditions were heavier,
58 less dormant, and prompt for germination (Matzrafi et al., 2021). Growing conditions and management
59 practices also influence Palmer amaranth sex dimorphism and flowering pattern (Korres et al., 2017; Rumpa
60 et al., 2019). Therefore, Palmer amaranth has shown plasticity to evolve and fast adapt under the current
61 conditions. Further scenarios show that global temperature warming can impact agriculture, and promote
62 niches for Palmer amaranth invasion/adaptation into new environments. Currently, it is estimated that the
63 greatest climatic risk of Palmer amaranth establishment are agronomic crops in Australia and Sub-Saharan
64 Africa (Kistner and Hatfield, 2018). Temperature is a key factor limiting Palmer amaranth expansion to
65 cooler geographies (Briscoe Runquist et al., 2019); however, under future climate change Palmer amaranth
66 is likely to expand northward into Canada and Northern Europe (Kistner and Hatfield, 2018; Briscoe
67 Runquist et al., 2019).

68 Palmer amaranth is already found in agronomic crops of South America (Larran et al., 2017; Küpper
69 et al., 2017) and Southern Europe (Milani et al., 2021). In the United States, Palmer amaranth is well
70 established in the Cotton Belt (Garetson et al., 2019; Bagavathiannan and Norsworthy, 2016) in the southern

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

In the southeastern US, early growing Palmer amaranth is well known to have a higher impact on cotton yields compared to late established plants (MacRae et al., 2013). In the northern states, Palmer amaranth impact on the agroecosystem is recent. Studies investigating Palmer amaranth in those locations are limited due to the plant classification as noxious weed species in some northern states (Yu et al., 2021). Nonetheless, the continuous Palmer amaranth dispersal and potential establishment across the northern United States is concerning and warrants investigations on species morphology in such environments. Understanding Palmer amaranth biology and growing strategies under different agroecosystems can enhance our knowledge on species adaptation and management practices. It can also aid in designing proactive and ecological tactics to limit the species range expansion, reduce its negative impact, and developing resilient and sustainable farming systems (MacLaren et al., 2020). Therefore, the objective of this study was to investigate the flowering pattern, sex dimorphism, biomass production, and height of Palmer amaranth cohorts growing under corn, soybean and bareground across five locations in the United States Midwest.

MATERIAL AND METHODS

Plant material and growing conditions

A Palmer amaranth accession (Per1) from Perkins County, Nebraska, with no reported herbicide resistance according to Oliveira et al. (2021) was selected for this study. Three weeks prior to the onset of the field experiments, seeds were planted in plastic trays containing potting-mix. Emerged seedlings (1 cm) were transplanted into 200 cm^{-3} plastic pots (a plant pot $^{-1}$). Palmer amaranth seedlings were supplied with adequate water and kept under greenhouse conditions at the University of Wisconsin-Madison, University of Nebraska-Lincoln, and Western Illinois University; and kept outdoors at the Perkins extension office in Grant, NE until the 2-3 leaf stage (5 to 8 cm height) when they were transported to the field.

Field study

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

Fields were conventionally tilled prior to crop planting. Corn hybrid and soybean varieties were planted in 76-cm row spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using

113 Daymet weather data from June through September across the five locations in 2018 and 2019 (Correndo
 114 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-metolachlor	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-metolachlor	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		

^a glyphosate, 840 g ae ha ^b S-metolachlor, g ai ha ^c S-metolachlor + trazine + mesotrione, + bicyclopyrone, g ai ha ^d saflufenacil + imazethapyr + pyroxasulfone, g ai ha

115 The field experimental units were three adjacent 9.1 m wide (12 rows at 76.2 cm row spacing) by 10.7
 116 m long. The experimental design were arranged in factorial design with three crops, two transplanting
 117 times simulating two cohorts, repeated across five locations. Each experimental unit was planted with
 118 corn, soybean, or kept under bareground. The two transplanting timings were June 1 (first cohort) and
 119 July 1 (second cohort). Palmer amaranth seedlings (potting mix + two seedlings) were transplanted (6 cm
 120 deep and 8 cm wide). Forty-eight plants were equidistantly placed (0.76 m apart) between rows within
 121 each crop (Figure 2). After a week, one plant was eliminated and one was kept, resulting in 24 plants per
 122 experimental unit and transplanting time (Figure 2). When needed, Palmer amaranth plants were supplied
 123 with water during the first week after transplanting.

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

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

132 Statistical analyses

133 The statistical analyses were performed using R statistical software version 4.0.1. Data analyses are
 134 stored at Zenodo (Oliveira, 2021).

135 Analyses of Palmer amaranth height and biomass were performed with a linear mixed model using *lmer*
 136 function from “lme4” package (Bates et al., 2015). Plant height and biomass were log transformed to meet
 137 model assumption of normality. In the model, crop (bareground, corn, soybean) was the fixed effect and
 138 year nested with location the random effects. Analysis of variance was performed with *anova* function

139 from “car” package (Fox and Weisberg, 2018). Marginal means and compact letter display were estimated
140 with *emmeans* and *cld* from packages “emmeans” and “multcomp” (Hothorn et al., 2008).

141 The Palmer amaranth flowering timing was estimated as cumulative flowering across all location. Dataset
142 was nested but id did not include Grant, NE. Palmer amaranth cumulative flowering estimation was
143 determined using an asymmetrical three parameter log logistic Weibull model of the drc package (Ritz et
144 al., 2015).

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

145 In this model, Y is the Palmer amaranth cumulative flowering, d is the upper limit (set to 100), and e is
146 the inflection point, and x day of year (doy).

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

152 Palmer amaranth sex dimorphism was fitted to a binary logistic regression (Bangdiwala, 2018). Binary
153 logistic regression is used for predicting binary classes, such as the probability of a plant being female in a
154 dioecious species. Prior to the analysis, all missing values were removed from the dataset. Also, data from
155 Grant was not used in this analysis due to the uniform plant harvesting at that location. The complete dataset
156 was splitted into 80% train and 20% test data. The 80% train is used for the model training and the 20% test
157 is used for checking how the model generalized on unseen dataset. With 80% dataset, a binary response
158 variable, male (0) and female (1), was fitted to a generalized linear model (*glm* function) including day of
159 year harvest, height, weight, crop and month as independent variables (without interaction). The model
160 family was binomial with a logit function. The model fit was assessed through pseudo R-squared values
161 (McFadden, Cox and Snell, Cragg and Uhler) and likelihood ratio using *nagelkerke* function (“rcompanion”
162 package). The marginal effects computation was performed with Average Marginal Effects (AMEs) at
163 every observed value of x and average across the results (Leeper, 2017) using *margins* function from
164 “margins” package. The rest 20% dataset was predicted using *predict* function with a cutoff estimation for
165 male or female using *performance* function. The model quality prediction from the classification algorithm
166 was measured with precision (*precision* function), recall (*recall* function) and F1-score (*f_meas* function)
167 using the “yardstick” package. The precision determines the accuracy of positive predictions (female
168 plants), recall determines the fraction of positives that were correctly identified, and F1-score is a weighted
169 harmonic mean of precision and recall with the best score of 1 and the worst score of 0. F1-score conveys
170 the balance between the precision and the recall (Yacoub and Axman, 2020).

RESULTS

171 Palmer amaranth height and biomass

172 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants
173 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3,
174 and 16.3 g plant⁻¹ in bareground, soybean and corn, respectively. Plants from the second cohort produced
175 62.6 g plant⁻¹ in bareground, followed by 6.3 g plant⁻¹ in soybean, and 1.4 g plant⁻¹.

176 Palmer amaranth height was more uniform across cohort timings, except when growing in corn (figure
 177 3B). Palmer amaranth plants from the first cohort were on average 69.2 cm tall in bareground, which
 178 was not different from the 70.7 cm tall plants from the second cohort timing ($P = 0.74$). In addition, no
 179 difference in Palmer amaranth height (69.3 cm) was detected from first cohort plants in soybean to first and
 180 second cohort plants in bareground ($P > 0.75$). Palmer amaranth plants from the second cohort were nearly
 181 10 cm lower compared to the first cohort in soybeans ($P = 0.04$). The tallest (first cohort) and smallest
 182 (second cohort) Palmer amaranth plants were found in corn. Palmer amaranth reached 85.2 and 38.2 cm
 183 tall, respectively.

184 **Palmer amaranth cumulative flowering**

185 Palmer amaranth plants from the first cohort growing in corn resulted in a longer flowering window
 186 compared to plants growing in bareground and soybean (Figure 4A). The 10% cumulative Palmer amaranth
 187 flowering in soybean, bareground and corn occurred at the end of June. Palmer amaranth reached 10%
 188 flowering in soybean, bareground and corn at doy 180, 180.9 and 181.7, respectively. The 50% Palmer
 189 amaranth cumulative flowering occurred in July. Palmer amaranth reached 50% flowering in bareground,
 190 soybean and corn at doy 193.4, 194.8, and 206.6, respectively. Similar trend was observed at 90%
 191 Palmer amaranth cumulative flowering. Palmer amaranth reached 90% flowering at doy 252.6 in corn
 192 (early September), which was 38 and 32 days after reaching 90% flowering in bareground and soybean,
 193 respectively.

194 Palmer amaranth cumulative flowering at the second cohort ranged from mid July to mid September
 195 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to
 196 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at
 197 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at
 198 doy 210.9, which was 6 days prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering,
 199 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; P
 200 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean
 201 (260.5; P = 0.66).

202 **Palmer amaranth sex dimorphism**

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

Table 2. Average marginal means of sex dimorphism logistic model. Factor pararamter 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.

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

DISCUSSION

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

225 Palmer amaranth grow and development in second cohort was limited due to the crop competitive ability
226 at advanced development stages. Palmer amaranth was transplanted when corn canopy was nearly closed,
227 which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was
228 lower compared to its first cohort. Under crop canopy (e.g., second cohort), Palmer amaranth flowering
229 window was near to similar in corn and soybean. Palmer amaranth growing without crop competition
230 produced the highest amounts of biomass and less extended flowering window. The Palmer amaranth
231 strategy in bareground was to invest biomass in growing plant width and height. Nonetheless, Palmer
232 amaranth produced 21% less biomass in second cohort compared to first cohort timing. In a bareground
233 study, early emerged Palmer amaranth without competition was 50% taller than late emerged plants
234 (Webster and Grey, 2015). These results suggest that crop competition is not the only factor limiting
235 late Palmer amaranth establishment. The limited growth of Palmer amaranth at second cohort is likely a
236 reduced plant response to day length, light availability and thermal units (e.g, growing degree days). It
237 is hypothesize that reduced day length contributed to smaller plants at second cohort as well as shorter
238 flowering period. A study in North Carolina and Illinois predicted that less than 10% Palmer amaranth
239 seedlings emergence occurred after June (Piskackova et al., 2021). In addition, Palmer amaranth negative
240 impact on soybean (Korres et al., 2020) and cotton (Webster and Grey, 2015) yields was higher when plants
241 were established near to crop planting.

242 Seed production was not evaluated due to plant harvest at initiation of flowering. Nonetheless, it is well
243 documented a strong positive correlation between Palmer amaranth biomass and seed production (Schwartz
244 et al., 2016; Spaunhorst et al., 2018). In our study, Palmer amaranth growing at first cohort accumulated an
245 overall 42% more biomass when compared to second cohort. Therefore, Palmer amaranth plants growing
246 in the second cohort is likely to produce less seeds regardless the cropping system. Our observation is
247 consistent with the findings that first Palmer amaranth cohort produced 50% more seeds per plant than
248 Palmer amaranth plants established six weeks later in bareground (Webster and Grey, 2015). Still, seed
249 production at second cohort is likely to replenish the soil seedbank. Seed production and deposition in
250 the seedbank is also a key factor for species perpetuation (Menges, 1987). Palmer amaranth can produce
251 hundred thousands seeds per plant (Schwartz et al., 2016; Keeley et al., 1987), and stay viable buried in
252 the seedbank for at least 36 months (Sosnoskie et al., 2013). Therefore, preventing Palmer amaranth seed

253 production or/and seed migration to its non-native habitat is an essential strategy to minimize weed impact
254 into agroecosystem (Davis et al., 2015).

255 An ecological approach to reduce seed production in Palmer amaranth is understanding its flowering
256 window. Our study suggests that Palmer amaranth flowering was slightly influenced by cropping systems
257 and cohort timings. Palmer amaranth growing in bareground and corn resulted in the overall shortest and
258 longest flowering window, respectively. When growing in soybean, Palmer amaranth flowering window
259 was similar to bareground at first cohort but similar to corn at second cohort timing. Plant flowering
260 initiation is complex and depends on biological and ecological factors (Lang, 1965). We hypothesize that
261 when growing in high competition (e.g., second cohort) and/or under low light/short day length, Palmer
262 amaranth plants tend to initiate flowering early, as well as having an extended flowering window. Early
263 flower initiation is plant strategy when growing in stress conditions. For example, when growing under
264 water stress, early flowering in Palmer amaranth resulted in a mismatch between female and male plants by
265 seven days (Mesgaran et al., 2021). A mismatch in Palmer amaranth male and female flowering period can
266 minimize plant outcross, and thus reduce plant seed production and exchange of resistant alleles (Jhala et
267 al., 2021). Sex dimorphism manipulation is considered a potential ecological pest control (McFarlane et al.,
268 2018; Schliekelman et al., 2005).

269 The mechanisms of sex-determination in plant species is intriguing and arouse the curiosity of many
270 scientists, including Charles Darwin (Darwin, 1888). In our study, the sex dimorphism model performance
271 was decent (AIC 0.64) considering the biology of plant flowering. A 1:1 male and female sex ratio is
272 a general evolutionary stable strategy for plant species perpetuation (Fisher, 1930). However, a slight
273 deviation from 1:1 sex ratio might occur in some dioecious species. For example, the dioecious *Halophila*
274 *stipulacea* is a female-biased plant in its native habitat, but the naturalized *H. stipulacea* have a 1:1 ratio
275 (Nguyen et al., 2018). Naturalized of *H. stipulacea* reduced female-male ratio to expand into its non-native
276 habitat (Nguyen et al., 2018). Also, biotic and/or abiotic stress can influence plant sex determination.
277 Palmer amaranth male-to-female ratio was greater under high plant densities (Korres and Norsworthy, 2017)
278 and after herbicide application (Rumpa et al., 2019). Our model estimated that late flowering, heavier and
279 taller Palmer amaranth plants deviated from 1:1 ratio in favor to female plants. It was reported that female
280 Palmer amaranth plants invested more in height, stem and biomass while male invested more in leaf area
281 and leaf dry weight under nutrient deficiency (Korres et al., 2017). Our model also estimated more female
282 plants in soybean and bareground compared to corn, which might linked to plant competition strategy
283 in each agroecosystem. Our results showed the influence of life-history and ecological traits on sexual
284 dimorphism in Palmer amaranth. Sexual dimorphism is documented in other dioecious species (Barrett and
285 Hough, 2013). For example, stronger female plant competition and greater male tolerance to herbivory was
286 reported in *Spinacia oleracea* (Pérez-Llorca and Sánchez Vilas, 2019). Research on candidate genes for
287 sex determination in *Amaranthus* species are currently underway but it is far to complete (Montgomery et
288 al., 2021, 2019). Further studies are also needed to understand the ecological basis of Palmer amaranth
289 flowering, including the plant behavior under climate change.

290 Our study demonstrated the Palmer amaranth plasticity to grow and develop into cropping-systems. Is
291 likely that Palmer amaranth range will continue to expanding into new geographies. Therefore, preventive
292 management is a priority to minimizing Palmer amaranth dispersal. Reactive management should focus on
293 early-season management programs, which would have a large negative effect on Palmer amaranth growth
294 and development. Tactics that promote early-season crop advantage against Palmer amaranth, including
295 early crop planting, crop rotation, plant width, preemergence applied herbicide, and crop residue (e.g. cover
296 crops) would minimize the negative impact of Palmer amaranth in agroecosystems. The aggressiveness

297 and differential Palmer amaranth adaptation to agroecosystem is striking and require national efforts to
298 minimize the species impact on economy and sustainability.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

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

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REFERENCES

- 306 A Frontier article expect the reference list to be included in this section. To make that happens, the below
307 syntax can be used. This feature is from Pandoc citeproc which is used with `frontier_article()` to
308 handle the bibliography
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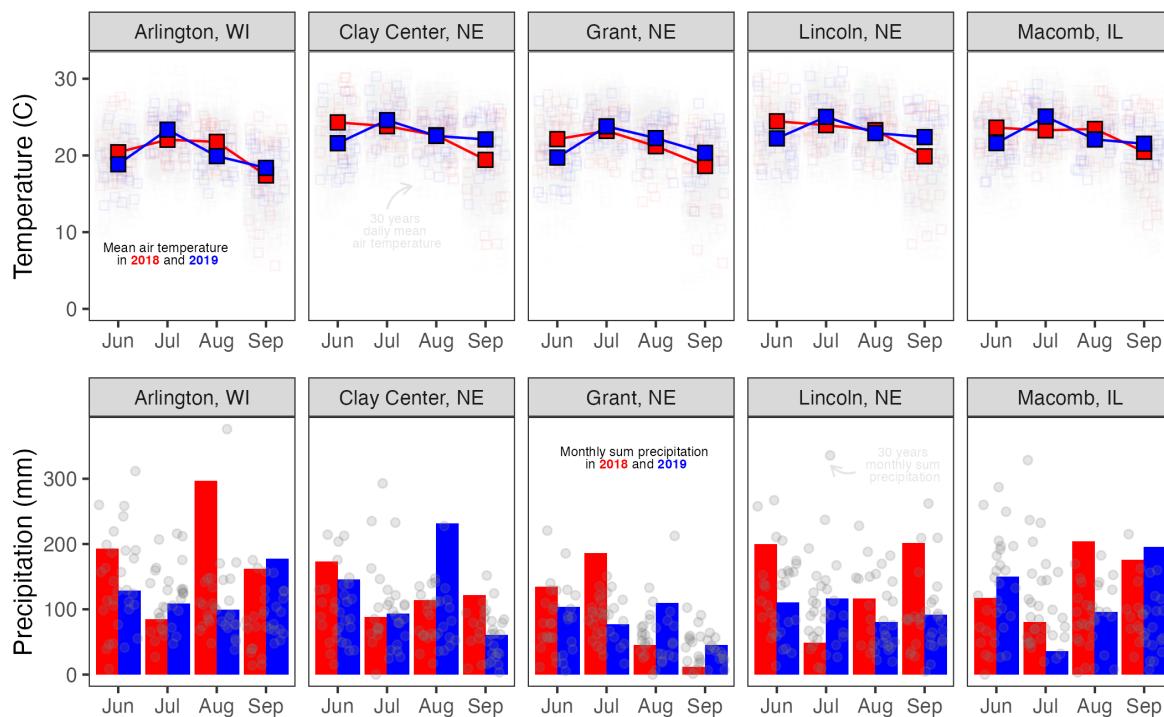


Figure 1. Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

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FIGURES

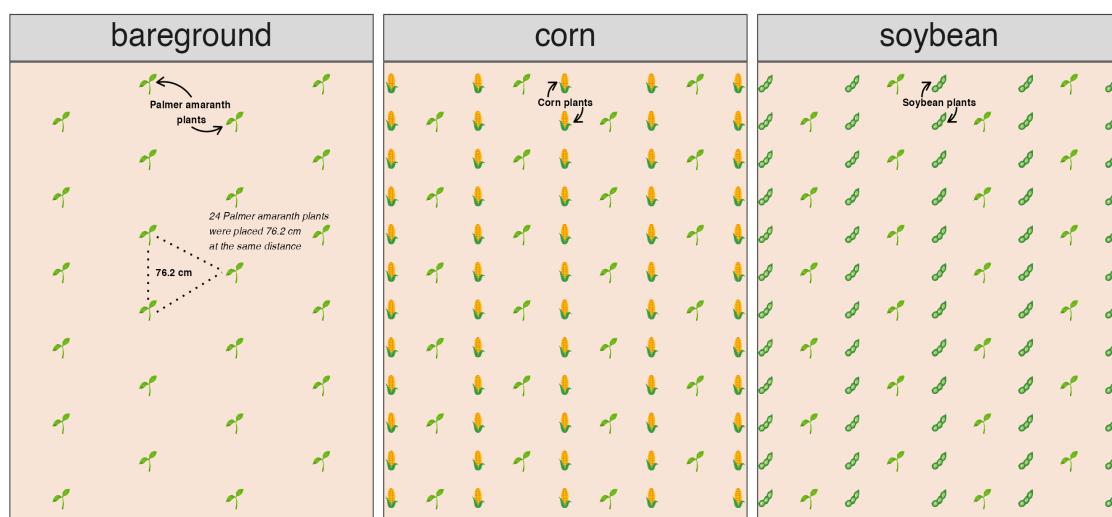


Figure 2. Palmer amaranth adaptation study layout of a plant cohort timing. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each experimental unit

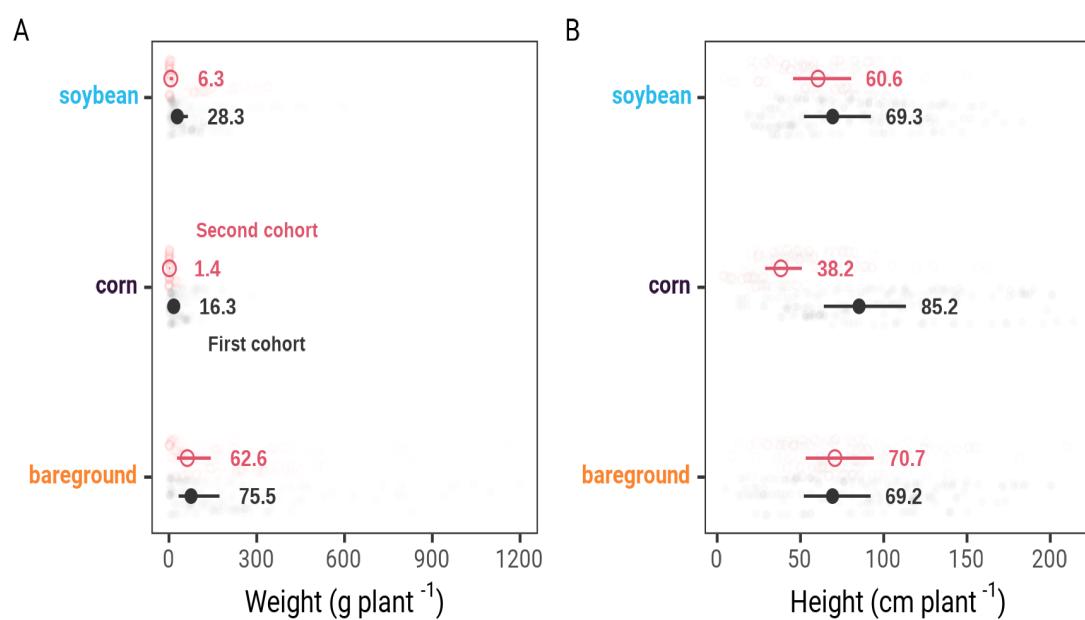


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

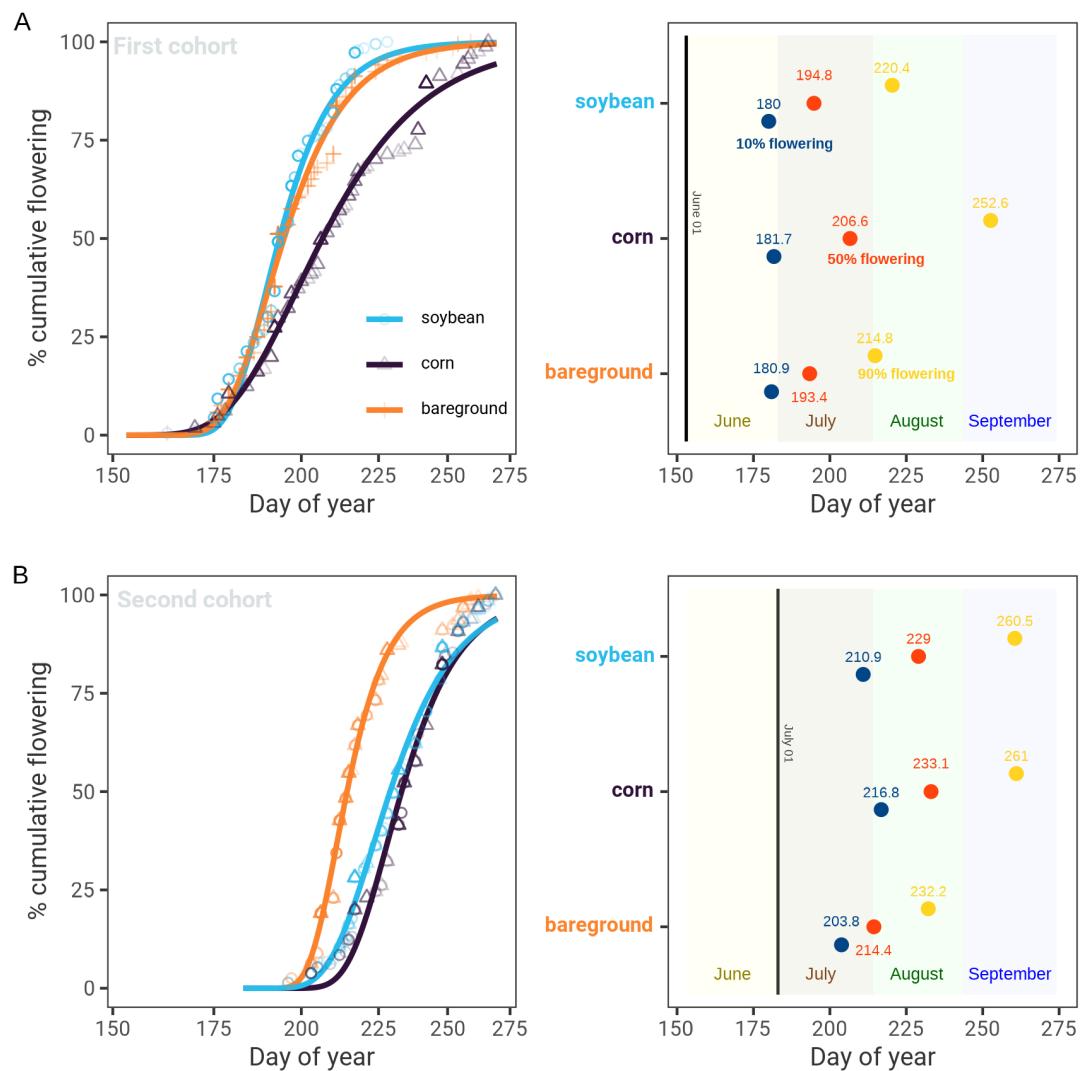


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

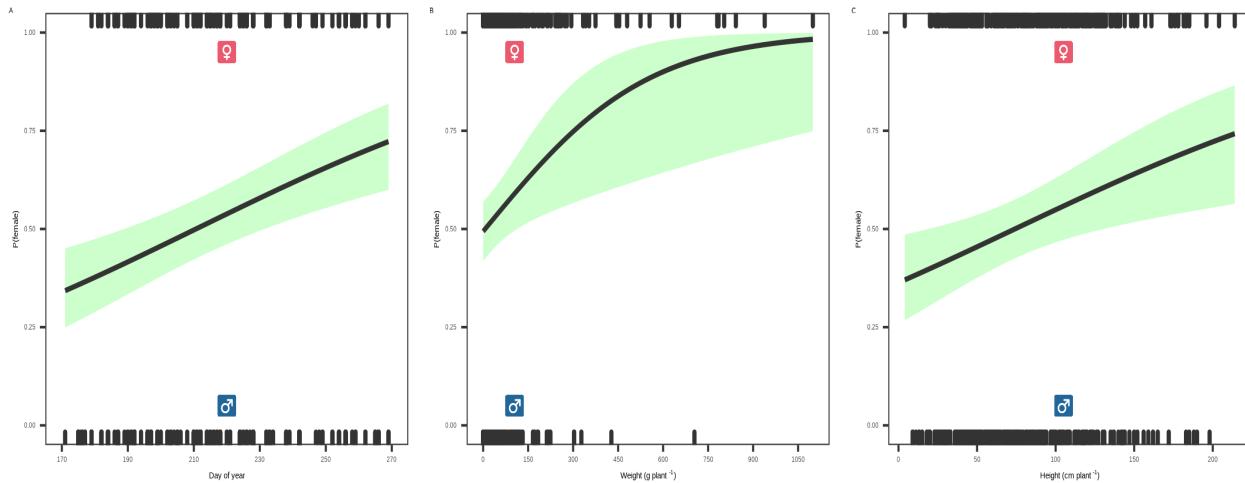


Figure 5. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

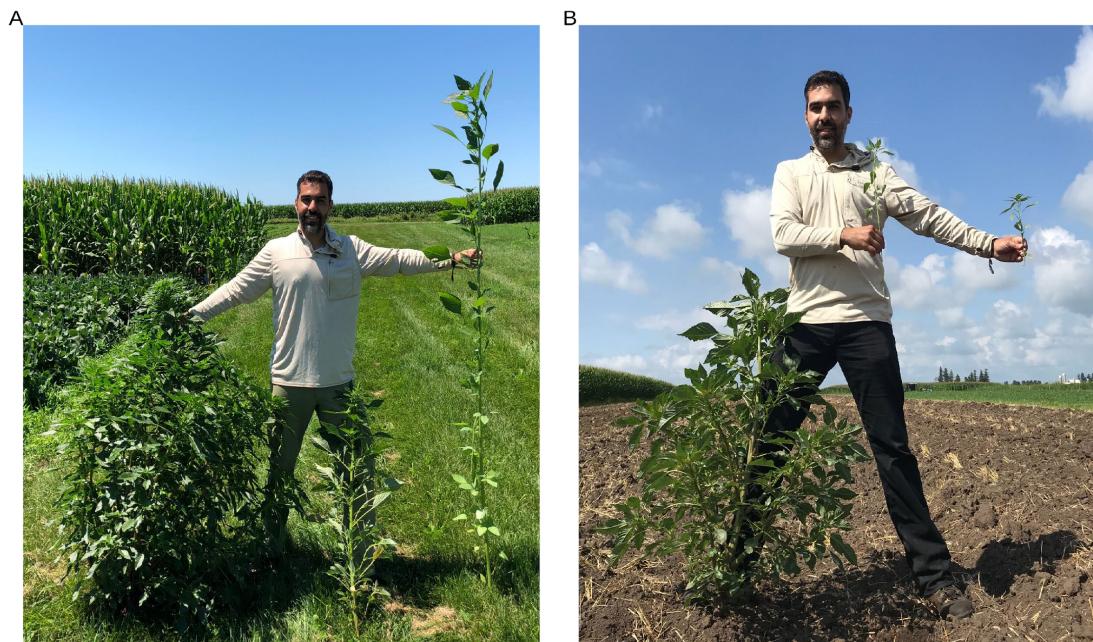


Figure 6. MCO (180 cm) holds harvested Palmer amaranth plants at 40 days after first cohort transplanting (A) and 33 days after second cohort transplanting (B). From left to right, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin