

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 US Midwest. Results demonstrated that first cohort of Palmer amaranth, established in June, produced 42% more biomass than plants from second cohort (established in July). The first Palmer amaranth cohort produced 75.5 g plant⁻¹ in bareground, 28.3 g plant⁻¹ in soybean and 16.3 g plant⁻¹ in corn, whereas the second Palmer amaranth cohort produced 62.6, 6.3, and 1.4 g plant⁻¹ in bareground, soybean and corn, respectively. Palmer amaranth height was more impacted when 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 increased as biomass and height increased. Our results showed the fast adaptation and plasticity of Palmer amaranth to grow and adapt to cropping systems from the US 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 to establish into cropping systems, including crop rotation (beyond corn and soybean), early/late crop planting, row spacing, cover crops, and effective chemical control programs.

Keywords: Evolution, Flowering, Management, Pigweed, Weed

INTRODUCTION

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

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

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

67 Palmer amaranth is already found in agronomic crops of South America (Larran et al., 2017; Küpper
68 et al., 2017) and Southern Europe (Milani et al., 2021). In the United States, Palmer amaranth is well
69 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 the US Midwest (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 new Palmer amaranth infestations in agronomic crops throughout northern United States 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 (Kei3) from Perkins County, Nebraska with no glyphosate resistance according to Oliveira et al. (2021) was selected for this study. Three weeks prior to the establishment of each cohort, 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°18'N, 89°29'W), Clay Center, NE (40.57'N, 9814'W), Grant, NE (XXX'N, XXX'W), Lincoln, NE (41.16'N, 96.42'W), and Macomb, IL (XXX'N, XXX'W).

112 Fields were conventionally tilled prior to crop planting. Corn and soybean were planted in 76-cm row
 113 spacing (Table 1). Monthly mean air temperature and total precipitation were obtained using Daymet
 114 weather data from June through September across the five locations in 2018 and 2019 (Correndo et al.,
 115 2021) (Figure 1)

Table 1. Field study attributes from Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

Attributes	Arlington, WI	Clay Center, NE	Grant, NE	Lincoln, NE	Macomb, IL
Bareground					
Corn	Weed control	glyphosate ^a / S-metolachlor ^b	saflufenacil + imazethapyr + pyroxasulfone ^c		
	Hybrid	NK0142 3120-EZ1	DKC60-67		
	Seeding rate	88956	86487		
	Weed control	glyphosate / S-metolachlor	S-metolachlor + trazine + mesotrione + bicyclopyrone ^d		
	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 + 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 glyphosate, 840 g ae ha; ^b S-metolachlor, 1324 g ai ha; ^c saflufenacil + imazethapyr + pyroxasulfone, 215 g ai ha; ^d S-metolachlor + trazine + mesotrione, + bicyclopyrone, 2409 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 filed experimental unit was planted with
 119 corn, soybean, or kept under bareground. The two transplant 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 to assure seedling survival.

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 harvested near soil surface and oven
 128 dried at 65 C until reaching constant weight before weigh (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 followed the methodology of plant harvest at flowering initiation, except
 131 in 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).

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

The Palmer amaranth flowering timing was estimated as cumulative flowering across all locations, except Grant, NE. Palmer amaranth cumulative flowering estimation was determined using an asymmetrical three parameter log logistic Weibull model of the *drc* package (Ritz et al., 2015).

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

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

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

A binary logistic regression was fitted to Palmer amaranth sex dimorphism. Binary logistic regression is used for predicting binary classes (Bangdiwala, 2018), such as the probability of a plant being female in a dioecious species. Prior to the analysis, missing values were removed from the dataset. Also, data from Grant was not used in this analysis due to the uniform plant harvesting at that location. The complete dataset was splitted into 80% train and 20% test data. The 80% train is used for the model training and the 20% test is used for checking model performance on unseen dataset. With 80% dataset, a generalized linear model (base R *glm* function) was fitted to binary response variable, the probability of being female (0 to male and 1 to female). The independent variables were day of year harvest, height, weight, and crop (without interaction). The model family was binomial with a logit function. The model fit was assessed through pseudo R-squared values (McFadden, Cox and Snell, Cragg and Uhler) and likelihood ratio using *nagelkerke* function from “rcompanion” package (Mangiafico, 2021). The marginal effects computation was performed with Average Marginal Effects (AMEs) at every observed value of x and average across the results (Leeper, 2017) using *margins* function from “margins” package (Leeper et al., 2021). The 20% test data was predicted using the *predict* function with a cutoff estimation for male or female using *performance* function from *ROCR* package (Sing et al., 2005). The model quality prediction from the classification algorithm was measured with precision (*precision* function), recall (*recall* function) and F1-score (*f_meas* function) using the “yardstick” package (Kuhn et al., 2021). The precision determines the accuracy of positive predictions (female plants), recall determines the fraction of positives that were correctly identified, and F1-score is a weighted harmonic mean of precision and recall with the best score of 1 and the worst score of 0 (Raoniar, 2021). F1-score conveys the balance between the precision and the recall (Yacoubi and Axman, 2020). The area under the receiver operating curve (AUC-ROC) was also estimated with *performance* function using the true positive and false positive rates. Higher the AUC, better the model is at distinguishing between female and male Palmer amaranth.

RESULTS

176 Palmer amaranth height and biomass

177 Palmer amaranth plants accumulated more biomass when growing in bareground compared to plants
178 growing in soybean and corn (figure 3A). Palmer amaranth plants in the first cohort produced 75.5, 28.3,
179 and 16.3 g plant⁻¹ in bareground, soybean and corn, respectively. Plants from the second cohort produced
180 62.6 g plant⁻¹ in bareground, followed by 6.3 g plant⁻¹ in soybean, and 1.4 g plant⁻¹.

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

189 Palmer amaranth cumulative flowering

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

199 Palmer amaranth cumulative flowering in the second cohort ranged from mid July to mid September
200 (Figure 4B). Palmer amaranth growing in the bareground resulted in earlier flowering time compared to
201 soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at
202 day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at
203 doy 210.9, which was 6 days prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering,
204 whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; P
205 = 0.00). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean
206 (260.5; P = 0.66).

207 Palmer amaranth sex dimorphism

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

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

Table 2. Average marginal means of Palmer amaranth sex dimorphism logistic model. Factor parameter 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.

DISCUSSION

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

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

Seed production was not evaluated due to plant harvest at initiation of flowering. Nonetheless, it is well documented a strong positive correlation between Palmer amaranth biomass and seed production (Schwartz et al., 2016; Spaunhorst et al., 2018). In our study, plants growing at first cohort accumulated an overall 42% more biomass when compared to second cohort. Therefore, Palmer amaranth plants growing in the

251 second cohort is likely to produce less seeds regardless the crop. Our observation is consistent with the
252 findings that first Palmer amaranth cohort produced 50% more seeds per plant than Palmer amaranth plants
253 established six weeks later in bareground (Webster and Grey, 2015). Still, seed production at second cohort
254 is likely to replenish the soil seedbank. Seed production and deposition in the seedbank is also a key factor
255 for species perpetuation (Menges, 1987). Palmer amaranth can produce hundred thousands seeds per plant
256 (Schwartz et al., 2016; Keeley et al., 1987), which can stay viable in the soil seedbank for at least 36 months
257 (Sosnoskie et al., 2013). Therefore, preventing Palmer amaranth seed production or/and seed migration to
258 non-native habitats is an essential strategy to minimize the species impact in agroecosystems (Davis et al.,
259 2015).

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

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

295 et al., 2021, 2019). Further studies are also needed to understand the ecological basis of Palmer amaranth
296 flowering, including the plant behavior under climate change.

297 Our study demonstrated the Palmer amaranth plasticity to grow and develop into arable land of US
298 Midwest. It is likely that Palmer amaranth range will continue to expanding into new geographies. The
299 migration of Palmer amaranth into the US Midwest will reshape the landscape as waterhemp and Palmer
300 amaranth will share the same habitat. The presence of Palmer amaranth and waterhemp will increase
301 the weed management complexity. Therefore, preventive management is a priority to minimizing Palmer
302 amaranth dispersal. Reactive management should focus on early-season management programs, which
303 would have a large negative effect on Palmer amaranth growth and development. Long-term tactics that
304 promote early-season crop advantage against Palmer amaranth, including diversity of crops in rotation,
305 early/late crop planting, plant width, and crop residue (e.g. cover crops) would minimize the negative
306 impact of Palmer amaranth to cropping systems. The aggressiveness and differential Palmer amaranth
307 adaptation to agroecosystem is striking and require national efforts to minimize the species impact on
308 sustainability and profitability of cropping systems.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

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

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315 sectors.

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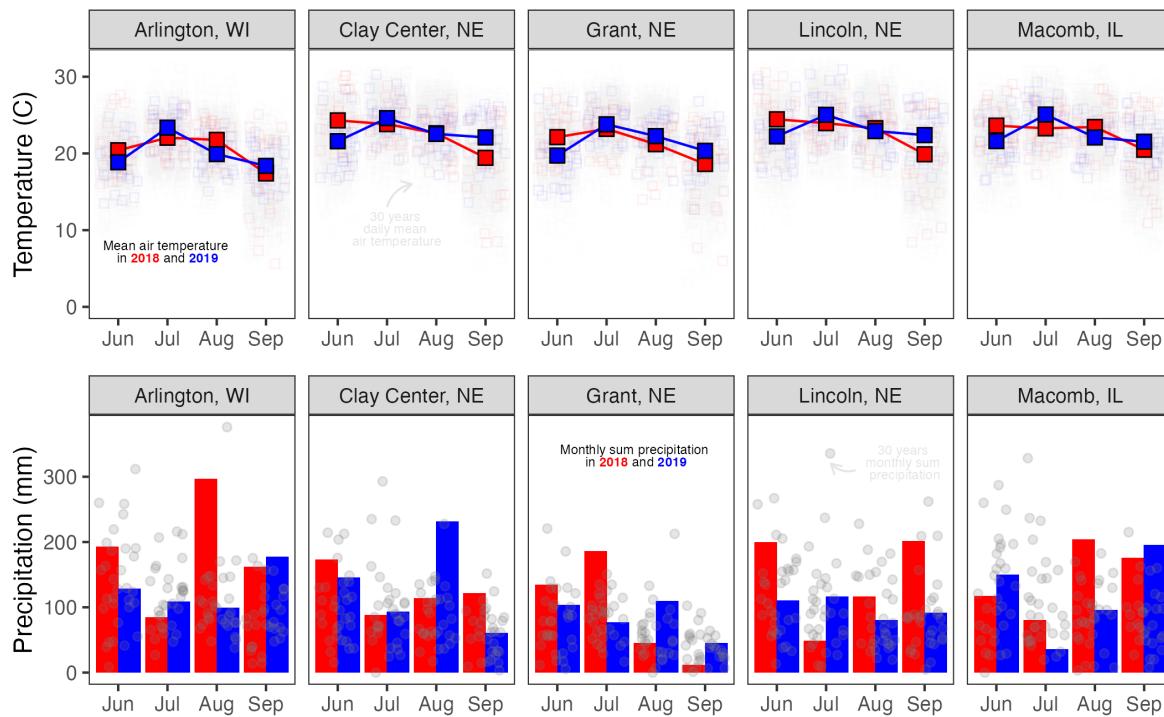


Figure 1. Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

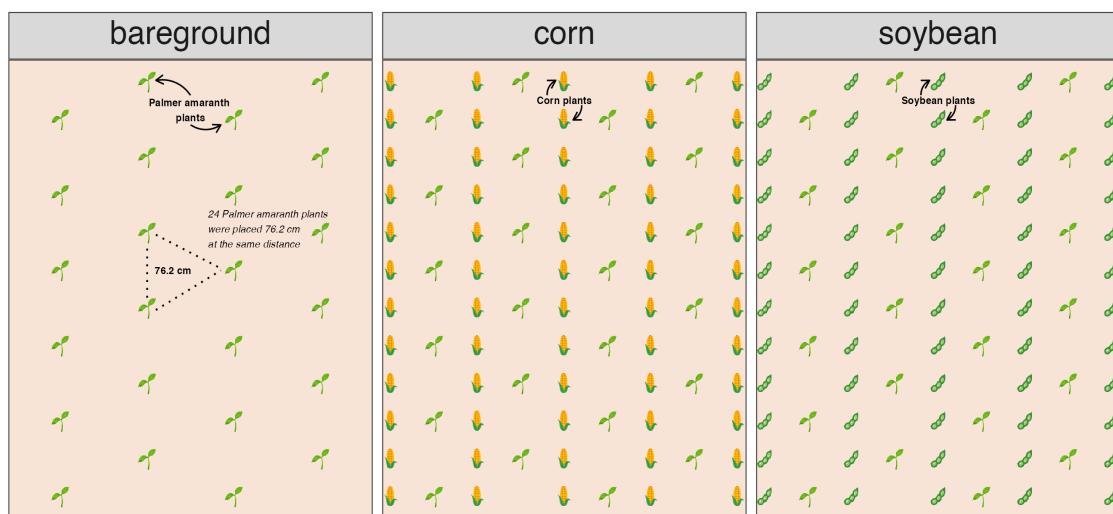


Figure 2. Palmer amaranth adaptation study layout of a plant cohort timing in bareground, corn, and soybean. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each field experimental unit

FIGURES

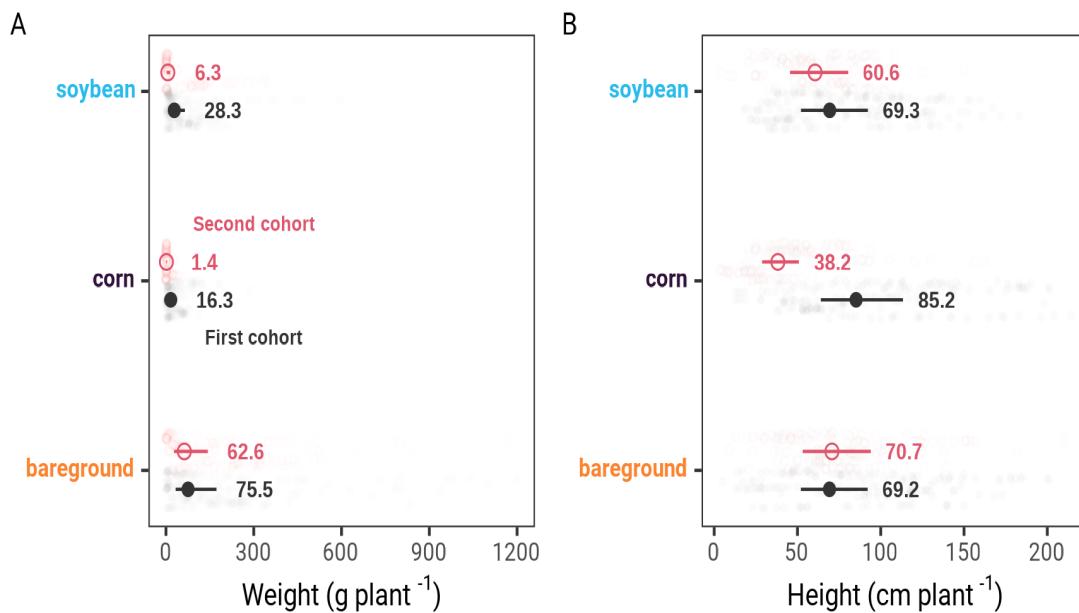


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

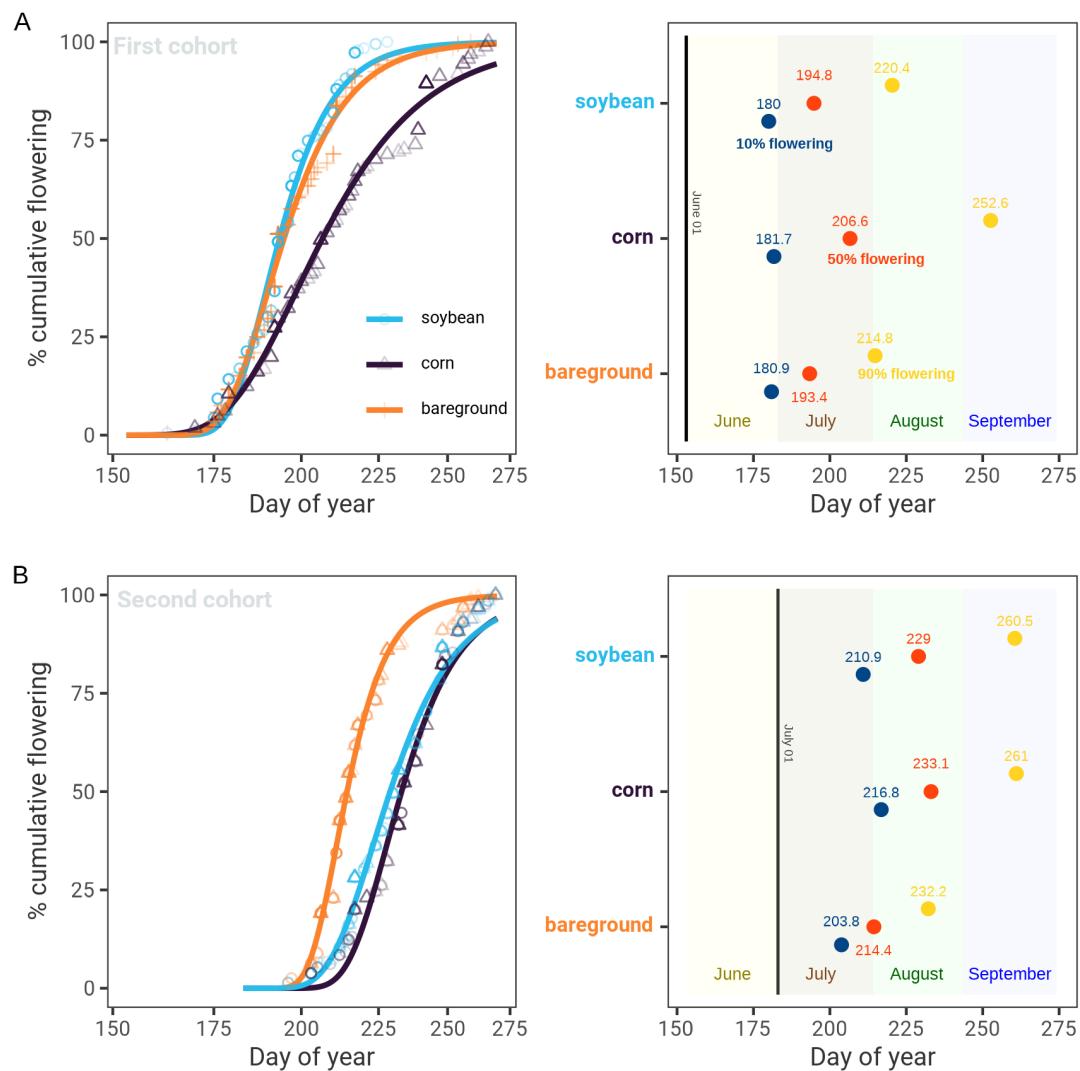


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second cohort transplanting time (B) nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

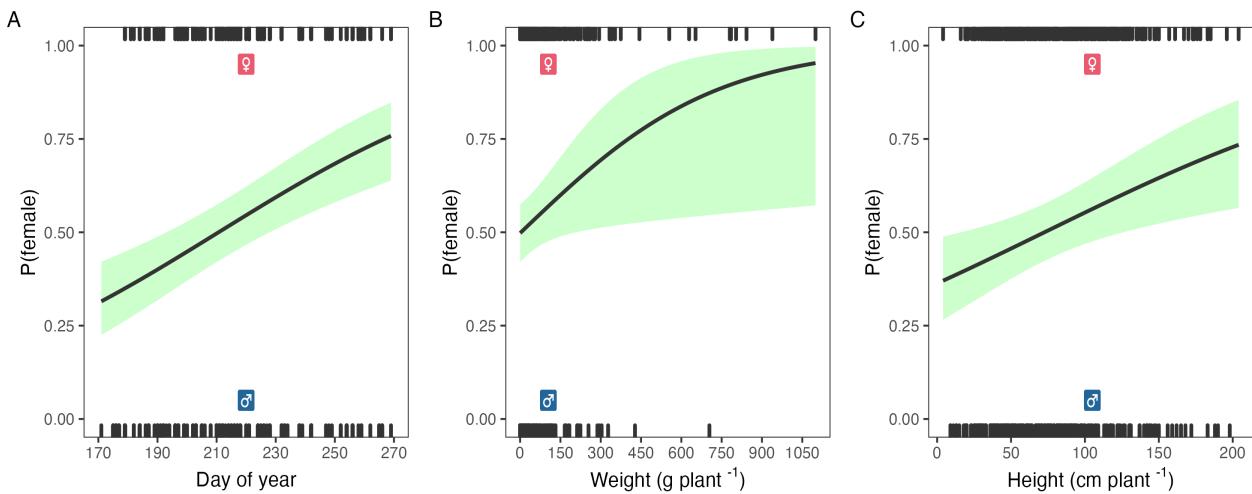


Figure 5. The probability (P) of being female Palmer amaranth by day of year (A), weight (B), and height (C). Black line represents the model estimation and shaded green the confidence intervals

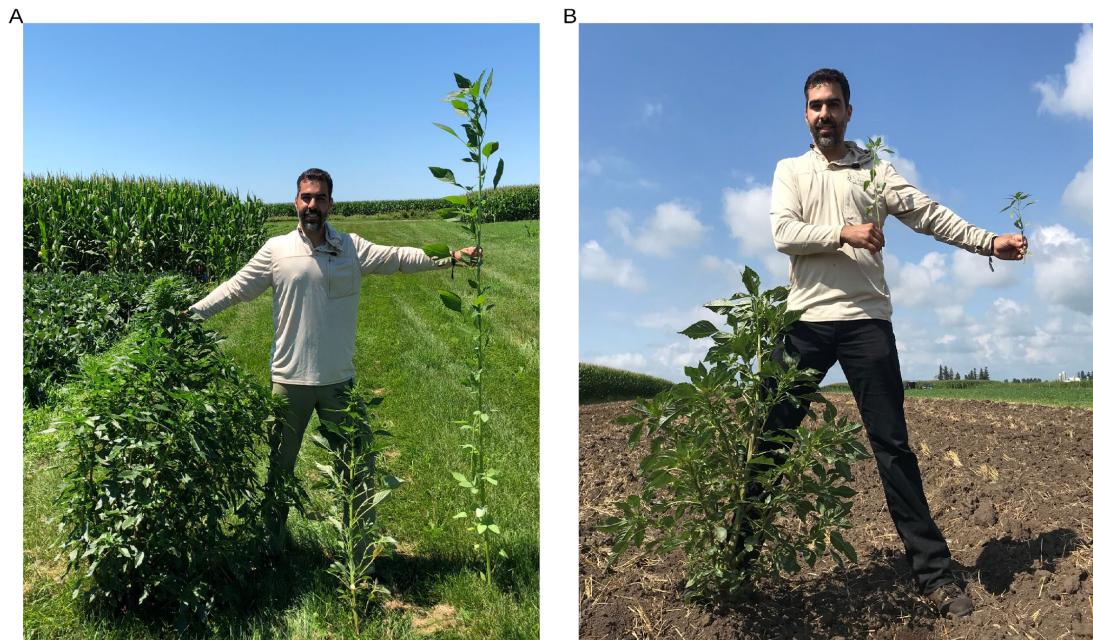


Figure 6. MCO (180 cm) holds harvested Palmer amaranth plants at 40 days after first cohort transplanting (A) and 33 days after second cohort transplanting (B) time. From left to right in each image, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin