

# 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. 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.,

26 2017), and plant propagules (Yu et al., 2021). The dispersal capacity of Palmer amaranth make the species  
27 one of the most successful cases of weed adaption to cropping systems.

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

43 Palmer amaranth is already found in agronomic crops of South America (Larran et al., 2017; Küpper et al.,  
44 2017) and Southern Europe (Milani et al., 2021). In the US, Palmer amaranth is well established at cotton  
45 fields (Garetson et al., 2019) and non-crop areas (Bagavathiannan and Norsworthy, 2016) in the southern  
46 United States but its range is expanding northward. For example, herbicide resistant Palmer amaranth is  
47 widespread in Nebraska (Oliveira et al., 2021), Michigan (Kohrt et al., 2017), Connecticut (Aulakh et al.,  
48 2021), and potential damaged to soybean fields in Illinois is reported (Davis et al., 2015). Successful cases  
49 of Palmer amaranth invasion and near to eradication is documented in Minnesota (Yu et al., 2021). No  
50 Palmer amaranth actively growing was found in Canada; however, Palmer amaranth seeds was detected in  
51 sweet potato slips (Page et al., 2021). Nonetheless, it seems fated the need to manage Palmer amaranth  
52 in agronomic crops throughout multiple environments in the near future. Strategies on Palmer amaranth  
53 management should encompass the agroecosystem level but not only attempts to eradicate the weed. Most  
54 tactics to manage Palmer amaranth are based on technology fixes (Scott, 2011), which are short-term (e.g.,  
55 herbicide and/or tillage) rather than long-term weed management. Palmer amaranth management should be  
56 built on minimizing the species ability to adapt, grow and develop into agroecossystems.

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

## MATERIAL AND METHODS

### 69 Plant material and growing conditions

70 The study was performed with a *A. palmeri* accession (Per1) from Perkins County, Nebraska. Per1  
71 accession collection is documented with no reported herbicide resistance (Oliveira et al., 2021). Three  
72 weeks prior to the field experiment, seeds were planted in plastic trays containing potting-mix. Emerged  
73 seedlings (1 cm) were transplanted into 200 cm<sup>3</sup> plastic pots (a plant pot-1). Palmer amaranth seedlings  
74 were supplied with adequate water and kept under greenhouse conditions at Arlington, Clay Center, Lincoln,  
75 and Macomb; and kept outdoors in Grant. Palmer amaranth seedlings were kept under greenhouse/outdoors  
76 until the onset of the experiment (2-3 leaf stage/5 to 8 cm height).

### 77 Field study

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

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

83 Monthly mean air temperature and sum precipitation were obtained using Daymet weather data from  
84 June through September across the five locations in 2018 and 2019 (Correndo et al., 2021) (Figure 1)

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

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

### 97 Statistical analyses

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

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

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

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

104 The doy for 10, 50, and 90% Palmer amaranth cumulative flowering were determined using the *ED*  
105 function of drc package. Also, the 10, 50, and 90% Palmer amaranth cumulative flowering were compared  
106 among agroecosystems and timings using the *EDcomp* function of drc package. The EDcomp function

107 compares the ratio of cumulative flowering using t-statistics, where P-value < 0.05 indicates that we fail to  
108 reject the null hypothesis.

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

## RESULTS

### 115 Cumulative flowering

116 Palmer amaranth growing in corn resulted in a longer flowering pattern compared to fallow and soybean  
117 at first cohort (Figure 2A). Nonetheless, the 10% cumulative Palmer amaranth flowering in soybean, fallow  
118 and corn occurred at the end of June. Palmer amaranth reached 10% flowering in soybean at doy 180, which  
119 was slightly different from fallow (doy 180.9;  $P = 0.01$ ) and corn (doy 181.7;  $P = 0.00$ ). The 50% Palmer  
120 amaranth cumulative flowering occurred in July. For example, Palmer amaranth reached 50% flowering in  
121 fallow at doy 193.4, followed by soybean (doy 194.8), corn (doy 206.6). Similar trend was observed at  
122 90% Palmer amaranth cumulative flowering. Palmer amaranth growing in corn reached 90% flowering  
123 at doy 252.6 (early September), which was 37.8 and 32.2 days after Palmer amaranth 90% flowering in  
124 fallow and soybean, respectively.

125 Palmer amaranth cumulative flowering at second cohort ranged from mid July to mid September (Figure  
126 2B). Palmer amaranth growing in fallow resulted in earlier flowering time compared to soybean and corn.  
127 Palmer amaranth growing in fallow reached 10%, 50%, and 90% flowering time at day 203.8, 214.4, and  
128 232.2, respectively. Palmer amaranth growing in soybean reached 10% flowering at doy 210.9, which  
129 was 6 days prior to corn ( $P$ -value = 0.00). Similar trend was observed at 50% flowering, whereas Palmer  
130 amaranth reached 50% flowering in corn (doy 233.0) 4 days after soybeans (doy 228.9;  $P = 0.00$ ). The 90%  
131 Palmer amaranth cumulative flowering occurred at same day in corn (260.9) and soybean (260.5;  $P = 0.66$ ).

### 132 Height and biomass

133 Palmer amaranth accumulated more biomass when growing in fallow compared to Palmer amaranth  
134 growing in soybean and corn (Figure 3A). At first cohort time, Palmer amaranth biomass was 78.3 g plant-1,  
135 26.4 g plant-1 and 14.9 g plant-1 in fallow, soybean and corn, respectively. Moreover, Palmer amaranth  
136 produce less biomass at cohort time. Palmer amaranth growing in fallow resulted in 49.2 g plant-1, 3.4 g  
137 plant-1 in soybean and 1.4 g plant when growing in corn.

138 The Palmer amaranth achieve 92.3 cm tall when growing at first cohort timing in corn (Figure 3B).

## DISCUSSION

139 Our study showed that Palmer amaranth flowering time, biomass and height varied within agroecosystems  
140 and cohort timing. In general, Palmer amaranth produced more biomass and taller plants when growing at  
141 first cohort rather than second cohort. At first cohort, resources (e.g., soil nutrients) and conditions (e.g.,  
142 light) were more timely available for both species, crop and weed. High biomass and taller Palmer amaranth  
143 plants are likely a weed strategy to compete for light in between crop rows in absence of canopy. In such  
144 condition, Palmer amaranth showed an extraordinary plasticity to adapt upon the agroecosystem. This is  
145 evident when comparing Palmer amaranth shape, and its extended flowering pattern when growing into  
146 corn compared to soybean. Palmer amaranth was taller and thinner when growing within corn. The Palmer

147 amaranth competition strategy was likely to mimic the crop grow and development (Figure 4). These results  
148 are concerning as breeding more competitive crop varieties is likely to select more competitive Palmer  
149 amaranth biotypes (Bravo et al., 2017).

150 Palmer amaranth grow and development at second cohort was limited due to the crop competitive ability  
151 at advanced development stages. Palmer amaranth was transplanted when corn canopy was nearly closed,  
152 which reduced Palmer amaranth competitiveness. As a result, Palmer amaranth height and biomass was  
153 lower compared to its first cohort. Under crop canopy, Palmer amaranth flowering pattern was near to  
154 similar in corn and soybean. Palmer amaranth growing without crop competition produced highest amounts  
155 of biomass and less extended flowering pattern. The Palmer amaranth strategy in bareground was to invest  
156 biomass in growing plant width and height. Nonetheless, Palmer amaranth produced 31% less biomass  
157 in second cohort compared to first cohort timing. In a bareground study, early emerged Palmer amaranth  
158 without competition was 50% taller than late emerged plants (Webster and Grey, 2015). These results  
159 suggests that crop competition is not the only factor limiting late Palmer amaranth establishment. The  
160 limited growth of Palmer amaranth at second cohort is likely a reduced plant response to thermal units (e.g.,  
161 growing degree days). It is hypothesize that reduced day length contributed to smaller plants at second  
162 cohort as well as shorter flowering period. A study in North Carolina and Illinois predicted that less than  
163 10% Palmer amaranth seedlings emergence occurred after June (Piskackova et al., 2021). In addition,  
164 Palmer amaranth negative impact on soybean (Korres et al., 2020) and cotton (Webster and Grey, 2015)  
165 yields was higher when plants were established near to crop planting.

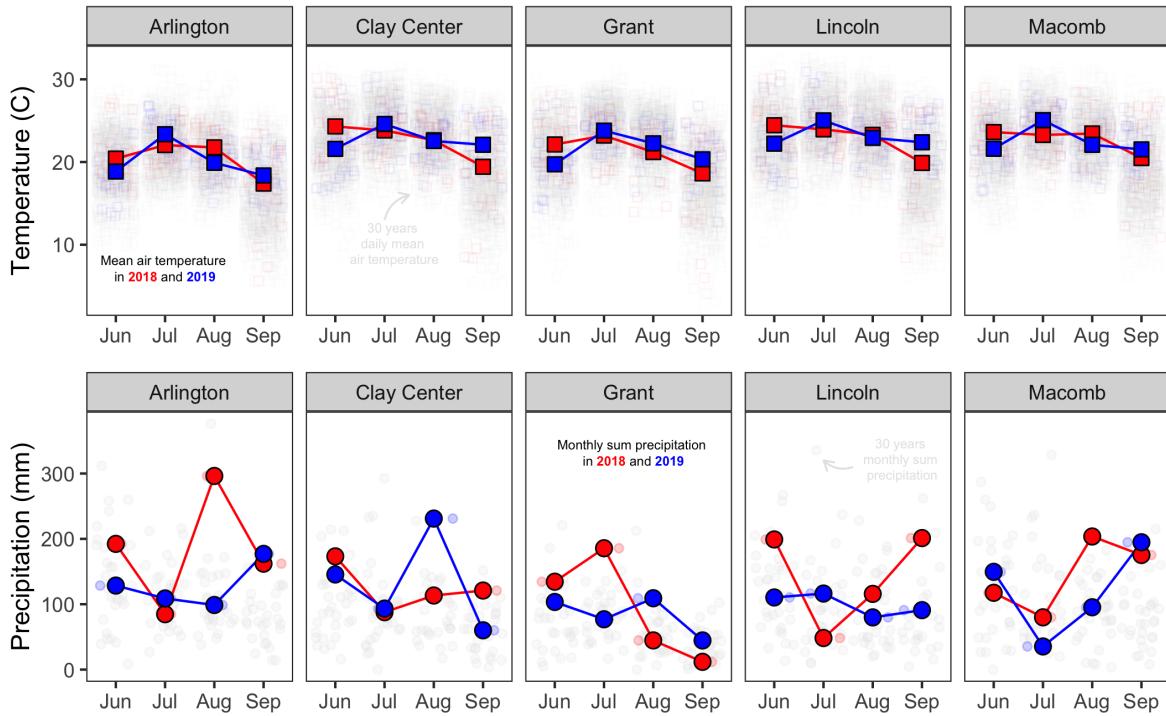
166 Seed production was not evaluated due to Palmer amaranth harvest at flowering time. Nonetheless, it  
167 is well documented a strong positive correlation between Palmer amaranth biomass and seed production  
168 (Schwartz et al., 2016; Spaunhorst et al., 2018). In our study, Palmer amaranth growing at first cohort  
169 accumulated an overall 50% more biomass when compared to second cohort. Therefore, Palmer amaranth  
170 plants growing in the second cohort is likely to produce less seeds regardless the agroecosystem. Our  
171 observation is consistent with the findings that first Palmer amaranth cohort produced 50% more seeds per  
172 plant than Palmer amaranth plants established six weeks later in bareground (Webster and Grey, 2015).  
173 Nonetheless, seed production at second cohort is likely to replenish the soil seedbank. Seed production and  
174 deposition in the seedbank is a key factor for species perpetuation (Menges, 1987). Palmer amaranth can  
175 produce hundred thousands seeds per plant (Schwartz et al., 2016; Keeley et al., 1987), and stay viable  
176 buried in the seedbank for at least 36 months (Sosnoskie et al., 2013).

177 Palmer amaranth flowering pattern was variable

178 Our study demonstrated the short-term Palmer amaranth plasticity to grow and develop into cropping-  
179 systems. Palmer amaranth management priority should focus on minimizing Palmer amaranth dispersal  
180 into new geographies. Early-season management programs would have a large negative effect in Palmer  
181 amaranth growth and development. Tactics that promote crop advantage against Palmer amaranth, including  
182 early crop planting, crop rotation, plant width, preemergence applied herbicide (Sanctis et al., 2021), and  
183 crop residue (e.g. cover crops) would minimize the negative impact of Palmer amaranth in agroecosystems.

## DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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



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

## AUTHOR CONTRIBUTIONS

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

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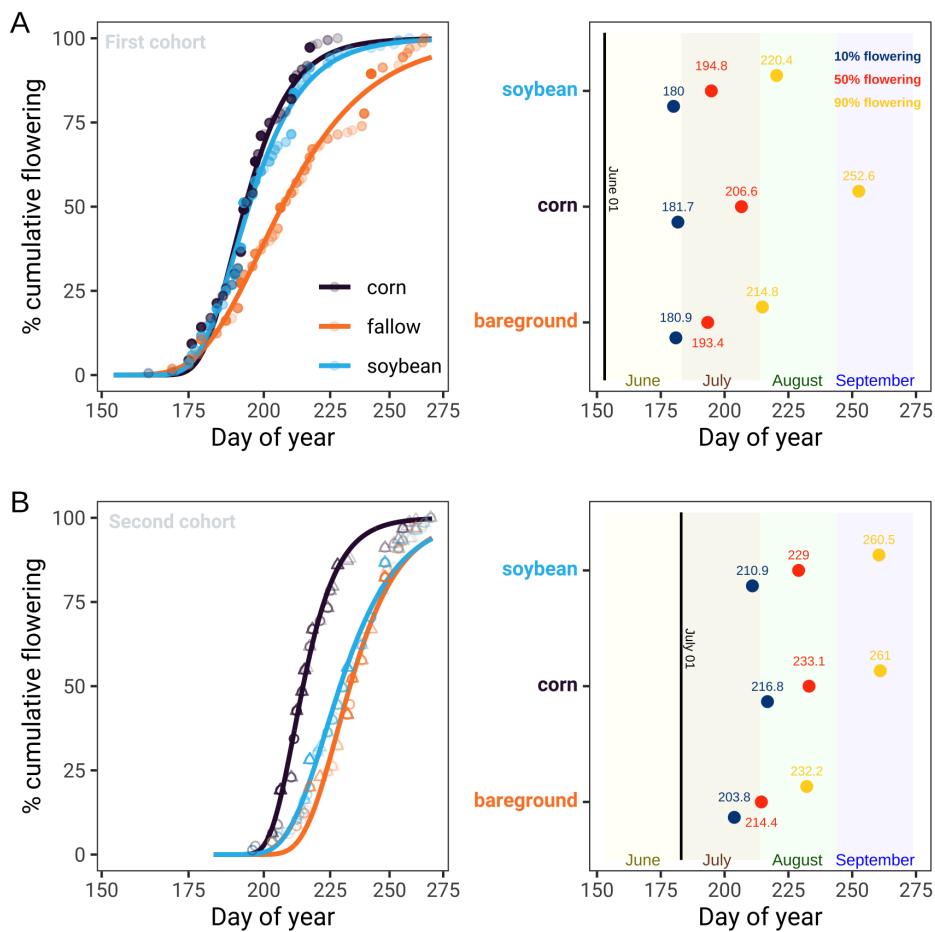
189 Funding: This work received no specific grant from any funding agency, commercial, or not-for-profit  
 190 sectors

## 1 SUPPLEMENTAL DATA

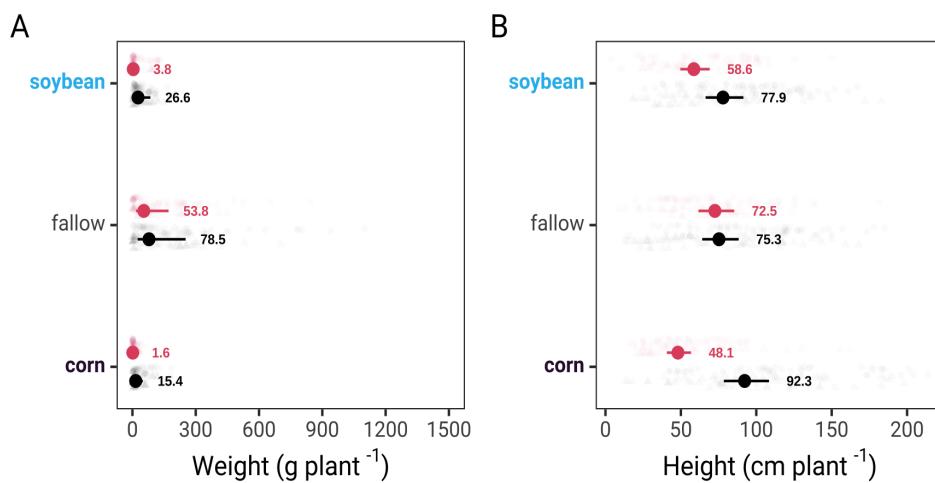
191 Supplementary Material should be uploaded separately on submission, if there are Supplementary Figures,  
 192 please include the caption in the same file as the figure. LaTeX Supplementary Material templates can be  
 193 found in the Frontiers LaTeX folder

## 2 REFERENCES

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



**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)



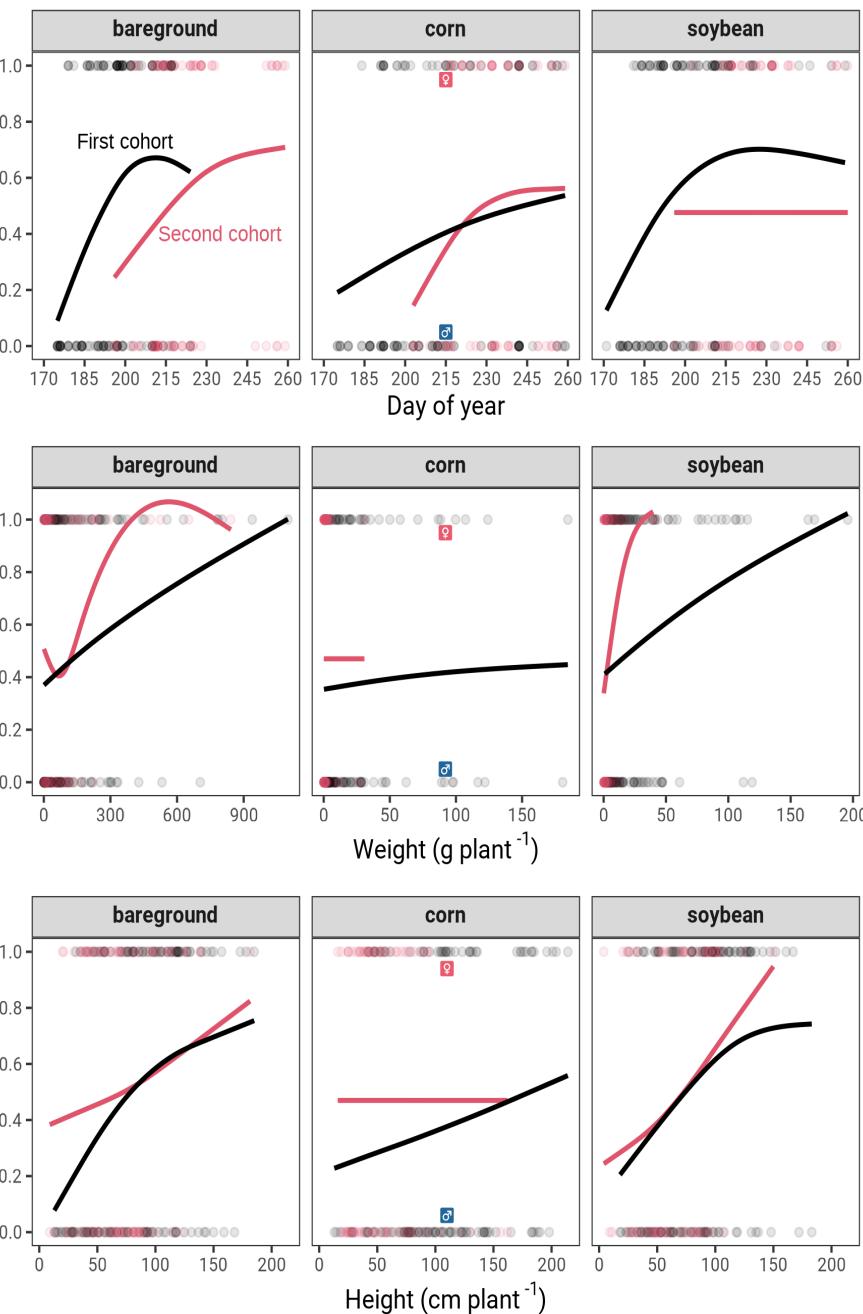
**Figure 3.** Palmer amaranth biomass (A) and height (B) growing in corn, fallow, and soybean across Arlington, Clay Center, Grant, Lincoln, and Macomb



**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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**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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