Weed Science

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Weed Biology and Ecology

Cite this article: Spaunhorst DJ, Devkota P, Johnson WG, Smeda RJ, Meyer CJ, Norsworthy JK (2018) Phenology of Five Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and Arkansas. Weed Sci 66:457–469. doi: 10.1017/wsc.2018.12

Received: 23 October 2017
Revised: 8 February 2018
Accepted: 15 February 2018

Associate Editor:
J. Anita Dille, Kansas State University

Key words:
Genetic and environmental variation; geographic range; pigweeds; seed production; weed biology

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Phenology of Five Palmer amaranth (*Amaranthus palmeri*) Populations Grown in Northern Indiana and Arkansas

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Abstract

Palmer amaranth (*Amaranthus palmeri* S. Watson) is a problematic weed encountered in U.S. cotton (*Gossypium hirsutum* L.) and soybean [*Glycine max* (L.) Merr.] production, with infestations spreading northward. This research investigated the influence of planting date (early, mid-, and late season) and population (AR, IN, MO, MS, NE, and TN) on *A. palmeri* growth and reproduction at two locations. All populations planted early or midseason at Throckmorton Purdue Agricultural Center (TPAC) and Arkansas Agriculture Research and Extension Center (AAREC) measured 196 and 141 cm or more, respectively. *Amaranthus palmeri* height did not exceed 168 and 134 cm when planted late season at TPAC and AAREC, respectively. Early season planted *A. palmeri* from NE grew to 50% of maximum height 8 to 13 d earlier than all other populations under TPAC conditions. In addition, the NE population planted early, mid-, and late season achieved 50% inflorescence emergence 5, 4, and 6 d earlier than all other populations, respectively. All populations established at TPAC produced fewer than 100,000 seeds plant^{-1}. No population planted at TPAC and AAREC produced more than 740 and 1,520 g plant^{-1} of biomass at 17 and 19 wk after planting, respectively. Planting date influenced the distribution of male and female plants at TPAC, but not at AAREC. *Amaranthus palmeri* from IN and MS planted late season had male-to-female plant ratios of 1.3:1 and 1.7:1, respectively. *Amaranthus palmeri* introduced to TPAC from NE can produce up to 7,500 seeds plant^{-1} if emergence occurs in mid-July. An NE *A. palmeri* population exhibited biological characteristics allowing it to be highly competitive if introduced to TPAC due to a similar latitudinal range, but was least competitive when introduced to AAREC. Although *A. palmeri* originating from different locations can vary biologically, plants exhibited environmental plasticity and could complete their life cycle and contribute to spreading populations.

Introduction

Palmer amaranth (*Amaranthus palmeri* S. Watson) is a dioecious (separate male and female plants) summer annual plant in the Amaranthaceae family, commonly referred to as pigweed. Species in the genus *Amaranthus* are found globally (Costea et al. 2005). Since the early 20th century, *A. palmeri* has expanded beyond its native range of Mexico and the southwestern United States, an area known as the Sonoran Desert, to areas north and east (Sauer 1957). More recently, *A. palmeri* and other weedy *Amaranthus* species have been found infesting midwestern and southern U.S. corn (*Zea mays* L.), cotton (*Gossypium hirsutum* L.), and soybean [*Glycine max* L. (Merr.)] production areas (Steckel 2007; Uva et al. 1997). Spread of *A. palmeri* is vectored by many natural factors. Li and Qiang (2009) found that rain and water runoff contribute to the spread of as many as 74 weed species, and more recently, Norsworthy et al. (2014) reported *A. palmeri* seed traveling as far as 114 m in rainwater. Other studies confirm dispersal of *Amaranthus* species via farm equipment, cotton gin trash, cover crop seed, livestock, and mallard ducks (*Anas platyrhynchos*) and other migratory birds (Farmer et al. 2017; Loux 2017; Norsworthy et al. 2009; Sprague 2014).

Crop yields are sensitive to *A. palmeri* competition (Bensch et al. 2003; Massinga et al. 2001). For example, 10 *A. palmeri* plants m^{-1} crop row reduced soybean grain yield by 68% (Klingaman and Oliver 1994). As a result, researchers suggest crop producers eliminate all *A. palmeri* plants before seed production (Davis et al. 2015; Norsworthy et al. 2014). Once *A. palmeri* is established in a crop field, effective management is challenging, because of

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season-long emergence. Jha and Norsworthy (2009) reported 40 or more *A. palmeri* plants m^{-2} emerged in two to three periods beginning in early May through mid-July in no-till soybean. Moreover, *A. palmeri* emergence in California has been reported to occur as late as October (Keeley et al. 1987). *Amaranthus palmeri* emergence is optimum (44%) when seed is buried no deeper than 2.5 cm, decreasing to 7% when buried under 5 cm of soil (Keeley et al. 1987). In a survey of crop producers across IA, IL, IN, MS, NC, and NE, 25% and 31% reported switching from conventional tillage to no- or reduced tillage systems, respectively, after adopting glyphosate-resistant cropping systems (Givens et al. 2009). Despite the benefits associated with no- and reduced tillage systems, *A. palmeri* are likely to emerge, as seeds are deposited and retained near the soil surface.

Amaranthus palmeri growth following emergence can be vigorous and can exceed that of similar species. For example, at 2 wk after planting, Sellers et al. (2003) observed the height of *A. palmeri* to be 3.7 cm greater than that of redroot pigweed (*Amaranthus retroflexus* L.), which was the second tallest of the *Amaranthus* species evaluated. Rapid *A. palmeri* growth throughout the growing season in California was reported by Keeley et al. (1987), where *A. palmeri* measured 210 cm in height 12 wk after a June 1 planting. In another study, Guo and Al-Khatib (2003) reported that *A. palmeri* biomass accumulation is more sensitive to cooler day and night air temperatures (15 and 10 C) than *A. retroflexus* and common waterhemp [*Amaranthus tuberculatus* (Moq.) J. D. Sauer]. When day and night air temperatures were increased (25 and 20 C to 35 and 30 C), *A. palmeri* accumulated more biomass than *A. retroflexus* or *A. tuberculatus* after 2, 3, and 4 wk of exposure (Guo and Al-Khatib 2003).

Previous research suggests that *A. palmeri* produces seed within 2 to 3 wk after flowering (Keeley et al. 1987). This is significant, as uncontrolled weeds that emerge later in the growing season produce seed and increase the weed seedbank. The quantity of *A. palmeri* seed that can be produced is closely linked to emergence timing. Sellers et al. (2003) found that early emerging *A. palmeri* may produce more than 250,000 seeds plant^{-1} over the course of a growing season. However, plants that emerge in September produce fewer than 100 seeds plant^{-1} at 9 wk after emergence (Keeley et al. 1987).

Studies have been conducted that compare growth and seed production among *Amaranthus* species (Guo and Al-Khatib 2003; Horak and Loughlin 2000; Sellers et al. 2003) and even between accessions (Bond and Oliver 2006; Davis et al. 2015; Heneghan and Johnson 2017). Bond and Oliver (2006) reported variation in leaf-area ratio, specific leaf area, net assimilation rate, and stem-to-leaf ratio among *A. palmeri* accessions, suggesting that different *A. palmeri* ecotypes exist. Davis et al. (2015) concluded that neither *A. palmeri* genotype nor its maternal environment negatively influence soybean grain yield and that *A. palmeri*'s damage niche is solely dependent on the quantity of seeds introduced. Understanding biological characteristics among *A. palmeri* populations and how those characteristics are affected by emergence timing may elucidate *A. palmeri's* ability to compete as a weed in northern IN and AR.

The research objectives of this study were to determine the influence of planting date (early, mid-, or late season) and population source (AR, IN, MO, MS, NE, and TN) on growth and reproduction of *A. palmeri* established at TPAC and AAREC. The hypothesis for this experiment was that growth, inflorescence emergence, and seed production of *A. palmeri* will vary between populations collected across the Midwest and Midsouth, as these populations have adapted to their local environment.

Materials and Methods

Site Description and Experimental Design

Field studies were conducted near Lafayette, IN, at Throckmorton Purdue Agricultural Center (TPAC) (40.298717°N, 86.901449°W) during the summers of 2013 and 2014 and at the Arkansas Agriculture Research and Extension Center (AAREC) in Fayetteville, AR (36.054893°N, 94.101722°W) in 2014. At TPAC, the soil type was a Throckmorton silt loam (fine-silty, mixed, superactive, mesic Mollic Oxyaquic Hapludalfs) with a pH of 6.7 and 3% organic matter. The soil type at AAREC was a Leaf silt loam (fine, mixed, active, thermic Typic Albaquults) with a pH of 5.6 and 1.7% organic matter. The experimental design was a randomized complete block design, with four replications conducted over two field seasons at TPAC and one season at AAREC. Two factors were evaluated, planting date with three levels (early, mid-, and late season) and population with five levels (TPAC location: AR, IN, MO, MS, and NE; AAREC location: AR, IN, MO, NE, and TN). The MS population was not planted at AAREC and the TN population was not planted at TPAC.

Amaranthus palmeri Seed Preparation

Amaranthus palmeri seeds were collected from 20 to 30 female plants near Fayetteville, AR; Evansville, IN; Greenville, MS; Chamois, MO; Lincoln, NE; and (location unknown) TN (Table 1; Figure 1). Seeds were stored in a cooler at 4 C for 3 mo before planting. *Amaranthus palmeri* seed not used in 2013 was placed in cold storage and used for the 2014 season.

Amaranthus palmeri Planting

AAREC

At both sites, the entire plot area where *A. palmeri* was planted was tilled once. Undesired plants that emerged after conventional tillage were controlled with 840 g ae ha^{-1} paraquat (Syngenta Crop Protection, 410 Swing Road, Greensboro, NC). Weeds between plots were removed by tillage as needed, while weeds within plots were hand pulled. At both study locations, a total of five *A. palmeri* populations were evaluated. At AAREC, *A. palmeri* seeds were directly planted into peat pellets (No. 736 Jiffy Peat Pellets, Hummert International, Earth City, MO) and germinated in the greenhouse. Day and night greenhouse air temperatures were set at 34 and 25 C, respectively. The early, mid-, and late season greenhouse planting occurred on May 1, June 2, and July 16, 2014, respectively (Table 2). Approximately 2 wk after seeding in the greenhouse, the entire peat pellet was transplanted in the field in three rows spaced 91 cm apart at a density of 1 plant m^{-1} row. In 2013, *A. palmeri* failed to emerge in the peat pellets; however, *A. palmeri* emergence was successful for the second run of the study in 2014. Growing degree days (GDD) were calculated using Equation 1.

$$\mathrm{GDD}_{10} = \left(\frac{\text{minimum temperature} + \text{maximum temperature}}{2}\right) - 10\,\mathrm{C} \quad [1]$$

This is a common metric used for measuring plant and insect development in agronomic systems (Gilmore and Rogers 1958).

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Table 1. Collection locations of Palmer amaranth (*Amaranthus palmeri*) populations and monthly air temperature and precipitation means.[a]

Population source[b]	Latitude	Longitude	Elev	30-yr weather means										
				Air temperature					Precipitation					
				May	June	July	Aug	Sept	May	June	July	Aug	Sept	Total[c]
	°N	°W	m	C					mm					
Fayetteville, AR	36.05989	94.16237	387	18.9	23.6	26.1	25.8	21.1	132	121	82	77	116	528
Evansville, IN	37.97499	87.57399	118	18.9	23.9	25.5	24.7	20.5	136	96	100	76	77	485
Chamois, MO	38.67501	91.76959	164	18.0	23.0	25.5	25.0	20.3	131	112	109	103	106	561
Greenville, MS	33.39772	91.03798	40	22.5	26.5	28.3	27.5	24.2	135	115	100	56	70	476
Lincoln, NE	40.82230	96.68489	358	16.9	22.5	25.3	24.2	18.9	109	110	86	89	77	471
Lafayette, IN	40.29871	86.90144	211	16.7	21.7	23.3	22.2	18.6	118	116	104	100	71	509

[a]Abbreviations: AR, Arkansas; Aug, August; Elev, elevation; IN, Indiana; MO, Missouri; MS, Mississippi; NE, Nebraska; Sept, September.
[b]Seeds were provided by weed science colleagues from each location. Approximately 20 to 30 female plants were collected from each location to represent a population. The source of the TN population established at Arkansas Agriculture Research and Extension Center, located near Fayetteville, AR, is unknown. The Throckmorton Purdue Agricultural Center is located 13 km south of Lafayette, IN.
[c]Average cumulative rainfall from May through September for Lafayette, IN, was included for reference.

TPAC

The study site at TPAC was established similarly to the AAREC site. Before planting at TPAC, approximately 300 seeds weighing 0.1 g from each location plus 1 cup of white silica sand were placed in a coin envelope (ULINE, 12575 Uline Drive, Pleasant Prairie, WI) and thoroughly mixed. At planting, a single coin envelope that contained mixed *A. palmeri* seed and sand was emptied into one planter unit. A total of three planter units spaced 40 cm apart were used to plant *A. palmeri* seed at a depth of 1.3 cm or less. Plots measured 2.3 by 7.6 m in size and included a 1.5-m buffer between replications. The small-plot weed seed planter was calibrated to disperse all contents in the coin envelope after one pass that measured 7.6 m. After emergence, *A. palmeri* were thinned to allow 20 cm of space between individual plants. Due to inconsistent mixing of *A. palmeri* seed and sand, spacing between individual *A. palmeri* plants occasionally exceeded 20 cm.

Amaranthus palmeri seeds from each population were planted in the field early, mid-, and late season (Table 3). At TPAC, the early season planting occurred on May 22, 2013, and May 27, 2014; the midseason planting on June 5, 2013, and June 6, 2014; and the late season planting on July 15, 2013, and July 18, 2014.

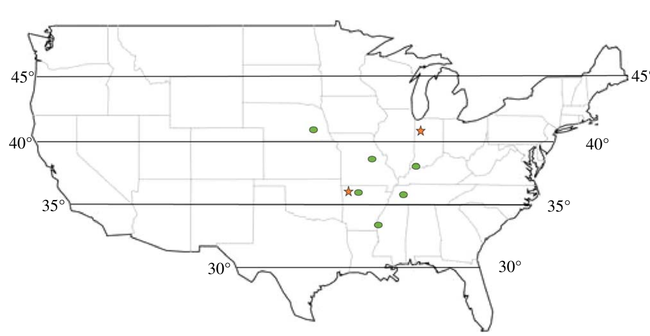

Figure 1. A map of the United States showing where Palmer amaranth (*Amaranthus palmeri*) populations were collected and the location of the experimental sites. Green circles represent the locations where *A. palmeri* seed was collected and orange stars represent the location of the experimental sites. The Indiana experimental site was located at the Throckmorton Purdue Agricultural Center near Lafayette, IN, and the Arkansas experimental site was located at the Arkansas Agriculture Research and Extension Center near Fayetteville, AR.

Weekly Data Collection

Amaranthus palmeri height was recorded weekly at both locations. A single plant representative of each plot was measured from the soil surface to the shoot apex or highest point of the reproductive structure, when reproductive structures were present. The same plants were not measured each week due to variation in growth within the populations. Percent inflorescence emergence was recorded weekly at TPAC, but not at AAREC. Inflorescence emergence was determined once reproductive structures ascended 0.6 cm above the shoot apex. Plants with emerged inflorescence were counted and divided by the total number of plants in the plot. At both study locations, all female and male plants were counted before *A. palmeri* was harvested to determine the ratio of male to female plants. Female plants were identified by spines located in bracts and rough inflorescence, in contrast to male plants with soft inflorescence and spineless bracts (Bryson and DeFelice 2009).

Amaranthus palmeri *Harvest*

Amaranthus palmeri planted early and midseason were harvested in 2013 at TPAC. The late season planting was not harvested in 2013 at TPAC, because mature seed was not present at time of harvest. Aboveground biomass from female plants was harvested on September 18, 2013, and September 13, 2014, at TPAC, and on September 12, 2014, for early and midseason plantings and

Table 2. Date of planting in the greenhouse, transplanting to peat pellets and field, and biomass harvest of five Palmer amaranth (*Amaranthus palmeri*) populations at three planting dates in a field study conducted at the Arkansas Agriculture Research and Extension Center in 2014.

A. palmeri	Early season	Midseason	Late season
	Date		
Greenhouse planting[a]	May 1	June 2	July 16
Transplant to peat plugs	May 6	June 6	July 21
Transplant to field[b]	May 12	June 16	August 1
Biomass harvest	September 12	September 12	October 3

[a]Day and night greenhouse temperatures were set to 34 and 25 C, respectively.
[b]Plants were irrigated at transplanting.

https://doi.org/10.1017/wsc.2018.12 Published online by Cambridge University Press

Table 3. Date of planting, seedling emergence, inflorescence emergence, seed maturation, and biomass harvest of five Palmer amaranth (*Amaranthus palmeri*) populations at three planting dates in a field study conducted at the Throckmorton Purdue Agricultural Center.

A. palmeri	2013			2014		
	Early season	Midseason	Late season	Early season	Midseason	Late season
	Date					
Planting	May 22	June 5	July 15	May 27	June 6	July 18
Seedling emergence[a–c]	June 6	June 11	August 1	June 5	June 11	July 26
Inflorescence emergence[d]	July 2	July 10	August 14	June 24	July 1	August 13
Seed maturation[e]	August 23	September 1	———	August 13	August 18	September 9
Biomass harvest[f]	September 18	September 18	———	September 13	September 13	September 13

[a]Date of first observed early season seedling emergence. Populations emerged no later than June 10, 2013 and June 7, 2014, respectively.
[b]Date of first observed midseason seedling emergence. Populations emerged no later than June 14 in 2013 and 2014.
[c]Date of first observed late season seedling emergence. All populations emerged on August 1, 2013, and all populations emerged no later than July 30, 2014.
[d]Inflorescence emergence was determined once reproductive structures emerged 0.6 cm above the apical meristem. Date recorded is when inflorescence emergence was first observed within each planting.
[e]Date of seed maturation was determined when seed appeared black and shiny. Mature seed was not observed at time of harvest in 2013 when *A. palmeri* was planted late season.
[f]*Amaranthus palmeri* planted late season were not harvested in 2013.

October 3, 2014, for the late season plating at AAREC, when shiny black seeds were present. Two pseudo-replicate biomass samples from the center row of each plot were taken by clipping female plants from the soil surface, placing them in separate paper bags, and storing them in forced-air dryers set at 40 C for 2 wk. After being dried, plant biomass was weighed, and reproductive structures were hand threshed to remove seed, after which *A. palmeri* stems were discarded and floral chaff was separated from seed using a vertical forced-air column tube. Seeds remaining at the bottom of the forced-air column tube were weighed. To determine total plant seed production and number of seeds per 0.1 g of seed, a single subsample of pure seed weighing approximately 0.1 g was quantified. The quantity of seeds extracted from the 0.1-g subsample was multiplied by total seed weight collected from each female plant to calculate seed production. The quantity of seed per gram of seed was a measurement used to determine seed size. The number of seeds per gram of seed measurement was recorded for both years at TPAC, but not at AAREC.

Statistical Analysis

All data were checked for normality and constant variance using PROC UNIVARIATE in SAS (v. 9.3; SAS Institute, 100 SAS Campus Drive, Cary, NC), and transformed when necessary and tested for appropriate interactions. Biomass and seed production data were subjected to ANOVA using the PROC MIXED procedure in SAS. Means were separated using Tukey's HSD at the 0.05 level of significance. Biomass data from both study locations were log transformed and seeds per plant data collected from AAREC and TPAC were log and square-root transformed, respectively. Study locations were analyzed separately. If the effect of year was significant at $\alpha \leq 0.05$, data were separated by year for the analysis. *Amaranthus palmeri* population and planting date were considered fixed effects, and replication was treated as a random effect. Biomass data from the 2013 late season planting at TPAC was not harvested in 2013, therefore seed production data were not recorded. In 2014 at TPAC, biomass from all three plantings was harvested.

Nonlinear regression analysis was conducted using a four-parameter logistic function (Equation 2) using SigmaPlot (SigmaPlot v. 12.5, Systat Software, San Jose, CA) that regressed plant height or percent inflorescence emergence against cumulative GDD_{10} since planting.

$$y = c + (d - c)/\left(1 + \left(\frac{x}{GDD_{50}}\right)^{(-b)}\right) \quad [2]$$

In this model, y is plant height or percent inflorescence emergence; GDD_{50} is the total number of growing degree days accumulated since planting for *A. palmeri* to grow to 50% of final height or inflorescence emergence, b is relative slope around parameter GDD_{50}; c is the lower limit, considered as 0; and d is the estimated maximum plant height or percent inflorescence emergence. At TPAC, data were pooled across years for the early and mid season planting dates, but data were separated by year for the late season planting date for growth regression analysis. The AR, IN, and MO populations planted late season in 2013 did not exhibit a sigmoidal growth pattern and could not be fit to the model. However, years were combined within each planting for regression analysis for percent inflorescence emergence data. At AAREC, growth regression analysis was conducted using data only from year 2014, as seedling establishment for year 2013 of the experiment failed. Predicted estimated means of maximum height, GDD_{50} to grow to 50% of final height, and GDD_{50} to 50% inflorescence emergence were separated within planting date. Alpha levels were adjusted using a Bonferroni correction (α/n, where n = total number of pairwise comparisons) when multiple comparisons were evaluated for each main effect, therefore maintaining an α level of 0.05 (Brosofske et al. 2001). Root mean-square error (RMSE) (Equation 3) and modeling efficiency coefficient (EF) (Equation 4) were calculated to test goodness of fit for the logistic model, where P_i is the predicted value, O_i is the observed value, n is the total number of observations, and $\overline{O}_i$ is the mean observed value (Archontoulis and Miguez 2015).

$$\text{RMSE} = \left[\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2\right]^{1/2} \quad [3]$$

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Table 4. Parameter estimates and the goodness of fit (RMSE and EF)[a] of the four-parameter logistic function[b] fit to height of five Palmer amaranth (*Amaranthus palmeri*) populations at three planting dates in a field study conducted at the Throckmorton Purdue Agricultural Center.[a]

Pop.	b^{c}	c^{c}	$d^{c,d}$	$GDD_{50}^{c,d}$	RMSE[e]	EF
		——— cm ———				
			Early season			
AR	4.8 ± 0.47	4.1 ± 2.9	216 ± 12 ab	853 ± 23 a	12.0	0.98
IN	4.3 ± 0.36	1.2 ± 2.9	196 ± 8 b	767 ± 18 bc	10.2	0.99
MO	4.2 ± 0.36	1.3 ± 3.0	225 ± 10 a	782 ± 21 bc	11.9	0.98
MS	4.1 ± 0.34	1.3 ± 3.5	252 ± 12 a	792 ± 21 ab	12.2	0.99
NE	4.6 ± 0.37	0.5 ± 3.3	201 ± 6 b	698 ± 13 c	11.5	0.99
			Midseason			
AR	4.2 ± 0.41	4.9 ± 2.3	223 ± 15 ab	784 ± 30 a	11.1	0.98
IN	4.0 ± 0.37	3.6 ± 2.6	198 ± 10 b	674 ± 20 a	11.1	0.98
MO	3.9 ± 0.40	3.0 ± 3.2	236 ± 14 ab	713 ± 26 a	13.4	0.98
MS	4.4 ± 0.35	4.6 ± 2.4	243 ± 11 a	720 ± 18 a	11.4	0.99
NE	5.0 ± 0.52	5.1 ± 3.0	207 ± 9 ab	665 ± 16 a	14.7	0.98
			Late season 2013[f]			
MS	5.6 ± 2.50	0.7 ± 2.9	168 ± 99 a	630 ± 151 a	7.4	0.97
NE	5.7 ± 0.58	0.5 ± 1.2	146 ± 9 a	541 ± 16 a	3.0	0.99
			Late season 2014			
AR	9.7 ± 1.1	1.4 ± 1.5	96 ± 3 c	402 ± 7 a	5.2	0.98
IN	10.2 ± 2.0	1.8 ± 3.0	112 ± 6 c	401 ± 11 a	10.1	0.96
MO	9.9 ± 1.1	2.3 ± 2.3	133 ± 5 ab	388 ± 7 a	7.8	0.98
MS	10.8 ± 2.4	1.9 ± 3.4	115 ± 7 bc	401 ± 12 a	11.6	0.95
NE	10.1 ± 1.2	3.0 ± 2.7	150 ± 5 a	383 ± 7 a	9.2	0.98

[a]Abbreviations: AR, Arkansas; EF, modeling efficiency coefficient; GDD, growing degree days; IN, Indiana; MO, Missouri; MS, Mississippi; NE, Nebraska; Pop., population; RMSE, root mean-square error.
[b]$Y = c + (d - c)/(1 + (x/(GDD_{50})^{-b})$, where Y is *A. palmeri* height, GDD_{50} is the accumulated GDD since planting that resulted in 50% of maximum plant height, b is the slope of the regression line at GDD_{50}, c is the minimum height, and d is the maximum height.
[c]Values are mean ± SE.
[d]Means ± SE within a column and within early, mid-, or late season planting followed by the same letter are not significantly different. Alpha levels were adjusted using a Bonferroni correction (α/n, where n = total number of pairwise comparisons).
[e]Smaller RMSE values indicate predicted values are closer to observed values.
[f]The four-parameter logistic function did not fit the growth of late season planted populations from AR, IN, and MO in 2013.

$$EF = 1 - \left[\sum_{i=1}^{n}(O_i - P_i)^2 / \sum_{i=1}^{n}(O_i - \overline{O}_i)^2\right] \quad [4]$$

The RMSE value describes how well the data fit the model. An RMSE value of zero suggests observed and predicted values are a perfect fit to the model. Moreover, EF values close to 1 suggest that model predictions are more accurate.

Data for the observed number of male to female plants from each location were compared with an expected 1:1 ratio (Equation 5) by subjecting data to a Pearson's chi-square test at $\alpha = 0.05$, with df = 1 and $\chi^2 = 3.841$ to determine whether the proportion of male to female plants represents a 1:1 ratio. Data were pooled across years for the TPAC location, and data for ARREC represent run 2 of the experiment. The following equation was used for calculating expected male and female plants.

$$y = 0.5\,(\text{male plants} + \text{female plants}) \quad [5]$$

To determine the effect of biomass on seed production, a Pearson correlation analysis (PROC CORR) was performed using SAS. Study locations were analyzed and presented separately for total seed production data.

Results and Discussion

Amaranthus palmeri *Growth and Inflorescence Emergence*

TPAC

Amaranthus palmeri populations collected from AR, IN, MO, MS, and NE survived and produced seed when seeded in northern IN at TPAC. A logistic regression model described (EF 0.95 to 0.99, RMSE 3.0 to 14.7) the relationship between *A. palmeri* plant height and GDDs as well as inflorescence emergence and GDDs (Tables 4 and 5). Height of late season planted *A. palmeri* populations collected from AR, IN, and MO could not be described by the logistical regression model in 2013; nonetheless, height increased as GDDs accumulated (Figure 2). Growth and inflorescence emergence varied among *A. palmeri* populations.

The maximum plant height estimated by the model for early season planted and midseason-planted *A. palmeri* from MS was 252 and 243 cm, respectively (Table 4). The estimated maximum height of early season planted *A. palmeri* populations from NE and IN were 20% to 22% shorter compared with the MS population. However, when these populations were planted mid- and late season in 2013, heights were similar among populations from MS and NE. The MS population was 23% taller than the IN

https://doi.org/10.1017/wsc.2018.12 Published online by Cambridge University Press

Table 5. Parameter estimates and the goodness of fit (RMSE and EF)[a] of the four-parameter logistic function[b] fit to inflorescence emergence of five Palmer amaranth (*Amaranthus palmeri*) populations at three planting dates in a field study conducted at the Throckmorton Purdue Agricultural Center.

Pop.	b[c]	c[c]	d[c]	GDD_{50}[c,d]	RMSE[e]	EF
			%			
			Early season			
AR	7.7 ± 0.7	0.7 ± 1.7	104 ± 2.4	687 ± 10 a	8.5	0.98
IN	8.9 ± 0.9	−1.8 ± 1.9	101 ± 1.8	589 ± 8 b	8.9	0.98
MO	8.5 ± 0.6	−0.4 ± 1.2	103 ± 1.5	680 ± 6 a	6.0	0.99
MS	8.6 ± 0.7	−1.3 ± 1.6	101 ± 1.6	600 ± 7 b	7.7	0.98
NE	13.1 ± 1.3	−1.1 ± 1.5	99 ± 1.1	536 ± 4 c	6.9	0.99
			Midseason			
AR	12.3 ± 2.0	3.5 ± 1.9	101 ± 2.6	637 ± 8 a	11.1	0.96
IN	6.5 ± 1.0	−0.1 ± 2.8	104 ± 3.6	535 ± 14 b	13.5	0.96
MO	10.9 ± 1.2	1.6 ± 1.4	102 ± 1.9	625 ± 6 a	8.0	0.98
MS	7.5 ± 0.9	1.0 ± 2.0	104 ± 2.8	582 ± 10 b	10.2	0.97
NE	6.9 ± 0.6	−0.8 ± 1.6	102 ± 1.7	489 ± 7 c	7.4	0.98
			Late season			
AR	27.8 ± 2.7	3.1 ± 0.9	100 ± 1.9	527 ± 2 a	5.1	0.98
IN	10.0 ± 1.9	−0.5 ± 2.5	104 ± 5.5	461 ± 10 b	11.1	0.95
MO	9.6 ± 1.7	−0.6 ± 2.3	105 ± 5.2	465 ± 9 b	9.9	0.97
MS	15.0 ± 2.0	0.8 ± 1.2	104 ± 3.2	526 ± 4 a	6.1	0.98
NE	11.2 ± 1.9	2.9 ± 2.5	103 ± 3.4	391 ± 8 c	10.5	0.97

[a]Abbreviations: AR, Arkansas; EF, modeling efficiency coefficient; GDD, growing degree days; IN, Indiana; MO, Missouri; MS, Mississippi; NE, Nebraska; Pop., population; RMSE, root mean-square error.
[b]$Y = c + (d - c)/(1 + (x/(GDD_{50})^{-b})$, where Y is *A. palmeri* percent inflorescence emergence, GDD_{50} is the accumulated growing degree days since planting that resulted in 50% of inflorescence emergence, b is the slope of the regression line at GDD_{50}, c is the minimum inflorescence emergence, and d is the maximum inflorescence emergence.
[c]Values are mean ± SE.
[d]Means ± SE within a column and within early, mid-, or late season planting followed by the same letter are not significantly different. Alpha levels were adjusted using a Bonferroni correction (α/n, where n = total number of pairwise comparisons).
[e]Smaller RMSE values indicate predicted values are closer to observed values.

population when planted midseason, but heights were similar when planted late season in 2014. Contrary to results for early season planted *A. palmeri* height, the NE population planted late season in 2014 was 30% to 56% taller than the AR, IN, and MS populations. It appears that plants from MS may be more competitive than plants from IN when emergence occurs early or midseason, because plants from the MS population were taller. It is possible that plants in the MS population that are adapted to warmer climates (Table 1) are more competitive and devote more energy to biomass production when grown in northern Indiana's environment. However, when *A. palmeri* emerged late season, the NE population was taller than the AR, IN, and MS populations. Over the course of a growing season, the change in plant height accumulation among populations gives evidence of the genetic plasticity of *A. palmeri*. Variation among *A. palmeri* accessions has been reported in other studies when grown in AR. Bond and Oliver (2006) found that 33% of AR accessions had 13% less leaf-area ratio compared with accessions collected from MO and MS.

GDDs for *A. palmeri* to grow to 50% of maximum plant height, as estimated by the model, were fewer as *A. palmeri* populations were planted later in the season. Total GDD for *A. palmeri* planted early, mid-, and late season 2013 and late season 2014 to grow to 50% of maximum height ranged from 698 to 853 GDD (155 GDD range), 665 to 784 GDD (119 GGD range), 541 to 630 GDD (89 GDD range), and 383 to 402 GDD (19 GDD range), respectively (Table 4). In 2014, a narrow range of 1 to 19 GDD among *A. palmeri* populations to grow to 50% of maximum height suggests these populations exhibit similar growth when planted late season because differences between populations were not observed (Table 4). Also, the strong influence of shorter day length to trigger flowering negated the potential for growth differences to develop between populations (Horak and Loughin 2000; Huang et al. 2000; Keeley et al. 1987). Similarly, *A. palmeri* planted midseason (119 GDD range) exhibited similar growth among populations at 50% of maximum height. However, a greater range of GDD (155) between populations to grow to 50% of maximum height, similar to that observed between the NE and AR populations, suggest a greater competitive ability may be present in the NE population when plants are established early season. The regression analysis that described midseason *A. palmeri* growth to 50% of maximum height exhibited a growth rate of 0.14 to 0.17 cm GDD^{-1} (unpublished data). These results agree with those previously reported by Horak and Loughlin (2000), in which *A. palmeri* planted mid-June grew 0.18 and 0.21 cm GDD^{-1} when measured at 100 and 87 cm, respectively.

Inflorescence emergence occurred in all *A. palmeri* populations and planting dates in this study. *Amaranthus palmeri* planted early and midseason achieved 50% inflorescence emergence no sooner than 536 and 489 GDD, respectively, after planting (Table 5). GDD to 50% inflorescence emergence ranged from 391 to 527 GDD for late season planted *A. palmeri*. This is equivalent to 34 to 46 d of daily maximum and minimum air temperatures of 27 and 16 C, respectively. Average daily June and July maximum and minimum air temperatures of 27 and 16 C, respectively, and an average day length of 14 to 15 h are expected in early summer in Lafayette, IN. Huang et al. (2000) reported that the phenological development of *A. retroflexus*, a species similar to *A. palmeri*, is sensitive to decreasing day length. Huang et al. (2000) reported the days from seedling emergence to end of seed set increased from 50.8 d when exposed to an 8-h photoperiod to 104.5 d when exposed to a 16-h photoperiod. The aforementioned authors also identified four development phases for *A. retroflexus* in response to photoperiod treatments. However, the authors did not indicate whether other *Amaranthus* species exhibit reproductive development phases similar to *A. retroflexus*.

At every planting date, the NE population attained 50% inflorescence emergence first (Figure 3; Table 5). In fact, 50% inflorescence emergence for early, mid-, and late season planting dates occurred 53, 46, and 70 GDD, respectively, earlier than the next closest population (IN). It is important to consider that the 30-yr average monthly air temperature at Lincoln, NE, and Lafayette, IN, from May through September deviate no more than 2 C between locations (Table 1). Moreover, both locations are similar in latitude and may help explain why the NE population was more successful than other populations when grown at TPAC (Figure 1). It is important to remember that one population was used from each state and by no means represents the diversity of *A. palmeri* within a state. For example, Schultz et al. (2015) reported substantial variation in herbicide sensitivity among 187 *A. tuberculatus* populations that were collected in MO. Mature *A. palmeri* seed were produced within 27 d of inflorescence

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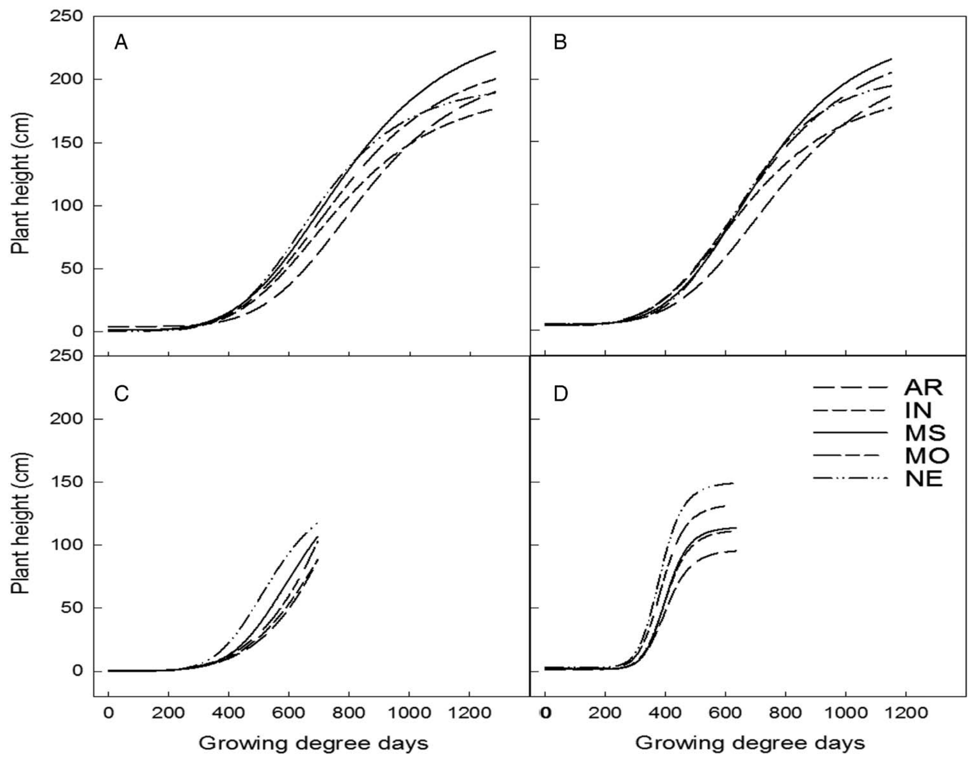

Figure 2. Influence of planting date on Palmer amaranth (*Amaranthus palmeri*) height for (A) early season planting, (B) midseason planting, (C) late season planting 2013, and (D) late season planting 2014 at Throckmorton Purdue Agricultural Center. Parameter estimates are provided in Table 4. Years were combined for early and midseason plantings, and years are presented separately for the late season plantings in 2013 and 2014. Growing degree day 0 represents the time of *A. palmeri* planting.

emergence or 53 d after *A. palmeri* were planted late season (Table 3). These results agree with those previously reported by Keeley et al. (1987), in which *A. palmeri* planted on August 1 in California produced seed within 42 d of planting. Bell and Tranel (2010) found that 9 d after pollination, up to 12% of the seed from female *A. tuberculatus* plants under greenhouse conditions germinated.

AAREC

The logistic regression model described (EF 0.87 to 0.98, RMSE 6.8 to 18.0) the relationship between *A. palmeri* height and GDD (Table 6; Figure 4). The predicted maximum height for all *A. palmeri* populations planted early and midseason at AAREC exceeded 140 cm (Table 6). Maximum height among populations was generally similar at the early and midseason plantings. However, *A. palmeri* from MO was 19% and 15% taller than the NE population when planted early and midseason, respectively. At the late season planting, all populations grew taller than the NE population. The local AR population was among the tallest at this site and measured 153% taller than the NE population. It is important to note that the northernmost *A. palmeri* population represented in this study was collected from Lincoln, NE (40.82230°N), and when introduced to AAREC late season, did not grow as tall as populations adapted to southern latitudes (33.39772 to 38.67501°N). These data support the idea that *A. palmeri* from NE have evolved under longer day lengths and populations that have evolved in areas with shorter day lengths are likely to grow taller when introduced to longitudes near the AAREC. Differences in GDD_{50} between populations at the early, mid-, or late seasons planting were not observed at the AAREC location.

Amaranthus palmeri *Biomass and Seed Production*

TPAC

The population by planting interaction was not significant in either year for biomass. Therefore, mean separations for main effects are presented. Biomass across *A. palmeri* populations ranged from 184 to 531 and 126 to 252 g $plant^{-1}$ in 2013 and 2014, respectively (Table 7). Sellers et al. (2003) reported *A. palmeri* biomass to exceed 800 g $plant^{-1}$ at 14 wk after planting in late May in MO. The MS population produced 189% more biomass per plant than the NE population in 2013. In 2014, populations collected from NE, MO, and MS produced 63%, 90%, and 100% more biomass per plant than IN, respectively. Parameter estimates that predicted maximum *A. palmeri* height were lower for IN and NE populations compared with MS. Less biomass accumulation in NE in 2013 and IN in 2014 compared with MS is likely attributable to shorter plant heights (Table 4).

Amaranthus palmeri planted early season weighed on average 75% more than *A. palmeri* planted midseason in 2013 (Table 7). In 2014, *A. palmeri* planted early and midseason produced similar amounts of biomass; however, *A. palmeri* planted early and midseason produced 164% or more biomass than late season planted *A. palmeri*.

Addition of seed to the soil seedbank is the only mechanism for annuals to ensure survival for more than one season. In 2013, a significant effect of population by planting date was not observed with number of seeds per plant; however, the population by planting date effect was significant in 2014 ($P = 0.0197$). Differences in population main effect was observed in 2013 with IN and AR populations. The IN population produced 209% more seed per plant than AR (Table 7). Planting date influenced the quantity of seeds per plant. *Amaranthus palmeri* planted early

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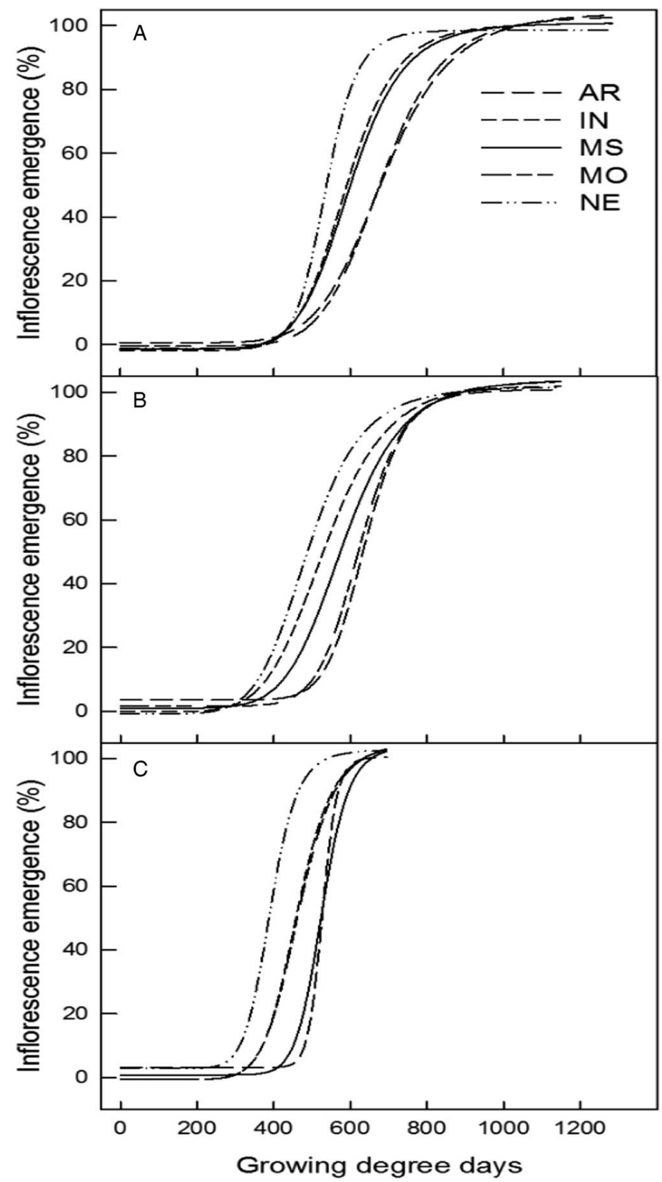

Figure 3. Influence of planting date on Palmer amaranth (*Amaranthus palmeri*) percent inflorescence emergence for (A) early season planting, (B) midseason planting, and (C) late season planting at Throckmorton Purdue Agricultural Center. Parameter estimates are provided in Table 5. Years were combined for early, mid-, and late season planting dates. Growing degree day 0 represents the time of *A. palmeri* planting.

season produced up to 113% more seed per plant than midseason-planted *A. palmeri*. In 2014, *A. palmeri* populations from IN, MO, MS, and NE that were planted late season produced 92% to 99% less seed than those populations planted midseason. However, the AR population planted mid- and late season produced similar quantities of seeds per plant (Table 7). In 2013, late season planted *A. palmeri* was not harvested, because no mature seeds were present at harvest. However, mature seeds were present on plants established late season in 2014 (Table 3). *Amaranthus palmeri* planted late season produced 47 to 7,443 seeds plant^{-1}. However, not all seeds in this study were likely to be viable and germinate the following season. In a study evaluating *A. palmeri* seedbank persistence, Jha et al. (2014) reported less than 1% of the total seedbank emerged after 4 yr.

Aboveground biomass and seed production (no. seeds plant^{-1}) were positively correlated, which indicated that plants with greater biomass produce more seeds than plants with less biomass (Figure 5A). Schwartz et al. (2016) also reported a positive correlation between aboveground biomass and seed production in two *Amaranthus* species, *A. palmeri* and *A. tuberculatus*. Data from this study and Schwartz et al. (2016) suggest that control failure or emergence of late season female *A. palmeri* plants that produce large amounts of biomass will produce seed for the next generation and replenish the soil seedbank.

The quantity of seeds per gram of seed was a measurement used to determine seed size. The population by planting date interaction was not observed in 2013; however, in 2014 the interaction influenced the number of seeds per gram of seed (P = 0.0433). Data from the population main effect suggest that *A. palmeri* collected from AR and MS had 21% to 28% fewer seeds g^{-1} of seed than *A. palmeri* from NE in 2013, suggesting that seeds produced by AR and MS populations were larger. Cidecydan and Malloch (1982) reported broadleaf dock (*Rumex obtusifolius* L.) germinating from seeds larger than 1.4 mm compared with 1.2- to 1.0-mm seed produced 46% more biomass at 31 d after planting. It is possible that maternal genetic background in the AR and MS populations resulted in heavier seeds, because female plants were likely pollinated by male plants from all populations. The main effect planting date did not influence the quantity of seed per gram of seed in 2013. In 2014, the number of seeds per gram of seed ranged from 2,596 to 3,991 across all populations and planting dates (Table 7). The quantity of seeds per gram of seed were similar between *A. palmeri* from AR planted early, mid-, and late season. The same trend was also observed with populations from IN, MO, and MS, but not NE. *Amaranthus palmeri* from NE planted late season had 52% fewer seeds per gram of seed than NE *A. palmeri* planted early or midseason.

AAREC

The population by planting date interaction did not influence *A. palmeri* biomass or seed production. *Amaranthus palmeri* biomass ranged from 418 to 1,513 g plant^{-1} across all populations (Table 8). The NE population produced the least amount of biomass. Populations from AR, IN, MO, and TN produced 25% to 41% more biomass than the NE population. The date of *A. palmeri* planting influenced biomass production. *Amaranthus palmeri* planted early season produced 25% and 102% more biomass per plant than *A. palmeri* planted mid- and late season, respectively. These data suggest that early emerging *A. palmeri* will be highly competitive with crops for light, water, and nutrients and agrees with results reported by Keeley et al. (1987). Thus, plants need to be controlled throughout the critical weed-free period to minimize crop yield loss.

Seed production per plant was similar between all *A. palmeri* populations (P = 0.1538). However, *A. palmeri* planted early and midseason produced the greatest quantity of seed. *Amaranthus palmeri* planted early and midseason produced 156% to 216% more seed per plant than *A. palmeri* planted late season. Thus, early and midseason emerging *A. palmeri* will rapidly replenish the soil seedbank and compete with crops if not controlled. It is also important to consider that late season planted *A. palmeri* produced 53,872 seeds plant^{-1}. Late season emerging *A. palmeri* will likely compete less with the current crop than early- or midseason emerging plants; however, plants that

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Table 6. Parameter estimates and the goodness of fit (RMSE and EF)[a] of the four-parameter logistic function[b] fit to height of five Palmer amaranth (*Amaranthus palmeri*) populations at three planting dates in a field study conducted at the Arkansas Agriculture Research and Extension Center.

Pop.	b^c	c^c	$d^{c,d}$	$GDD_{50}{}^{c,d}$	RMSE[e]	EF
			——— cm ———			
			Early season			
AR	6.9 ± 0.6	11.1 ± 2.5	163 ± 3 ab	926 ± 12 a	9.5	0.98
IN	5.6 ± 0.6	9.0 ± 3.3	155 ± 4 ab	947 ± 19 a	11.1	0.98
MO	6.5 ± 0.7	11.1 ± 3.4	168 ± 4 a	929 ± 17 a	12.3	0.98
NE	5.4 ± 1.1	6.6 ± 5.3	141 ± 8 b	990 ± 37 a	18.0	0.94
TN	6.4 ± 0.9	7.8 ± 4.0	153 ± 5 ab	949 ± 22 a	14.6	0.96
			Midseason			
AR	6.7 ± 1.1	5.5 ± 8.0	171 ± 6 ab	803 ± 20 a	15.7	0.96
IN	7.0 ± 0.8	5.3 ± 5.5	172 ± 4 ab	774 ± 13 a	10.5	0.98
MO	6.5 ± 0.9	5.0 ± 7.2	187 ± 5 a	801 ± 17 a	13.6	0.97
NE	7.0 ± 1.0	4.3 ± 6.3	163 ± 4 b	788 ± 16 a	12.4	0.97
TN	6.9 ± 0.8	6.2 ± 5.3	167 ± 3 b	770 ± 13 a	10.0	0.98
			Late season			
AR	5.1 ± 1.7	1.9 ± 11.1	134 ± 16 a	687 ± 40 a	13.2	0.95
IN	12.0 ± 3.5	9.0 ± 5.5	97 ± 3 a	627 ± 16 a	10.9	0.95
MO	16.3 ± 12.5	10.5 ± 7.1	75 ± 4 b	617 ± 21 a	14.6	0.87
NE	9.2 ± 3.0	7.5 ± 3.9	53 ± 2 c	614 ± 24 a	6.8	0.92
TN	6.7 ± 2.5	4.0 ± 9.0	96 ± 9 ab	665 ± 37 a	14.0	0.92

[a]Abbreviations: AR, Arkansas; EF, modeling efficiency coefficient; GDD, growing degree days; IN, Indiana; MO, Missouri; NE, Nebraska; Pop., population; TN, Tennessee; RMSE, root mean-square error.
[b]$Y = c + (d - c)/(1 + (x/(GDD_{50})^{-b})$, where Y is *A. palmeri* height, GDD_{50} is the accumulated growing degree days since planting that resulted in 50% of maximum plant height, b is the slope of the regression line at GDD_{50}, c is the minimum height, and d is the maximum height.
[c]Values are mean ± SE.
[d]Means ± SE within a column and within early, mid-, or late season planting followed by the same letter are not significantly different. Alpha levels were adjusted using a Bonferroni correction (α/n, where n = total number of pairwise comparisons).
[e]Smaller RMSE values indicate predicted values are closer to observed values.

produce up to 54,000 seeds plant^{-1} will be problematic for crop producers in future cropping seasons. Aboveground biomass and seed production (no. seeds plant^{-1}) were positively correlated and were similar to the trend observed at TPAC (Figure 5B).

Amaranthus palmeri seed production without crop competition has been reported in excess of 250,000 seeds plant^{-1} (Keeley et al. 1987; Sellers et al. 2003). Total *A. palmeri* seed production per plant at TPAC did not exceed 100,000 seeds plant^{-1} and was less than seed production per plant at AAREC (250,000 seeds plant^{-1}) (unpublished data). Lower seed production per plant can be attributed to greater intraspecific *A. palmeri* competition, as *A. palmeri* plants were planted closer to one another at TPAC (20 cm by 40 cm) than at AAREC (100 cm by 91 cm), Missouri (70 to 100 cm by 150 cm [Sellers et al. 2003]), and California (33 cm by 100 cm [Keeley et al. 1987]) locations. Therefore, seed production per plant at TPAC represents a scenario of a heavy *A. palmeri* infestation, whereas seed production at AAREC, Missouri, and California characterizes seed production per plant in areas with low to moderate *A. palmeri* infestations.

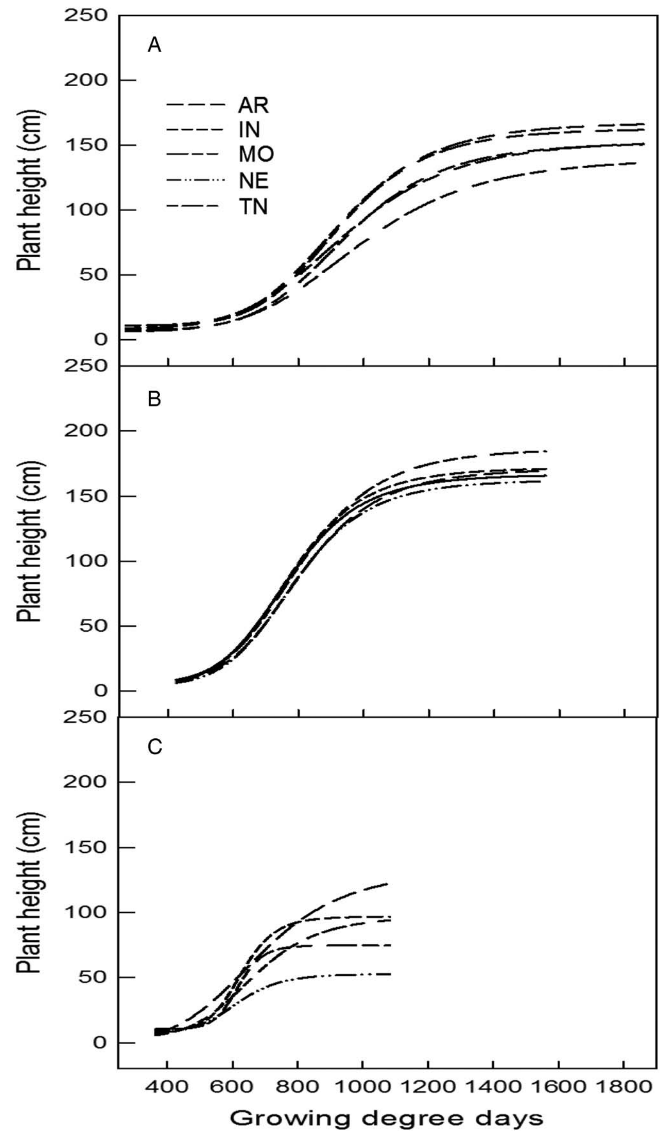

Figure 4. Influence of planting date on Palmer amaranth (*Amaranthus palmeri*) height for (A) early season planting, (B) midseason planting, and (C) late season planting at Arkansas Agriculture Research and Extension Center. Parameter estimates are provided in Table 6. Growing degree day 0 represents the time of *A. palmeri* planting.

Frequency of Male and Female Amaranthus palmeri

TPAC

Sex determination of all late season planted *A. palmeri* from MS in 2014 and AR in both years was not recorded before biomass harvest. Results from the chi-square analysis suggest that *A. palmeri* populations from NE planted early, mid-, or late season and AR planted early or midseason had an equal distribution of male to female plants (Table 9). This result agrees with previous research by Keeley et al. (1987), in which the male-to-female plant ratio was observed to be 1:1. However, late season planted *A. palmeri* populations from IN and MS had 20% and 40% more male plants than female plants, respectively. The MO population was the only population not to have an equal distribution of male to female plants when *A. palmeri* were planted midseason. This population had 23% more male plants than female plants. When *A. palmeri* was planted early season, there was an equal distribution of male and female plants in all populations.

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Table 7. Palmer amaranth (*Amaranthus palmeri*) biomass and seed production of five *A. palmeri* populations established at three planting dates in a field study conducted at the Throckmorton Purdue Agricultural Center.[a]

		A. palmeri					
		Biomass[b,c]		Seed production[b]			
Pop.	Planting	2013	2014	2013	2014	2013	2014
		—— g plant^{-1} ——		—— Seeds plant^{-1} [d] ——		—— Seeds g^{-1} ——	
AR		398 ab	139 ab	15,663 b	——	2,193 b	——
IN		344 ab	126 b	48,412 a	——	2,709 ab	——
MS		531 a	252 a	32,708 ab	——	2,389 b	——
MO		414 ab	240 a	24,093 ab	——	2,619 ab	——
NE		184 b	206 a	31,941 ab	——	3,036 a	——
	Early	477 a	258 a	41,584 a	——	——	——
	Mid	272 b	232 a	19,543 b	——	——	——
	Late[e]	——	88 b	——	——	——	——
AR	Early	——[f]	——	——	19,090 c-f	——	3,275 a-c
AR	Mid	——	——	——	4,619 e-g	——	2,862 bc
AR	Late	——	——	——	47 g	——	2,659 c
IN	Early	——	——	——	49,701 a-c	——	3,798 ab
IN	Mid	——	——	——	38,962 a-d	——	3,646 a-c
IN	Late	——	——	——	3,078 fg	——	3,779 ab
MS	Early	——	——	——	42,226 a-c	——	3,255 a-c
MS	Mid	——	——	——	27,080 b-e	——	3,268 a-c
MS	Late	——	——	——	266 g	——	3,062 a-c
MO	Early	——	——	——	47,349 a-c	——	3,586 a-c
MO	Mid	——	——	——	79,523 ab	——	3,687 a-c
MO	Late	——	——	——	1,056 fg	——	3,438 a-c
NE	Early	——	——	——	83,598 a	——	3,852 ab
NE	Mid	——	——	——	94,759 a	——	3,991 a
NE	Late	——	——	——	7,443 d-g	——	2,596 c

[a]Abbreviations: AR, Arkansas; IN, Indiana; MO, Missouri; MS, Mississippi; NE, Nebraska; Pop., population.
[b]Means within a column followed by the same letter are not statistically different at the 0.05 probability level as determined by Tukey's HSD. The means for main effects (population and planting date) were separated when interaction terms were not significant. When population by planting date was significant, means were separated within the interaction.
[c]Data were log transformed and backtransformed for presentation.
[d]Data were square-root transformed and backtransformed for presentation.
[e]Late season planting was not harvested in 2013.
[f]A solid black bar (——) within a column suggests the interaction term and/or main effect was not significant. Means were not presented for main effects when the interaction was significant.

A trend of more male than female plants observed in populations from IN, MO, and MS that emerged mid- or late season, may suggest there is less potential for seedbank increase when plants are not controlled. However, it is important to consider that *A. palmeri* emergence in mid-July has the potential to produce as many as 7,443 seeds plant^{-1} at 8 wk after planting.

AAREC

All *A. palmeri* populations established early, mid-, and late season at AAREC exhibited a 1:1 ratio of male to female plants (Table 10). Thus, late season emerging *A. palmeri* from other geographies that are introduced to AAREC may have more female plants than late season–established *A. palmeri* introduced to TPAC. Differences between latitude, climate, and weather may have resulted in the differences observed between the two locations. Moreover, the study conducted at TPAC had higher *A. palmeri* densities than the AAREC location. This may have resulted in more intraspecific competition, possibly influencing the distribution of male to female plants.

Environmental Implications

Results from this study show that *A. palmeri* seed introduced to TPAC (northern IN) from NE can induce inflorescence emergence earlier and produce more seeds per plant than other populations, while maintaining a high growth rate; however, this conclusion may not reflect all *A. palmeri* populations from NE. Precipitation accumulation and mean temperature between locations where *A. palmeri* seeds were collected differed by as much as 90 mm and 5.6 C from May through September. For example, mean 30-yr precipitation accumulation from May through September in Chamois, MO, is 561 mm, compared with 471 mm in Lincoln, NE, and May mean air temperature in Greenville, MS, is 22.5 C compared with 16.9 C in Lincoln, NE.

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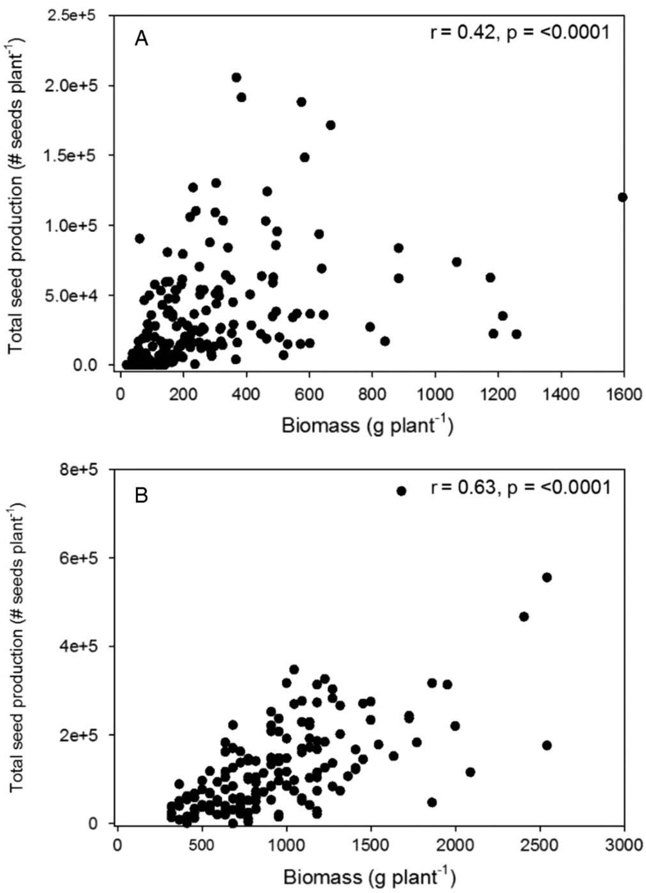

Figure 5. Correlation between Palmer amaranth (*Amaranthus palmeri*) biomass (g plant^{-1}) and total seed production (no. of seeds plant^{-1}) for (A) Throckmorton Purdue Agricultural Center ($n = 195$) and (B) Arkansas Agriculture Research and Extension Center ($n = 161$).

However, the environment in which the NE population has evolved resembles that of Lafayette, IN (located 13 km north of TPAC), for the 30-yr monthly air temperature from May through September more closely than other environments where *A. palmeri* seed was collected.

Table 8. Palmer amaranth (*Amaranthus palmeri*) biomass and seed production of five *A. palmeri* populations established at three planting dates in a field study at the Arkansas Agriculture Research and Extension Center.[a]

Population	Planting	Biomass[b,c]	Seed production[b,c]
		g plant^{-1}	Seeds plant^{-1}
AR		919 a	——[d]
IN		959 a	——
MO		951 a	——
NE		734 b	——
TN		1,037 a	——
	Early	1,202 a	170,399 a
	Mid	961 b	137,852 a
	Late	596 c	53,872 b

[a]Abbreviations: AR, Arkansas; IN, Indiana; MO, Missouri; NE, Nebraska; TN, Tennessee.
[b]Means within a column and main effect followed by the same letter are not statistically different at the 0.05 probability level as determined by Tukey's HSD.
[c]Data were log transformed and backtransformed for presentation.
[d]A solid black bar (——) within a column suggests the main effect was not significant.

Table 9. Pearson's chi-square analysis of male and female Palmer amaranth (*Amaranthus palmeri*) frequency at the Throckmorton Purdue Agricultural Center in 2013 and 2014.[a]

		Observed			Expected			
Population[b]	Planting	Male	Female	Total	Male	Female	χ^{2c}	P value
AR	Early	203	187	390	195	195	0.65	0.4178
	Mid	240	208	448	224	224	2.28	0.1305
IN	Early	148	169	317	158	158	1.39	0.2382
	Mid	224	229	453	226	226	0.05	0.8142
	Late	182	145	327	163	163	4.18	0.0407
MO	Early	164	138	302	151	151	2.23	0.1346
	Mid	191	147	338	169	169	5.72	0.0167
	Late	160	181	341	170	170	1.29	0.2554
MS	Early	163	132	295	147	147	3.25	0.0710
	Mid	185	189	347	187	187	0.04	0.8361
	Late	140	84	224	112	112	14.0	0.0002
NE	Early	211	230	441	220	220	0.81	0.3656
	Mid	285	248	533	266	266	2.56	0.1090
	Late	224	207	431	215	215	0.67	0.4129

[a]Abbreviations: AR, Arkansas; IN, Indiana; MO, Missouri; MS, Mississippi; NE, Nebraska.
[b]At biomass harvest, male and female reproductive structures were unable to be identified from late season planted *A. palmeri* from AR in both years and MS in 2014.
[c]A chi-square value greater than 3.841 suggests that there was not a 1:1 ratio of male:female *A. palmeri* plants.

The *A. palmeri* population collected from MS has evolved in an environment with shorter day length and monthly mean air temperatures in excess of those of other locations where *A. palmeri*

Table 10. Pearson's chi-square analysis of male and female Palmer amaranth (*Amaranthus palmeri*) frequency at the Arkansas Agriculture Research and Extension Center in 2014.[a]

		Observed			Expected			
Population	Planting	Male	Female	Total	Male	Female	χ^{2b}	P value
AR	Early	34	50	84	42	42	1.52	0.2170
	Mid	43	36	79	40	40	0.31	0.5776
	Late	35	34	69	35	35	0.01	0.9323
IN	Early	26	42	68	34	34	1.88	0.1701
	Mid	45	39	84	42	42	0.21	0.6434
	Late	43	23	66	33	33	3.03	0.0817
MO	Early	37	41	78	39	39	0.10	0.7488
	Mid	48	38	86	43	43	0.58	0.4458
	Late	37	31	68	34	34	0.26	0.6069
NE	Early	28	33	61	31	31	0.20	0.6508
	Mid	41	36	77	39	39	0.16	0.6870
	Late	24	37	61	31	31	1.38	0.2392
TN	Early	42	31	73	37	37	0.83	0.3626
	Mid	49	33	82	41	41	1.56	0.2115
	Late	35	34	69	35	35	0.01	0.9323

[a]Abbreviations: AR, Arkansas; IN, Indiana; MO, Missouri; NE, Nebraska; TN, Tennessee.
[b]A chi-square value greater than 3.841 suggests that there was not a 1:1 ratio of male:female *A. palmeri* plants.

https://doi.org/10.1017/wsc.2018.12 Published online by Cambridge University Press

seeds were collected. *Amaranthus palmeri* adapted to an environment with high temperatures and introduced to an environment with cooler average temperatures may have benefited the MS population's growth, as this population was among the tallest. Griffith and Watson (2006) reported common cocklebur (*Xanthium strumarium* L.) populations collected from central IN and Isabella County, MI, that were planted further north in Chatham, MI, were mostly similar or larger in height and produced more primary branches than the same plants grown in their native environment. However, frost prevented *X. strumarium* populations from central IN and Isabella County, MI, from producing seeds. In Lafayette, IN, a 50% probability for air temperatures to dip below 0 C occurs from October 10 to 15. If *A. palmeri* can produce mature seed 53 d after planting, as was observed in this study, it is unlikely that seed will be produced before the first frost if emergence occurs in early September. Lafayette, IN, and Lincoln, NE, are located at similar latitudes, meaning that these two locations are exposed to similar day lengths. Therefore, *A. palmeri* that has adapted to Lafayette's climate will likely initiate reproductive structures at similar times as populations from Lincoln, NE.

Amaranthus palmeri from NE that was established at AAREC produced the least biomass when compared with all other populations grown at AAREC. These data suggest that changes in the latitudinal gradient influence biomass production of *A. palmeri*. However, all populations established at AAREC produced similar quantities of seed.

We reject the null hypothesis that *A. palmeri* populations exhibit similar growth rates and inflorescence emergence. The AR population was less competitive in growth compared with the IN, MO, MS, and NE populations when established at IN due to more GDD needed to attain 50% maximum height. However, the AR population did produce heavier seeds than other populations. In contrast to *A. palmeri* height and biomass production at TPAC, *A. palmeri* height and biomass in southern latitudes were similar. However, the latitude of the native site of a population appears to influence *A. palmeri* height and biomass in cases in which populations from latitudes higher than 40°N are established in latitudes near 36°N. A fundamental management practice is to deter *A. palmeri* introduction and seed spread to noninfested fields. Monitoring *A. palmeri* emergence throughout the growing season in areas know to be infested will allow growers to make timely herbicide applications, as *A. palmeri* grows rapidly in a short period of time. Management of late season emerging plants should not be neglected, as these plants flower and produce seed much faster than early season–emerging plants. Successful control of *A. palmeri* requires an integrated weed management approach, and preventing seed introduction is the first step toward successful weed management.

Acknowledgments. The authors would like to thank the United Soybean Board for funding this research. We would also like to thank the members of Purdue Weed Science for their assistance in data collection and Yixuan Qui from Purdue Statistical Consulting Service for assistance in statistical analysis. *Amaranthus palmeri* seed was graciously provided by Travis Legleiter, Tom Eubank, Kevin Bradley, and Lowell Sandell.

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