

Growth and fecundity of Palmer amaranth escaping glufosinate in soybean with and without grass competition

Research Article

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Abstract

Field experiments were conducted at Clayton and Rocky Mount, North Carolina, during the summer of 2020 to determine the growth and fecundity of Palmer amaranth plants that survived glufosinate with and without grass competition in soybean crops. Glufosinate (590 g ai ha⁻¹) was applied at early postemergence (when Palmer amaranth plants were 5 cm tall), mid-postemergence (7–10 cm), and late postemergence (>10 cm) and at orthogonal combinations of those timings. Nontreated Palmer amaranth was grown in weedy (i.e., intraspecific and grass competition), weed-free in-crop (WFIC), and weed-free fallow (WFNC) conditions for comparisons. No Palmer amaranth plants survived the sequential glufosinate applications and control decreased as the plants were treated at a larger size in both experiments. The apical and circumferential growth rate of Palmer amaranth surviving glufosinate was reduced by more than 44% compared with the WFNC Palmer amaranth. The biomass of Palmer amaranth plants that survived glufosinate was reduced by more than 87% compared with the WFNC Palmer amaranth. The fecundity of Palmer amaranth that survived glufosinate was reduced by more than 70% compared with WFNC Palmer amaranth. Palmer amaranth plants that survived glufosinate were as fecund as the WFIC Palmer amaranth in both experiments in soybean fields. The results prove that despite the significant vegetative growth rate decrease of Palmer amaranth that survived glufosinate, plants can be as fecund as nontreated plants. The trends in growth and fecundity of Palmer amaranth that survives glufosinate with and without grass competition were similar. These results suggest that glufosinate-treated grass weeds may not reduce the growth or fecundity of Palmer amaranth that survives glufosinate.

Introduction

Palmer amaranth is a pervasive and ubiquitous weed throughout the southeastern United States, and its biology and the widespread evolution of herbicide resistance in this species contributes to the complexity of management (Webster and Grey 2015; Webster and Nichols 2012). Palmer amaranth can grow 0.5 to 2.5 cm per day and produce 250,000 to 500,000 seeds per plant (Mahoney et al. 2021; Sellers et al. 2003a). Because Palmer amaranth is an obligate outcrosser, offspring will be genetically diverse, which can facilitate rapid adaptation to weed management tactics (Chandi et al. 2013; Darmency 2018; Owen 2016). In tandem with competitive biological traits, Palmer amaranth has evolved resistance to herbicides from nine unique groups, and multiple herbicide-resistant populations are common (González-Torralva et al. 2020; Heap 2023; Mahoney et al. 2020). If not controlled, Palmer amaranth can reduce soybean yield by 14% to 68% (Basinger et al. 2019; Klingaman and Oliver 1994). Only a few postemergence herbicides remain effective for Palmer amaranth control in soybean grown in the southeastern United States.

Glufosinate is an effective, nonselective, fast-acting contact herbicide that inhibits glutamine synthetase (EC 6.3.1.2; categorized as a Group 10 herbicide by the Weed Science Society of America [WSSA]), resulting in the production of reactive oxygen species that disrupt cell membrane integrity (Takano et al. 2019). Palmer amaranth control with glufosinate can be greatly reduced if applied to plants taller than 10 cm, reflecting the importance of spray coverage (Jones et al. 2022; Steckel et al. 1997). Although glufosinate is efficacious, overreliance on it has led to the evolution of several isolated glufosinate-resistant Palmer amaranth populations

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(Carvalho-Moore et al. 2022; Priess et al. 2022). Annual grass control with glufosinate is more variable than annual broadleaf control (Beyers et al. 2002; Bradley et al. 2000; Burke et al. 2005; Culpepper et al. 2000). Additionally, glufosinate has no soil residual activity; weeds will emerge later in the season if no other control tactic is implemented (Anonymous 2017; Krausz et al. 1999). Plants can exhibit reduced growth after a sublethal herbicide dose, but a sublethal dose can also stimulate growth (Belz 2018; Cedergreen 2008). Previous research reported that weed growth is not hormetic after surviving glufosinate or a related herbicide (i.e., a cell membrane disruptor) (Cedergreen 2008; Haarmann et al. 2021). Quantifying the growth of Palmer amaranth that survives glufosinate is important for determining putative yield loss if those plants are allowed to interfere with the crop (Everman et al. 2008; Page et al. 2012). For example, Palmer amaranth that exhibited reduced growth after injury still significantly reduced cotton yield, highlighting the importance of quantifying the growth of plants escaping glufosinate (Sosnoskie et al. 2014).

Previous research demonstrated that large Palmer amaranth (≥ 10 cm) treated with glufosinate in the vegetative or reproductive stage significantly reduced fecundity (Jha and Norsworthy 2012; Jones et al. 2022; Scruggs et al. 2020). The fecundity of the glufosinate-treated Palmer amaranth was compared with the fecundity of plants in weedy nontreated controls, which may not be a true representation of the fecundity reduction due to the high levels of inter- and intraspecific competition. Additionally, the research reporting the fecundity of Palmer amaranth in the vegetative stage that survived glufosinate did not also report that grass weeds or later emerging weeds were controlled, whereas other research reporting the fecundity of surviving Palmer amaranth in the reproductive stage did control other weeds before glufosinate was applied (Jones et al. 2022; Scruggs et al. 2020). Controlling grass and later-emerging weeds could influence the growth and fecundity of Palmer amaranth escaping glufosinate (Adler et al. 2018; Qasem and Hill 1994).

Currently, the growth and fecundity of vegetative-stage Palmer amaranth plants that survive glufosinate with and without grass competition have not been documented with soybean. Thus, the objectives of this research were to quantify the growth and fecundity of Palmer amaranth that survives an application of glufosinate with and without grass competition compared with weedy and weed-free, nontreated Palmer amaranth in soybean fields.

Materials and Methods

Two separate field experiments were each conducted with soybean to determine the response of Palmer amaranth growth and fecundity with and without grass competition (hereafter referred to as the No Grass Competition and Grass Competition experiments) after surviving glufosinate. The experiments were established at two locations in North Carolina during the 2020 growing season: Rocky Mount, in Edgecombe County (35.89°N, 77.68°W), and Clayton, in Johnston County (35.66°N, 78.51°W). The Rocky Mount site has a soil mosaic of Goldsboro fine sandy loam (fine-loamy, siliceous, subactive, thermic Aquic Paleudult) and Norfolk loamy sand (fine-loamy, kaolinitic, thermic Typic Kandiudult). The Clayton site has a soil mosaic of Norfolk loamy sand (fine-loamy, kaolinitic, thermic Typic Kandiudult), Rains sandy loam (fine-loamy, siliceous, semiactive, thermic Typic Paleaquults), Varina loamy sand (fine, kaolinitic, thermic Plinthic Paleudult), and a Wagram loamy sand (loamy, kaolinitic, thermic Arenic

Kandiudult). The Palmer amaranth populations at each experiment location are resistant to acetolactate synthase (EC 2.2.1.6)-inhibiting herbicides (WSSA Group 2) and glyphosate (WSSA Group 9). The field sites were cultivated and bedded prior to soybean planting to control established weeds, but pre-emergence herbicides were not applied to ensure maximum emergence of weed seedlings for each experiment. The Rocky Mount and Clayton sites were planted on June 9 and 10, respectively. The soybean variety 'CZ 6515LL' was planted on the raised beds at a rate of 272,000 seeds ha^{-1} with a row spacing of 91 cm at both locations.

The experimental design for both experiments was a randomized complete block with four replications. Individual plots were 3.6 m wide by 9.0 m long. Glufosinate treatments were applied at three timings: early postemergence (5-cm-tall Palmer amaranth), mid-postemergence (7- to 10-cm-tall Palmer amaranth), late postemergence (>10 cm Palmer amaranth), and at orthogonal combinations of those timings. The three application timings were separated by 7 d. Three additional treatments were included in the experiments for comparison: a weedy nontreated in-crop control (NTC), a weed-free in-crop (WFIC), and weed-free no-crop (WFNC) for a total of 10 treatments. The WFIC and WFNC plots were sprayed with glufosinate at the early postemergence timing, but 10 Palmer amaranth plants were arbitrarily selected within the center 3 m of the plots and covered with a plastic cup before herbicide application. The WFIC and WFNC plots were hand-weeded weekly thereafter. Glufosinate was applied with a CO_2 -pressurized backpack sprayer calibrated to deliver 140 L ha^{-1} at 165 kPa with TeeJet XR110002 flat-fan nozzles (Spraying Systems Co., Glendale Heights, IL) 46 cm above the target weed height. Glufosinate was applied at a rate of 590 g ai ha^{-1} with 10 g L^{-1} ammonium sulfate at all timings. Glufosinate was applied at approximately 2 h of solar noon and temperatures above 30 C with relative humidity greater than 30% to avoid environment-induced control reductions (Coetzer et al. 2001; Sellers et al. 2003b). S-metolachlor (1,071 g ai ha^{-1}) was applied to all plots (except the NTC) using the methods described above, 3 d after the late postemergence application, to control later-emerging weeds and mitigate confounding effects of inter- and intraspecific competition on growth and fecundity that was not attributable to plants that survived glufosinate in both experiments. In the No Grass Competition experiment, clethodim (280 g ai ha^{-1}) was applied to control grass species using the methods described above, 10 d after the late postemergence application to avoid control antagonism (Burke et al. 2005). Palmer amaranth control was visually estimated 35 d after treatment using a 0% to 100% scale, where 0% equals no control and 100% equals complete control. Palmer amaranth plants that emerged after glufosinate applications were not rated because glufosinate has no soil residual activity (Krausz et al. 1999). Density counts (plants 0.25 m^{-2}) by species were recorded at 35 d after treatment, respectively, in both experiments.

Palmer amaranth plants that survived glufosinate were marked with a flag (10 plants plot^{-1}) 7 d after each application timing, respectively. Plants were visually inspected for herbicide damage before flagging (i.e., chemical excisions, leaf necrosis, and meristem regrowth). Ten Palmer amaranth plants were arbitrarily selected for data collection in the NTC, WFIC, and WFNC plots. Weekly measurements of plant apical height and canopy circumference (widest point) were recorded on the flagged plants from 1 wk until 6 wk after the last treatment (WAT). Circumference was measured as a metric for apical dominance (Cline 1997). At the end of the

Table 1. No Grass Competition experiment regression parameters from the four-parameter Gompertz equation to model apical and canopy circumferential growth of Palmer amaranth treated with glufosinate.^{a,b}

Location	Treatment	Apical					Canopy circumference				
		Regression parameters					Regression parameters				
		<i>a</i>	<i>b</i>	<i>x</i> 0	<i>y</i> 0	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>x</i> 0	<i>y</i> 0	<i>r</i> ²
Clayton	NTC	68.79	0.59	3.17	19.59	0.98	4.22	0.01	3.15	9.67	0.89
	WFNC	165.55	0.9	2.45	17.15	0.99	81.21	0.04	2.98	25.96	0.97
	WFIC	205.85	1.23	2.98	17.94	0.99	135.58	0.69	2.59	60.12	0.93
	EPOST	61.91	1.38	3.43	4.63	0.99	27.04	0.25	1.93	14.32	0.97
	MPOST	130.78	1.05	4.03	11.25	0.99	40.66	0.05	2.97	23.83	0.78
	LPOST	100.05	1.51	5.13	16.9	0.97	62.73	2.33	5.68	24.52	0.83
Rocky Mount	NTC	–	–	–	–	0.84	10.64	0.04	1.97	23.07	0.99
	WFNC	164.92	1.6	3.38	9.18	0.99	48.58	0.2	3.44	21.11	0.97
	WFIC	121.08	1.59	2.43	–0.38	0.97	–	–	–	–	0.79
	MPOST	26.88	0.55	4.31	8.68	0.99	24.06	0.04	3.97	22.51	0.92
	LPOST	23.69	1.22	5.01	10.75	0.89	16.75	0.05	4.03	22.2	0.74

^aAbbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

^bIn cells with a dash (–) growth was best modeled with a linear equation. Apical growth: Palmer amaranth under NTC conditions with soybean at Rocky Mount: $y = -2.2 + 7.9 \cdot x$. Circumference growth: Palmer amaranth under WFIC conditions with soybean at Rocky Mount $y = 33.7 + 7.8 \cdot x$.

season, three surviving female Palmer amaranth plants (if present) were collected from each plot. When possible, female plants were selected from the previously flagged plants. If no flagged female Palmer amaranth plants remained in a plot, additional plants were selected that indicated they had survived a glufosinate application. Harvested plants were placed in a drier at 60 C for 72 h. After drying, the plants were weighed to determine biomass. Following drying, the plants were threshed by hand to remove seeds from the florets, and seeds were separated from plant residues using sieves and a forced air column separator (South Dakota Seed Blower; Seedburo Equipment Company, Chicago, IL). Unimbibed crush tests were used during the cleaning process to determine whether seeds were viable or nonviable (Sawma and Mohler 2002). A small number of aborted seeds were separated along with the plant residue before final fecundity testing. Samples were cleaned again with forced air to further remove plant residue. The total number of seeds produced by each female plant was extrapolated by determining the mass of five 100-seed subsamples for each treatment (Sellers et al. 2003a). The total number of seeds produced was calculated using Equation 1:

$$T = \left(\frac{W}{S} \right) * 100 \quad [1]$$

where *W* equals the total seed mass, *S* equals the average mass of the five 100-seed subsamples, and *T* equals the calculated number of seeds produced.

After female Palmer amaranth plants were harvested and soybean reached physiological maturity, soybean was harvested with a two-row plot combine equipped with a weighing scale. Soybean yields from both experiments and sites were adjusted to 16% moisture. The weedy, nontreated plots were not harvested due to severe weed infestations. The WFIC plots were not harvested.

Statistical Analysis

Palmer amaranth control, growth, fecundity, and soybean yield data from both experiments were subjected to ANOVA using the GLIMMIX procedure with SAS software (v.9.4; SAS Institute Inc., Cary, NC), where $\alpha = 0.05$. Location, treatment, and their interactions were considered the main effects, whereas replication

was considered a random effect. Palmer amaranth biomass, control, and fecundity means were separated using Tukey's honestly significant difference test ($P \leq 0.05$). Palmer amaranth control data from nontreated plots and treatments that incurred complete control (e.g., 100% control) were excluded from statistical analysis so as to not violate the constant variance assumption of ANOVA. Ninety-five percent confidence intervals were calculated to determine whether any treatment was similar to the treatments excluded from the analysis.

Palmer amaranth apical and circumferential growth throughout the growing season were modeled using a four-parameter Gompertz equation with Sigmaplot software (v. 14.0; Systat Software, San Jose, CA) as follows:

$$y = y_0 + a \left(\frac{-(x-x_0)}{b} \right) \quad [2]$$

where *y* equals growth, *y*0 equals the *y*-intercept, *a* equals an upper asymptote, *x* equals the time in weeks, *x*0 equals the *x*-intercept, and *b* equals the slope at *x*. If apical or circumferential growth did not fit the four-parameter Gompertz equation, the growth was modeled with a linear equation using Sigmaplot software (v. 14.0) as follows:

$$y = y_0 + a * x \quad [3]$$

where *y* equals growth rate, *y*0 equals the *y*-intercept, *a* equals the slope, and *x* equals time in weeks. Regression parameters for the apical and circumferential growth are provided in Tables 1 and 2.

Results and Discussion

Palmer Amaranth Control Following Glufosinate Application Timings

No Grass Competition Experiment

Palmer amaranth control was affected by location ($P = 0.0003$) and application timing ($P < 0.0001$), and the interaction ($P < 0.0001$) was significant. Therefore, data were analyzed by location and application timing. Palmer amaranth control with the early postemergence and sequential applications was greater than 90%; however, surviving plants were observed following the early

Table 2. Grass Competition experiment regression parameters from the four-parameter Gompertz equation to model apical and canopy circumferential growth of Palmer amaranth treated with glufosinate.^{a,b}

Location	Treatment	Apical					Canopy circumference				
		Regression parameters					Regression parameters				
		<i>a</i>	<i>b</i>	<i>x</i> ₀	<i>y</i> ₀	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>x</i> ₀	<i>y</i> ₀	<i>r</i> ²
Clayton	NTC	103.07	1.33	3.3	13.19	0.99	13.83	0.02	3.01	25.4	0.65
	WFNC	234.38	1.86	3.06	6.61	0.99	157.73	0.45	2.41	65.11	0.98
	WFIC	216.8	1.77	3.17	10.19	0.99	89.48	0.41	2.31	60.96	0.87
	EPOST	83.87	1.07	3.64	6.7	0.99	40.2	0.05	3	18.62	0.97
	MPOST	99.81	1.38	3.94	10.45	0.99	23.88	0.05	2.95	23.6	0.97
	LPOST	234.97	3.48	7.28	13.93	0.97	21.01	0.01	3.27	22.65	0.94
Rocky Mount	NTC	–	–	–	–	0.94	7.83	0.02	3.1	29.49	0.5
	WFNC	170.91	1.46	3.48	10.4	0.99	130.88	0.04	3	43.18	0.96
	WFIC	160.89	1.92	3.87	8.41	0.99	67.77	1.16	2.33	24.66	0.99
	MPOST	57.89	0.82	4.51	11.19	0.99	24.8	0.03	3.94	26.95	0.87
	LPOST	16.06	0.31	4.99	13.34	0.99	–2.46	–0.05	4.85	29.95	0.18

^aAbbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

^bIn cells with a dash (–) growth was best modeled with a linear equation. Apical growth: Palmer amaranth under NTC conditions at Rocky Mount: $y = -4.3 + 10.6^x$.

Table 3. Palmer amaranth control with glufosinate (590 g ai ha⁻¹) from the No Grass and Grass Competition experiments 35 d after treatment.^{a,b,c}

Treatment	No grass competition		Grass competition ^d
	Clayton	Rocky Mount	
	% (SE)		
EPOST	95 (4) a	100 (0) a	93 (4) a
MPOST	66 (6) c	75 (10) c	68 (6) b
LPOST	45 (3) d	81 (3) bc	61 (4) b
EPOST fb MPOST	100 (0) a	100 (0) a	100 (0) a
EPOST fb LPOST	100 (0) a	100 (0) a	100 (0) a
MPOST fb LPOST	100 (0) a	100 (0) a	100 (0) a
EPOST fb MPOST fb LPOST	100 (0) a	100 (0) a	100 (0) a

^aAbbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); fb, followed by; LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm).

^bSimilar letters within columns are not different according to Tukey's honest significant differences ($P \leq 0.05$).

^cTreatments that violated the constant variance assumption were not included in the analysis, but 95% confidence intervals were used to determine whether values were similar.

^dDue to the lack of an interaction between location and application timing for the Grass Competition experiment, data were pooled across location.

postemergence application at Clayton (Table 3). Control was reduced when glufosinate was applied at the mid-postemergence and late postemergence timings and were less effective than the early postemergence and sequential applications (Table 3). The pattern of decreased control as Palmer amaranth size increased at the time of application was similar to previous studies, regardless of crop (Coetzer et al. 2002; Everman et al. 2007; Randell et al. 2020). Clethodim effectively controlled all grass species that were not controlled by glufosinate as demonstrated by no plants being found in the treated plots (Table 3).

Grass Competition Experiment

Grass weed composition differed between the Clayton and Rocky Mount locations: large crabgrass (*Digitaria sanguinalis* L. Scop.) was present at Clayton; and bermudagrass (*Cynodon dactylon* L.), goosegrass (*Elusine indica* L.), large crabgrass, and Texas panicum (*Panicum texana* L.) were present at Rocky Mount (Table 4). Palmer amaranth control was affected by application timing ($P < 0.0001$), but neither the location ($P = 0.23$) nor the interaction ($P = 0.23$) was significant; thus, control data were analyzed by

application timing averaged over the location (Table 3). Early postemergence and sequential glufosinate applications provided the greatest Palmer amaranth control, whereas the mid-post-emergence and late postemergence applications on larger Palmer amaranth were less effective (Table 3). These results align with those of the No Grass Competition experiment and other studies investigating glufosinate efficacy on various weed sizes (Coetzer et al. 2002; Everman et al. 2007; Randell et al. 2020). Lack of grass control with the mid-postemergence and late postemergence glufosinate treatments was evident, but the grass weed densities differed across locations, with greater grass weed density at Clayton compared to Rocky Mount (Table 4).

Growth and Fecundity of Palmer Amaranth Surviving Glufosinate

No Grass Competition Experiment

No Palmer amaranth plants survived sequential applications of glufosinate, nor did any plants survive glufosinate when applied early postemergence at the Rocky Mount location; therefore, growth rate and fecundity data were not measured in these treatments. Differential control between locations resulted in significant main effects and interactions ($P < 0.0001$); thus, apical and circumferential growth were analyzed by location and treatment.

Across locations, the Palmer amaranth plants growing under WFIC and WFNC conditions exhibited the greatest apical growth rate followed by the plants under NTC conditions and those that survived glufosinate (Figure 1; Table 5). The differential apical growth between Palmer amaranth plants growing under WFNC and WFIC conditions at Rocky Mount but not at Clayton suggests that the apical growth of Palmer amaranth is affected by soybean competition and varies under different environmental conditions. Palmer amaranth plants that survived the mid-postemergence application exhibited a greater growth rate than plants that survived the early postemergence and late postemergence applications at Clayton (Figure 1; Table 5). Regardless of timing, Palmer amaranth plants that survived glufosinate at Clayton did not resume apical growth until 1 WAT (Figure 1). At Rocky Mount, the growth rate of Palmer amaranth plants that survived the mid-postemergence application was higher than plants that survived the late postemergence application (Figure 1; Table 5).

Table 4. Weed species density with various glufosinate treatments from the No Grass and Grass Competition experiments 35 d after treatment.^{a,b}

Location	Treatment	AMAPA	BRAAP	DIGSA	ELEIN	PANDI
Plants 0.25 m ⁻²						
No Grass Competition						
Clayton	NTC	50	–	15	0.5	–
	EPOST	1	–	0	0	–
	MPOST	6	–	0	0	–
	LPOST	18	–	0	0	–
Rocky Mount	NTC	33	3	1	0	1
	EPOST	0	0	0	0	0
	MPOST	7	0	0	0	0
	LPOST	5	0	0	0	0
Grass Competition						
Clayton	NTC	34	–	35	0	–
	EPOST	1	–	12	0	–
	MPOST	4	–	6	0	–
	LPOST	15	–	10	0	–
Rocky Mount	NTC	40	4	0	3	0
	EPOST	0	0	0	0	0
	MPOST	10	1	1	0	0
	LPOST	11	0	1	0	0

^aAbbreviations: AMAPA, Palmer amaranth; BRAAP, bermudagrass; DIGSA, large crabgrass; ELEIN, goosegrass; EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; PANTE, Texas panicum.

^bA dash (–) indicates the species was not present.

Palmer amaranth plants that survived glufosinate applied mid-postemergence and late postemergence at Rocky Mount did not resume apical growth until 4 and 3 WAT, respectively (Figure 1). Average final height reductions for Palmer amaranth that survived glufosinate at Clayton were more than 40% and 58% compared with plants grown under WFIC and WFNC conditions, respectively, whereas height reductions of Palmer amaranth that survived glufosinate at Rocky Mount were more than 69% and 76%, respectively, compared with plants that grew under WFIC and WFNC conditions (Figure 1).

Palmer amaranth plants at both locations that grew under WFNC conditions exhibited the greatest circumferential growth rate, with decreasing values for those grown under WFIC then NTC conditions, and those that survived glufosinate (Figure 2; Table 5). This result suggests that soybean competition significantly affects vegetative growth in the absence of competition from other species. Palmer amaranth plants that survived glufosinate at both locations did not resume circumferential growth until 1 and 2 WAT, respectively (Figure 2). At Clayton, average final circumference reductions of Palmer amaranth that survived glufosinate were 75% and 82%, respectively, compared with those that were grown under WFIC and WFNC conditions (Figure 2). At Rocky Mount average circumferential reductions of Palmer amaranth plants that survived glufosinate were 78% compared with plants that were grown under WFNC conditions (Figure 2).

Female biomass of Palmer amaranth was affected by location and application timing ($P < 0.0001$) with a significant interaction ($P < 0.0001$); biomass data were analyzed by location and treatment. No differences in Palmer amaranth biomass were observed between the WFNC and WFIC treatments at Clayton. However, the WFNC treatment at Rocky Mount resulted in greater biomass (Table 6). Palmer amaranth surviving glufosinate resulted in biomass accumulation similar to that of the NTC, and all were lower than the WFNC treatments at both locations (Table 6). At Rocky Mount, Palmer amaranth that grew under WFIC conditions were not significantly different from those that survived

glufosinate or that grew under NTC conditions (Table 6). Average biomass reductions of Palmer amaranth that survived glufosinate were 92% and 96% in Clayton and Rocky Mount, respectively, compared with Palmer amaranth plants that grew under WFIC (Clayton-only) and WFNC conditions.

Fecundity of Palmer amaranth was affected by application timing ($P < 0.0001$) but not location ($P = 0.84$). Although the interaction was nonsignificant ($P = 0.89$), fecundity data were analyzed by treatment and location because Palmer amaranth survived only the early postemergence application at the Clayton location.

Seed mass of Palmer amaranth was greatest from plants that grew under WFIC and WFNC conditions and from plants that survived glufosinate applied mid-postemergence and late postemergence at Clayton (Table 7). The smallest seeds came from Palmer amaranth plants grown at Clayton under NTC conditions followed by plants that survived the early postemergence and mid-postemergence applications (Table 7). Seed size was not different among treatments at Rocky Mount (Table 7). At both locations, Palmer amaranth grown under WFNC conditions were the most fecund, followed by those grown under WFIC and NTC conditions, and those that survived glufosinate (Table 7). That fecundity of Palmer amaranth grown under WFIC conditions was not different from plants grown under NTC conditions or those that survived glufosinate is likely a function of intraspecific competition. The fecundity of Palmer amaranth that survived glufosinate did not differ among treatments within the location (Clayton: 8,639 to 34,544 seeds plant⁻¹; Rocky Mount: 4,525 to 6,861 seeds plant⁻¹) (Table 7). Average fecundity reductions for Palmer amaranth that survived glufosinate were 87% and 97% compared with plants that grew under WFNC conditions at Clayton and Rocky Mount, respectively (Table 7).

Grass Competition Experiment

Since no Palmer amaranth plants survived sequential applications of glufosinate, growth and fecundity are not reported. Additionally, Palmer amaranth plants survived glufosinate applied early postemergence at Clayton but not Rocky Mount; thus, the growth and fecundity for this treatment cannot be reported because there were no surviving plants at Rocky Mount. Significant main effects and interactions ($P < 0.0001$) were detected; thus, apical and circumferential growth were analyzed by location and treatment.

The apical growth of Palmer amaranth plants was greatest in those grown under WFIC and WFNC conditions followed by NTC conditions, and for Clayton, plants that survived glufosinate (Figure 3; Table 5). Plants under WFNC conditions exhibited the greatest growth rate, followed by WFNC conditions, then NTC conditions, then those that survived glufosinate when it was applied at mid-postemergence, and then finally, at Rocky Mount, plants that survived glufosinate at late postemergence (Figure 3; Table 5). The differential apical growth between Palmer amaranth plants under WFNC and WFIC conditions at both locations suggests that its apical growth is affected by environmental conditions and soybean competition. Palmer amaranth that survived the mid-postemergence application exhibited a greater growth rate than those that survived the late postemergence application at Rocky Mount (Figure 3; Table 5). Palmer amaranth plants that survived glufosinate at Clayton did not resume apical growth until 1 WAT, whereas the plants that survived glufosinate resumed apical growth 2 WAT at Rocky Mount (Figure 3). At Clayton, average height reductions for Palmer amaranth that survived glufosinate were 52% to 64% compared with plants that

Table 5. Apical and canopy circumferential growth rate of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments.^{a,b}

Treatment	Apical growth		Circumference growth	
	Clayton	Rocky Mount	Clayton	Rocky Mount
	cm week ⁻¹ (\pm SE)			
No Grass Competition				
NTC	15 (0.2) c	9 (0.2) cde	6 (1.0) c	6 (0.3) b
WFNC	33 (0.2) a	24 (0.5) b	46 (5.0) a	31 (2.2) a
WFIC	35 (0.4) a	11 (0.8) cde	34 (2.7) b	9 (2.6) b
EPOST	10 (1.2) cde	NS	7 (2.2) c	NS
MPOST	23 (0.9) b	6 (0.5) de	10 (1.4) c	7 (0.8) b
LPOST	12 (0.3) cd	5 (0.3) e	9 (0.6) c	7 (0.9) b
EPOST fb MPOST	NS	NS	NS	NS
EPOST fb LPOST	NS	NS	NS	NS
MPOST fb LPOST	NS	NS	NS	NS
EPOST fb MPOST fb LPOST	NS	NS	NS	NS
Grass Competition				
NTC	17 (0.8) b	11 (0.6) c	6 (0.3) c	6 (0.2) c
WFNC	33 (1.0) a	25 (0.9) a	36 (3.6) a	31 (2.5) a
WFIC	31 (2.3) a	20 (1.3) b	27 (3.4) b	15 (1.4) b
EPOST	14 (2.7) bc	NS	10 (1.5) c	NS
MPOST	15 (1.4) bc	10 (0.9) c	8 (0.5) c	7 (0.8) c
LPOST	11 (1.4) c	5 (0.4) d	7 (0.8) c	7 (0.5) c
EPOST fb MPOST	NS	NS	NS	NS
EPOST fb LPOST	NS	NS	NS	NS
MPOST fb LPOST	NS	NS	NS	NS
EPOST fb MPOST fb LPOST	NS	NS	NS	NS

^aAbbreviations: EPOST, early postemergence (5 cm); fb, followed by; LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NS, no survivors; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

^bSimilar letters within columns for the No Grass and Grass Competition experiments are not different according to Tukey's honestly significant difference test ($\alpha \leq 0.05$).

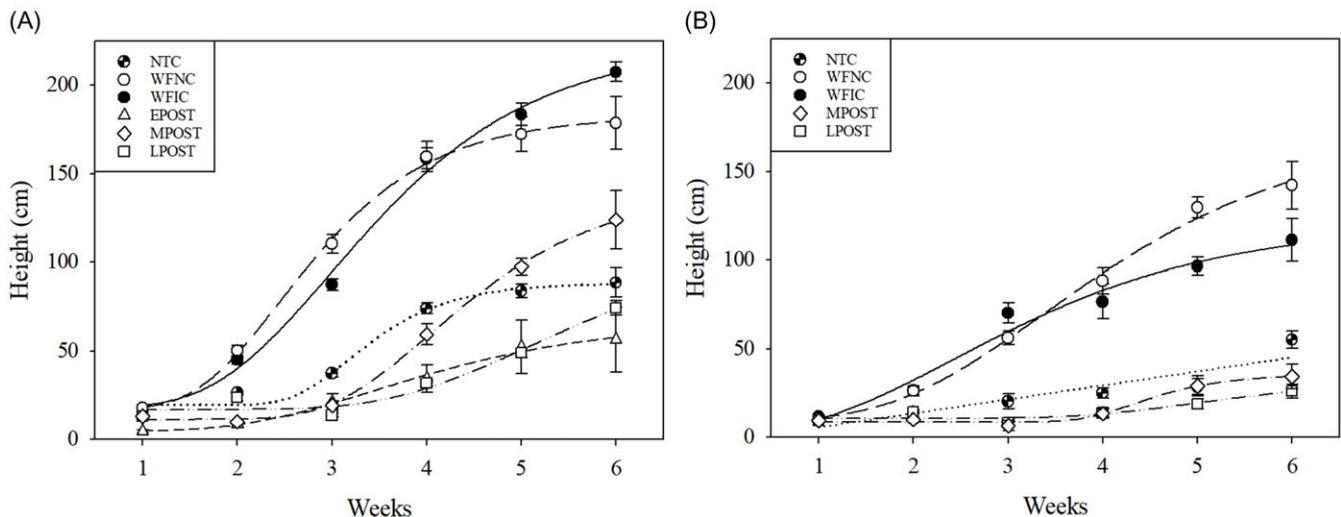


Figure 1. Plant height of Palmer amaranth plants treated with glufosinate from the No Grass Competition experiments conducted with soybean crops at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began 1 wk after the first application. Apical growth was modeled with a four-parameter Gompertz equation except for the Palmer amaranth plants under NTC conditions at Rocky Mount, which were modeled with a linear equation. Abbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

grew under WFIC and WFNC conditions (Figure 3). At Rocky Mount, average final height reductions for Palmer amaranth that survived glufosinate were 50% to 76% and 60% to 80% compared with plants that grew under WFIC and WFNC conditions, respectively (Figure 3).

Canopy circumference growth was greatest for Palmer amaranth plants that grew under WFNC conditions, followed by plants that grew under WFIC and NTC conditions, and plants that survived glufosinate at both locations (Figure 4; Table 5). Palmer amaranth plants that survived the early postemergence,

mid-postemergence, and late postemergence applications at Clayton did not resume apical growth until 2, 1, and 0.25 WAT, respectively (Figure 4). At Rocky Mount, plants that survived the mid-postemergence and late postemergence applications did not resume apical growth until 1 and 3 WAT, respectively (Figure 4). At Clayton, average final circumference reductions of Palmer amaranth that survived glufosinate were 63% to 71% and 73% to 79% compared with reductions of plants grown under WFIC and WFNC conditions, respectively, and the circumference reductions that occurred at Rocky Mount were similar (Figure 4).

Table 6. Biomass of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments.^{a,b}

Treatment	No grass competition		Grass competition	
	Clayton	Rocky Mount	Clayton	Rocky Mount
	g plant ⁻¹ (±SE)			
NTC	50 (6) b	19 (5) b	32 (7) b	27 (4) b
WFNC	633 (121) a	616 (72) a	332 (55) a	759 (122) a
WFIC	592 (120) a	66 (24) b	164 (42) a	118 (17) b
EPOST	46 (19) b	NS	30 (19) b	NS
MPOST	60 (11) b	32 (6) b	29 (8) b	54 (14) b
LPOST	37 (7) b	22 (6) b	35 (7) b	31 (3) b
EPOST fb MPOST	NS	NS	NS	NS
EPOST fb LPOST	NS	NS	NS	NS
MPOST fb LPOST	NS	NS	NS	NS
EPOST fb MPOST fb LPOST	NS	NS	NS	NS

^aAbbreviations: EPOST, early postemergence (5 cm); fb, followed by; LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NS, no survivors; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

^bSimilar letters within columns are not different according to Tukey's honestly significant difference test ($\alpha \leq 0.05$).

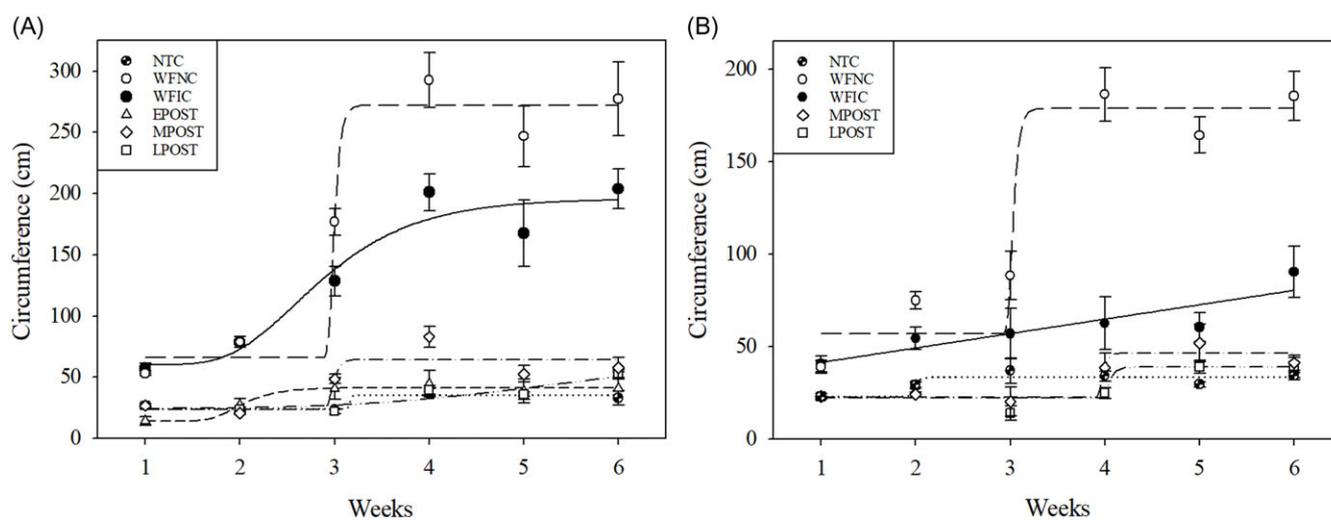


Figure 2. Canopy circumference of Palmer amaranth plants treated with glufosinate from the No Grass Competition experiments conducted with soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began 1 wk after the first application. Circumference growth was modeled with a four-parameter Gompertz equation except for the Palmer amaranth plants under WFIC conditions at Rocky Mount, which were modeled with a linear equation. Abbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

Accumulated female biomass of Palmer amaranth was affected by location ($P = 0.01$) and application timing ($P < 0.0001$), and the interaction ($P < 0.0001$) was significant; thus, female biomass data were analyzed by location and application timing. Palmer amaranth biomass across locations and treatments was nearly identical to that measured after the No Grass Competition experiment (Table 6). Average biomass reductions of Palmer amaranth that survived glufosinate were 94% compared with that of plants that grew under WFIC/WFNC and WFNC conditions at Clayton and Rocky Mount, respectively (Table 6).

Fecundity was affected by location ($P = 0.004$) and application timing ($P < 0.0001$). The interaction between the main effects was significant ($P < 0.0001$); thus, fecundity data were analyzed by location and application timing.

Seeds were larger from Palmer amaranth plants that were subjected to less competition (WFNC and WFIC) compared with plants subjected to greater competition or herbicide treatment (NTC, and treated at mid-postemergence and late postemergence) at Clayton (Tables 4 and 7). In addition, Palmer amaranth plants that survived the early postemergence application exhibited an

intermediate seed size (Table 7). Seed size at Rocky Mount was different. Seeds from Palmer amaranth plants grown under NTC conditions were the smallest, whereas seeds from plants grown under WFIC conditions and plants treated postemergence were the largest (Table 7). The seeds from the plants that grew under WFNC conditions and those that were treated late postemergence were intermediate in size at Rocky Mount (Table 7). The fecundity of Palmer amaranth plants that survived glufosinate did not differ among application timings within location (Clayton: 3,831 to 12,394 seeds plant⁻¹; Rocky Mount: 5,084 to 11,833 seeds plant⁻¹) (Table 7). Average fecundity reductions for Palmer amaranth that survived glufosinate were 84% and 87% compared with plants grown under WFNC conditions at the Clayton and Rocky Mount sites, respectively (Table 7).

Soybean Yield

No Grass Competition Experiment

The main effects (location and application timing, $P < 0.0001$) and interaction ($P = 0.02$) were significant for soybean yield; thus, yield

Table 7. Seed mass and fecundity of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments.^{a,b}

Treatment	Seed mass		Fecundity	
	Clayton	Rocky Mount	Clayton	Rocky Mount
	g 100 seeds ⁻¹ (±SE)		seeds plant ⁻¹ (±SE)	
No Grass Competition				
NTC	0.027 (0.0006) c	0.032 (0.0008)	12,484 (3,114) b	2,041 (818) b
WFNC	0.034 (0.0008) a	0.032 (0.0006)	163,606 (2,9690) a	170,167 (30,469) a
WFIC	0.032 (0.00006) ab	0.034 (0.0007)	10,835 (2,446) b	23,006 (9,968) b
EPOST	0.030 (0.0007) b	NS	34,544 (10,651) b	NS
MPOST	0.031 (0.0009) b	0.035 (0.0009)	21,068 (5,034) b	6,861 (1,671) b
LPOST	0.033 (0.0004) a	0.032 (0.0007)	8,639 (2,639) b	4,525 (1,428) b
EPOST fb MPOST	NS	NS	NS	NS
EPOST fb LPOST	NS	NS	NS	NS
MPOST fb LPOST	NS	NS	NS	NS
EPOST fb MPOST fb LPOST	NS	NS	NS	NS
Grass Competition				
NTC	0.030 (0.0003) c	0.029 (0.0003) c	10,069 (3,296) b	8,217 (5,547) b
WFNC	0.032 (0.0004) a	0.032 (0.0005) bc	55,530 (15,430) a	166,265 (27,604) a
WFIC	0.032 (0.0007) ab	0.035 (0.0008) a	25,443 (6,124) ab	34,662 (7,840) b
EPOST	0.031 (0.0002) bc	NS	11,115 (7,387) b	NS
MPOST	0.029 (0.0002) c	0.035 (0.0009) a	12,394 (3,683) b	11,833 (7,308) b
LPOST	0.029 (0.0002) c	0.034 (0.0008) ab	3,831 (2,080) b	5,084 (977) b
EPOST fb MPOST	NS	NS	NS	NS
EPOST fb LPOST	NS	NS	NS	NS
MPOST fb LPOST	NS	NS	NS	NS
EPOST fb MPOST fb LPOST	NS	NS	NS	NS

^aAbbreviations: EPOST, early postemergence (5 cm); fb, followed by; LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NS, no survivors; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop

^bSimilar letters within columns for the No Grass and Grass Competition experiments are not different according to Tukey's honestly significant difference test ($\alpha \leq 0.05$).

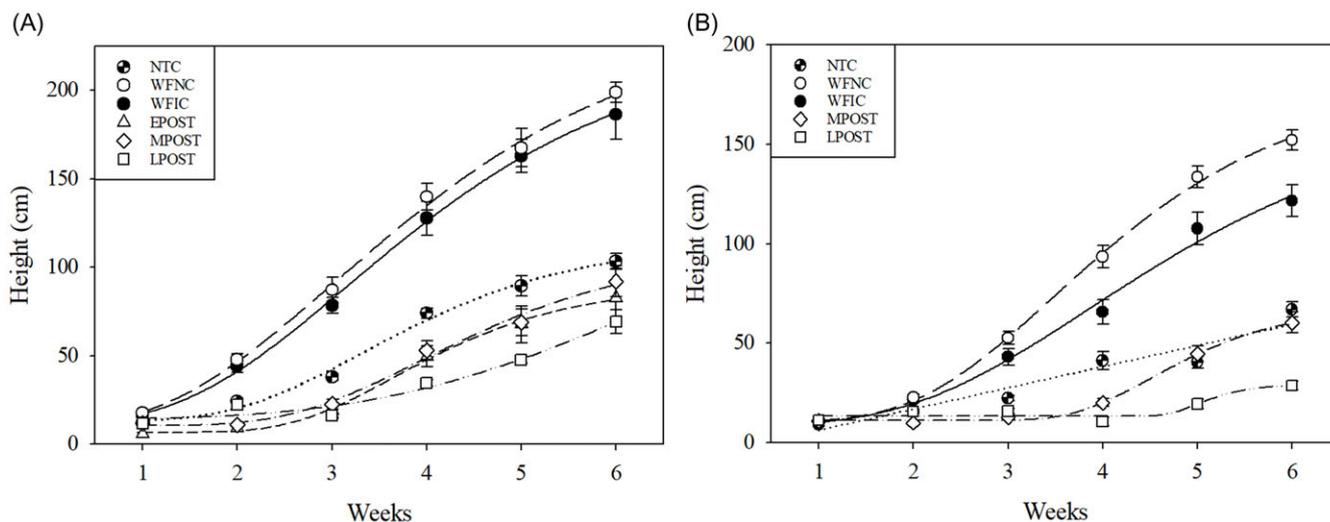


Figure 3. Height of Palmer amaranth plants treated with glufosinate from the Grass Competition experiments conducted in soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began 1 wk after the first application. Apical growth was modeled with a four-parameter Gompertz equation except for the Palmer amaranth plants under NTC conditions at Rocky Mount, which were modeled with a linear equation. Abbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

data were analyzed across location and glufosinate application. On average, soybean yield was higher at Clayton (4,433 kg ha⁻¹) than Rocky Mount (3,188 kg ha⁻¹). Lesser soybean yields were incurred with mid-postemergence and late postemergence applications at Clayton; no difference in soybean yield was detected between the early postemergence and all sequential applications (Table 8). A decrease in crop yields with herbicides applied to larger weeds later in the growing season has been observed by previous researchers (Fickett et al. 2013; Johnson and Hoverstad 2002). No difference in soybean yield was detected in applications at Rocky Mount (Table 8).

Grass Competition Experiment

Soybean yield was significantly affected by location ($P < 0.001$) but not application timing ($P = 0.22$), the interaction between the main effects was not significant ($P = 0.62$), thus soybean yield data were analyzed by location. Soybean yield was greater at Clayton (4,509 kg ha⁻¹) than Rocky Mount (3,502 kg ha⁻¹). The soybean yields from this experiment were comparable to those of soybean treated with glufosinate only (Aulakh and Jhala 2015; Craigmyle et al. 2013).

These results indicate that the vegetative growth of Palmer amaranth that survive a glufosinate application is reduced when

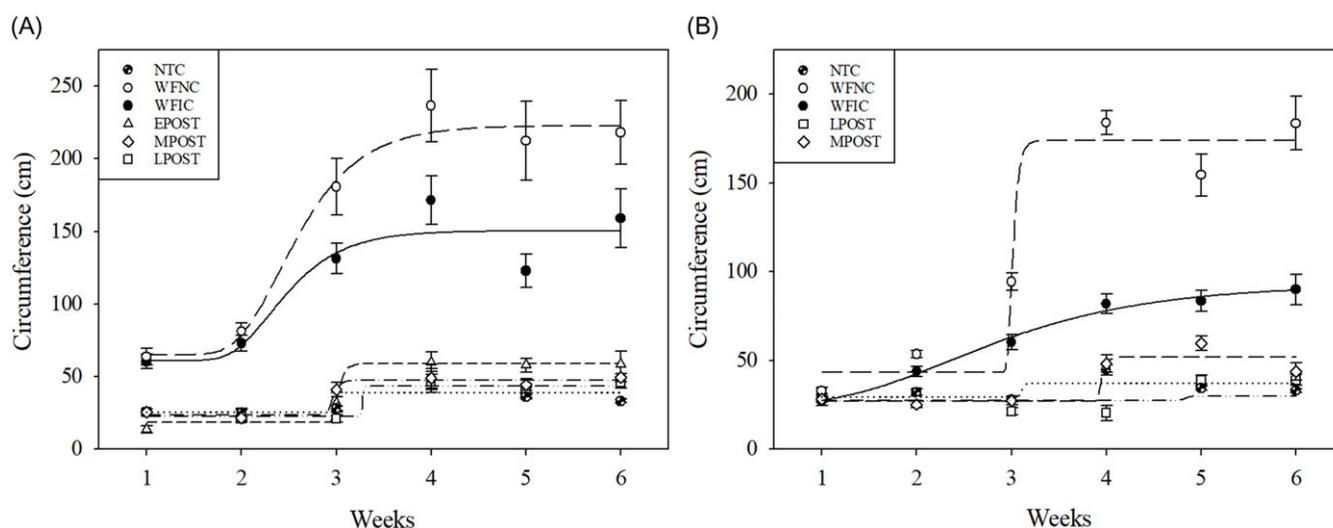


Figure 4. Canopy circumference growth of Palmer amaranth plants treated with glufosinate from the Grass Competition experiments conducted with soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began 1 wk after the first application. Circumference growth was modeled with a four-parameter Gompertz equation. Abbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm); NTC, nontreated control; WFIC, weed-free nontreated in-crop; WFNC, weed-free nontreated no-crop.

Table 8. Soybean yield with various glufosinate treatments from the No Grass Competition experiments.^{a,b}

Treatment	kg ha ⁻¹ (±SE)	
	Clayton	Rocky Mount
EPOST	4653 (242) a	3060 (130)
MPOST	3748 (406) bc	2900 (197)
LPOST	3530 (426) c	2852 (140)
EPOST fb MPOST	4508 (42) ab	3546 (178)
EPOST fb LPOST	4933 (346) a	3594 (189)
MPOST fb LPOST	4934 (207) a	3260 (67)
EPOST fb MPOST fb LPOST	4724 (92) a	3001 (275)

^aAbbreviations: EPOST, early postemergence (5 cm); fb, followed by; LPOST, late postemergence (>10 cm); MPOST, mid-postemergence (7–10 cm).

^bSimilar letters within column are not different according to Tukey's honestly significant difference test ($P \leq 0.05$).

growing with or without intraspecific grass weed competition compared with Palmer amaranth plants that grow under WFIC and WFNC conditions. The apical and circumferential growth of Palmer amaranth plants that survive glufosinate will resume reduced growth after treatment regardless of interspecific and intraspecific competition, and will continue to interfere with the crop. The loss of apical dominance or increased circumferential growth was not realized with Palmer amaranth plants that survived glufosinate in either experiment. This result parallels the reduced branching response exhibited by glufosinate-treated Palmer amaranth (Haarmann et al. 2021). Inseparable biomass of plants treated with glufosinate at different sizes has been demonstrated in previous research (Tharp et al. 1999). This result further demonstrates that Palmer amaranth exhibits the plasticity to accumulate similar size biomass regardless of size when treated with glufosinate, grass competition, or crop. Plant gender was not determined for Palmer amaranth plants, but previous research has provided evidence that gender does not affect the vegetative growth of dioecious *Amaranthus* species (Jones et al. 2019; Mahoney et al. 2021).

Since the collected female Palmer amaranth that survived glufosinate from all experiments produced seed, those that survived glufosinate produced viable ovules (stigmas). Previous

research has shown that nontreated Palmer amaranth grown in fields of weed-free soybean produced 40,000 to 550,000 seeds plant⁻¹ (Mahoney et al. 2021). The fecundity of the Palmer amaranth plants under WFIC conditions has been observed in other previous research with similar intraspecific competition levels (Bensch et al. 2003; Webster and Gray 2015). Although the plants under WFIC conditions in these experiments produced fewer seeds than those from the NTC, the fact that Palmer amaranth that survives glufosinate has the plasticity to overcome herbicide injury to produce the same number of seeds as that of a weed-free nontreated plant is noteworthy. It is also important to highlight the differential densities in each treatment that would also influence field-scale seed production (Table 4). However, the presence of a weed-free crop reduced the biomass and fecundity of Palmer amaranth the same as plants that survived glufosinate, which highlights the importance of crop competition (Swanton and Weise 1991). Palmer amaranth in the vegetative stage that survived glufosinate in these experiments were more fecund than similar plants in the reproductive stage that survived glufosinate and related herbicides (de Sanctis et al. 2021; Jha and Norsworthy 2012; Scruggs et al. 2020). Although the Palmer amaranth in the reproductive stage that survived glufosinate investigated by Jha and Norsworthy (2012) and Scruggs et al. (2020) produced fewer seeds, the glufosinate rate (656 to 820 g ai ha⁻¹) was significantly higher than that used in the present research (590 g ai ha⁻¹), suggesting that fecundity of Palmer amaranth that survives glufosinate may be rate-dependent. Additionally, experiments mentioned previously were conducted with 76-cm row spacing, whereas the current experiments were conducted with 91-cm row spacing, suggesting that row spacing could be an effective tactic for reducing seed production.

While direct comparisons cannot be made across experiments, Palmer amaranth that survived glufosinate with and without grass competition exhibited similar growth and fecundity. Future research should determine the growth and fecundity of Palmer amaranth that survives glufosinate in glufosinate-tolerant crops other than soybean due to the different vegetative architecture (Hartzler et al. 2004; Nordby and Hartzler 2004). Although glufosinate is not the most efficacious grass herbicide, the injury

incurred by the grass weeds in this research may have negated any competitive advantage compared with grass weeds treated with a herbicide with no grass control (i.e., dicamba) (Terra et al. 2007). Although farmers would likely apply glyphosate or an acetyl CoA carboxylase (EC 6.4.1.2; WSSA Group 1)-inhibiting herbicide to control grasses, this research provides further evidence that glufosinate should not be relied on solely for weed control. In tandem, future research determining the fecundity of plants that survive a herbicide treatment should include making controlled crosses of surviving male and female plants to determine the fitness and herbicide susceptibility of the offspring.

Practical Implications

The results of this study further bolster the concept of applying glufosinate to small Palmer amaranth plants, which results in greater control. Sequential applications of glufosinate eliminated Palmer amaranth survivors, but other tactics (chemical and nonchemical) should be implemented to reduce selection pressure on resistant plants. Palmer amaranth that survived glufosinate exhibited reduced growth, but yield loss is likely attributable to early season competition. Although direct comparisons cannot be made across the experiments, the competition of glufosinate-treated grass likely does influence Palmer amaranth growth and fecundity. However, these plants are still interfering with the crop and could result in a reduction in harvest efficiency. More importantly, Palmer amaranth that survives glufosinate will produce seed (approximately 3,800 to 25,000 seeds plant⁻¹), which is equivalent to nontreated plants that grow with soybean. This result is very important because any Palmer amaranth escape adds a substantial number of seeds to soil to be controlled in subsequent growing seasons. This result should provide caution of using only a single glufosinate application because even 5-cm plants survived and produced several thousand seeds.

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