

Palmer amaranth (*Amaranthus palmeri*) adaptation to agroecosystems

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2 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 (Ward et al., 2013). The species has showed a remarkable capacity to evolve resistance to herbicides. Palmer amaranth has evolved resistance to eight herbicide sites of action (Heap, 2021), increasing the weed management complexity (Lindsay et al., 2017). Uncontrolled Palmer amaranth in competition for water, light and nutrients can drastically reduce crop yields (Berger et al., 2015). 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.

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. On the other hand, Palmer amaranth is a prolific seed producer with a C4 photosynthetic apparatus (Ward et al., 2013). 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

25 (Yu et al., 2021). Therefore, Palmer amaranth dispersal capacity make the species one of the most successful
26 cases of weed adaption to cropping systems.

27 Light and temperature are likely the main environment requirements for Palmer amaranth successful
28 adaptation. Palmer amaranth is reported with an extended germination period (Jha et al., 2010). Germination
29 of Palmer amaranth is triggered by 18 C soil temperature (Keeley et al., 1987), and optimal germination
30 and biomass production occur at 35/30 C day and night temperatures (Guo and Al-Khatib, 2003). Water
31 has not shown to limit Palmer amaranth fitness. Under continuous water stress, Palmer amaranth survived
32 and produced at least 14000 seeds plant-1 (Chahal et al., 2018). Also, seeds from Palmer amaranth growing
33 under water stress conditions were heavier, less dormant, and prompt for germination (Matzrafi et al.,
34 2021). The continuous global temperature warming can impact agriculture and promote niches for Palmer
35 amaranth invasion/adaptation into new environments. Currently, it is estimated that the greatest climatic
36 risk of Palmer amaranth establishment are agronomic crops in Australia and Sub-Saharan Africa (Kistner
37 and Hatfield, 2018). Temperature is a key factor limiting Palmer amaranth expansion to cooler geographies
38 (Briscoe Runquist et al., 2019); however, under future climate change Palmer amaranth is likely to expand
39 northward into Canada and Northern Europe (Kistner and Hatfield, 2018; Briscoe Runquist et al., 2019).

40 Palmer amaranth is already documented in agronomic crops of South America (Larran et al., 2017;
41 Küpper et al., 2017) and Southern Europe (Milani et al., 2021). In the US, Palmer amaranth is established
42 at crop (Garetson et al., 2019) and non-crop land (Bagavathiannan and Norsworthy, 2016) in the warm
43 southern United States but its range is expanding to cool temperatures northward. For example, herbicide
44 resistant Palmer amaranth is widespread in Nebraska (Oliveira et al., 2021), Michigan (Kohrt et al., 2017),
45 and Connecticut (Aulakh et al., 2021). Successful cases of Palmer amaranth invasion and near to eradication
46 is reported in Minnesota (Yu et al., 2021). No Palmer amaranth actively growing was found in Canada;
47 however, Palmer amaranth seeds was detected in sweet potato slips (Page et al., 2021). Nonetheless, it seems
48 fated the need to manage Palmer amaranth in agronomic crops throughout multiple environments in the
49 near future. Therefore, strategies on Palmer amaranth management should encompass the agroecosystem
50 level but not only attempts to eradicate the weed. Most tactics to manage Palmer amaranth are based on
51 technology fixes (Scott, 2011), which are short-term (e.g., herbicide and/or tillage) rather than long-term
52 weed management.

53 The continuous Palmer amaranth dispersal and potential establishment into northern United States warrant
54 investigations on species morphology growing in such environments. Understanding Palmer amaranth
55 biology and growing strategies under different agroecosystems can enhance our knowledge on species
56 adaptation. It can also aid on designing proactive and ecological tactics to limit the species range expansion,
57 reduce its negative impact, and design resilient and sustainable farming systems (MacLaren et al., 2020).
58 Therefore, the objective of this study was to investigate the flowering pattern, biomass production, and
59 height of Palmer amaranth growing under in corn, soybean and fallow at two timings across five locations
60 in the mid/upper United States Midwest.

MATERIAL AND METHODS

61 Plant material and growing conditions

62 The study was performed with a *A. palmeri* accession (Per1) from Perkins County, Nebraska. Per1
63 accession collection is documented with no reported herbicide resistance (Oliveira et al., 2021). Three
64 weeks prior to the field experiment, seeds were planted in plastic trays containing potting-mix. Emerged
65 seedlings (1 cm) were transplanted into 200 cm⁻³ plastic pots (a plant pot-1). Palmer amaranth seedlings
66 were supplied with adequate water and kept under greenhouse conditions at Arlington, Clay Center, Lincoln,

67 and Macomb; and kept outdoors in Grant. Palmer amaranth seedlings were kept under greenhouse/outdoors
68 until the onset of the experiment (2-3 leaf stage/5 to 8 cm height).

69 Field study

70 The experiment was conducted in 2018 and 2019 under field conditions at five locations: Arlington
71 (Washington County, Wisconsin), Clay Center (Clay County, Nebraska), Grant (Perkins County, Nebraska),
72 Lincoln (Lancaster County, Nebraska), and Macomb (McDonough County, Illinois).

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

75 The field experimental unit were six adjacent 9.1 m wide (12 rows at 72.2 cm row spacing) by 10.7
76 m long. Each experimental unit was planted with corn or soybean (DSR-1950 R2Y at 296,400 seeds ha
77 ⁻¹), or under fallow condition. Palmer amaranth seedlings (potting mix + two seedlings) were and gently
78 transferring to the ground (6 cm deep and 8 cm wide). Twenty-four plants were equidistantly placed (0.76
79 m apart) between rows within each agroecosystems. After a week, one was eliminated and one was kept.
80 There were two transplant timing: first (June 1) and second (July 1). There were 24 Palmer amaranth plants
81 in each experimental unit, with a total of 144 plants for each location. The study was repeated twice.

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

87 Statistical analyses

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

90 The cumulative Palmer amaranth flowering estimation was determined using a asymmetrical three
91 parameter log logistic Weibull model of the drc package (Ritz et al., 2015).

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

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

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

99 Palmer amaranth height and biomass were performed with a linear mixed model using *lmer* function from
100 “lme4” package (Bates et al., 2015). Plant height and biomass were transformed to meet model assumption
101 of normality. In the model, agroecosystem (crop, soybean, fallow) was the fixed effect and year nested with
102 location the random effects. Analysis of variance was performed with *anova* function from “car” package
103 (Fox and Weisberg, 2018). Marginal means and compact letter display were estimated with *emmeans* and
104 *cld* from packages “emmeans” and *multcomp* (Hothorn et al., 2008).

RESULTS

105 Cumulative flowering

106 Palmer amaranth cumulative flowering from first transplant timing ranged from late June to early
107 September. Palmer amaranth growing in corn resulted in a longer flowering pattern compared to fallow
108 and soybean. Palmer amaranth reached 10% flowering in soybean at doy 180, which was slightly different
109 from fallow (doy 180.9; $P = 0.01$) and corn (doy 181.7; $P = 0.00$). Nonetheless, the 10% cumulative
110 Palmer amaranth flowering in soybean, fallow and corn occurred at the end of June. The 50% Palmer
111 amaranth cumulative flowering occurred in July. For example, Palmer amaranth reached 50% in fallow at
112 doy 193.4, followed by soybean (doy 194.8), corn (doy 206.6). Similar trend was observed at 90% Palmer
113 amaranth cumulative flowering. Palmer amaranth growing in corn reached 90% flowering at doy 252.6
114 (early September), which was 37.8 and 32.2 days after Palmer amaranth 90% flowering in fallow and
115 soybean, respectively.

116 Palmer amaranth cumulative flowering from second transplanting timing ranged from mid July to mid
117 September. All cumulative flowering comparisons among agroecosystems were significant ($P < 0.00$).
118 Palmer amaranth growing in fallow resulted in earlier flowering time compared to soybean and corn. Palmer
119 amaranth growing in fallow reached 10%, 50%, and 90% flowering time at day 203.8, 214.4, and 232.2,
120 respectively. Palmer amaranth growing in soybean reached 10% flowering at doy 210.9, which was 6 days
121 prior to corn (P -value = 0.00). Similar trend was observed at 50% flowering, whereas Palmer amaranth
122 reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9; $P = 0.00$). The 90% Palmer
123 amaranth cumulative flowering occurred at same day in corn (260.9) and soybean (260.5; $P = 0.66$).

124 Height and biomass

125 Palmer amaranth accumulated more biomass when growing in fallow compared to Palmer amaranth
126 growing in soybean and corn. At first transplanting time, Palmer amaranth biomass was 78.3 g plant-1,
127 26.4 g plant-1 and 14.9 g plant-1 in fallow, soybean and corn, respectively. Palmer amaranth produce less
128 biomass at second transplanting time. For example, Palmer amaranth growing in fallow resulted in 49.2 g
129 plant-1, 3.4 g plant-1 in soybean and 1.4 g plant when growing in corn.

DISCUSSION

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

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

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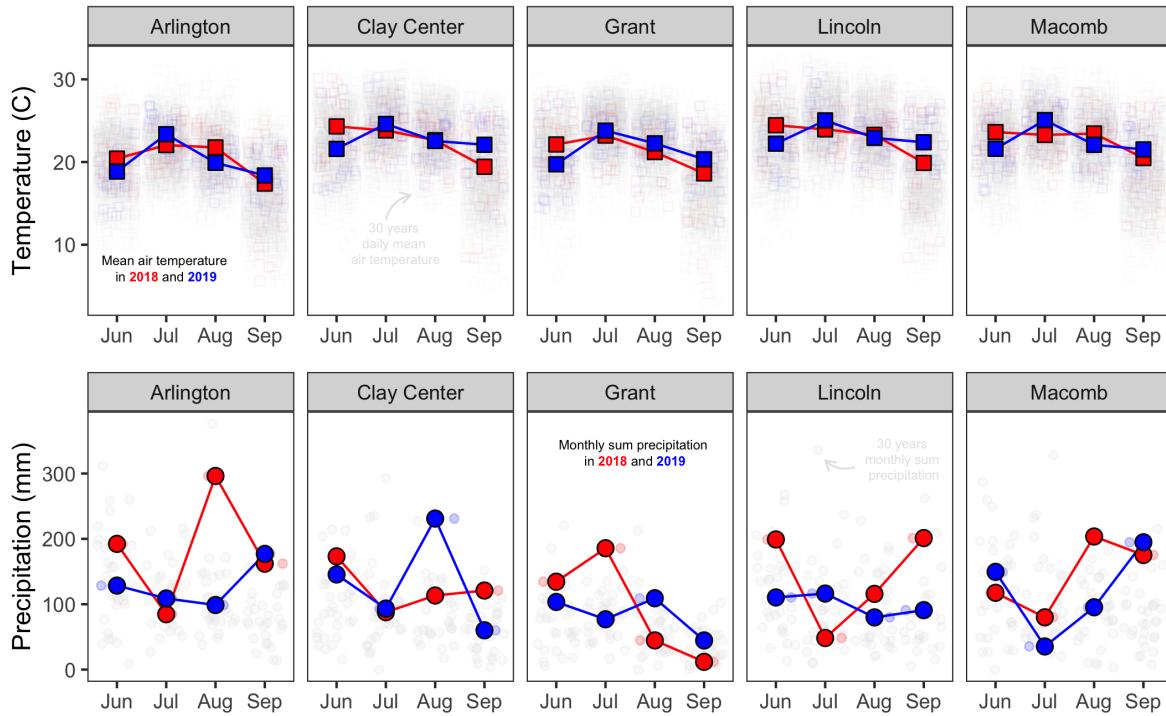


Figure 1. Mean average temperature (C) and monthly sum precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

1 SUPPLEMENTAL DATA

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

2 REFERENCES

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

FIGURES

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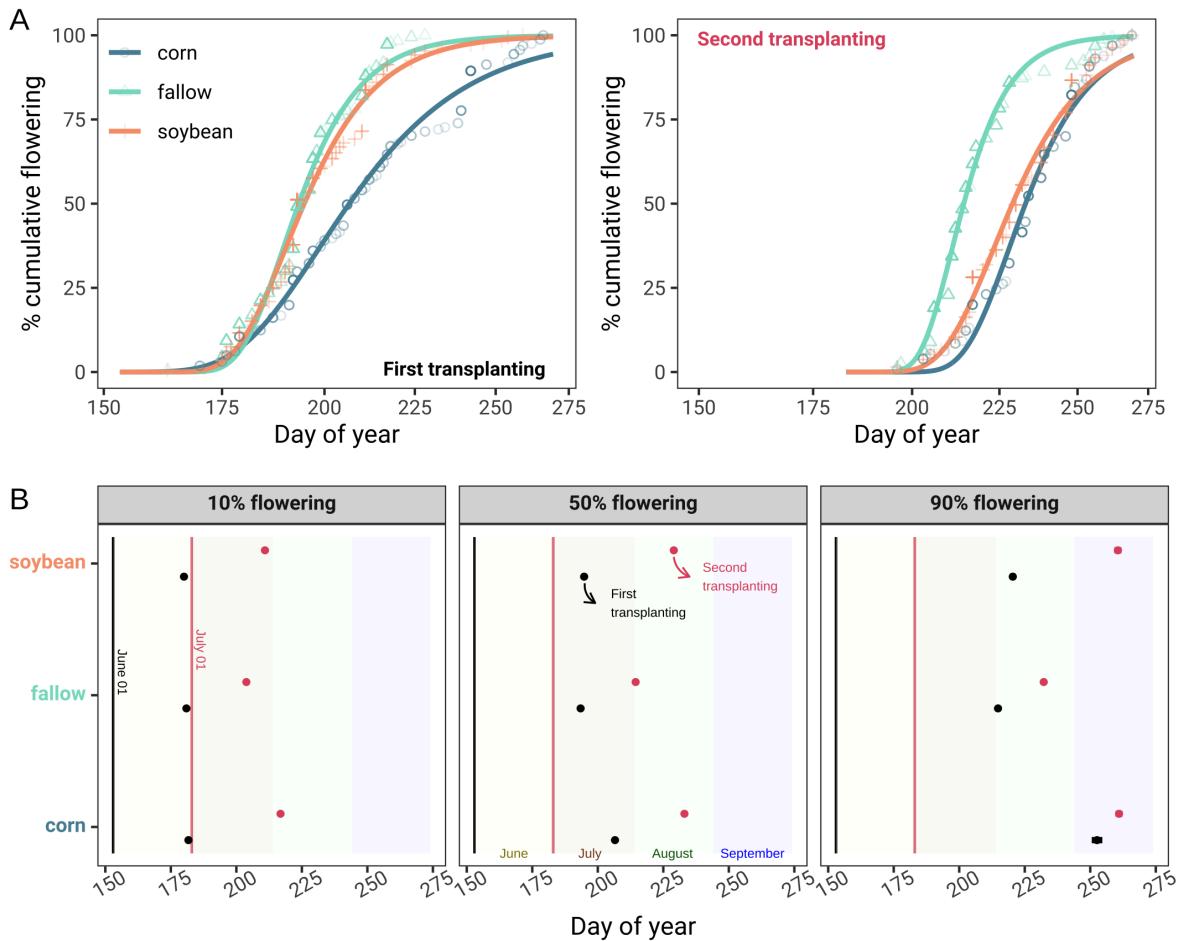


Figure 2. Cumulative flowering of Palmer amaranth at first and second transplant timing (A) and day of year of 10, 50, and 90 cumulative flowering at first and second transplant timing (B)

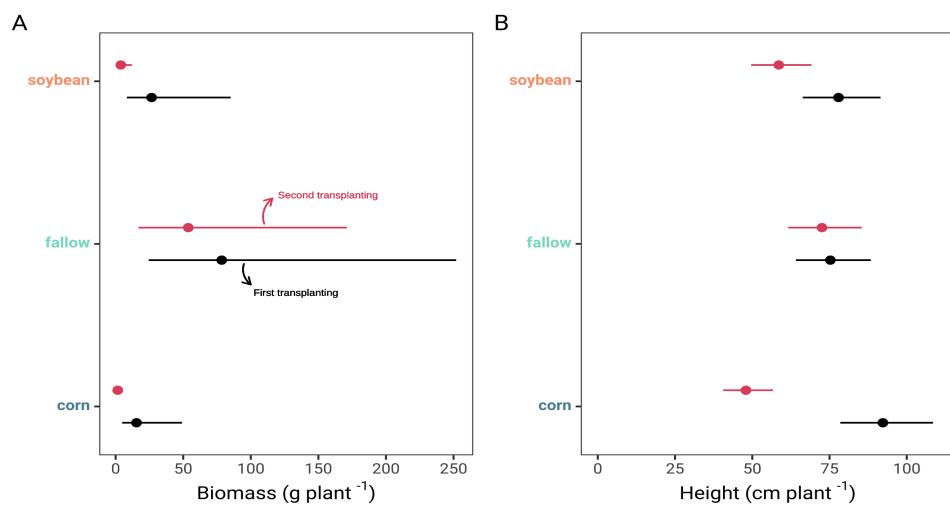


Figure 3. Palmer amaranth biomass (A) and height (B) growing in corn, fallow, and soybean across Arlington, Clay Center, Grant, Lincoln, and Macomb



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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