

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. 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). The first Palmer amaranth first 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.

26 **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 (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 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 ('N, 'W), Lincoln, NE (41.16'N, 96.42'W), and Macomb, IL ('N, '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

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

^a glyphosate, 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 m
 117 long. The experimental design were arranged in factorial design with three crops, two transplanting times
 118 simulating two cohorts, repeated across five locations. Each filed 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 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).

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

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

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

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

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

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 in 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 goodness of fit was 0.23, 0.32, 0.40 using pseudo R-squared test from McFadden, Cox and
207 Snell, and Cragg and Uhler, respectively. The likelihood ratio test showed a p-value of < 0.00. The average
208 marginal effects showed that Palmer amaranth growing in corn resulted in 14.8% less females plants (Table
209 2). 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 AUC 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 effects of Palmer amaranth sex dimorphism logistic model. Factor pararamter values (crop and bareground) is shown compared 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.

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, which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was lower compared to its first cohort. 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.

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 second cohort is likely to produce less seeds regardless the crop. Our observation is consistent with the findings that first Palmer amaranth cohort produced 50% more seeds per plant than Palmer amaranth plants established six weeks later in bareground (Webster and Grey, 2015). Still, seed production at second cohort is likely to replenish the soil seedbank. Seed production and deposition in the seedbank is also a key factor for species perpetuation (Menges, 1987). Palmer amaranth can produce hundred thousands seeds per plant

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

257 An ecological approach to reduce Palmer amaranth seed production is understanding plant biology,
258 including flowering pattern. Our study suggests that Palmer amaranth flowering was slightly influenced by
259 crops and cohort timings. Palmer amaranth growing in bareground and corn resulted in the overall shortest
260 and longest flowering window, respectively. The shortest flowering window of second cohorts of Palmer
261 amaranth growing in bareground highlighted the impact of photoperiod on flowering. When growing in
262 soybean, Palmer amaranth flowering window was similar to bareground at first cohort but similar to corn
263 at second cohort timing. Plant flowering initiation is complex and depends on biological and ecological
264 factors (Lang, 1965). We hypothesize that when growing in high competition (e.g., second cohort), Palmer
265 amaranth plants tend to initiate flowering early, as well as having an extended flowering window. A study
266 has shown that non-native Palmer amaranth initiated flowering two weeks prior to the native waterhemp in
267 Iowa (Baker, 2021). Early flower initiation could also be a plant strategy when growing in stress conditions.
268 For 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 leaf
285 area and leaf dry weight under nutrient deficiency (Korres et al., 2017). Our model also estimated more
286 female plants in soybean and bareground compared to corn, which might be 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 from complete (Montgomery
292 et 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

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

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

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

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REFERENCES

- Aulakh, J. S., Chahal, P. S., Kumar, V., Price, A. J., and Guillard, K. (2021). Multiple herbicide-resistant Palmer amaranth (*Amaranthus palmeri*) in Connecticut: Confirmation and response to POST herbicides. *Weed Technology* 35, 457–463. doi:10.1017/wet.2021.6.
- Bagavathiannan, M. V., and Norsworthy, J. K. (2016). Multiple-Herbicide Resistance Is Widespread in Roadside Palmer Amaranth Populations. *PLOS ONE* 11, e0148748. doi:10.1371/journal.pone.0148748.
- Baker, R. (2021). Comparative analysis of Palmer amaranth (*Amaranthus palmeri*) and waterhemp (*A. Tuberculatus*) in Iowa. doi:10.31274/etd-20210609-11.
- Bangdiwala, S. I. (2018). Regression: Binary logistic. *International Journal of Injury Control and Safety Promotion* 25, 336–338. doi:10.1080/17457300.2018.1486503.
- Barrett, S. C. H., and Hough, J. (2013). Sexual dimorphism in flowering plants. *Journal of Experimental Botany* 64, 67–82. doi:10.1093/jxb/ers308.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using Lme4. *Journal of Statistical Software* 67, 1–48. doi:10.18637/jss.v067.i01.
- Berger, S. T., Ferrell, J. A., Rowland, D. L., and Webster, T. M. (2015). Palmer Amaranth (*Amaranthus palmeri*) Competition for Water in Cotton. *Weed Science* 63, 928–935. doi:10.1614/WS-D-15-00062.1.
- Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2017). Differentiation of Life-History Traits among Palmer Amaranth Populations (*Amaranthus palmeri*) and Its Relation to Cropping Systems and Glyphosate Sensitivity. *Weed Science* 65, 339–349. doi:10.1017/wsc.2017.14.

- 331 Bravo, W., Leon, R. G., Ferrell, J. A., Mulvaney, M. J., and Wood, C. W. (2018). Evolutionary Adaptations
332 of Palmer Amaranth (*Amaranthus palmeri*) to Nitrogen Fertilization and Crop Rotation History Affect
333 Morphology and Nutrient-Use Efficiency. *Weed Science* 66, 180–189. doi:10.1017/wsc.2017.73.
- 334 Briscoe Runquist, R. D., Lake, T., Tiffin, P., and Moeller, D. A. (2019). Species distribution models
335 throughout the invasion history of Palmer amaranth predict regions at risk of future invasion and reveal
336 challenges with modeling rapidly shifting geographic ranges. *Sci Rep* 9, 2426. doi:10.1038/s41598-
337 018-38054-9.
- 338 Chahal, P. S., Barnes, E. R., and Jhala, A. J. (2021). Emergence pattern of Palmer amaranth (*Amaranthus*
339 *palmeri*) influenced by tillage timings and residual herbicides. *Weed Technology* 35, 433–439.
340 doi:10.1017/wet.2020.136.
- 341 Chahal, P. S., Irmak, S., Jugulam, M., and Jhala, A. J. (2018). Evaluating Effect of Degree of Water Stress
342 on Growth and Fecundity of Palmer amaranth (*Amaranthus palmeri*) Using Soil Moisture Sensors.
343 *Weed Science* 66, 738–745. doi:10.1017/wsc.2018.47.
- 344 Correndo, A. A., Moro Rosso, L. H., and Ciampitti, I. A. (2021). Retrieving and processing agro-
345 meteorological data from API-client sources using R software. *BMC Research Notes* 14, 205.
346 doi:10.1186/s13104-021-05622-8.
- 347 Darwin, C. (1888). *The Different Forms of Flowers on Plants of the Same Species*. J. Murray Available at:
348 <http://books.google.com?id=7uMEAAAAYAAJ>.
- 349 Davis, A. S., Schutte, B. J., Hager, A. G., and Young, B. G. (2015). Palmer Amaranth (*Amaranthus palmeri*)
350 Damage Niche in Illinois Soybean Is Seed Limited. *Weed Science* 63, 658–668. doi:10.1614/WS-D-14-
351 00177.1.
- 352 Farmer, J. A., Webb, E. B., Pierce, R. A., and Bradley, K. W. (2017). Evaluating the potential for weed seed
353 dispersal based on waterfowl consumption and seed viability. *Pest Management Science* 73, 2592–2603.
354 doi:10.1002/ps.4710.
- 355 Fisher, R. A. (1930). The genetical theory of natural selection. *Eugen Rev* 22, 127–130. Available at:
356 <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2984947/> [Accessed August 12,
357 2021].
- 358 Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications Available at:
359 <http://books.google.com?id=uPNrDwAAQBAJ>.
- 360 Garetson, R., Singh, V., Singh, S., Dotray, P., and Bagavathiannan, M. (2019). Distribution of herbicide-
361 resistant Palmer amaranth (*Amaranthus palmeri*) in row crop production systems in Texas. *Weed*
362 *Technology* 33, 355–365. doi:10.1017/wet.2019.14.
- 363 Guo, P., and Al-Khatib, K. (2003). Temperature effects on germination and growth of redroot pigweed
364 (*Amaranthus retroflexus*), Palmer amaranth (*A. Palmeri*), and common waterhemp (*A. rudis*). *Weed*
365 *Science* 51, 869–875. doi:10.1614/P2002-127.
- 366 Hartzler, B., and Anderson, M. (2016). Palmer amaranth: It's here, now what? 10.
- 367 Heap, I. (2021). Internation Herbicide-Resistant Weed Database. Available at: <http://www.weedscience.org/Home.aspx> [Accessed July 26, 2021].
- 368
- 369 Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models.
370 *Biometrical Journal* 50, 346–363. doi:10.1002/bimj.200810425.

- 371 Jha, P., Norsworthy, J. K., Riley, M. B., and Bridges, W. (2010). Annual Changes in Temperature and Light
372 Requirements for Germination of Palmer Amaranth (*Amaranthus palmeri*) Seeds Retrieved from Soil.
373 *Weed Science* 58, 426–432. doi:10.1614/WS-D-09-00038.1.
- 374 Jhala, A. J., Norsworthy, J. K., Ganie, Z. A., Sosnoskie, L. M., Beckie, H. J., Mallory-Smith, C.
375 A., Liu, J., Wei, W., Wang, J., and Stoltzenberg, D. E. (2021). Pollen-mediated gene flow and
376 transfer of resistance alleles from herbicide-resistant broadleaf weeds. *Weed Technology* 35, 173–187.
377 doi:10.1017/wet.2020.101.
- 378 Keeley, P. E., Carter, C. H., and Thullen, R. J. (1987). Influence of Planting Date on Growth of Palmer
379 Amaranth (*Amaranthus palmeri*). *Weed Science* 35, 199–204. doi:10.1017/S0043174500079054.
- 380 Kistner, E. J., and Hatfield, J. L. (2018). Potential Geographic Distribution of Palmer
381 Amaranth under Current and Future Climates. *Agricultural & Environmental Letters* 3, 170044.
382 doi:10.2134/ael2017.12.0044.
- 383 Klingaman, T. E., and Oliver, L. R. (1994). Palmer Amaranth (*Amaranthus palmeri*) Interference in
384 Soybeans (*Glycine max*). *Weed Science* 42, 523–527. doi:10.1017/S0043174500076888.
- 385 Kohrt, J. R., Sprague, C. L., Nadakuduti, S. S., and Douches, D. (2017). Confirmation of a Three-Way
386 (Glyphosate, ALS, and Atrazine) Herbicide-Resistant Population of Palmer Amaranth (*Amaranthus
387 palmeri*) in Michigan. *Weed Science* 65, 327–338. doi:10.1017/wsc.2017.2.
- 388 Korres, N. E., and Norsworthy, J. K. (2017). Palmer Amaranth (*Amaranthus palmeri*) Demographic and
389 Biological Characteristics in Wide-Row Soybean. *Weed Science* 65, 491–503. doi:10.1017/wsc.2017.12.
- 390 Korres, N. E., Norsworthy, J. K., FitzSimons, T., Roberts, T. L., and Oosterhuis, D. M. (2017). Differential
391 Response of Palmer Amaranth (*Amaranthus palmeri*) Gender to Abiotic Stress. *Weed Science* 65,
392 213–227. doi:10.1017/wsc.2016.34.
- 393 Korres, N. E., Norsworthy, J. K., Mauromoustakos, A., and Williams, M. M. (2020). Soybean density and
394 Palmer amaranth (*Amaranthus palmeri*) establishment time: Effects on weed biology, crop yield, and
395 economic returns. *Weed Science* 68, 467–475. doi:10.1017/wsc.2020.41.
- 396 Kuhn, M., Vaughan, D., and RStudio (2021). *Yardstick: Tidy Characterizations of Model Performance*.
397 Available at: <https://CRAN.R-project.org/package=yardstick> [Accessed August 24,
398 2021].
- 399 Küpper, A., Borgato, E. A., Patterson, E. L., Netto, A. G., Nicolai, M., Carvalho, S. J. P. de, Nissen, S.
400 J., Gaines, T. A., and Christoffoleti, P. J. (2017). Multiple Resistance to Glyphosate and Acetolactate
401 Synthase Inhibitors in Palmer Amaranth (*Amaranthus palmeri*) Identified in Brazil. *Weed Science* 65,
402 317–326. doi:10.1017/wsc.2017.1.
- 403 Lang, A. (1965). “Physiology of flower initiation,” in *Differenzierung und Entwicklung / Differentiation
404 and Development* Handbuch der Pflanzenphysiologie / Encyclopedia of Plant Physiology., ed. A. Lang
405 (Berlin, Heidelberg: Springer), 1380–1536. doi:10.1007/978-3-642-50088-6_39.
- 406 Larran, A. S., Palmieri, V. E., Perotti, V. E., Lieber, L., Tuesca, D., and Permingeat, H. R. (2017). Target-site
407 resistance to acetolactate synthase (ALS)-inhibiting herbicides in *Amaranthus palmeri* from Argentina.
408 *Pest Management Science* 73, 2578–2584. doi:10.1002/ps.4662.
- 409 Leeper, T. J. (2017). Interpreting Regression Results using Average Marginal Effects with R’s margins. 31.

- 410 Leeper, T. J., Arnold, J., Arel-Bundock, V., and Long, J. A. (2021). *Margins: Marginal Effects*
411 *for Model Objects*. Available at: <https://CRAN.R-project.org/package=margins>
412 [Accessed August 24, 2021].
- 413 Lenth, R. V., Buerkner, P., Herve, M., Love, J., Riebl, H., and Singmann, H. (2021). *Emmeans: Estimated*
414 *Marginal Means, aka Least-Squares Means*. Available at: <https://CRAN.R-project.org/package=emmeans> [Accessed August 24, 2021].
- 415 Lindsay, K., Popp, M., Norsworthy, J., Bagavathiannan, M., Powles, S., and Lacoste, M. (2017). PAM:
416 Decision Support for Long-Term Palmer Amaranth (*Amaranthus palmeri*) Control. *Weed Technology*
417 31, 915–927. doi:10.1017/wet.2017.69.
- 418 MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., and Dehnen-Schmutz, K. (2020). An ecological
419 future for weed science to sustain crop production and the environment. A review. *Agron. Sustain. Dev.*
420 40, 24. doi:10.1007/s13593-020-00631-6.
- 421 MacRae, A. W., Webster, T. M., Sosnoskie, L. M., Culpepper, A. S., and Kichler, J. M. (2013). Cotton
422 Yield Loss Potential in Response to Length of Palmer Amaranth (*Amaranthus palmeri*) Interference.
423 17, 6.
- 424 Mangiafico, S. (2021). *Rcompanion: Functions to Support Extension Education Program Evaluation*.
425 Available at: <https://CRAN.R-project.org/package=rcompanion> [Accessed August
426 24, 2021].
- 427 Massinga, R. A., Currie, R. S., Horak, M. J., and Boyer, J. (2001). Interference of Palmer amaranth in corn.
428 *Weed Science* 49, 202–208. doi:10.1614/0043-1745(2001)049[0202:IOPAIC]2.0.CO;2.
- 429 Matzrafi, M., Osipitan, O. A., Ohadi, S., and Mesgaran, M. B. (2021). Under pressure: Maternal effects
430 promote drought tolerance in progeny seed of Palmer amaranth (*Amaranthus palmeri*). *Weed Science*
431 69, 31–38. doi:10.1017/wsc.2020.75.
- 432 McFarlane, G. R., Whitelaw, C. B. A., and Lillico, S. G. (2018). CRISPR-Based Gene Drives for Pest
433 Control. *Trends in Biotechnology* 36, 130–133. doi:10.1016/j.tibtech.2017.10.001.
- 434 Menges, R. M. (1987). Weed Seed Population Dynamics during Six Years of Weed Management Systems
435 in Crop Rotations on Irrigated Soil. *Weed Science* 35, 328–332. Available at: <http://www.jstor.org/stable/4044593>.
- 436 Mesgaran, M. B., Matzrafi, M., and Ohadi, S. (2021). Sex dimorphism in dioecious Palmer amaranth
437 (*Amaranthus palmeri*) in response to water stress. *Planta* 254, 17. doi:10.1007/s00425-021-03664-7.
- 438 Milani, A., Panizzo, S., Farinati, S., Iamonico, D., Sattin, M., Loddo, D., and Scarabel, L. (2021). Recent
439 Discovery of *Amaranthus palmeri* S. Watson in Italy: Characterization of ALS-Resistant Populations
440 and Sensitivity to Alternative Herbicides. *Sustainability* 13, 7003. doi:10.3390/su13137003.
- 441 Montgomery, J. S., Giacomini, D. A., Weigel, D., and Tranel, P. J. (2021). Male-specific Y-chromosomal
442 regions in waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *New*
443 *Phytologist* 229, 3522–3533. doi:10.1111/nph.17108.
- 444 Montgomery, J. S., Sadeque, A., Giacomini, D. A., Brown, P. J., and Tranel, P. J. (2019). Sex-specific
445 markers for waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth (*Amaranthus palmeri*). *Weed*
446 *Science* 67, 412–418. doi:10.1017/wsc.2019.27.

- 449 Morgan, G. D., Baumann, P. A., and Chandler, J. M. (2001). Competitive Impact of Palmer Amaranth
450 (Amaranthus palmeri) on Cotton (*Gossypium hirsutum*) Development and Yield. *Weed Technology* 15,
451 408–412. doi:10.1614/0890-037X(2001)015[0408:CIOPAA]2.0.CO;2.
- 452 Nguyen, H. M., Kleitou, P., Kletou, D., Sapir, Y., and Winters, G. (2018). Differences in flowering sex
453 ratios between native and invasive populations of the seagrass *Halophila stipulacea*. *Botanica Marina*
454 61, 337–342. doi:10.1515/bot-2018-0015.
- 455 Oliveira, M. C. (2021). *Maxwelco/palmer_adaptation*. Zenodo Available at: <https://doi.org/10.5281/zenodo.5236831>.
- 456
- 457 Oliveira, M. C., Gaines, T. A., Patterson, E. L., Jhala, A. J., Irmak, S., Amundsen, K., and Knezevic, S.
458 Z. (2018). Interspecific and intraspecific transference of metabolism-based mesotrione resistance in
459 dioecious weedy Amaranthus. *The Plant Journal* 96, 1051–1063. doi:10.1111/tpj.14089.
- 460 Oliveira, M. C., Giacomini, D. A., Arsenijevic, N., Vieira, G., Tranel, P. J., and Werle, R. (2021).
461 Distribution and validation of genotypic and phenotypic glyphosate and PPO-inhibitor resistance in
462 Palmer amaranth (Amaranthus palmeri) from southwestern Nebraska. *Weed Technology* 35, 65–76.
463 doi:10.1017/wet.2020.74.
- 464 Page, E. R., Nurse, R. E., Meloche, S., Bosveld, K., Grainger, C., Obeid, K., Filotas, M., Simard, M.-J., and
465 Laforest, M. (2021). Import of Palmer amaranth (Amaranthus palmeri S. Wats.) Seed with sweet potato
466 (*Ipomea batatas* (L.) Lam) slips. *Can. J. Plant Sci.*, CJPS-2020-0321. doi:10.1139/CJPS-2020-0321.
- 467 Pérez-Llorca, M., and Sánchez Vilas, J. (2019). Sexual dimorphism in response to herbivory and
468 competition in the dioecious herb *Spinacia oleracea*. *Plant Ecol* 220, 57–68. doi:10.1007/s11258-
469 018-0902-7.
- 470 Piskackova, T. A. R., Reberg-Horton, S. C., Richardson, R. J., Jennings, K. M., Franca, L., Young, B. G.,
471 and Leon, R. G. (2021). Windows of action for controlling palmer amaranth (Amaranthus palmeri)
472 using emergence and phenology models. *Weed Research* 61, 188–198. doi:10.1111/wre.12470.
- 473 Price, A. J., Balkcom, K. S., Culpepper, S. A., Kelton, J. A., Nichols, R. L., and Schomberg, H. (2011).
474 Glyphosate-resistant Palmer amaranth: A threat to conservation tillage. *Journal of Soil and Water
475 Conservation* 66, 265–275. doi:10.2489/jswc.66.4.265.
- 476 Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. (2015). Dose-Response Analysis Using R. *PLOS ONE*
477 10, e0146021. doi:10.1371/journal.pone.0146021.
- 478 Rumpa, M. M., Krausz, R. F., Gibson, D. J., and Gage, K. L. (2019). Effect of PPO-Inhibiting Herbicides
479 on the Growth and Sex Ratio of a Dioecious Weed Species Amaranthus palmeri (Palmer Amaranth).
480 *Agronomy* 9, 275. doi:10.3390/agronomy9060275.
- 481 Sauer, J. (1957). Recent Migration and Evolution of the Dioecious Amaranths. *Evolution* 11, 11–31.
482 doi:10.2307/2405808.
- 483 Sauer, J. D. (1972). The dioecious amaranths: A new species name and major range extensions. *Madroño*
484 21, 426–434. Available at: <http://www.jstor.org/stable/41423815>.
- 485 Sbatella, G. M., and Wilson, R. G. (2010). Isoxaflutole Shifts Kochia (*Kochia scoparia*) Populations in
486 Continuous Corn. *Weed Technology* 24, 392–396. doi:10.1614/WT-D-09-00023.1.
- 487 Schliekelman, P., Ellner, S., and Gould, F. (2005). Pest Control by Genetic Manipulation of Sex Ratio.
488 *Journal of Economic Entomology* 98, 18–34. doi:10.1093/jee/98.1.18.

- 489 Schwartz, L. M., Norsworthy, J. K., Young, B. G., Bradley, K. W., Kruger, G. R., Davis, V. M., Steckel,
490 L. E., and Walsh, M. J. (2016). Tall Waterhemp (*Amaranthus tuberculatus*) and Palmer amaranth
491 (*Amaranthus palmeri*) Seed Production and Retention at Soybean Maturity. *Weed Technology* 30,
492 284–290. doi:10.1614/WT-D-15-00130.1.
- 493 Scott, D. (2011). The Technological Fix Criticisms and the Agricultural Biotechnology Debate. *J Agric
494 Environ Ethics* 24, 207–226. doi:10.1007/s10806-010-9253-7.
- 495 Sosnoskie, L. M., Webster, T. M., and Culpepper, A. S. (2013). Glyphosate Resistance Does Not
496 Affect Palmer Amaranth (*Amaranthus palmeri*) Seedbank Longevity. *Weed Science* 61, 283–288.
497 doi:10.1614/WS-D-12-00111.1.
- 498 Spaunhorst, D. J., Devkota, P., Johnson, W. G., Smeda, R. J., Meyer, C. J., and Norsworthy, J. K. (2018).
499 Phenology of Five Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and
500 Arkansas. *Weed Science* 66, 457–469. doi:10.1017/wsc.2018.12.
- 501 Team, R. C. (2021). *R: The R Project for Statistical Computing*. Vienna, Austria: R Foundation for Statistical
502 Computing Available at: <https://www.r-project.org/> [Accessed August 24, 2021].
- 503 Tranel, P. J., Riggins, C. W., Bell, M. S., and Hager, A. G. (2011). Herbicide Resistances in *Amaranthus
504 tuberculatus*: A Call for New Options. *J. Agric. Food Chem.* 59, 5808–5812. doi:10.1021/jf103797n.
- 505 Van Wychen, L. (2020). 2020 Survey of the most common and troublesome weeds in grass crops, pasture,
506 and turf in the United States and Canada. Available at: [https://wssa.net/wp-content/
uploads/2020-Weed-Survey_grass-crops.xlsx](https://wssa.net/wp-content/
507 uploads/2020-Weed-Survey_grass-crops.xlsx).
- 508 Wang, J. L., Klessig, D. F., and Berry, J. O. (1992). Regulation of C4 Gene Expression in Developing
509 Amaranth Leaves. *The Plant Cell* 4, 173–184. doi:10.1105/tpc.4.2.173.
- 510 Ward, S. M., Webster, T. M., and Steckel, L. E. (2013). Palmer Amaranth (*Amaranthus palmeri*): A Review.
511 *Weed Technology* 27, 12–27. doi:10.1614/WT-D-12-00113.1.
- 512 Webster, T. M., and Grey, T. L. (2015). Glyphosate-Resistant Palmer Amaranth (*Amaranthus palmeri*)
513 Morphology, Growth, and Seed Production in Georgia. *Weed Science* 63, 264–272. doi:10.1614/WS-D-
514 14-00051.1.
- 515 Wu, C., and Owen, M. D. K. (2014). When Is the Best Time to Emerge: Reproductive Phenology and
516 Success of Natural Common Waterhemp (*Amaranthus rudis*) Cohorts in the Midwest United States?
517 *Weed Science* 62, 107–117. Available at: <http://www.jstor.org/stable/43700638>.
- 518 Yacoubi, R., and Axman, D. (2020). Probabilistic Extension of Precision, Recall, and F1 Score for
519 More Thorough Evaluation of Classification Models. in *Proceedings of the First Workshop on
520 Evaluation and Comparison of NLP Systems* (Online: Association for Computational Linguistics),
521 79–91. doi:10.18653/v1/2020.eval4nlp-1.9.
- 522 Yu, E., Blair, S., Hardel, M., Chandler, M., Thiede, D., Cortilet, A., Gunsolus, J., and Becker, R. (2021).
523 Timeline of Palmer amaranth (*Amaranthus palmeri*) invasion and eradication in Minnesota. *Weed
524 Technology*, 1–31. doi:10.1017/wet.2021.32.

FIGURES

525 \begin{figure}

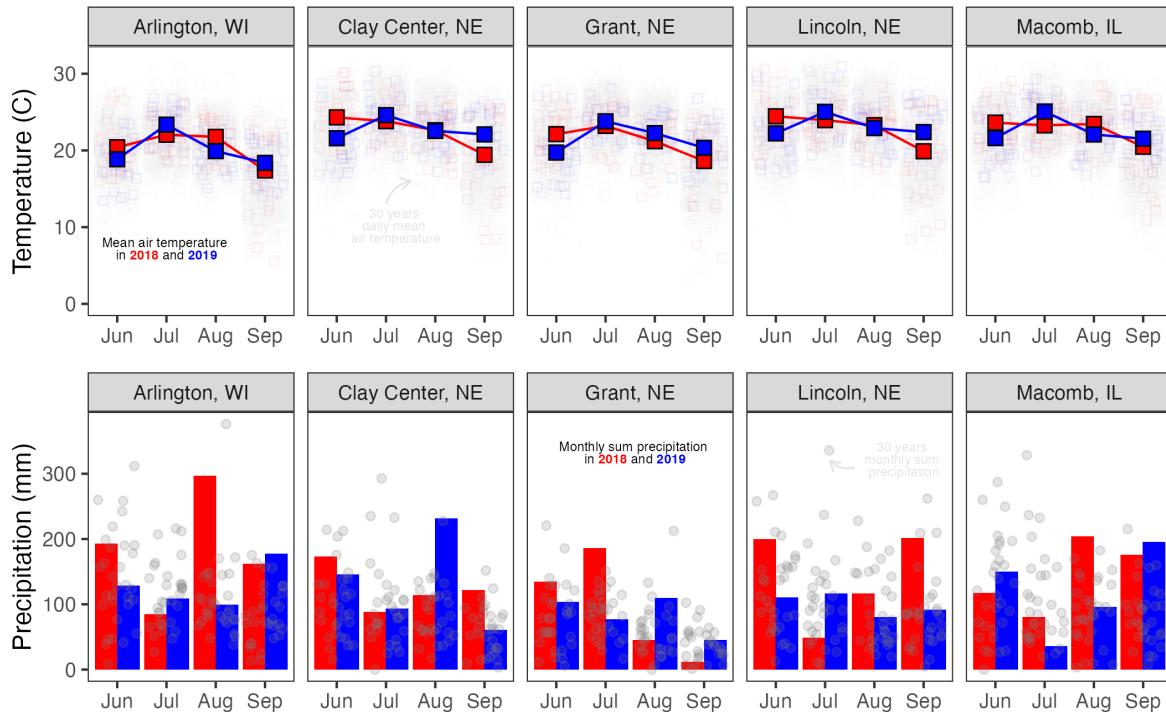


Figure 1. Mean average temperature (C) and total monthly precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE and Macomb, IL

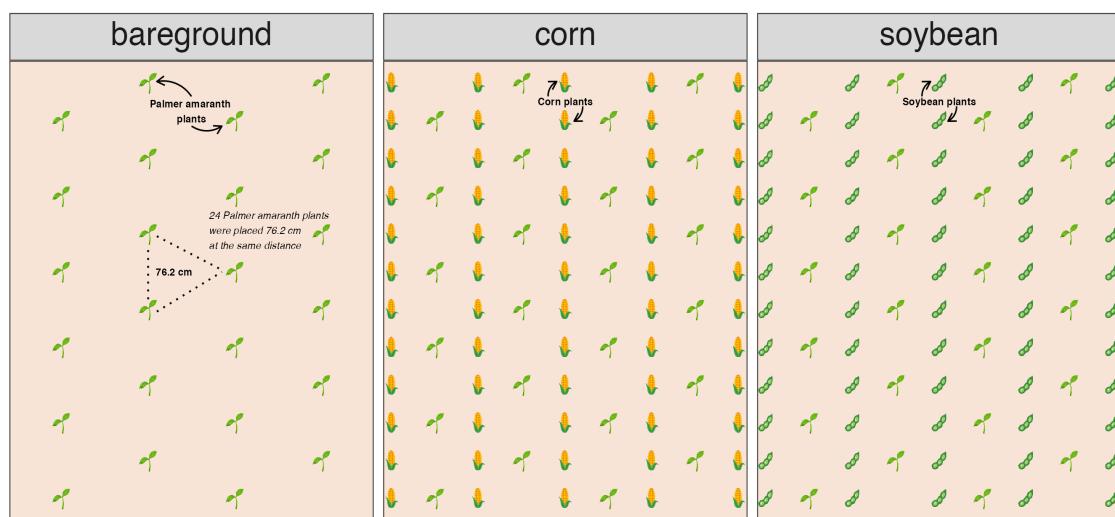
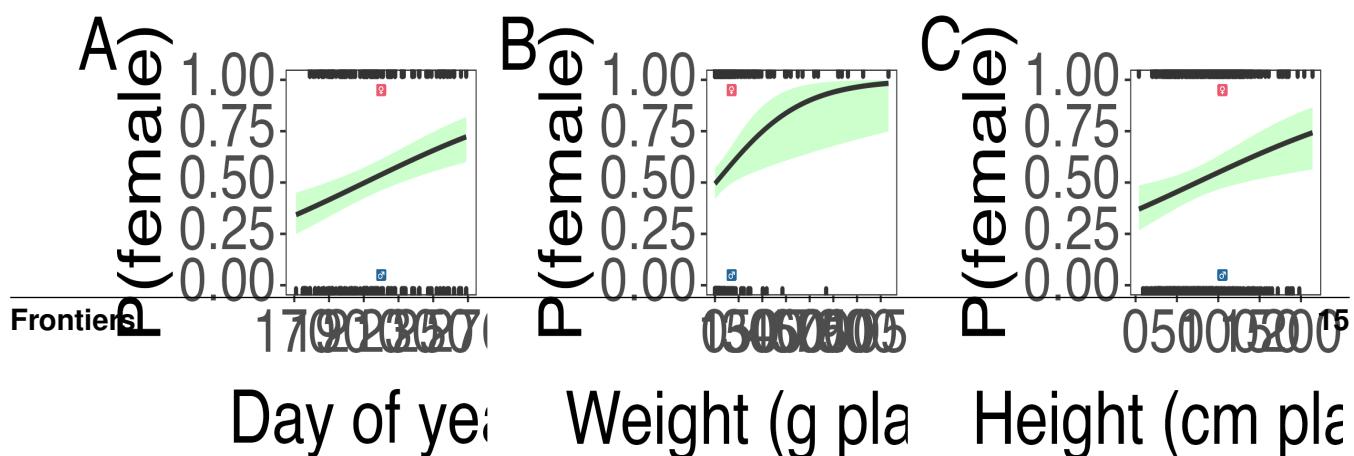


Figure 2. Palmer amaranth adaptation study layout of a plant cohort timing in bareground, corn, and soybean. Twenty-four Palmer amaranth plants were place 76.2 cm apart in each field experimental unit



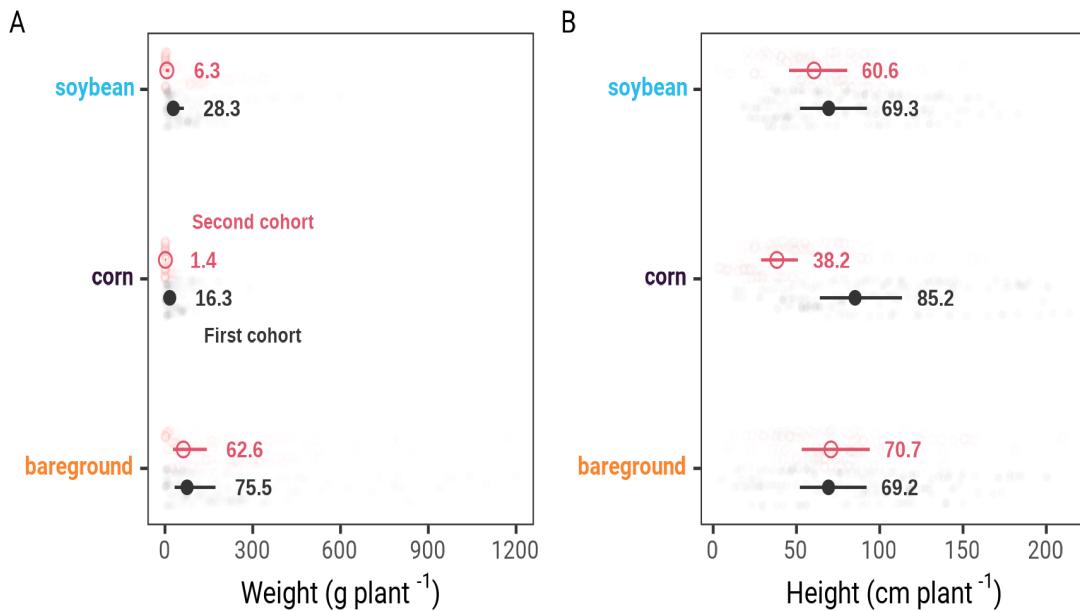


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

527

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528 \caption{The probability (P) of being female Palmer amaranth by day of year (A), weight (B), and height
 529 (C). Back line represents the model estimation and shade green the 95% confidence intervals}
 530 \end{figure}}

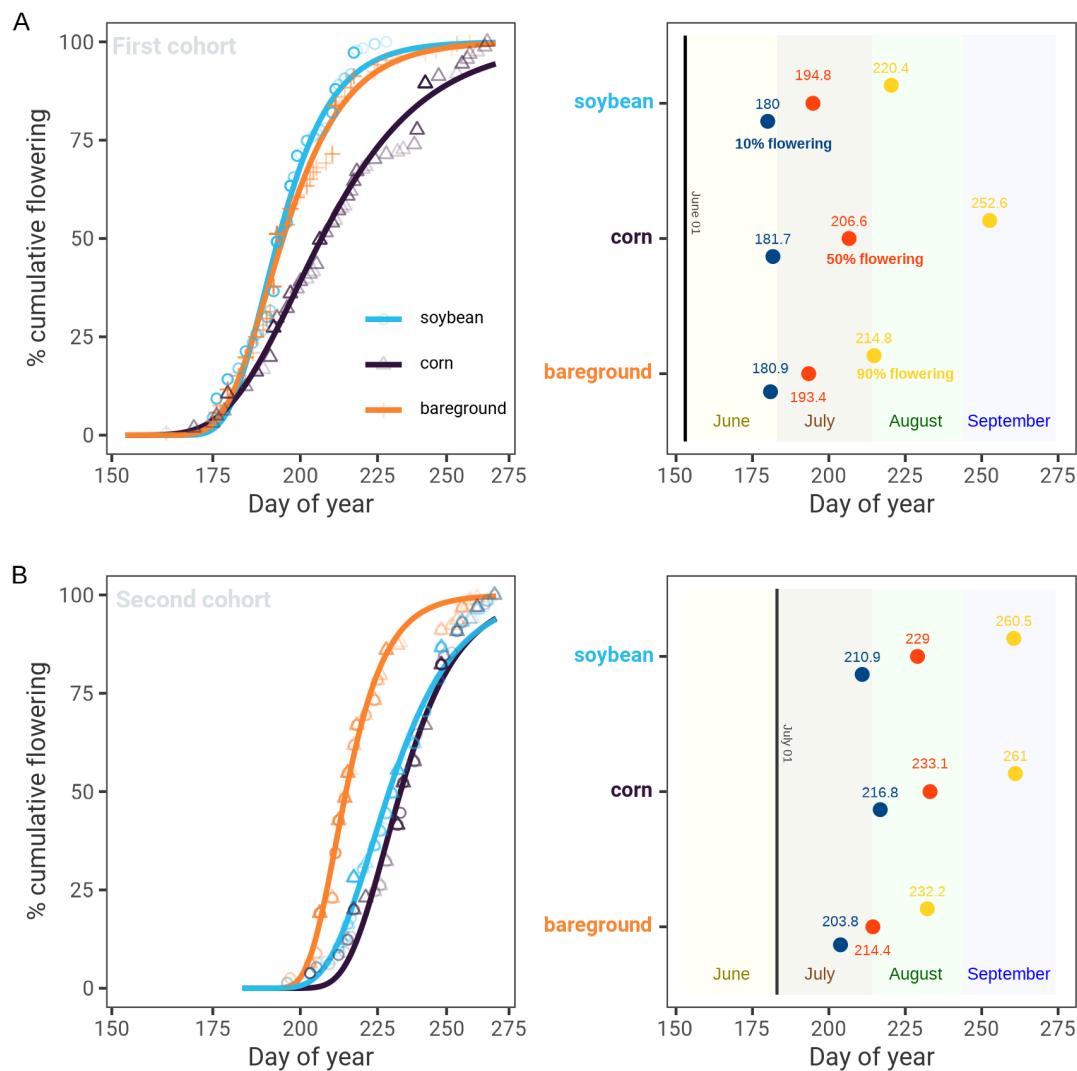


Figure 4. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second cohort transplanting time (B) nested across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

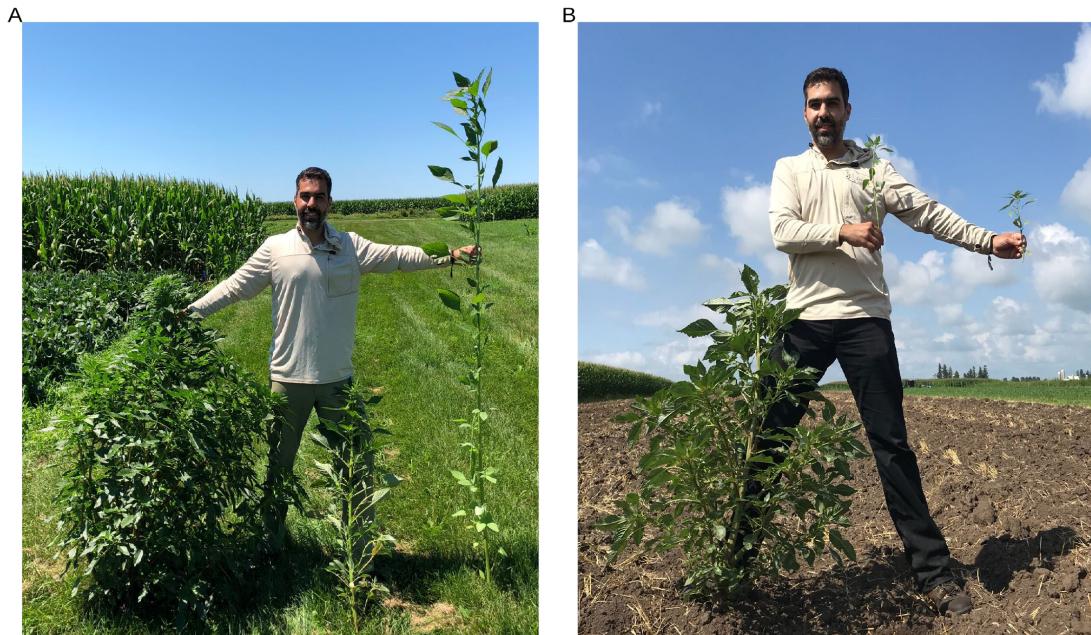


Figure 5. MCO (180 cm) holds harvested Palmer amaranth plants at 40 days after first cohort transplanting (A) and 33 days after second cohort transplanting (B) time. From left to right in each image, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin