Palmer amaranth (*Amaranthus palmeri*) adaptation to agroecossystems

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ABSTRACT

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Keywords: Evolution Flowering Management Pigweed Weed

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 . The species 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). 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. 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 adaptation. 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). 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). Also, seeds from Palmer amaranth growing under water stress conditions were heavier, less dormant, and prompt for germination (Matzrafi et al., 2021). 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 documented 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 crop (Garetson et al., 2019) and non-crop land (Bagavathiannan and Norsworthy, 2016) in the warm southern United States but its range is expanding to cool temperatures northward. For example, herbicide resistant Palmer amaranth is widespread in Nebraska (Oliveira et al., 2021), Michigan (Kohrt et al., 2017), and Connecticut (Aulakh et al., 2021). Successful cases of Palmer amaranth invasion and near to eradication is reported 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. Therefore, 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. Strategies to manage Palmer amaranth should be built on minimizing the species ability to adapt, grow and develop into agroecossystems.

The continuous Palmer amaranth dispersal and potential establishment into northern United States 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, biomass production, and height of Palmer amaranth growing under corn, soybean and fallow 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 *A. palmeri* 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 (Washington County, Wisconsin), Clay Center (Clay County, Nebraska), Grant (Perkins County, Nebraska), Lincoln (Lancaster County, Nebraska), and Macomb (McDonough County, Illinois).

A glyphosate-resistant soybean cultivar (DSR-1950 R2Y at 296,400 seeds ha 1), and a corn hybrid were planted at

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)

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 (DSR-1950 R2Y at 296,400 seeds ha 1), or under fallow 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 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, fallow) 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

Cumulative flowering

Palmer amaranth growing in corn resulted in a longer flowering pattern compared to fallow and soybean (Figure 2A). Palmer amaranth reached 10% flowering in soybean at doy 180, which was slightly different from fallow (doy 180.9; P = 0.01) and corn (doy 181.7; P = 0.00). Nonetheless, the 10% cumulative Palmer amaranth flowering in soybean, fallow and corn occurred at the end of June. The 50% Palmer amaranth cumulative flowering occurred in July. For example, Palmer amaranth reached 50% in fallow 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 fallow and soybean, respectively.

Palmer amaranth cumulative flowering from second transplanting timing ranged from mid July to mid September (Figure 2). All cumulative flowering comparisons among agroecossystems were significant ($P < 0.00$) Palmer amaranth growing in fallow resulted in earlier flowering time compared to soybean and corn. Palmer amaranth growing in fallow 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).

Height and biomass

Palmer amaranth accumulated more biomass when growing in fallow compared to Palmer amaranth growing in soybean and corn (Figure 3). At first transplanting time, Palmer amaranth biomass was 78.3 g plant-1, 26.4 g plant-1 and 14.9 g plant-1 in fallow, soybean and corn, respectively. Palmer amaranth produce less biomass at second transplanting time. For example, Palmer amaranth growing in fallow resulted in 49.2 g plant-1, 3.4 g plant-1 in soybean and 1.4 g plant when growing in corn.

For example, Palmer amaranth growing at first cohort accumulated 90%, 85% and 31% more biomass when compared to second cohort at corn, soybean and fallow, respectively

In addition, Palmer amaranth growing in corn and soybean at second cohort had a similar end-season flowering pattern.

DISCUSSION

Our study showed the Palmer amaranth flowering pattern, grow and development varied within agroecossystems and timing. 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. Thus, Palmer amaranth growing strategy was to mimic the crop species (Figure 4). In contrast, at second cohort, Palmer amaranth grow and development was limited due to the crop competitive ability at advanced development stages.

Taller Palmer amaranth plants is a strategy to compete for light in between crop rows in absence of canopy. For example, at first cohort, corn and Palmer amaranth had abundant light to grow and develop, which likely aid its extended the flowering pattern. However, at second cohort, Palmer amaranth was transplanted when corn canopy was nearly closed, which reduced Palmer amaranth competition. As a result, Palmer amaranth height and biomass was nearly 50% and 90% lower compared to its first cohort, respectively. Similar trend was observed to Palmer amaranth growing in soybeans. Palmer amaranth growing without crop competition produced highest amount of biomass. The Palmer amaranth strategy in fallow was to invest biomass in growing plant width and height. Nonetheless, Palmer amaranth produced 31% less biomass in second cohort compared to first cohort timing. Therefore, crop competition was not the only factor limiting Palmer amaranth growing in the second cohort.

It was not evaluate seed production due to Palmer amaranth harvest at early flowering. Nonetheless, it is reported 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 nearly 50% more overall biomass when compared to second cohort. Therefore, Palmer amaranth plants growing in the second cohort is likely to produce less seeds regardless the agroecossystem. Seed production and deposition in the seedbank is a key factor for species perpetuation (Menges, 1987). Palmer amaranth germination is influenced by soil depth and seed viable seeds were fount after 36 months buried in the seedbank (Sosnoskie et al., 2013). Therefore, tactics that promote crop advantage against Palmer amaranth, including early crop planting, preemergence applied herbicide, and crop residue (e.g. cover crops) can minimize the negative impact of Palmer amaranth in agroecossystems.

Palmer amaranth has shown to be responsive to to thermal units (e.g, growing degree days). A study in North Carolina demonstrated that Palmer amaranth emergence in response to soil temperature, with seedlings emerging before July prior to crop canopy closure (Piskackova et al., 2021). In addition, in a bareground study, Palmer emergence emergence pattern in Nebraska was influenced by soil management. Early tillage resulted in 90% Palmer amaranth emergence in June

can cause significant soybean yield loss (Korres et al., 2019)

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: 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.

ACKNOWLEDGMENTS

Funding: This work received no specific grant from any funding agency, commercial, or not-for-profit sectors

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

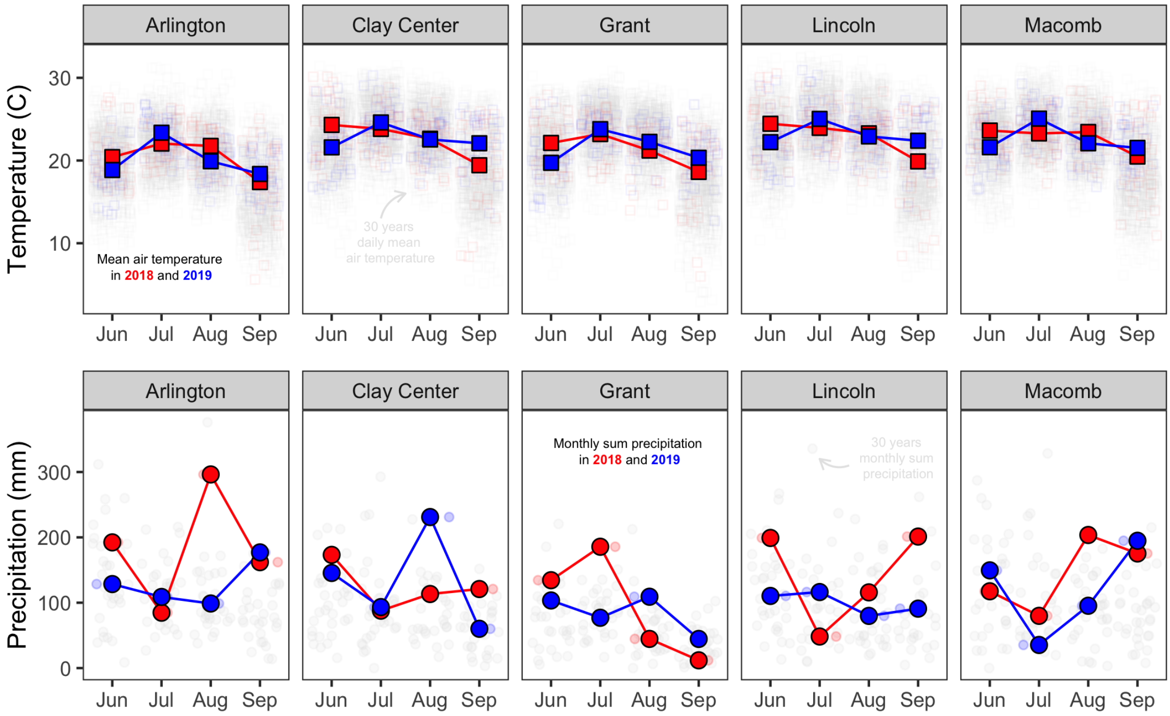

Figure 1. Mean average temperature (C) and montly sum precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

2 REFERENCES

A reference list should be automatically created here. However it won't. Pandoc will place the list of references at the end of the document instead. There are no convenient solution for now to force Pandoc to do otherwise. The easiest way to get around this problem is to edit the LaTeX file created by Pandoc before compiling it again using the traditional LaTeX commands.

FIGURES

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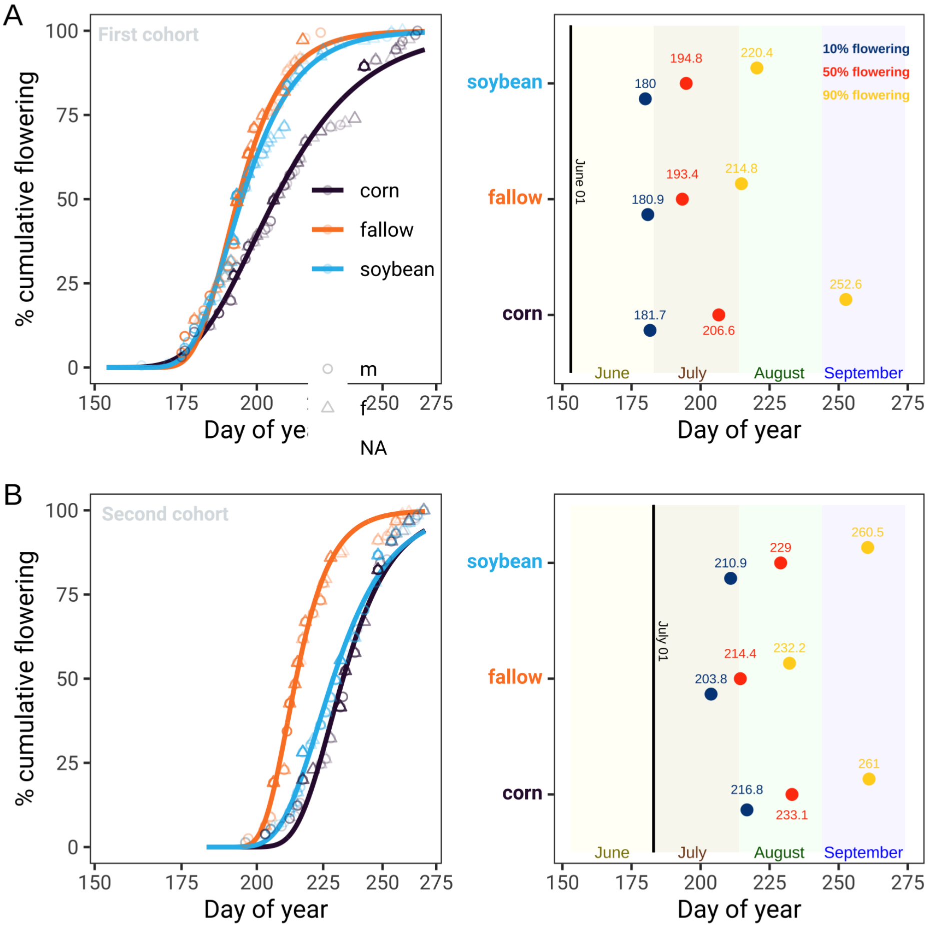

Figure 2. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

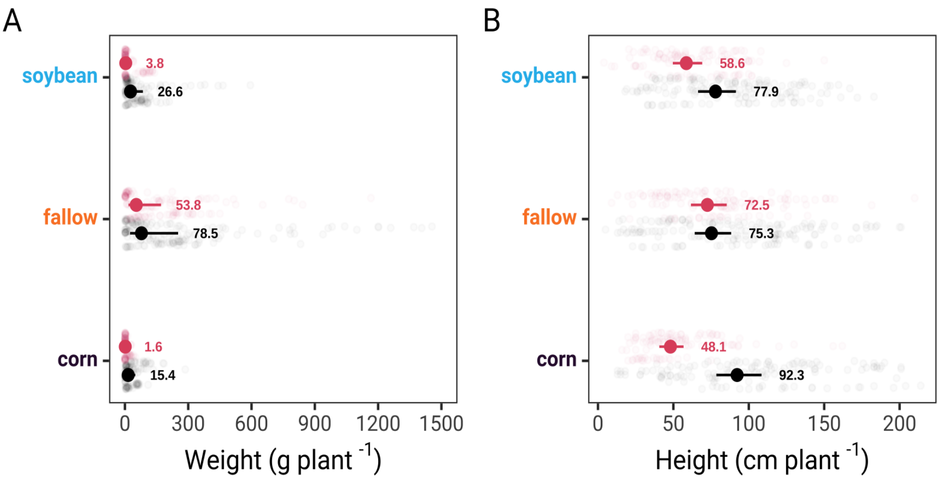

Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, fallow, and soybean across Arlington, Clay Center, Grant, Lincoln, and Macomb

Figure 4. Harvest Palmer amaranth plants at 40 days after first transplant timing. From left to right, Palmer amaranth growing in fallow, soybean and corn in Arlington, Wisconsin

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