Adaptation of Palmer amaranth (*Amaranthus palmeri*) to agroecossystems

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2 ABSTRACT

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INTRODUCTION

- 7 Palmer amaranth (Amaranthus palmeri S. Watson) is currently considered one of the most economically
- 8 damaged weed species to cropping systems in the United States (Ward et al., 2013). The species has showed
- 9 a remarkable capacity to evolve resistance to herbicides. Palmer amaranth has evolved resistance to eight
- 10 herbicide sites of action (Heap, 2021), increasing the weed management complexity (Lindsay et al., 2017).
- 11 Uncontrolled Palmer amaranth in competition for water, light and nutrients can drastically reduce crop
- 12 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)
- 14 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
- 17 is likely a result of human-assisted selection in combination with species biology. Farm mechanization,
- 18 conservation agriculture (e.g., no-till), and reliance on herbicides for weed management are the main human
- 19 mediated selection of Palmer amaranth to cropping systems. On the other hand, Palmer amaranth is a
- 20 prolific seed producer with a C4 photosynthetic apparatus (Ward et al., 2013). With a dioecy nature, Palmer
- 21 amaranth male and female plants are obligate outcrosser species, increasing the chances of exchanging
- 22 herbicide resistant alleles among plants (Oliveira et al., 2018). Also, Palmer amaranth small seed size (e.g,
- 23 1 mm) tend to thrive in no-tillage systems (Price et al., 2011), and spread across locations through farm
- 24 equipment (Sauer, 1972), manure (Hartzler and Anderson, 2016), animals (Farmer et al., 2017), and plant

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

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

The continuous Palmer amaranth dispersal and potential establishment into northern United States warrant investigations on species morphology growing 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 in corn, soybean and fallow at two timings across five locations in the mid/upper United States Midwest.

MATERIAL AND METHODS

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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 (7 to 10 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 The field experimental unit were six adjacent 9.1 m wide (12 rows at 72.2 cm row spacing) by 10.7
- 74 m long. Each experimental unit was planted with corn or soybean, or under fallow condition. Palmer
- 75 amaranth seedlings were transplanted to the field experiment by making a whole in the soil (6 cm deep
- 76 and 8 cm wide); and gently transferring to the ground (potting mix + two seedlings). After a week, one
- 77 was eliminated and one was kept. There were two transplant timing: first (June 1st) and second (July 1st).
- 78 There were 24 Palmer amaranth plants in each experimental unit, with a total of 144 plants. The study was
- 79 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
- 82 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

- 85 The statistical analyses were performed using R statistical software version 4.0.1. Data across locations
- 86 and year were combined.
- 87 The cumulative Palmer amaranth flowering estimation was determined using a asymmetrical three
- 88 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
- 90 XXX, and x day of year (doy).
- The doy for 10, 50, and 90% Palmer amaranth cumulative flowering were determined using the ED
- 92 function of drc package. Also, the 10, 50, and 90% Palmer amaranth cumulative flowering were compared
- 93 among crop/fallow and timings using the *EDcomp* function of drc package. The EDcomp function compares
- 94 the ratio of cumulative flowering using t-statistics, where P-value < 0.05 indicates that we fail to reject the
- 95 null hypothesis.
- Palmer amaranth height and biomass were performed with a linear mixed model using *lmer* function
- 97 from "lme4" package (Bates et al., 2015). Plant height and biomass were transformed to meet model
- 98 assumption of normality. In the model, agroecosystem (crop, soybean, fallow) was the fixed effect and
- 99 year nested with location the random effects. Analysis of variance was performed with *anova* function
- 100 from "car" package (Fox and Weisberg, 2018). Marginal means and compact letter display were estimated
- 101 with emmeans and cld from packages "emmeans" and multcomp (Hothorn et al., 2008)

RESULTS

102 Subsection 1

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04 Subsection 2

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- 110 substantial delay during the production process.

1 DISCUSSION

DISCLOSURE/CONFLICT-OF-INTEREST STATEMENT

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

AUTHOR CONTRIBUTIONS

- 113 MCO design, wrote,
- The statement about the authors and contributors can be up to several sentences long, describing the tasks
- of individual authors referred to by their initials and should be included at the end of the manuscript before
- 116 the References section.

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2 SUPPLEMENTAL DATA

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- do otherwise. The easiest way to get around this problem is to edit the LaTeX file created by Pandoc before
- 124 compiling it again using the traditional LaTeX commands.

FIGURES

- 125 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.
- 127 *Weed Technology* 35, 457–463. doi:10.1017/wet.2021.6.
- 128 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.
- 130 Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using
- 131 Lme4. Journal of Statistical Software 67, 1–48. doi:10.18637/jss.v067.i01.
- 132 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.

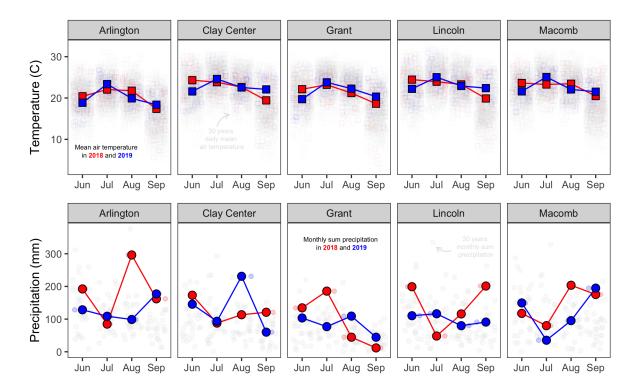


Figure 1. Mean average temperature (C) and montly sum precipitation (mm) at Arlington, WI, Clay Center, NE, Grant, NE, Lincoln, NE and Macomb, IL

- Briscoe Runquist, R. D., Lake, T., Tiffin, P., and Moeller, D. A. (2019). Species distribution models throughout the invasion history of Palmer amaranth predict regions at risk of future invasion and reveal challenges with modeling rapidly shifting geographic ranges. *Sci Rep* 9, 2426. doi:10.1038/s41598-018-38054-9.
- 138 Chahal, P. S., Irmak, S., Jugulam, M., and Jhala, A. J. (2018). Evaluating Effect of Degree of Water Stress
 139 on Growth and Fecundity of Palmer amaranth (Amaranthus palmeri) Using Soil Moisture Sensors.
 140 Weed Science 66, 738–745. doi:10.1017/wsc.2018.47.
- Farmer, J. A., Webb, E. B., Pierce, R. A., and Bradley, K. W. (2017). Evaluating the potential for weed seed
 dispersal based on waterfowl consumption and seed viability. *Pest Management Science* 73, 2592–2603.
 doi:10.1002/ps.4710.
- Fox, J., and Weisberg, S. (2018). *An R Companion to Applied Regression*. SAGE Publications Available at: http://books.google.com?id=uPNrDwAAQBAJ.
- Garetson, R., Singh, V., Singh, S., Dotray, P., and Bagavathiannan, M. (2019). Distribution of herbicide resistant Palmer amaranth (Amaranthus palmeri) in row crop production systems in Texas. Weed
 Technology 33, 355–365. doi:10.1017/wet.2019.14.
- Guo, P., and Al-Khatib, K. (2003). Temperature effects on germination and growth of redroot pigweed
 (Amaranthus retroflexus), Palmer amaranth (A. Palmeri), and common waterhemp (A. rudis). Weed
 Science 51, 869–875. doi:10.1614/P2002-127.
- 152 Hartzler, B., and Anderson, M. (2016). Palmer amaranth: It's here, now what? 10.

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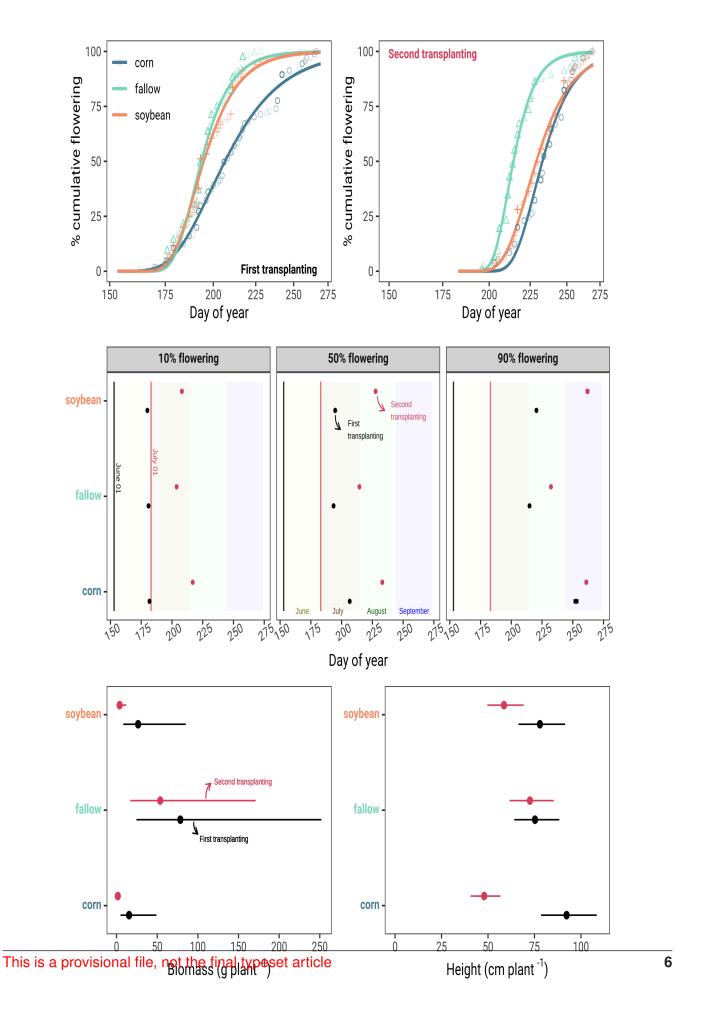


Figure 2. Figure caption

153 Heap, I. (2021). Internation Herbicide-Resistant Weed Database. Available at: http://www.

- weedscience.org/Home.aspx [Accessed July 26, 2021].
- 155 Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models.
- 156 *Biometrical Journal* 50, 346–363. doi:10.1002/bimj.200810425.
- 157 Jha, P., Norsworthy, J. K., Riley, M. B., and Bridges, W. (2010). Annual Changes in Temperature and Light
- Requirements for Germination of Palmer Amaranth (Amaranthus palmeri) Seeds Retrieved from Soil.
- 159 *Weed Science* 58, 426–432. doi:10.1614/WS-D-09-00038.1.
- 160 Keeley, P. E., Carter, C. H., and Thullen, R. J. (1987). Influence of Planting Date on Growth of Palmer
- Amaranth (Amaranthus palmeri). Weed Science 35, 199–204. doi:10.1017/S0043174500079054.
- 162 Kistner, E. J., and Hatfield, J. L. (2018). Potential Geographic Distribution of Palmer
- Amaranth under Current and Future Climates. Agricultural & Environmental Letters 3, 170044.
- doi:10.2134/ael2017.12.0044.
- 165 Klingaman, T. E., and Oliver, L. R. (1994). Palmer Amaranth (Amaranthus palmeri) Interference in
- Soybeans (Glycine max). Weed Science 42, 523–527. doi:10.1017/S0043174500076888.
- 167 Kohrt, J. R., Sprague, C. L., Nadakuduti, S. S., and Douches, D. (2017). Confirmation of a Three-Way
- (Glyphosate, ALS, and Atrazine) Herbicide-Resistant Population of Palmer Amaranth (Amaranthus
- palmeri) in Michigan. Weed Science 65, 327–338. doi:10.1017/wsc.2017.2.
- 170 Küpper, A., Borgato, E. A., Patterson, E. L., Netto, A. G., Nicolai, M., Carvalho, S. J. P. de, Nissen, S.
- J., Gaines, T. A., and Christoffoleti, P. J. (2017). Multiple Resistance to Glyphosate and Acetolactate
- Synthase Inhibitors in Palmer Amaranth (Amaranthus palmeri) Identified in Brazil. Weed Science 65,
- 173 317–326. doi:10.1017/wsc.2017.1.
- 174 Larran, A. S., Palmieri, V. E., Perotti, V. E., Lieber, L., Tuesca, D., and Permingeat, H. R. (2017). Target-site
- 175 resistance to acetolactate synthase (ALS)-inhibiting herbicides in Amaranthus palmeri from Argentina.
- 176 *Pest Management Science* 73, 2578–2584. doi:10.1002/ps.4662.
- 177 Lindsay, K., Popp, M., Norsworthy, J., Bagavathiannan, M., Powles, S., and Lacoste, M. (2017). PAM:
- Decision Support for Long-Term Palmer Amaranth (Amaranthus palmeri) Control. Weed Technology
- 179 31, 915–927. doi:10.1017/wet.2017.69.
- 180 MacLaren, C., Storkey, J., Menegat, A., Metcalfe, H., and Dehnen-Schmutz, K. (2020). An ecological
- future for weed science to sustain crop production and the environment. A review. *Agron. Sustain. Dev.*
- 40, 24. doi:10.1007/s13593-020-00631-6.
- 183 Massinga, R. A., Currie, R. S., Horak, M. J., and Boyer, J. (2001). Interference of Palmer amaranth in corn.
- Weed Science 49, 202–208. doi:10.1614/0043-1745(2001)049[0202:IOPAIC]2.0.CO;2.
- 185 Matzrafi, M., Osipitan, O. A., Ohadi, S., and Mesgaran, M. B. (2021). Under pressure: Maternal effects
- promote drought tolerance in progeny seed of Palmer amaranth (Amaranthus palmeri). Weed Science
- 187 69, 31–38. doi:10.1017/wsc.2020.75.
- 188 Milani, A., Panozzo, S., Farinati, S., Iamonico, D., Sattin, M., Loddo, D., and Scarabel, L. (2021). Recent
- Discovery of Amaranthus palmeri S. Watson in Italy: Characterization of ALS-Resistant Populations
- and Sensitivity to Alternative Herbicides. *Sustainability* 13, 7003. doi:10.3390/su13137003.

Frontiers 7

191 Morgan, G. D., Baumann, P. A., and Chandler, J. M. (2001). Competitive Impact of Palmer Amaranth

- (Amaranthus palmeri) on Cotton (Gossypium hirsutum) Development and Yield. Weed Technology 15,
- 408–412. doi:10.1614/0890-037X(2001)015[0408:CIOPAA]2.0.CO;2.
- 194 Oliveira, M. C., Gaines, T. A., Patterson, E. L., Jhala, A. J., Irmak, S., Amundsen, K., and Knezevic, S.
- Z. (2018). Interspecific and intraspecific transference of metabolism-based mesotrione resistance in
- dioecious weedy Amaranthus. *The Plant Journal* 96, 1051–1063. doi:10.1111/tpj.14089.
- 197 Oliveira, M. C., Giacomini, D. A., Arsenijevic, N., Vieira, G., Tranel, P. J., and Werle, R. (2021).
- Distribution and validation of genotypic and phenotypic glyphosate and PPO-inhibitor resistance in
- Palmer amaranth (Amaranthus palmeri) from southwestern Nebraska. *Weed Technology* 35, 65–76.
- 200 doi:10.1017/wet.2020.74.
- 201 Page, E. R., Nurse, R. E., Meloche, S., Bosveld, K., Grainger, C., Obeid, K., Filotas, M., Simard, M.-J., and
- Laforest, M. (2021). Import of Palmer amaranth (Amaranthus palmeri S. Wats.) Seed with sweet potato
- 203 (Ipomea batatas (L.) Lam) slips. *Can. J. Plant Sci.*, CJPS-2020-0321. doi:10.1139/CJPS-2020-0321.
- 204 Price, A. J., Balkcom, K. S., Culpepper, S. A., Kelton, J. A., Nichols, R. L., and Schomberg, H. (2011).
- 205 Glyphosate-resistant Palmer amaranth: A threat to conservation tillage. Journal of Soil and Water
- 206 *Conservation* 66, 265–275. doi:10.2489/jswc.66.4.265.
- 207 Ritz, C., Baty, F., Streibig, J. C., and Gerhard, D. (2015). Dose-Response Analysis Using R. *PLOS ONE*
- 208 10, e0146021. doi:10.1371/journal.pone.0146021.
- 209 Sauer, J. (1957). Recent Migration and Evolution of the Dioecious Amaranths. *Evolution* 11, 11–31.
- 210 doi:10.2307/2405808.
- 211 Sauer, J. D. (1972). The dioecious amaranths: A new species name and major range extensions. *Madroño*
- 21, 426-434. Available at: http://www.jstor.org/stable/41423815.
- 213 Scott, D. (2011). The Technological Fix Criticisms and the Agricultural Biotechnology Debate. J Agric
- 214 Environ Ethics 24, 207–226. doi:10.1007/s10806-010-9253-7.
- 215 Ward, S. M., Webster, T. M., and Steckel, L. E. (2013). Palmer Amaranth (Amaranthus palmeri): A Review.
- 216 *Weed Technology* 27, 12–27. doi:10.1614/WT-D-12-00113.1.
- 217 Yu, E., Blair, S., Hardel, M., Chandler, M., Thiede, D., Cortilet, A., Gunsolus, J., and Becker, R. (2021).
- Timeline of Palmer amaranth (Amaranthus palmeri) invasion and eradication in Minnesota. Weed
- 219 *Technology*, 1–31. doi:10.1017/wet.2021.32.