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

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ABSTRACT

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INTRODUCTION

Palmer amaranth (*Amaranthus palmeri* S. Watson) is currently considered one of the most economically damaged weed species to cropping systems in the United States. Unmanaged Palmer amaranth in competition for water, light and nutrients can drastically impact on crop yields (Berger et al., 2015). For example, Palmer amaranth is documented with potential to reduce 91%, 68%, and 54% of corn (Massinga et al., 2001), soybean (Klingaman and Oliver, 1994), and cotton (Morgan et al., 2001) yields, respectively. Moreover, Palmer amaranth has showed a remarkable capacity to evolve resistance to herbicides. To date, Palmer amaranth has evolved resistance to eight herbicide sites of action (Heap, 2021), increasing the weed management complexity (Lindsay et al., 2017). Thus, Palmer amaranth poses an economical risk to sustainable agriculture.

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

Light and temperature are likely the main environment requirements for Palmer amaranth successful grow and development. Palmer amaranth is reported with an extended germination period (Jha et al., 2010). Germination of Palmer amaranth is triggered by 18 C soil temperature (Keeley et al., 1987), and optimal germination and biomass production occur at 35/30 C day and night temperatures (Guo and Al-Khatib, 2003). Palmer amaranth germination is also human-mediated by tillage timings and preemergence-applied herbicides (Chahal et al., 2021). Water has not shown to limit Palmer amaranth fitness. Under continuous water stress, Palmer amaranth survived and produced at least 14000 seeds plant-1 (Chahal et al., 2018). Seeds from Palmer amaranth growing with limited water conditions were heavier, less dormant, and prompt for germination (Matzrafi et al., 2021). Growing conditions and management practices also influence Palmer amaranth sex dimorphism and flowering pattern (Korres et al., 2017; Rumpa et al., 2019). The continuous global temperature warming can impact agriculture and promote niches for Palmer amaranth invasion/adaptation into new environments. Currently, it is estimated that the greatest climatic risk of Palmer amaranth establishment are agronomic crops in Australia and Sub-Sahara Africa (Kistner and Hatfield, 2018). Temperature is a key factor limiting Palmer amaranth expansion to cooler geographies (Briscoe Runquist et al., 2019); however, under future climate change Palmer amaranth is likely to expand northward into Canada and Northern Europe (Kistner and Hatfield, 2018; Briscoe Runquist et al., 2019).

Palmer amaranth is already found in agronomic crops of South America (Larran et al., 2017; Küpper et al., 2017) and Southern Europe (Milani et al., 2021). In the US, Palmer amaranth is well established at cotton fields (Garetson et al., 2019) and non-crop areas (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), Michigan (Kohrt et al., 2017), Connecticut (Aulakh et al., 2021), and potential damaged to soybean fields in Illinois is reported (Davis et al., 2015). In Iowa, a study showed that Palmer amaranth is still not well adapted compared to waterhemp (*Amaranthus tuberculatus*) (Baker, 2021). Successful cases of Palmer amaranth invasion and near to eradication is documented in Minnesota (Yu et al., 2021). No Palmer amaranth actively growing was found in Canada; however, Palmer amaranth seeds was detected in sweet potato slips (Page et al., 2021). Nonetheless, it seems fated the need to manage Palmer amaranth in agronomic crops throughout multiple environments in the near future. Strategies on Palmer amaranth management should encompass the agroecosystem level but not only attempts to eradicate the weed. Most tactics to manage Palmer amaranth are based on technology fixes (Scott, 2011), which are short-term (e.g., herbicide and/or tillage) rather than long-term weed management. Palmer amaranth management should be built on minimizing the species ability to adapt, grow and develop into agroecossystems.

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

MATERIAL AND METHODS

Plant material and growing conditions

The study was performed with a Palmer amaranth accession (Per1) from Perkins County, Nebraska. Per1 accession collection is documented with no reported herbicide resistance (Oliveira et al., 2021). Three weeks prior to the field experiment, 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 Arlington, Clay Center, Lincoln, and Macomb; and kept outdoors in Grant. Palmer amaranth seedlings were kept under greenhouse/outdoors until the onset of the experiment (2-3 leaf stage/5 to 8 cm height).

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 ('N, 'W), Grant (('N, 'W)), Lincoln (('N, 'W)), and Macomb (('N, 'W)).

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

Table 1. Field study attributes

Attributes		Arlington, WI	Clay Center, NE	Grant, NE	Lincoln, NE	Macomb, IL
Bareground						
	Weed control	glyphosate	saflufenacil + imazethapyr + pyroxasulfone			
Corn						
	Hybrid		DKC60-67			
	Seeding rate		86487			
	Weed control	glyphosate / S-metolachor	S-metolachlor + trazine + mesotrione, + bicyclopyrone			
Soybean						
	Variety	DSR-1950	AG21X8			
	Seeding rate	296400	321237			
	Weed control	glyphosate / S-metolachor	saflufenacil + imazethapyr + pyroxasulfone			
Planting day		May 10 to 20	May 10 to 14			
Soil						
	Type		Crete Silt Loam			
	Ratio (sand-clay-silt)		58-25-6.5			
	pH	6.6	6.5			
	Organic matter (%)		3			

The field experimental unit were six adjacent 9.1 m wide (12 rows at 72.2 cm row spacing) by 10.7 m long. Each experimental unit was planted with corn or soybean, or under bareground condition. Palmer amaranth seedlings (potting mix + two seedlings) were and gently transferring to the ground (6 cm deep and 8 cm wide). Twenty-four plants were equidistantly placed (0.76 m apart) between rows within each agroecossystems. After a week, one was eliminated and one was kept. There were two transplant timing: first (June 1) and second (July 1). There were 24 Palmer amaranth plants in each experimental unit, with a total of 144 plants for each location. The study was repeated twice.

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

Statistical analyses

The statistical analyses were performed using R statistical software version 4.0.1. Data across locations and year were combined.

The cumulative Palmer amaranth flowering estimation was determined using a 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 XXX, 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 agroecossystems and timings 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.

Palmer amaranth gender was fitted to a binary logistic regression (Bangdiwala, 2018). Binary logistic regression is used for predicting binary classes, such as the probability of female in dioecious plants. Prior to the analysis, all 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 whole dataset was splitted into 80% train and 20% test data. The 80% train is used for the model training and the rest 20% is used for checking how the model generalized on unseen dataset. With 80% dataset, a binary response variable, male (0) and female (1), was fitted to a generalized linear model (*glm* function) including day of year harvest, height, weight, crop and month as independent variables. 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 ("rcompanion" package). The marginal effects computation was performed with Average Marginal Effects at every observed value of x and average across the results (AMEs) (Leeper, 2017) using *margins* function from "margins" package. The rest 20% dataset was predicted using *predict* function with a cutoff estimation for male or female using *performance* function. The model quality prediction from the classification algorithm was measure with precision (*precision* function), recall (*recall* function) and F1 score (*f_meas* function) using "yardstick" package. 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. F1 score conveys the balance between the precision and the recall.

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 transformed to meet model assumption of normality. In the model, agroecosystem (crop, soybean, bareground) was the fixed effect and year nested with location the random effects. Analysis of variance 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" and "multcomp" (Hothorn et al., 2008).

RESULTS

Palmer amaranth height and biomass

Palmer amaranth accumulated more biomass when growing in bareground compared to Palmer amaranth growing in soybean and corn (figure 2A). At first cohort time, Palmer amaranth biomass was 75.5 g plant-1, 28.3 g plant-1 and 16.3 g plant-1 in bareground, soybean and corn, respectively. At second cohort timing, Palmer amaranth produced 62.6 g plant in bareground, followed by 6.3 g plant in soybean, and 1.4 g plant in corn.

Palmer amaranth height was more uniform across cohort timings, except when growing in corn (figure 2B). Palmer amaranth achieved 69.2 cm tall when growing at first cohort timing in bareground, which was not different to 70.7 cm tall at second cohort timing (P = 0.74). In addition, no difference in Palmer amaranth height (69.3 cm) was found in soybean at first cohort compared to bareground ($P > 0.75$). At second cohort in soybean, Palmer amaranth was near to 10 cm lower compared to its first cohort time (P = 0.04). The tallest and smallest Palmer amaranth plants were found in corn. Palmer amaranth reached 85.2 cm tall at first cohort and 38.2 cm at second cohort timings.

Palmer amaranth cumulative flowering

Palmer amaranth growing in corn resulted in a longer flowering pattern compared to bareground and soybean at first cohort (figure3A). Nonetheless, the 10% cumulative Palmer amaranth flowering in soybean, bareground and corn occurred at the end of June. Palmer amaranth reached 10% flowering in soybean at doy 180, which was slightly different from bareground (doy 180.9; $P = 0.01$) and corn (doy 181.7; $P = 0.00$). The 50% Palmer amaranth cumulative flowering occurred in July. For example, Palmer amaranth reached 50% flowering in bareground at doy 193.4, followed by soybean (doy 194.8), corn (doy 206.6). Similar trend was observed at 90% Palmer amaranth cumulative flowering. Palmer amaranth growing in corn reached 90% flowering at doy 252.6 (early September), which was 37.8 and 32.2 days after Palmer amaranth 90% flowering in bareground and soybean, respectively.

Palmer amaranth cumulative flowering at second cohort ranged from mid July to mid September (figure3B). Palmer amaranth growing in bareground resulted in earlier flowering time compared to soybean and corn. Palmer amaranth growing in bareground reached 10%, 50%, and 90% flowering time at day 203.8, 214.4, and 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at doy 210.9, which was 6 days prior to corn (P-value = 0.00). Similar trend was observed at 50% flowering, whereas Palmer amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; $P = 0.00$). The 90% Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean (260.5; $P = 0.66$).

Palmer amaranth gender

The model fit was 0.23, 0.32, 0.40 with using pseudo R squared test from McFadden, Cox and Snell, and Cragg and Uhler, respectively. The likelihood ratio test showed a p-value of < 0.00. The average marginal effects showed that Palmer amaranth growing in corn resulted in 14.5% less females plants (Table 2). Moreover, increasing a unit doy increases the probability of having a female plant by 0.4% (Table 2 and Figure4A). Similar trend is observed to weight as well as height, whereas the probability of being female increase by 0.2% (Figure 4B) and 0.1% (Figure 4C) when a unit of weight (g) and height (cm) increases, respectively.

Table 2. Average marginal means of gender logistic model. Factor pararemter values (e.g. crop) is shown related to soybean.

Term	AME	SE	Lower	Upper	Z-score	P-value
crop_bareground	-0.048	0.054	-0.154	0.059	-0.876	0.381
crop_corn	-0.148	0.052	-0.250	-0.046	-2.842	0.004
doyh	0.004	0.001	0.003	0.006	4.959	0.000
height	0.002	0.001	0.001	0.003	2.953	0.003
weight	0.001	0.000	0.000	0.001	2.179	0.029

[a] Average Marginal Effects. [b] Standard Error.

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

DISCUSSION

Our study showed that Palmer amaranth biomass, height, flowering pattern and gender varied within agroecossystems and cohort timings. In general, Palmer amaranth produced more biomass and taller plants when growing at first cohort rather than second cohort. At first cohort, resources (e.g., soil nutrients) and conditions (e.g., light) were more timely available for both species, crop and weed. 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 condition, Palmer amaranth showed an extraordinary plasticity to adapt upon the agroecosystem. This is evident when comparing Palmer amaranth canopy shape, and its extended flowering pattern when growing into corn compared to soybean. The Palmer amaranth competition strategy was to mimic the crop grow and development (Figure 4). These results suggests that Palmer amaranth can fast evolve life-history traits to adapt into agroecossystems and cultural practices, including nitrogen fertilization (Bravo et al., 2018). Our results highlight the Palmer amaranth as a threat to agroecossystems as breeding more competitive crop varieties is likely to select more competitive biotypes (Bravo et al., 2017).

Palmer amaranth grow and development at second cohort was limited due to the crop competitive ability at advanced development stages. Palmer amaranth was transplanted when corn canopy was nearly closed, which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was lower compared to its first cohort. Under crop canopy (e.g., second cohort), Palmer amaranth flowering pattern was near to similar in corn and soybean. Palmer amaranth growing without crop competition produced highest amounts of biomass and less extended flowering pattern. The Palmer amaranth strategy in bareground was to invest biomass in growing plant width and height. Nonetheless, Palmer amaranth produced 21% 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 suggests 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 thermal units (e.g, growing degree days). It is hypothesize that reduced day length contributed to smaller plants at second cohort as well as shorter flowering period. 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). I our study, Palmer amaranth growing at first cohort accumulated an overall 36% more biomass when compared to second cohort. Therefore, Palmer amaranth plants growing in the second cohort is likely to produce less seeds regardless the agroecossystem. 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 (Schwartz et al., 2016; Keeley et al., 1987), and stay viable buried in the seedbank for at least 36 months (Sosnoskie et al., 2013). Therefore, preventing Palmer amaranth seed production or/and seed migration to its non-native habitat is an essential strategy to minimize weed impact into agroecossystem (Davis et al., 2015).

An ecological approach to reduce seed production in Palmer amaranth is understanding its flowering pattern. Our study suggests that Palmer amaranth flowering pattern was slightly influenced by cropping systems and cohort timings. Palmer amaranth growing in bareground and corn resulted in the overall shortest and longest flowering pattern, respectively. When growing in soybean, Palmer amaranth flowering pattern was similar to bareground at first cohort but similar to corn at second cohort timing. Plant flowering initiation is complex and it depends on biological and ecological factors (Lang, 1965). We hypothesize that when growing in high competition (e.g., second cohort), Palmer amaranth plants tend to initiate flowering early, as well as having an extended flowering pattern. Early flower initiation is plant strategy when growing in stress conditions. For example, when growing under water stress, early flowering in Palmer amaranth resulted in a mismatch between female and male plants by seven days (Mesgaran et al., 2021). A mismatch in Palmer amaranth male and female flowering period can minimize plant outcross, and thus reduce plant seed production. Sex dimorphism manipulation is considered a potential ecological pest control (McFarlane et al., 2018; Schliekelman et al., 2005).

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

Our study demonstrated the short-term Palmer amaranth plasticity to grow and develop into cropping-systems. Is likely that Palmer amaranth range will continue to expanding to new geographies. 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. Tactics that promote early-season crop advantage against Palmer amaranth, including early crop planting, crop rotation (Oliveira et al., 2021), plant width, preemergence applied herbicide (Sanctis et al., 2021), and crop residue (e.g. cover crops) would minimize the negative impact of Palmer amaranth in agroecossystems. The aggressiveness and differential Palmer amaranth adaptation to agroecosystem is striking and require national efforts to minimize the species impact on economy and sustainability.

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

Flower manipulation is a promising ecological Palmer amaranth but it is not well understood.

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: 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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1 SUPPLEMENTAL DATA

Supplementary Material should be uploaded separately on submission, if there are Supplementary Figures, please include the caption in the same file as the figure. LaTeX Supplementary Material templates can be found in the Frontiers LaTeX folder

2 REFERENCES

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FIGURES

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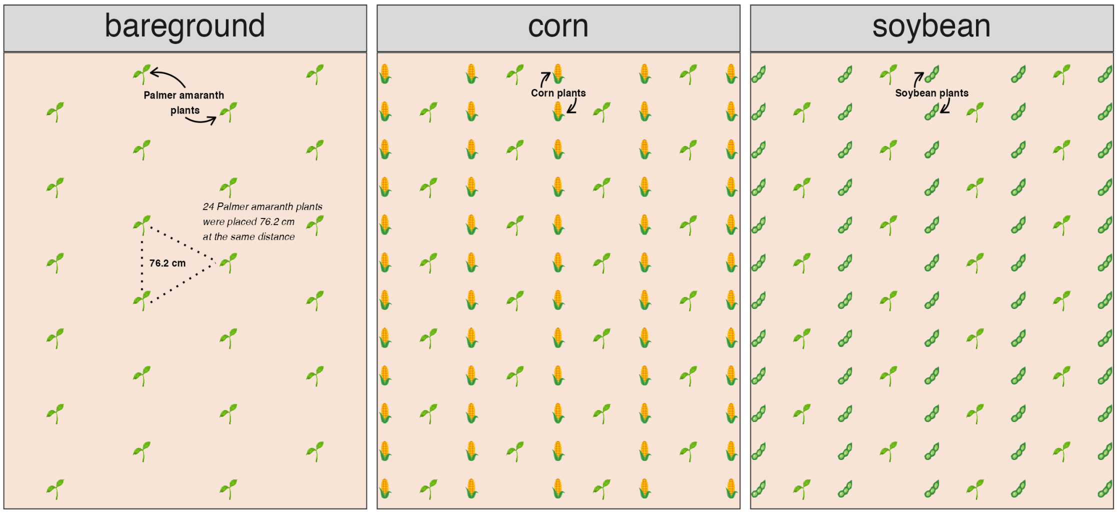
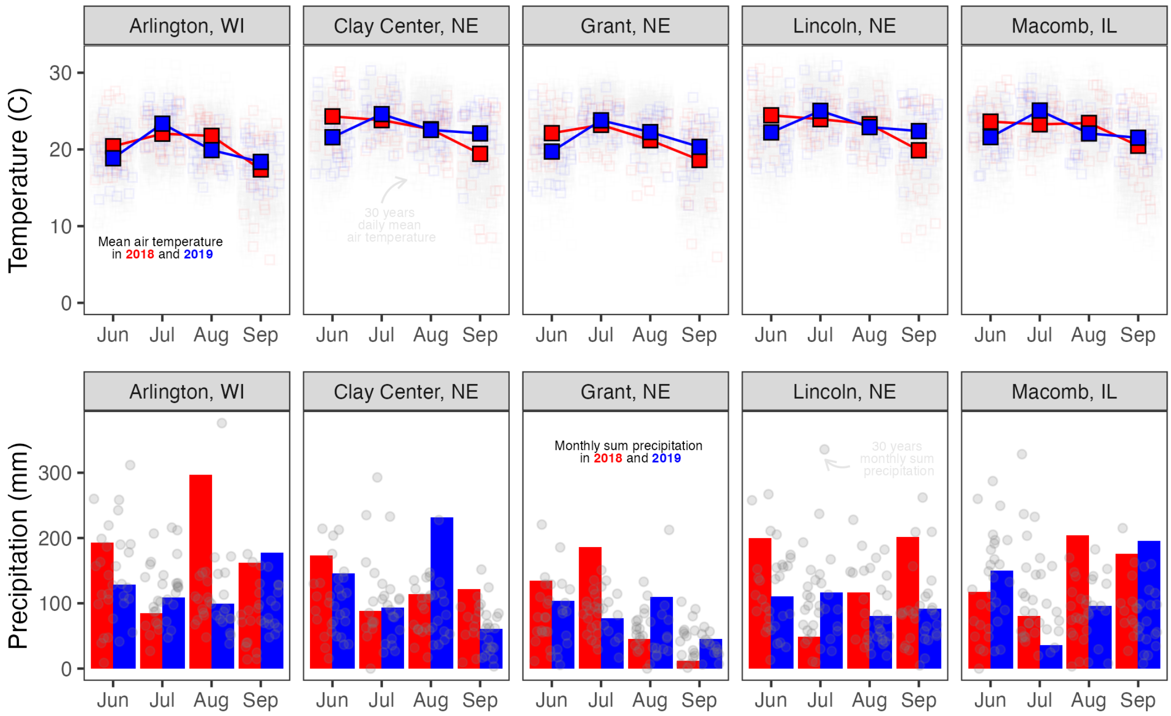


Figure 1. Mean average temperature (C) and montly sum precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL



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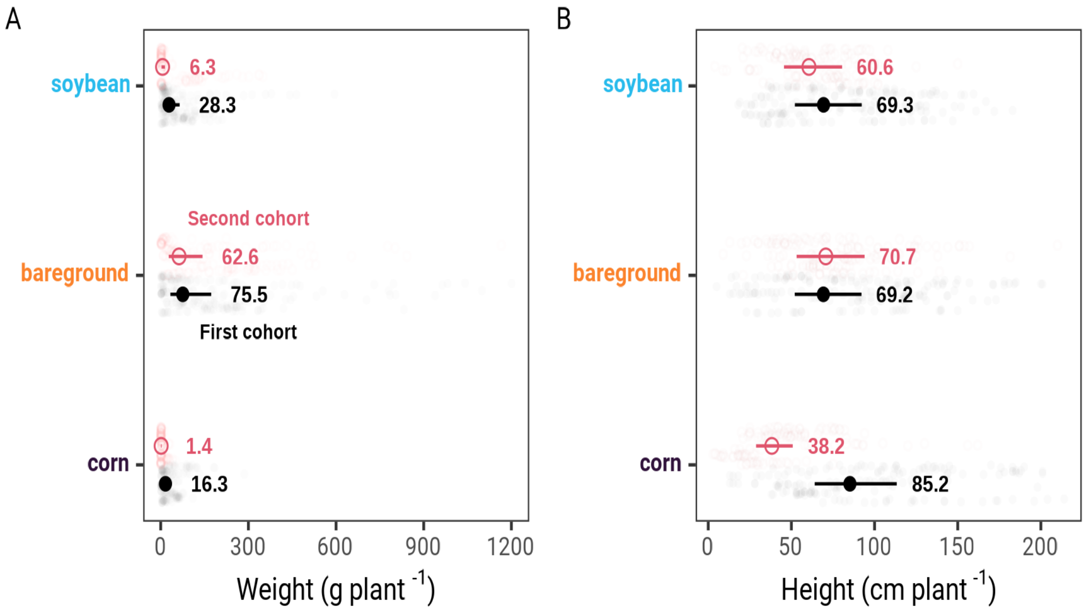

Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, bareground, and soybean across Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

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Figure 4. MCO (180 cm) holding harvested Palmer amaranth plants at 40 days after first transplant (1st cohort, A) and 33 days after second transplant (2nd cohort, B). From left to right, Palmer amaranth growing in bareground, soybean and corn in Arlington, Wisconsin

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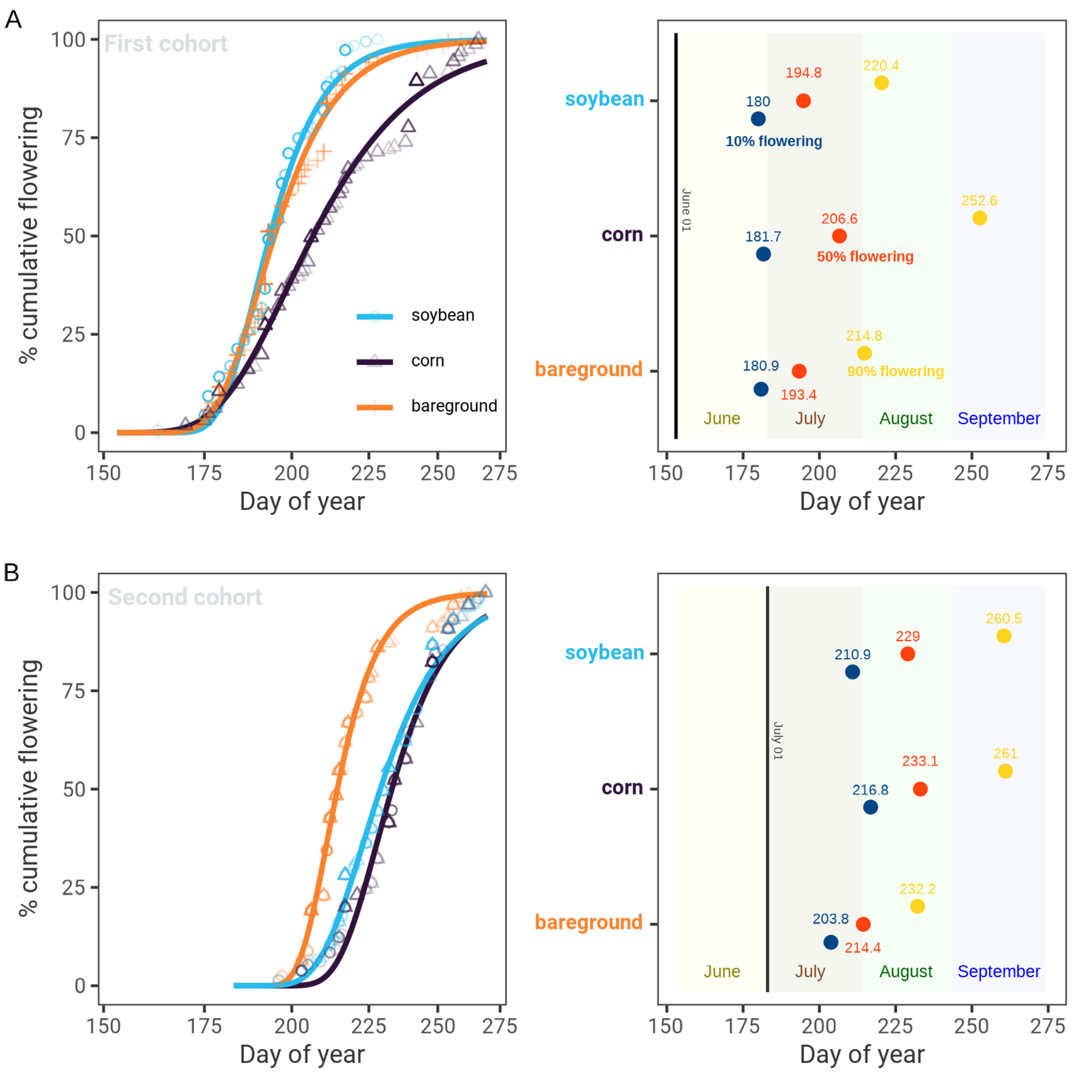

Figure 5. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

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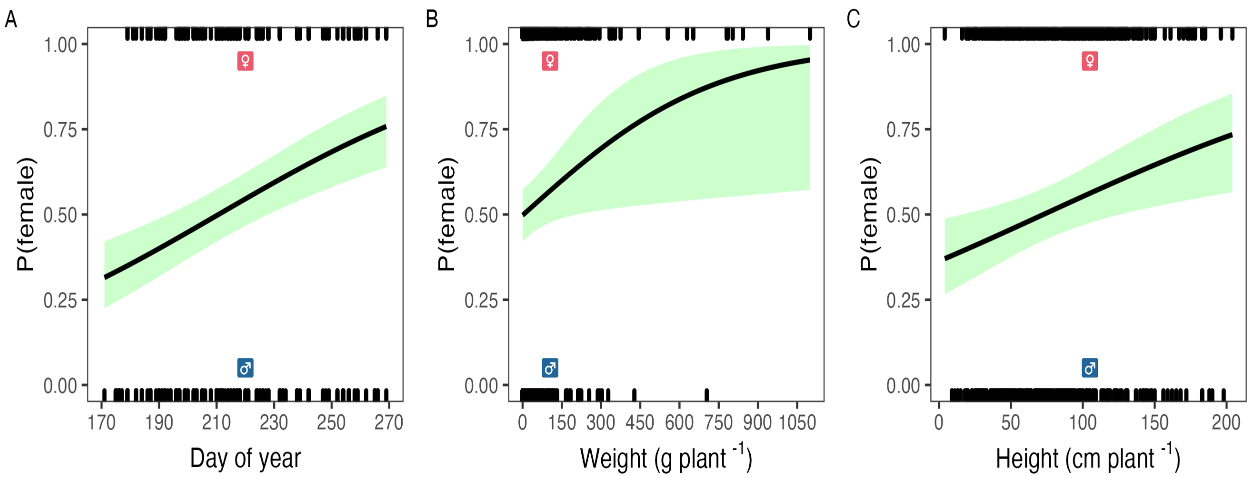

Figure 6. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

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