

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 to 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 from United States Midwest. Palmer amaranth is likely to continue its expansion northward. Therefore, preventing plant dispersal into new habitats 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 intensive use of herbicides for weed management
41 are 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). Waterhemp, an *Amaranthus* species, is the most troublesome species in that geography (Tranel et al., 2011). Nonetheless, 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 can increase. It seems certain the need to manage Palmer amaranth in agronomic crops throughout novel 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

100 Plant material and growing conditions

101 A Palmer amaranth accession (Kei3) from Perkins County, Nebraska, with no reported herbicide resistance
102 according to Oliveira et al. (2021) was selected for this study. Three weeks prior to the onset of the field
103 experiments, seeds were planted in plastic trays containing potting-mix. Emerged seedlings (1 cm) were
104 transplanted into 200 cm⁻³ plastic pots (a plant pot⁻¹). Palmer amaranth seedlings were supplied with
105 adequate water and kept under greenhouse conditions at the University of Wisconsin-Madison, University
106 of Nebraska-Lincoln, and Western Illinois University; and kept outdoors at the Perkins extension office in
107 Grant, NE until the 2-3 leaf stage (5 to 8 cm height) when they were transported to the field.
108

Field study

109 The experiment was conducted in 2018 and 2019 under field conditions at five locations: Arlington, WI
110 (43°18'N, 89°29'W), Clay Center, NE (40.57'N, 9814'W), Grant, NE (XXX'N, XXX'W), Lincoln, NE
111 (41.16'N, 96.42'W), and Macomb, IL (XXX'N, XXX'W).

112 Fields were conventionally tilled prior to crop planting. Corn hybrid and soybean varieties were planted
 113 in 76-cm row spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using
 114 Daymet weather data from June through September across the five locations in 2018 and 2019 (Correndo
 115 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	NK0142 3120-EZ1	DKC60-67		
	Seeding rate	88956	86487		
	Weed control	glyphosate ^a / S-metolachlor ^b	S-metolachlor + trazine + mesotrione + bicyclopyrone ^c		
	Stage at 1 st cohort	V2-3			
	Stage at 2 nd cohort	V6-7			
	Planting day	April 30, 2018 / May 5, 2019	May 10, 2018/19		
	Fertilization	N (46-0-0) at 157 kg ha ⁻¹			
Soybean	Variety	DSR-1950	AG21X8		
	Seeding rate	296400	321237		
	Weed control	glyphosate / S-metolachlor	saflufenacil + imazethapyr ^d + pyroxasulfone		
	Stage at 1 st cohort	V1-2			
	Stage at 2 nd 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		

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

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

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

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

133 Statistical analyses

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

136 Analyses of Palmer amaranth height and biomass were performed with a linear mixed model using *lmer*
 137 function from “lme4” package (Bates et al., 2015). Plant height and biomass were log transformed to meet

138 model assumption of normality. In the model, crop (bareground, corn, soybean) and cohort time (first
 139 and second) were the fixed effects and year nested with location the random effects. Analysis of variance
 140 was performed with *anova* function from “car” package (Fox and Weisberg, 2018). Marginal means and
 141 compact letter display were estimated with *emmeans* and *cld* from packages “*emmeans*” (Lenth et al.,
 142 2021) and “*multcomp*” (Hothorn et al., 2008), respectively.

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

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

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

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

154 Palmer amaranth sex dimorphism was fitted to a binary logistic regression (Bangdiwala, 2018). Binary
 155 logistic regression is used for predicting binary classes, such as the probability of a plant being female in
 156 a dioecious species. Prior to the analysis, all missing values were removed from the dataset. Also, data
 157 from Grant was not used in this analysis due to the uniform plant harvesting at that location. The complete
 158 dataset was splitted into 80% train and 20% test data. The 80% train is used for the model training and the
 159 20% test is used for checking model performance on unseen dataset. With 80% dataset, a binary response
 160 variable, male (0) and female (1), was fitted to a generalized linear model (base R *glm* function) including
 161 day of year harvest, height, weight, crop and month as independent variables (without interaction). The
 162 model family was binomial with a logit function. The model fit was assessed through pseudo R-squared
 163 values (McFadden, Cox and Snell, Cragg and Uhler) and likelihood ratio using *nagelkerke* function from
 164 “rcompanion” package (Mangiafico, 2021). The marginal effects computation was performed with Average
 165 Marginal Effects (AMEs) at every observed value of x and average across the results (Leeper, 2017) using
 166 *margins* function from “margins” package (Leeper et al., 2021). The rest 20% dataset was predicted using
 167 *predict* function with a cutoff estimation for male or female using *performance* function. The model quality
 168 prediction from the classification algorithm was measured with precision (*precision* function), recall (*recall*
 169 function) and F1-score (*f_meas* function) using the “yardstick” package (Kuhn et al., 2021). The precision
 170 determines the accuracy of positive predictions (female plants), recall determines the fraction of positives
 171 that were correctly identified, and F1-score is a weighted harmonic mean of precision and recall with the
 172 best score of 1 and the worst score of 0. F1-score conveys the balance between the precision and the recall
 173 (Yacoub and Axman, 2020).

RESULTS

174 Palmer amaranth height and biomass

175 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants
 176 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3,

177 and 16.3 g plant⁻¹ in bareground, soybean and corn, respectively. Plants from the second cohort produced
178 62.6 g plant⁻¹ in bareground, followed by 6.3 g plant⁻¹ in soybean, and 1.4 g plant⁻¹.

179 Palmer amaranth height was more uniform across cohort timings, except when growing in corn (figure
180 3B). Palmer amaranth plants from the first cohort were on average 69.2 cm tall in bareground, which
181 was not different from the 70.7 cm tall plants from the second cohort timing ($P = 0.74$). In addition, no
182 difference in Palmer amaranth height (69.3 cm) was detected from first cohort plants in soybean to first and
183 second cohort plants in bareground ($P > 0.75$). Palmer amaranth plants from the second cohort were nearly
184 10 cm lower compared to the first cohort in soybeans ($P = 0.04$). The tallest (first cohort) and smallest
185 (second cohort) Palmer amaranth plants were found in corn. Palmer amaranth reached 85.2 and 38.2 cm
186 tall, respectively.

187 **Palmer amaranth cumulative flowering**

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

197 Palmer amaranth cumulative flowering at the second cohort ranged from mid July to mid September
198 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to
199 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at
200 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at
201 doy 210.9, which was 6 days prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering,
202 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; P
203 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean
204 (260.5; P = 0.66).

205 **Palmer amaranth sex dimorphism**

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

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

DISCUSSION

216 Our study showed that Palmer amaranth biomass, height, flowering window and sex varied within crops and
217 cohort timings. In general, first cohort of Palmer amaranth plants were heavier and taller when compared
218 to the second cohort. At first cohort, resources (e.g., soil nutrients) and conditions (e.g., light) were more

Table 2. Average marginal means of Palmer amaranth sex dimorphism logistic model. Factor pararamter values (crop and bareground) is shown compared to soybean.

Term	AME ^a	SE ^b	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.

219 timely available for the species. High biomass and taller Palmer amaranth plants are likely a weed strategy
 220 to compete for light in between crop rows in absence of canopy. In such conditions, Palmer amaranth
 221 showed an extraordinary plasticity to adapt upon the agroecosystem. This is evident when comparing
 222 Palmer amaranth canopy shape. The Palmer amaranth competition (e.g., light) strategy was to mimic
 223 the crop grow and development (Figure 6). These results suggests that Palmer amaranth can fast evolve
 224 life-history traits to adapt into cropping systems and cultural practices, which was also showed in a study
 225 varying nitrogen fertilization (Bravo et al., 2018). Our results highlight the Palmer amaranth as a threat to
 226 field crops as breeding more competitive crop varieties is likely to select more competitive weed biotypes
 227 (Bravo et al., 2017).

228 Palmer amaranth grow and development in second cohort was limited due to the crop competitive ability
 229 at advanced development stages. Plants were transplanted at greater crop height, which reduced Palmer
 230 amaranth competitiveness. As a result, Palmer amaranth height and biomass was lower compared to its
 231 first cohort. Palmer amaranth growing without crop competition produced the highest amounts of biomass.
 232 The Palmer amaranth strategy in bareground was to invest biomass in growing plant width and height.
 233 Nonetheless, Palmer amaranth produced 17% less biomass in second cohort compared to first cohort
 234 timing. In a bareground study, early emerged Palmer amaranth without competition was 50% taller than
 235 late emerged plants (Webster and Grey, 2015). These results suggest that crop competition is not the only
 236 factor limiting late Palmer amaranth establishment. The limited growth of Palmer amaranth at second
 237 cohort is likely a reduced plant response to day length, light availability and thermal units (e.g, growing
 238 degree days). The *Amaranthus* species are sensitive to photoperiod (Wu and Owen, 2014). It is hypothesize
 239 that reduced day length contributed to smaller plants at second cohort regardless the crop. A study in North
 240 Carolina and Illinois predicted that less than 10% Palmer amaranth seedlings emergence occurred after
 241 June (Piskackova et al., 2021). In addition, Palmer amaranth negative impact on soybean (Korres et al.,
 242 2020) and cotton (Webster and Grey, 2015) yields was higher when plants were established near to crop
 243 planting.

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

253 (Schwartz et al., 2016; Keeley et al., 1987), and stay viable buried in the seedbank for at least 36 months
254 (Sosnoskie et al., 2013). Therefore, preventing Palmer amaranth seed production or/and seed migration to
255 its non-native habitat is an essential strategy to minimize the species impact into agroecosystem (Davis et
256 al., 2015).

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

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

294 Our study demonstrated the Palmer amaranth plasticity to grow and develop into arable land of US
295 Midwest. Is likely that Palmer amaranth range will continue to expanding into new geographies. The
296 migration of Palmer amaranth into the US Midwest will reshape the landscape as waterhemp and Palmer

297 amaranth will share the same habitat. The presence of Palmer amaranth and waterhemp will increase
298 the weed management complexity. Therefore, preventive management is a priority to minimizing Palmer
299 amaranth dispersal. Reactive management should focus on early-season management programs, which
300 would have a large negative effect on Palmer amaranth growth and development. Long-term tactics that
301 promote early-season crop advantage against Palmer amaranth, including diversity of crops in rotation,
302 early/late crop planting, plant width, and crop residue (e.g. cover crops) would minimize the negative
303 impact of Palmer amaranth to cropping systems. The aggressiveness and differential Palmer amaranth
304 adaptation to agroecosystem is striking and require national efforts to minimize the species impact on
305 sustainability and economy.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

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

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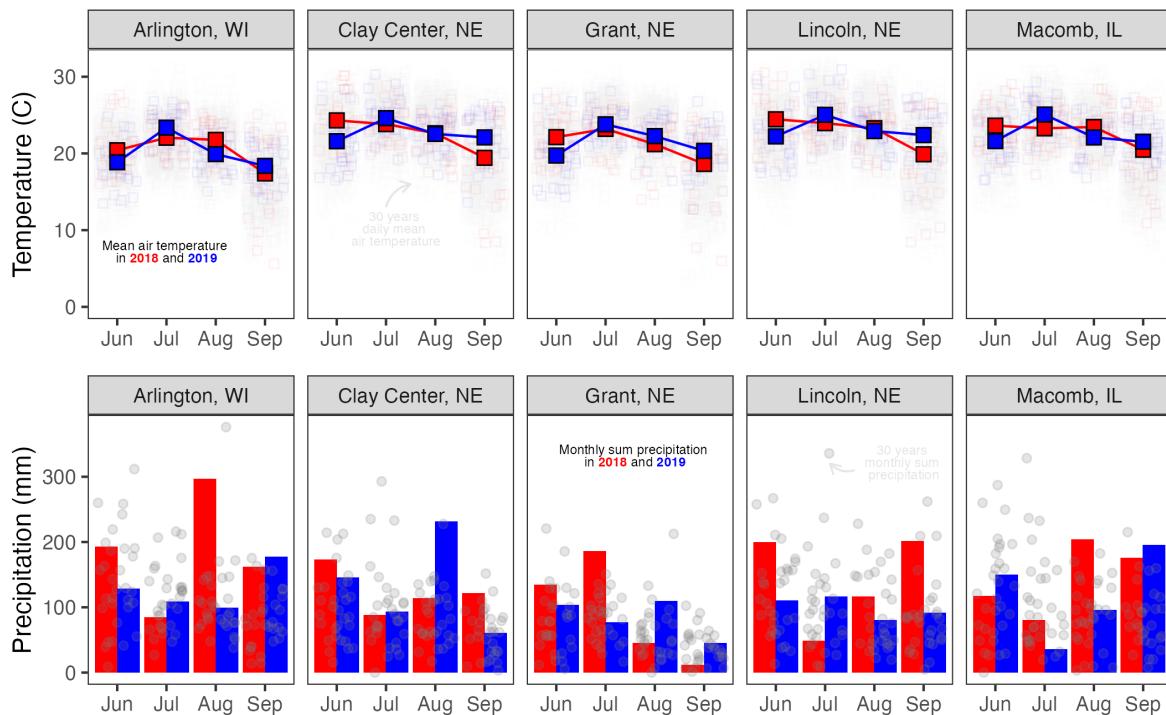


Figure 1. Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE and Macomb, IL

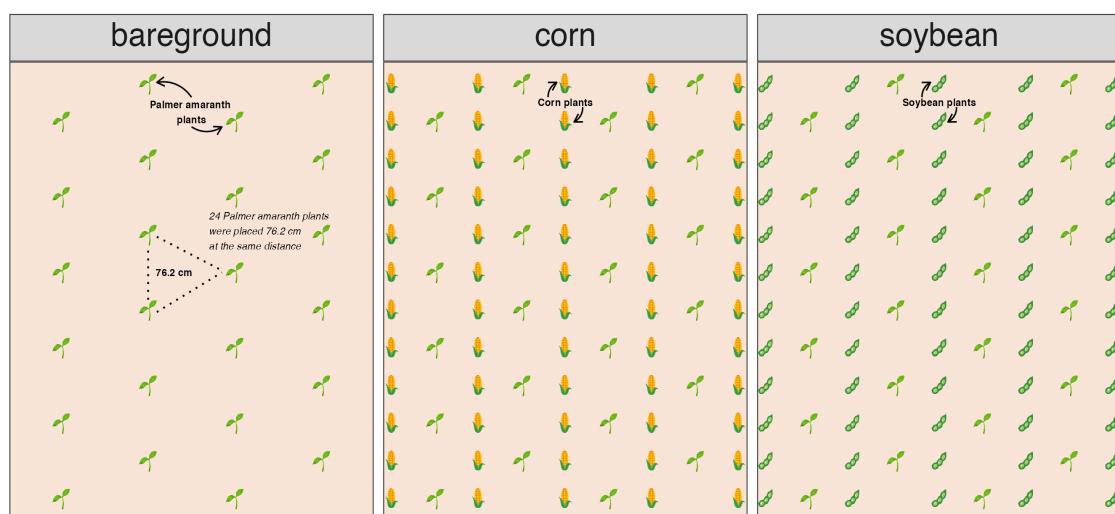


Figure 2. Palmer amaranth adaptation study layout of a plant cohort timing in bareground, corn, and soybean. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each experimental unit

FIGURES

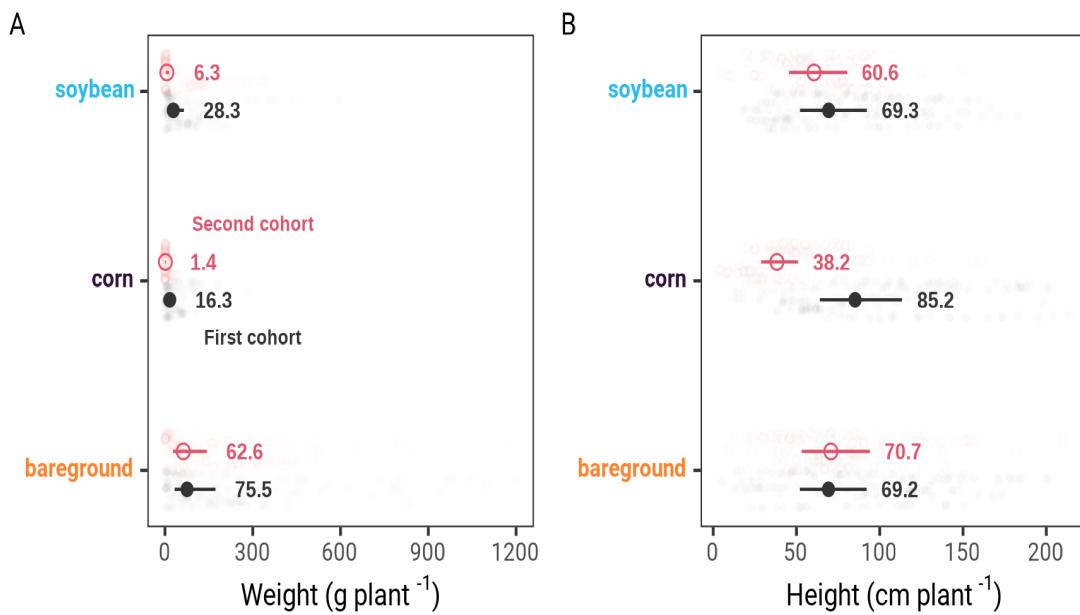


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

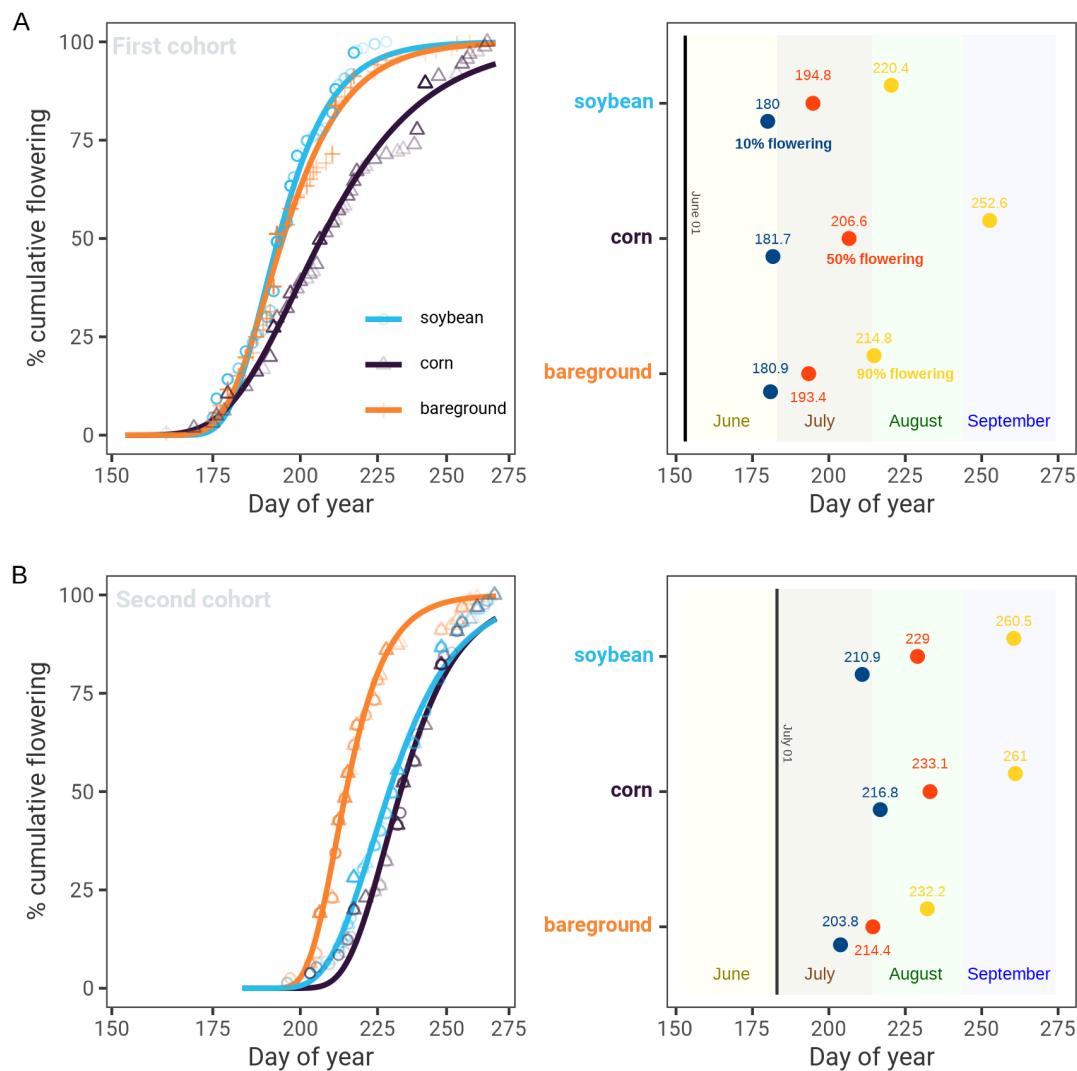


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B) nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

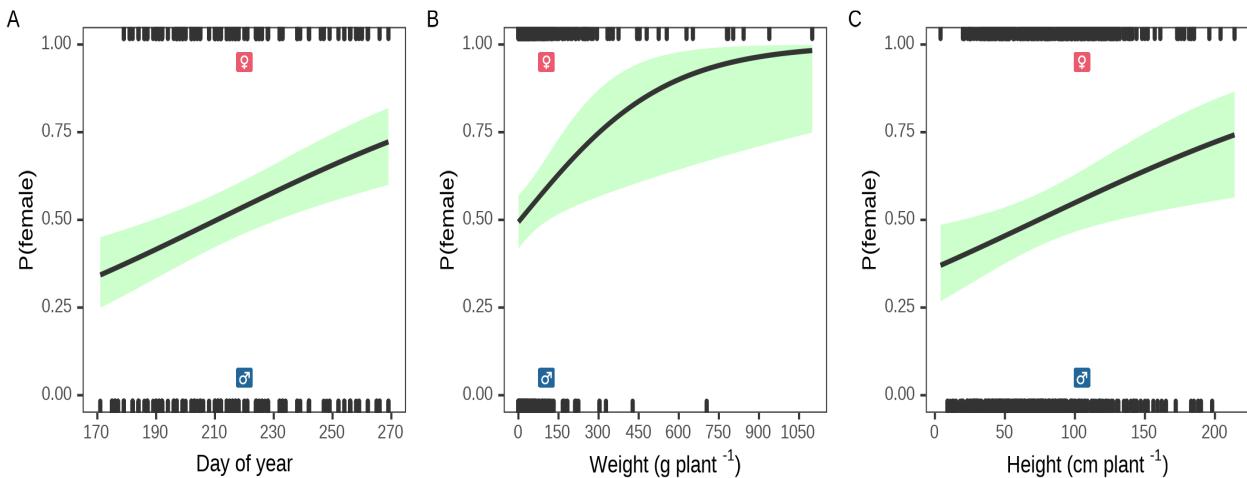


Figure 5. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

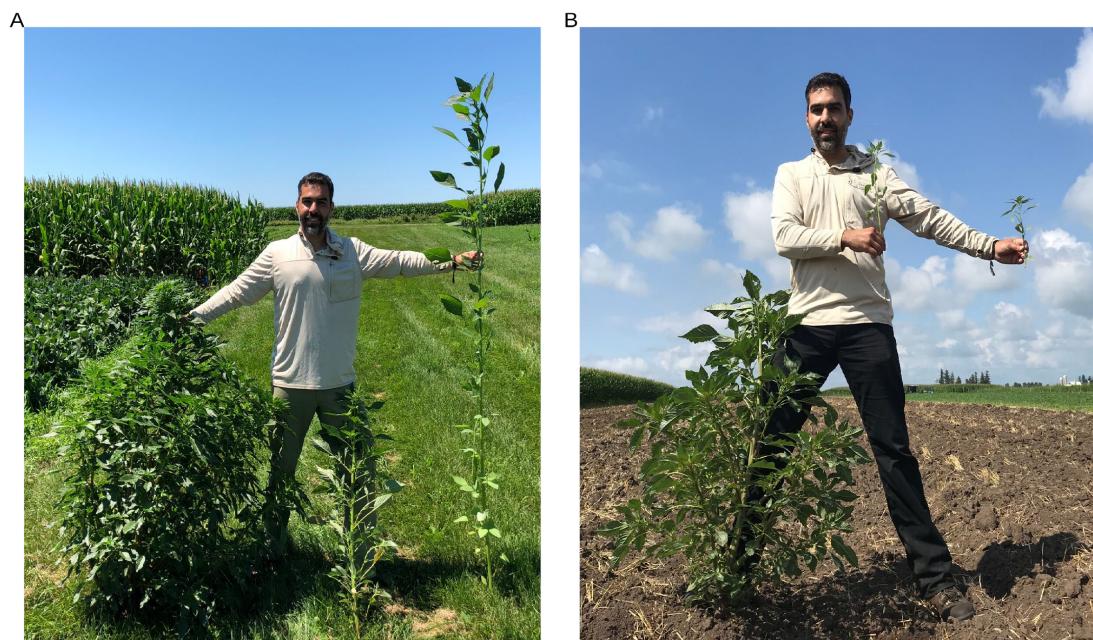


Figure 6. MCO (180 cm) holds harvested Palmer amaranth plants at 40 days after first cohort transplanting (A) and 33 days after second cohort transplanting (B) time. From left to right, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin