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Palmer Amaranth (*Amaranthus palmeri*) Demographic and Biological Characteristics in Wide-Row Soybean

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Knowledge of Palmer amaranth demographics and biology is essential for the development and implementation of weed management strategies. A field experiment was conducted to investigate the effects of Palmer amaranth density on seedling mortality, flowering initiation, and flowering progress throughout the growing season and biomass production and fecundity in wide-row soybean. The experimental design was a randomized complete block design with three levels of Palmer amaranth density-clusters: high, medium, and low. Palmer amaranth mortality rate was greater at high Palmer amaranth population density-cluster, reaching a peak within 30 to 40 d after Palmer amaranth emergence (DAE) (0.55 and 0.80 for 2014 and 2015, respectively), in comparison with mortality rate at medium and lower density-clusters. Likewise, as Palmer amaranth density increased, biomass and seed production per unit area of the weed also increased. Biomass production at the high density-cluster in 2014 was 664.7 g m^{-2} compared with 542.9 and 422.1 g m^{-2} at medium and low density-clusters, respectively. Similarly, biomass production at high density-cluster in 2015 was 100.6 g m^{-2} compared with 37.3 and 34.2 at medium and low density-clusters, respectively. In addition, seeds produced at high density-cluster were 1.5 million and 245,400 seeds m^{-2} for 2014 and 2015, respectively. Seed production was reduced by 29% and 54% in 2014 and by 65% and 75% in 2015 at medium and low density-clusters, respectively. Earlier flowering initiation (i.e., between 30 to 40 DAE) occurred in higher Palmer amaranth density-clusters, indicating a trade-off between reproduction and survival at high densities and more stressed environments for species survival. Palmer amaranth male-to-female sex ratio was greater at high densities, 1.3 and 1.9, compared with lower densities of 0.6 to 0.7 and 0.7 to 0.8 in 2014 and 2015, respectively. The plasticity of Palmer amaranth population and population-structure regulation, vegetative growth, and flowering shifts at various levels of intraspecific competition (i.e., high vs. low population density-clusters) and the trade-off between these biological transitions merits further investigation.

Nomenclature: Palmer amaranth, *Amaranthus palmeri* S. Wats.; soybean, *Glycine max* (L.) Merr.

Key words: Cluster analysis, cohort analysis, fecundity, flowering, life table analysis, male-to-female sex ratio, phenology, weed population dynamics

Palmer amaranth is one of the most problematic weeds in soybean, cotton (*Gossypium hirsutum* L.), and corn (*Zea mays* L.) in the southern United States (Riar et al. 2013; Webster and Nichols 2012), causing substantial yield losses when not adequately controlled (Culpepper et al. 2006; Green and Owen 2011; Massinga et al. 2001; Morgan et al. 2001). The occurrence of Palmer amaranth becomes even more concerning due to the evolution of multiple herbicide-resistant biotypes. Palmer amaranth has evolved resistance to multiple herbicide modes of action such as 5-enol-pyruvylshikimate-3-phosphate synthase, acetolactate synthase, and 4-hydroxyphenylpyruvate dioxygenase inhibitors; microtubule assembly inhibitors; and photosystem II inhibitors (Heap 2017; Jhala et al. 2014; Molin et al. 2016). Future management strategies will rely on an improved understanding of weed biology and ecology with particular emphasis on population demographics (Puricelli et al. 2002). This information can be used for improvements in crop management decisions (Bussan et al. 2000; Norsworthy et al. 2007). Norsworthy et al. (2016), for example, evaluated the effectiveness of various fall management programs and herbicide regimes based on Palmer amaranth density.

Demography is the study of a population as it responds to intrinsic and extrinsic factors that act upon it (Hutchings 1997; Werner and Caswell 1977). Growth of individuals, fecundity, and mortality or survival are the main parameters that affect weed populations; inclusion of these parameters in demographic studies secures the accuracy of the

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study's outcome (Boutin and Harper 1991). Weed seed germination, seedling emergence, and seedling establishment, including those for Palmer amaranth, have been mostly investigated as isolated events (Hakansson 1986; Jha and Norsworthy 2009; Kropff et al. 1993), but in our research these were considered collectively to facilitate an integrated analysis of Palmer amaranth demographics. In addition, the deviation of male-to-female sex ratio from the 1:1 relationship was assessed, as evidence in the literature on *Amaranthus* species is contradictory. Costea et al. (2005) recorded a tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer] male-to-female sex ratio close to 1:1, although Lemen (1980) found that the proportion of male plants in a population of common waterhemp (*Amaranthus rudis* Sauer) from Illinois was 0.33. Conversely, Menalled et al. (2004) reported a marginally higher male-to-female ratio in common waterhemp plants grown under different compost-amended treatments compared with those with compost-free treatments. Based on field observations, Neve et al. (2011) used a 3:1 male-to-female ratio for modeling herbicide resistance in Palmer amaranth.

The highly plastic manner by which weeds, particularly Palmer amaranth, respond to stressful conditions (e.g., self-thinning, adjustments in size and biomass production, alterations in resources allocation or phenology) (Jha et al. 2008; Korres et al. 2016, 2017) necessitates a detailed demographic approach. Methodologies that fail to consider and quantify the plasticity of weed response to stresses are prone to failure.

Representations of weed population dynamics have largely been accomplished using demographic models (Freckleton and Stephens 2009; Holst et al. 2007). Demographic data in the form of life tables provide important means of quantifying the impact of biotic and abiotic stresses on population parameters such as mortality (Roach 2003; White 1980). There are two major types of life tables, the current or period life tables and the generation or cohort life tables. The former evaluates the mortality rates of an entire population at one moment of time, whereas the latter, as in this work, follows a given cohort of births over its entire life span (Kalisz et al. 2014; Salguero-Gomez and de Kroon 2010).

Life table analysis has been used widely in studies on invasive plants, insects (Asiimwe et al. 2007; Kalisz et al. 2014; Salguero-Gomez and de Kroon 2010), weed biological control (Bellows and Driesche 1999), and toxicological effects of herbicides (Saska et al. 2016). Surprisingly, no demographic studies on Palmer amaranth in row crops using life table analysis have been reported so far, to the best of our knowledge.

Knowledge of Palmer amaranth biology and demography can be a valuable tool in relation to the implementation of various management options of this species. The objectives of this study are to investigate (1) Palmer amaranth seedling mortality patterns, (2) flowering initiation and cumulative flowering, and (3) fecundity and biomass production as affected by Palmer amaranth density in soybean.

Materials and Methods

Experiment Establishment. Field experiments were conducted at the University of Arkansas–Agriculture Research and Extension Center, Fayetteville, AR, during the summers of 2014 and 2015 to investigate Palmer amaranth demographics in 92-cm wide-row soybean. The soil texture was a silt loam (fine, mixed, active, thermic Typic Albaquults) with 34% sand, 53% silt, 13% clay, 1.5% organic matter, and a pH between 6.5 and 6.9. Prior to crop planting, the seedbed was prepared by disking followed by a field cultivator (Kongskilde Industries, Hudson, IL). A glufosinate-resistant soybean cultivar (i.e., Pioneer® 95L01 maturity group 4.6 and Credenz® 4748 maturity group 4.7 for the first and second years, respectively) was planted in four-row plots at 320,000 seeds per ha^{-1} on June 24, 2014, and June 25, 2015. Differences between soybean densities among plots or between years were statistically insignificant when soybean densities were analyzed taking plot and year as random effects (unpublished data). Plots were 6-m long and 2.5-m wide. A few days after soybean planting, Palmer amaranth seeds collected from a local population were spread by hand between the middle two rows of the plot to create a range of targeted Palmer amaranth population densities (i.e., 1, 10, 100, 1,000, and 10,000 plants m^{-2}) and slightly covered with soil. The targeted densities were underachieved, so a generated range of Palmer amaranth densities, as it is described in Life Table and Statistical Analyses section, was developed.

Glyphosate (Roundup® PowerMax, Monsanto Company, St. Louis, IL) and glufosinate (Liberty® 280 SL, Bayer CropScience, Research Triangle Park, NC) were sprayed at 870 g ae ha^{-1} and 594 g ai ha^{-1}, respectively; the former prior to soybean planting and the latter after crop planting but prior to Palmer amaranth sowing to ensure the control of weed vegetation. A CO_2-pressurized backpack sprayer consisting of a handheld boom that contained four

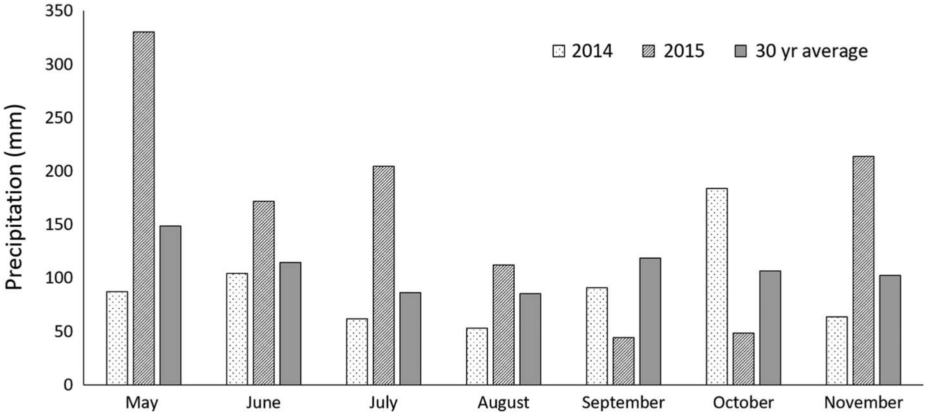

Figure 1. Monthly precipitation during the experimental period and 30-yr average rainfall in Fayetteville, AR (data obtained from www.srh.noaa.gov).

110015 flat-fan nozzles (TeeJet® Technologies, Springfield, IL) calibrated to deliver 140 L ha^{-1} at 276 kPa was used. Experimental plots were routinely hand weeded during the entire experimental period to remove other weed species and were irrigated when rainfall did not occur approximately within a 1-wk period, using a Valley remote irrigation system (Valmont Industries, Valley, NE) that delivered 12.5 mm of water per irrigation run (approx. 3- to 5-h time period).

Sampling and Data Measurements. Flags marked 1-m^2 sampling quadrats in the center of each plot as an area to assess Palmer amaranth demographic and biological characteristics every 10 to 15 d after Palmer amaranth emergence (DAE) throughout the growing period. Soybean plants at the top of the bed were included within the area of the sampling quadrat. The experiment was set up as a randomized complete block design with four replications. Unfortunately, unsuitable weather conditions, particularly in the second year of the study, when notable deviations from the 30-yr averages for monthly precipitation totals occurred (Figure 1), did not permit targeted Palmer amaranth densities. These were monitored by counting the emergence and establishment of Palmer amaranth seedlings on a daily basis until their population reached a stable state (i.e., until seedling population did not increase) approximately 20 DAE. After this period, Palmer amaranth plants within each quadrat were counted at 10- to 15-d intervals, i.e., 30, 40, 55, 65, and 75 DAE for both experimental years (Figure 2).

A sunfleck ceptometer (AccuPAR, model LP-80, Decagon Devices, Pullman, WA) was used to record

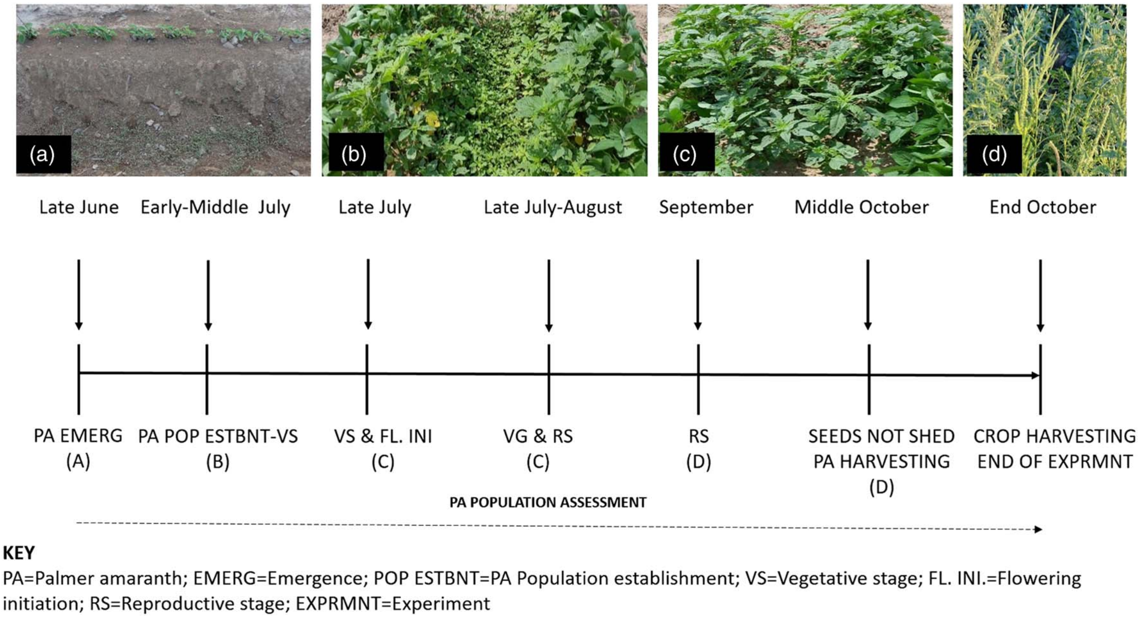

Figure 2. Palmer amaranth life cycle stages in relation to the stages and transitions under investigation in this research.

light interception for each experimental plot. Recordings were taken above and below the crop and Palmer amaranth canopy from two predetermined points within sampling quadrats under uniform sky conditions between 1100 and 1400 hours every 10 to 15 DAE. Two measurements were taken from each plot, and the plot average from each block was used for statistical analysis. The results presented here are estimated based on the percentage fractional transmission of light (Equation 1) (Liu et al. 2012)

$$F_r = \left(1 - \frac{I}{I_0}\right) \times 100 \qquad [1]$$

where F_r is fractional light interception (%), I_0 is photosynthetically active radiation (µmol m^{-2} s^{-1}) above crop and Palmer amaranth canopy, and I is photosynthetically active radiation below crop and Palmer amaranth canopy.

Palmer amaranth density, flower initiation, subsequent number of flowering plants, and average height of all Palmer amaranth plants within the sampling area were measured every 10 to 15 d, whereas dry biomass and seed production were measured at final harvest. All plants in the 1-m^2 sampling quadrat were cut at ground level prior to soybean harvesting and before seeds were shed for the evaluation of weed dry biomass and seed production (Figure 2). Harvested plants were separated by gender, placed in paper bags, and dried in the greenhouse at 32/25 C for 3 wk before threshing. Collected seeds from female plants were separated from plant tissue using a series of sieves, with the bracts and other plant debris removed by gently blowing air over the seeds as they were transferred between sieves. A minimum of five subsamples of 100 seeds from each female plant within each plot were weighed for the determination of female plant seed production, and the total number of seeds produced per female plant was extrapolated for the entire seed sample and expressed on square-meter basis. Seed-cleaning procedures were standardized across treatments and years.

The male-to-female sex ratio was calculated from the actual counts of male and female Palmer amaranth plants within each sampling quadrat at approximately 120 DAE, just prior to soybean harvesting. Palmer amaranth plant gender was determined based on the inflorescence characteristics and pollen production.

Life Table and Statistical Analyses. A hierarchical cluster analysis, using Ward's minimum variance method, was performed to categorize Palmer amaranth densities into three separate clusters for low, medium, and high density-clusters. Life table analyses were employed to investigate the weed demographics during the experimental season based on these density-clusters. Hierarchical clustering is a process that considers each entity as a separate cluster. At each step, two of the clusters that are close to each other are merged into a single cluster. This process continues until only one cluster that contains the entire data set remains. The routine will produce a nested hierarchy of n partitions, where n is the number of entities in the data set. Partitions represent nonoverlapping clusters, and once two entities become members of the same cluster, they are never again partitioned. This type of clustering is the most appropriate for small data sets, as in this study (Milligan and Cooper 1987).

Survivorship and mortality rates for each of the three Palmer amaranth density-clusters up to 75 DAE were evaluated using life table analysis as described by Begon et al. (2006) and Preston et al. (2001). Each of the three Palmer amaranth density-clusters was considered as a group of individuals all emerging in the same time period; survivorship and mortality rates were estimated for each sampling period (i.e., life stage). Specifically, a cohort-based life table analysis, as in this work, was calculated by analyzing the actual mortality of individuals (i.e., the cohort) from birth to the death of the last member of the cohort (Begon et al. 2006; Preston et al. 2001). Once the life stages have been defined (i.e., sampling occasion in Table 1) and the number of individuals in each age class has been counted (i.e., average population of Palmer amaranth within each density cohort, denoted as a_t in Table 1), the values of other variables such as survivorship and mortality can be calculated. Survivorship (l_t), for example, is a standardized ratio of the number of individuals at a given life stage relative to the number of individuals at $t = 0$. The first survivorship value entered in any life table (l_0, $t = 0$) is always 1.0, because 100% of individuals are observed at the first stage (Table 1).

$$l_{t_i} = \frac{a_{t_i}}{a_{t_0}} \qquad [2]$$

where a_t is the average number of individuals for each cohort at each sampling occasion and t is the stage at each sampling occasion; i is an element of natural numbers $N_0 = \{0, 1, 2, 3\ldots\}$ i.e., $i \in N_0$.

Table 1. Life table analysis for low, medium, and high Palmer amaranth density-clusters up to 75 days after Palmer amaranth emergence for both 2014 and 2015 experimental periods.[a]

	Sampling occasion	Low density-cluster				Medium density-cluster				High density-cluster			
Year	DAE	a_t	l_t	d_t	q_t	a_t	l_t	d_t	q_t	a_t	l_t	d_t	q_t
2014	20	51.0	1	0.08	0.08	143.1	1	0.13	0.13	825.4	1	0.28	0.28
	30	46.1	0.92	0.16	0.17	125.3	0.87	0.14	0.14	596.2	0.72	0.40	0.55
	40	38.2	0.76	0.06	0.08	104.1	0.75	0.11	0.11	265.0	0.32	0.12	0.38
	55	35.3	0.70	0.04	0.06	92.7	0.65	0.09	0.09	163.6	0.20	0.04	0.22
	65	33.0	0.66	0.12	0.17	84.4	0.59	0.13	0.13	128.0	0.15	0.004	0.023
	75	27.2	0.54			73.7	0.50			125.0	0.15		
2015	20	78.3	1	0.49	0.49	263.2	1	0.40	0.36	913.8	1	0.30	0.29
	30	40.2	0.51	0.38	0.75	168.2	0.60	0.50	0.85	647.0	0.71	0.60	0.83
	40	10.0	0.13	0.03	0.25	25.8	0.10	0.04	0.46	111.2	0.12	0.05	0.46
	55	7.5	0.09	0.02	0.23	14.0	0.05	0.02	0.34	60.6	0.07	0.025	0.30
	65	5.8	0.07	0.02	0.31	9.2	0.04	0.01	0.20	37.4	0.01	0.01	0.24
	75	4.0	0.05			7.4	0.03			29.0	0.03		

[a] DAE, days after Palmer amaranth emergence; a_t, total number of individuals observed each sampling occasion; l_t, proportion of original number of individuals surviving at each sampling occasion (survivorship); d_t, proportion of original number of individuals dying from one to the succeeding sampling occasion (mortality); q_t, mortality rate from one to the succeeding sampling occasion.

Actual mortality (d_t) is the reduction in number of individuals between each sampling occasion, calculated by subtracting survivorship values:

$$d_{t_i} = l_{t_i} - l_{t_{i+1}} \qquad [3]$$

where t is the stage at each sampling occasion and $i \in N_0$.

Mortality rate (q_t), an estimate of mortality intensity at each sampling occasion, is calculated as follows:

$$q_{t_i} = \frac{d_{t_i}}{l_{t_i}} \qquad [4]$$

where t is the stage at each sampling occasion and $i \in N_0$.

An unbalanced one-way ANOVA was used, due to differences in sample sizes among population density treatments resulting from cluster analysis, to analyze Palmer amaranth biological characteristics, i.e., biomass production, fecundity, and flowering, using JMP Pro v. 12.0.1 (SAS Institute, Carey, NC) software. The relationship between light interception by the crop and Palmer amaranth canopy and Palmer amaranth cumulative flowering was determined by correlation analysis. The measurements of fractional light interception and corresponding cumulative flowering from each sampling occasion and each Palmer amaranth density across the entire experimental period were used as variables in correlation analysis. Transformations based on natural logarithms were conducted to secure assumptions of normality. SigmaPlot v. 13.0 (Systat Software, San Jose, CA) was used to fit a three-parameter sigmoidal model to the cumulative number of Palmer amaranth flowering plants (based on initiation of flowering) as they were recorded through the entire experimental period for each Palmer amaranth density.

Results and Discussion

Palmer Amaranth Demographics. The resulting range of Palmer amaranth plants in each cluster were different between 2014 and 2015 because of higher precipitation, particularly in the second year (Figure 1), which necessitated the adoption of a hierarchical cluster analysis. Based on this analysis three density-clusters were classified in 2014 with the high density-cluster having 697 to 927 plants m^{-2}, the medium having 84 to 252 plants m^{-2}, and the low having 23 to 66 plants m^{-2} (Figure 3a). In 2015 the three density-clusters were high with 745 to 1178 plants m^{-2}, medium with 186 to 389 plants m^{-2}, and low with 29 to 118 plants m^{-2} (Figure 3b). Life tables were constructed for each Palmer amaranth density-cluster, with stages defined as sampling occasions for each year (Table 1). Life table data can provide great insight into the demographics of a population. Quantifying density-specific mortality rates, for example, enables us to distinguish patterns and make predictions mostly related with the timing of implementation measures to control Palmer amaranth infestations. A large proportion of the

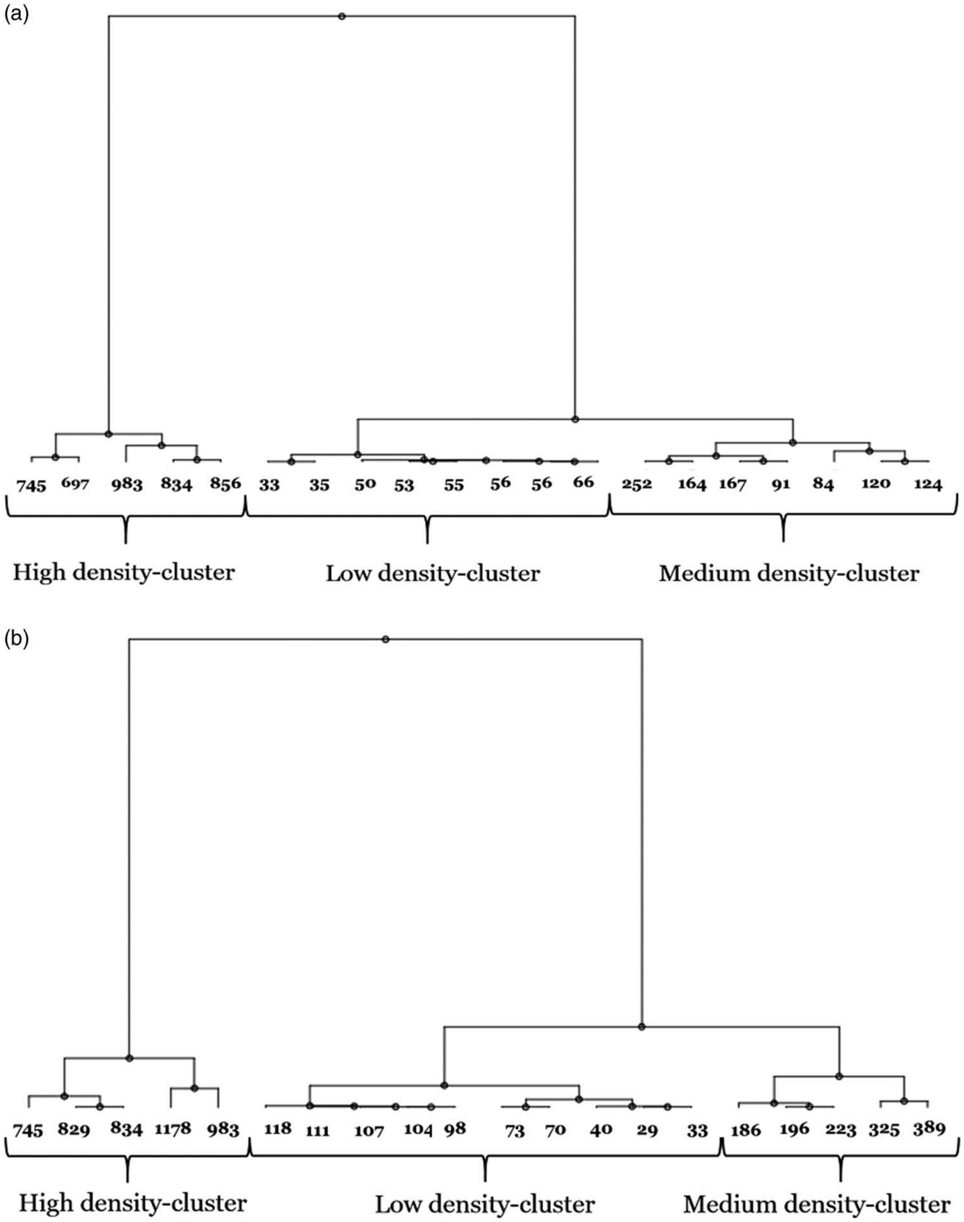

Figure 3. Palmer amaranth density-clusters for 2014 (a) and 2015 (b) experimental periods as determined by cluster analysis on actual weed densities at the beginning of the experimental period i.e., 20 d after Palmer amaranth emergence (DAE).

Palmer amaranth population did not survive to later ages, particularly in high density-clusters (Table 1). The lower survivorship values at later life cycle stages of high Palmer amaranth density-cluster, for example, are indicative of the higher mortality rates this population exhibited at the earliest life cycle stages (Figure 4). Survivorship curves have traditionally been used in plant demography studies, although it is difficult to discern the pattern of mortality by examining the changes in the slope of a survival curve (Carey et al. 1992). Thus, mortality rate was used to evaluate changes in Palmer amaranth density for each sampling occasion (Figure 4a and b). Excluding the adult stage (approx. 120 DAE), when every individual plant entering is destined to die, the highest rates of mortality were observed between 30 to 40 DAE in both years (Figure 4a and b). Mortality rates were increased in higher Palmer amaranth densities, although a secondary peak of mortality rate occurred for the low Palmer amaranth density at 55 to 65 DAE following a relatively steady population state between 40 to 55 DAE (Figure 4a and b). Blackman and Templeman (1938) reported an increased mortality of annual broadleaf species [i.e., wild radish (*Raphanus raphanistrum* L.) and wild mustard (*Sinapis arvensis* L.)] in spring cereal crops at approximately 65

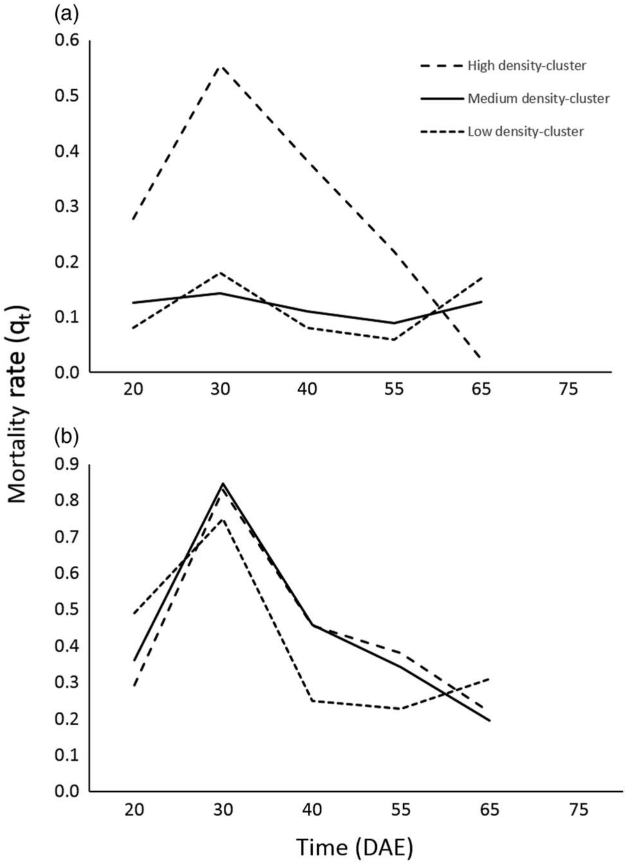

Figure 4. Palmer amaranth mortality rate as estimated by life table analysis under low, medium, and high Palmer amaranth density-clusters up to 75 d after Palmer amaranth emergence (DAE) during 2014 (a) and 2015 (b) experimental periods.

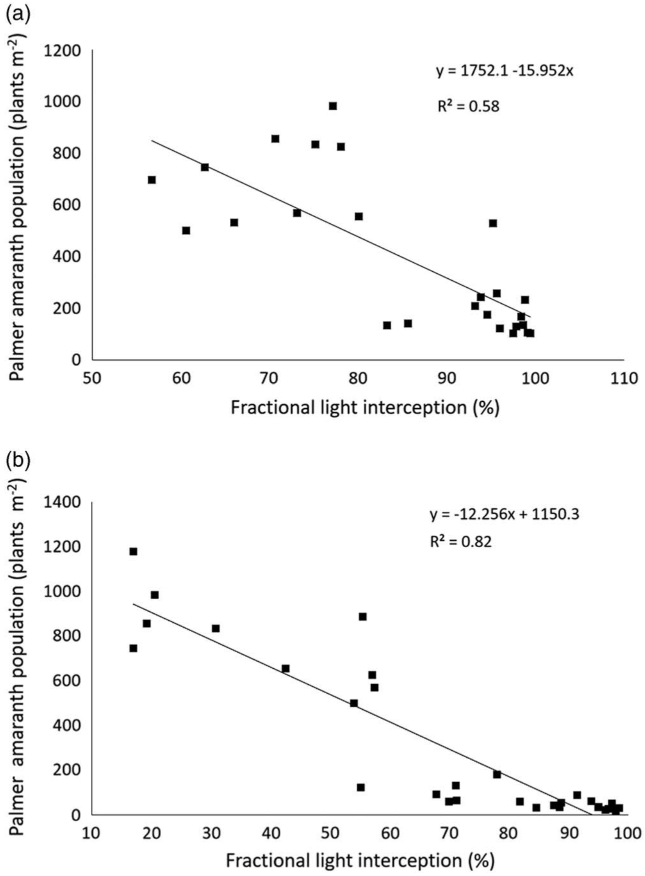

Figure 6. Relationship between high Palmer amaranth density-cluster and light interception by the soybean and Palmer amaranth canopies for 2014 (a) and 2015 (b) experimental periods.

DAE as the crop canopy was fully developed and light interception by the crop canopy reached its maximum.

Air temperature in both years was below the optimal range for maximum photosynthesis (Figure 5) up to 60 to 65 DAE, which might partially explain the decrease in Palmer amaranth density within this time period, as the effects of competition for light and nutrients on plants with weaker performance are enhanced. Net photosynthetic rate in Palmer amaranth plants grown outdoors during the summer months in Salt Lake City, Utah, was found to be temperature dependent (i.e., optimal range between 35 to 45 C), resulting in reduced photosynthetic rates of approximately 50% of the maximum rate at 25 C (Ehleringer 1983). In addition, there may be mechanisms other than environmental ones that cause reductions in Palmer amaranth density, such as those mechanisms that result in senescence following the developmental shift to reproduction.

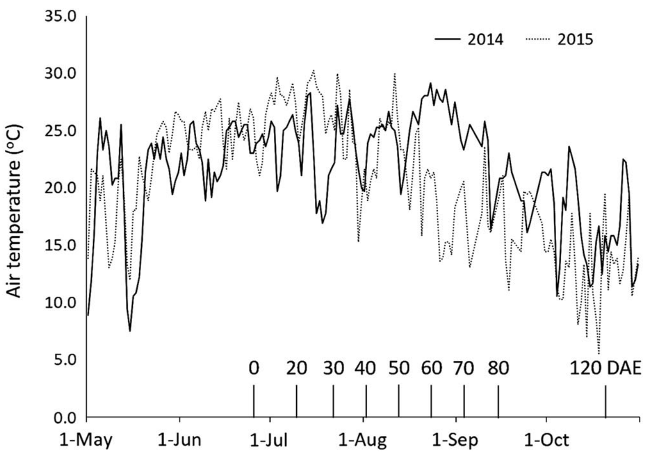

Figure 5. Daily means of air temperature throughout the experimental period in 2014 and 2015 (data obtained from www.srh.noaa.gov). Days after Palmer amaranth emergence (DAE) as an ancillary *x*-axis scale are shown within figure.

Palmer amaranth density was found to be negatively correlated with interception of solar radiation by the soybean and Palmer amaranth canopies. This trend was observed for all Palmer amaranth densities, especially the higher density (Figure 6a and b), in which the correlation

Table 2. Segmentation of Palmer amaranth population prior to soybean harvesting for gender evaluation and male-to-female sex ratio determination.

		Male[a]	Female[a]			
Year	Palmer amaranth density-cluster	Plants m^{-2}	Plants m^{-2}	SE[b]	M/F ratio[c]	SE[d]
2014	High	75.8 (4.5)	52.6 (3.9)	7.91 (0.20)	1.3	0.14
	Medium	28.8 (3.4)	44.3 (3.8)	7.07 (0.17)	0.7	0.19
	Low	11.7 (2.4)	15.9 (2.6)	6.87 (0.16)	0.6	0.18
2015	High	18.9 (2.8)	10.9 (2.4)	3.46 (0.43)	1.9	0.24
	Medium	3.0 (1.1)	3.7 (1.5)	2.85 (0.36)	0.8	0.17
	Low	2.1 (0.7)	4.2 (1.4)	2.62 (0.34)	0.7	0.17

[a] Numbers in the parentheses represent the mean of the natural log-transformed male and female Palmer amaranth counts.
[b] SE of the untransformed and natural log-transformed (in parentheses) of male and female counts (i.e., different sample size with unequal variances).
[c] Male-to-female (M/F) ratio was estimated based on the untransformed male and female Palmer amaranth counts.
[d] SE of the male-to-female sex ratio (i.e., different sample sizes with unequal variances).

coefficient was equal to 0.58 and 0.82 for 2014 and 2015, respectively. The correlation coefficient was 0.28 and 0.16 in 2014 and 0.79 and 0.61 in 2015 for medium ($N_{2014} = 35$ and $N_{2015} = 30$) and low ($N_{2014} = 40$ and $N_{2015} = 60$) Palmer amaranth densities, respectively (unpublished data; N represents sample size for correlation analysis and not Palmer amaranth density). Ngouajio and Ernest (2004) reported a reduction in weed density as light transmission was decreased by the use of colored polyethylene mulches. However, the ability of Palmer amaranth to tolerate growth under low-light environments through increases of specific leaf area has been reported (Jha et al. 2008). The results presented in this work indicate the importance of light manipulation in reducing the density of Palmer amaranth. The use of early-maturing cultivars, an increasingly popular strategy in the midsouthern United States for avoiding drought and reducing irrigation cost, planted at higher crop densities for earlier canopy closure, hence greater light interception (Seversike and Purcell 2006), is a cultural method that can reduce Palmer amaranth density and biomass production (Korres et al. 2015). Nevertheless, increased soybean seeding rates in conjunction with appropriate row-width adjustments can make this production system cost prohibitive for some growers.

The differential response of male and female plants under different Palmer amaranth densities is noteworthy (Table 2). Particularly at high density, the increase of male plants compared with female plants (i.e., male-to-female ratio > 1) is statistically different ($\alpha = 0.057$ and $\alpha = 0.05$ for 2014 and 2015 experiments, respectively) compared with medium and low Palmer amaranth densities. The reverse relationship was observed at the medium and lower Palmer amaranth densities, where females dominated (i.e., male-to-female ratio < 1) (Table 2). This resulted in significantly different male-to-female ratios between high Palmer amaranth density-clusters in comparison with medium and low Palmer amaranth density-clusters for

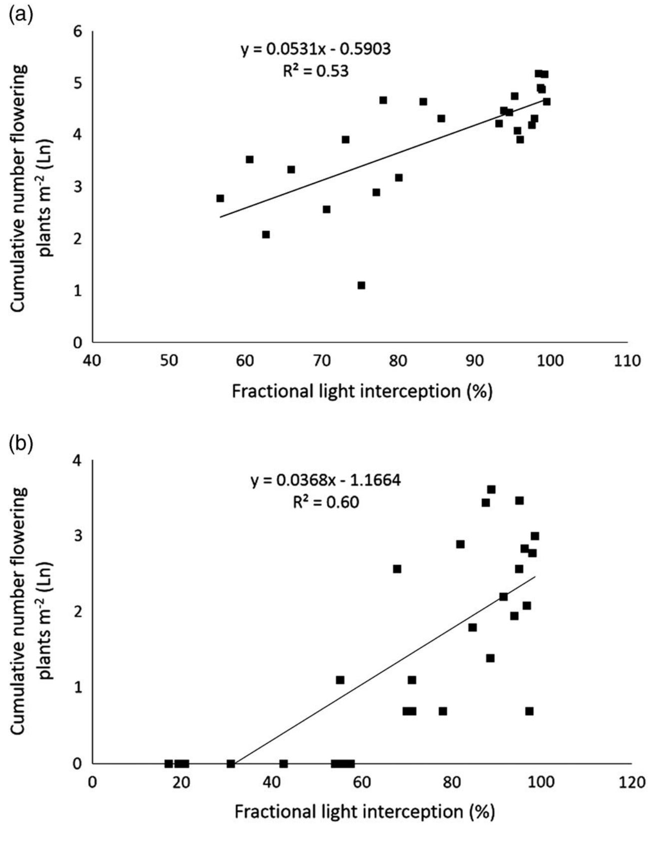

Figure 7. Relationship between cumulative number of flowering plants at high population density and light interception by crop and Palmer amaranth canopy for 2014 (a) and 2015 (b) experimental periods.

Table 3. Coefficients and related statistics of the three-parameter sigmoidal model (Figure 8) fit onto cumulative number of Palmer amaranth flowering plants for each Palmer amaranth density throughout the experimental period.

Year	Density-cluster	Model parameters[a]	Coefficient	SE	*t*-test	P value	R^2
2014	High	α	134.4	4.62	29.1	<0.0001	0.98
		b	7.7	0.95	8.16	0.0005	
		χ_o	56.2	1.19	47.39	<0.0001	
	Medium	α	86.6	5.36	16.15	<0.0001	0.94
		b	8.5	1.65	5.18	0.0035	
		χ_o	55.7	2.14	28.03	<0.0001	
	Low	α	30.9	2.60	11.85	<0.0001	0.96
		b	9.0	2.45	3.68	0.0142	
		χ_o	59.9	3.14	17.72	<0.0001	
2015	High	α	23.7	0.71	33.4	<0.0001	0.99
		b	6.2	0.76	8.16	0.0012	
		χ_o	58.3	0.85	68.73	<0.0001	
	Medium	α	6.5	0.066	98.61	<0.0001	0.99
		b	5.7	0.27	20.97	<0.0001	
		χ_o	56.6	0.28	198.91	<0.0001	
	Low	α	4.1	0.13	31.73	<0.0001	0.99
		b	6.7	0.71	9.42	0.0007	
		χ_o	66.1	0.84	78.38	<0.0001	

[a] α, upper asymptote; b, inflection point; χ_o, lower asymptote

both experiment years. Male-to-female ratios between medium and low Palmer amaranth density-clusters were nonsignificantly different for both years. The differential occurrence in reproduction between males and females and the differences in sex ratios could be due to environmental requirements that are different for each Palmer amaranth gender. This could explain the alterations of Palmer amaranth gender expression at different densities, namely various regimes of intraspecific competition. Palmer amaranth female plants under various nutrient deficiencies and light regimes were showing a negative energy feedback (i.e., a reversibility in photosynthetic performance at high light intensities and in nitrogen- and phosphorus-deficient environments) despite their ability, compared with male Palmer amaranth plants, to respond to stressful abiotic conditions more efficiently (Korres et al. 2017).

Palmer Amaranth Biological Characteristics. Reproduction is the last stage to consider in demographic analyses, and a large number of factors affect this stage (Fox 2007). Fractional light interception by the soybean and Palmer amaranth canopies was positively correlated ($R^2 = 0.53$ and 0.60 for 2014 and 2015, respectively) with Palmer amaranth flowering initiation and cumulative number of flowering plants (Figure 7a and b). Increases in fractional light interception caused earlier flowering initiation and consequent increases in the cumulative number of Palmer amaranth flowering plants. This trend was observed for all Palmer amaranth densities, especially at the highest density in both experiments (Figure 7a and b). The correlation coefficients for medium and low Palmer amaranth density-clusters were 0.40 and 0.49 for 2014 and 0.51 and 0.36 for 2015, respectively, and were lower than those observed under higher Palmer amaranth densities in both years.

Various factors such as planting date can influence the phenology of flowering, and therefore the transition from vegetative to reproductive development in Palmer amaranth (Keely et al. 1987). Plant density is also known to affect temporal patterns of flowering (Lyons and Mully 1992). A sigmoidal model, the parameters of which are shown in Table 3, was used to examine the relationship of cumulative flowering to Palmer amaranth density (Figure 8a and b). Earlier flowering at the higher Palmer amaranth density was observed between 30 and 40 DAE for both experiments (Figure 8a and b) and was10 to 20 d earlier compared with low Palmer amaranth density. This may be an example of a trade-off between reproduction and species survival that could explain the flowering initiation earlier in the season under high densities and a more stressed environment. Increases in light interception by soybean and Palmer amaranth canopies resulted in significant decrease in Palmer amaranth population at high density (Figure 6), whereas they resulted in a significant increase in

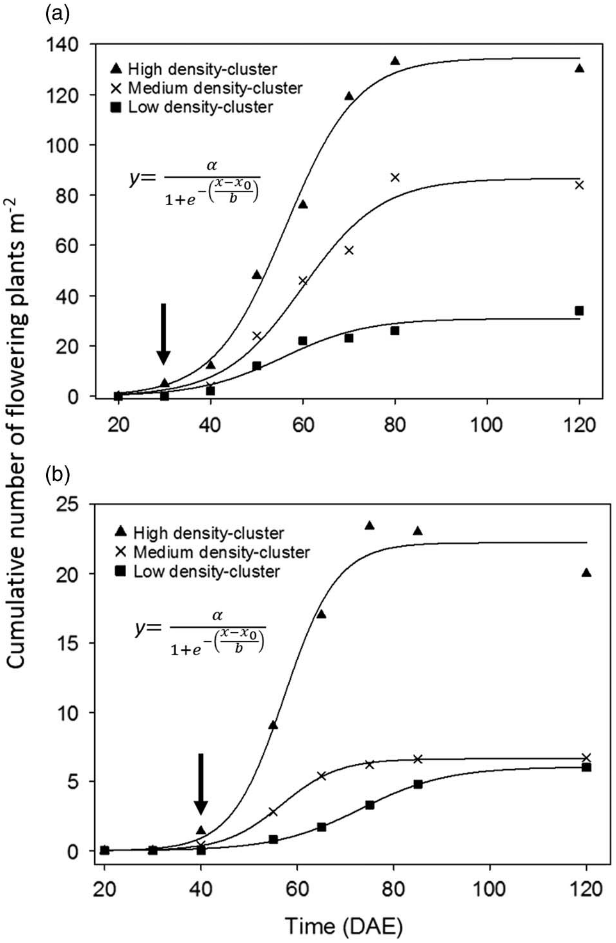

Figure 8. Relationships between Palmer amaranth density-clusters and cumulative number of flowering plants for 2014 (a) and 2015 (b) experimental periods. Arrows indicate the initiation of flowering at high Palmer amaranth density. DAE, days after Palmer amaranth emergence.

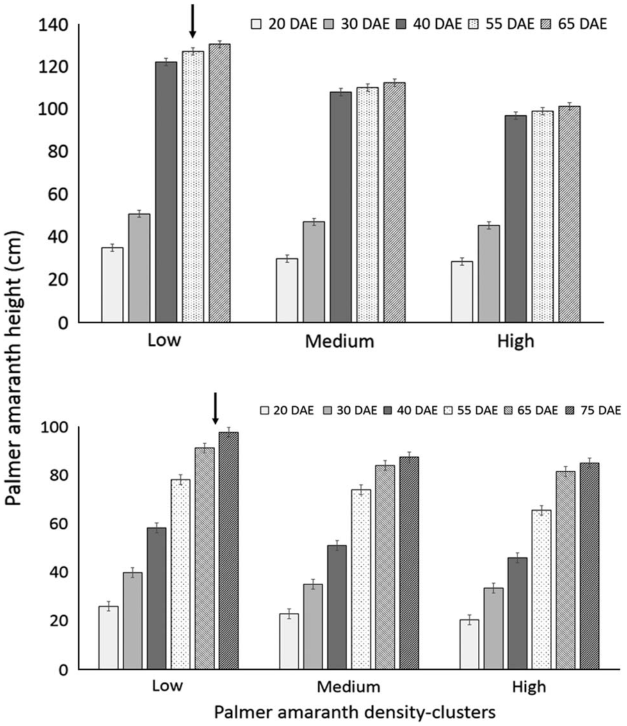

Figure 9. Effects of Palmer amaranth density-clusters on plant height during the growing season for 2014 (top) and 2015 (bottom) experimental periods. Arrows indicate plant height differences at low Palmer amaranth density compared with those at higher densities. Vertical bars represent the pooled SEs of different sample sizes with unequal variances. DAE, days after Palmer amaranth emergence.

cumulative number of Palmer amaranth flowering plants per square meter (Figure 7). Reports in the literature on nonphotoperiodic flowering or stress-induced flowering (i.e., the tendency to flower under unsuitable growth conditions) indicate that factors responsible for stress-induced flowering include, among others, light stress (i.e., low or high light intensity) (Takeno 2012). As stated by Adams et al. (2009), acceleration of flowering under shade could be another adaptive mechanism by the plants.

Flowering reached a plateau i.e., the entire Palmer amaranth population was reproductive, between 70 and 80 DAE, particularly at the highest Palmer amaranth density; whereas a relatively noticeable increase of cumulative number of Palmer amaranth flowering plants per square meter was observed beyond that period for the low density (Figure 8a and b). Alterations of flowering time in response to population density at very short time periods after emergence indicate a level of plasticity in response to intraspecific competition. This phenological attribute is of great importance, as selection of earlier-flowering ecotypes is likely to increase the risk of seed release prior to soybean harvest with possible evasion of the at-harvest, nonherbicide weed control strategies, as investigated by Norsworthy et al. (2016).

Palmer amaranth plants at low density continued growing after flower initiation up to 55 and 65 DAE for 2014 and 2015, respectively. Significantly taller plants ($\alpha = 0.05$) were observed at the low density (i.e., 130 and 95 cm in 2014 and 2015, respectively) compared with plants at the high density (i.e., 100 and 83 cm in 2014 and 2015, respectively) (Figure 9). This is an indication of an extended vegetative growth period at lower densities, possibly due to reduced intraspecific competition and greater resource availability. The results from this research indicate the ability of Palmer amaranth to easily adapt to various pressure regimes, since plants grown under high density invest in reproductive output earlier than those grown under less suppressive conditions. The plasticity of Palmer amaranth definitely deserves further investigation, since knowledge of the species

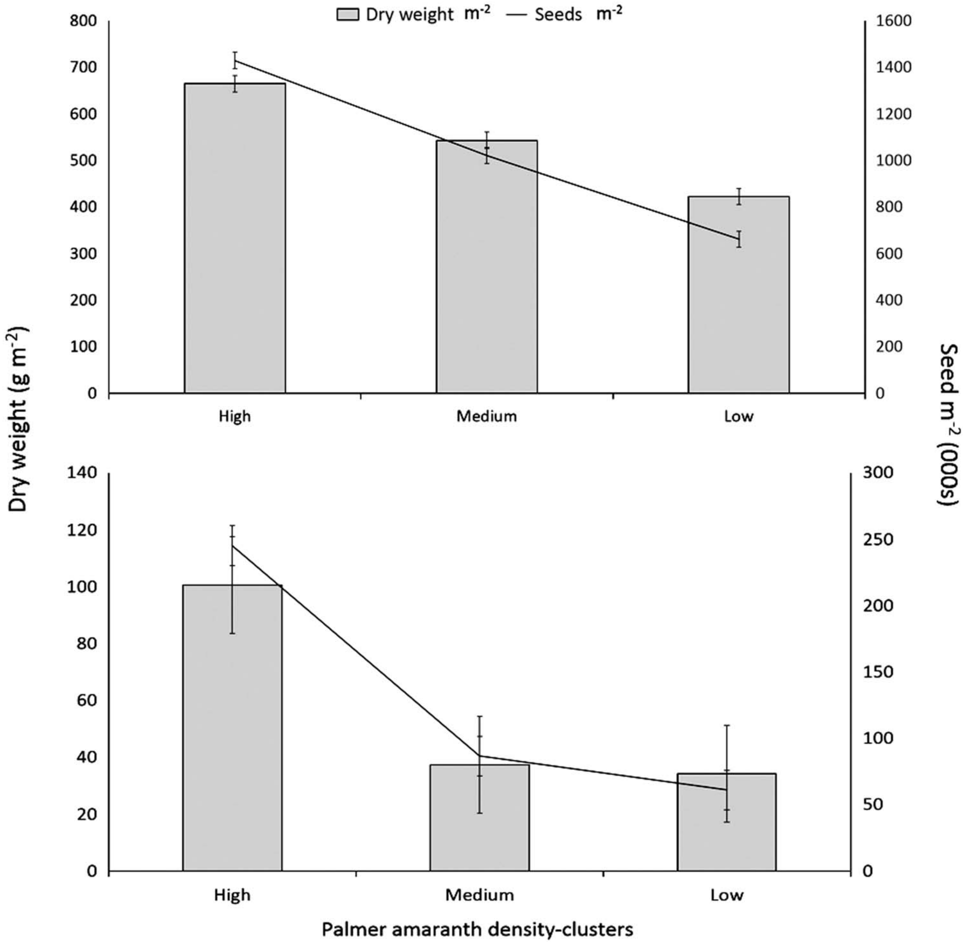

Figure 10. Effects of Palmer amaranth density-clusters on dry matter production and seed production at harvesting in the 2014 (a) and 2015 (b) experimental periods. Vertical bars represent the pooled SEs of different sample sizes with unequal variances.

behavioral attributes in the face of the current lack of simple solutions for management (Strek 2014) could be invaluable for improving the implementation of Palmer amaranth control options.

Many studies have shown that high densities compared with low densities exhibit greater biomass and seed production per area (Hendrix 1994; Korres et al. 2015). Similar results were observed in this study, as the relationship between Palmer amaranth biomass and seed production per unit area increased with increases in Palmer amaranth density (Figure 10a and b). Increases in Palmer amaranth biomass production of 20% and 40% were observed in 2014 at the high density compared with the medium and low densities, respectively, whereas biomass production at high density increased by 60% and 65% in 2015 compared with medium and low densities, respectively. In addition, seed production per square meter in 2014 was increased by 30% and 50% at the high Palmer amaranth density in relation to medium and low densities, respectively, whereas the corresponding values for 2015 were 65% and 75% (Figure 10a and b). Norsworthy et al. (2016) reported a strong relationship between Palmer amaranth density and seed production under various harvest weed seed control techniques aiming to control glyphosate-resistant Palmer amaranth in wide-row soybean. Significantly greater biomass production on a per-plant basis at the low Palmer amaranth density (unpublished data) was not adequate to compensate for the production of biomass and seeds per square meter at higher plant densities.

Practical Implementations and Future Research. Increased light interception reduced Palmer amaranth density but promoted earlier flowering initiation within 30 to 40 DAE. In addition, the highest mortality was observed within this time period in both years. If weed control is successful in the first 4 to 5 wk after soybean emergence, seed production from existing Palmer amaranth plants may be prevented in a wide-row soybean production system. Nevertheless, late-flowering Palmer amaranth may require additional weed control measures later in the growing season to prevent additions to the soil seedbank. The ability of Palmer amaranth to exhibit flowering-time shifts and bipolar adaptation strategies requires further investigation on how these characteristics can optimize the implementation of Palmer amaranth control strategies. Male-to-female sex ratio alterations such as those we observed at high and low Palmer amaranth densities require further research. Further research is also required for the determination of factors that could possibly affect Palmer amaranth sex expression in favor of either maleness or femaleness, as manipulation of gender expression could prove to be of great importance in integrated Palmer amaranth management. Another interesting question, in conjunction with this research, is how late Palmer amaranth emergence affects flowering initiation. Clay et al. (2016) reported that the growth of Palmer amaranth planted over 6-wk intervals (i.e., early, mid, and late) was unaffected under South Dakota conditions, and flowering commenced about the same time for all sowing dates. Finally, development of Palmer amaranth demographic studies under various cropping systems would enhance our knowledge on the biology and phenology of this weed.

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