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

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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 surviving glufosinate with and without grass competition in soybean. Glufosinate (590 g ai ha^{-1}) was applied at early postemergence (5 cm Palmer amaranth height), mid-postemergence (7-10 cm), and late postemergence (>10 cm) and at orthogonal combinations of those timings. Non-treated 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 for both experiments. The apical and circumference growth rate of Palmer amaranth surviving glufosinate was reduced by more than 44% when compared to the WFNC Palmer amaranth. The biomass of Palmer amaranth plants surviving glufosinate was reduced by more than 87% when compared to the WFNC Palmer amaranth. The fecundity of Palmer amaranth surviving glufosinate was reduced by more than 70% when compared to WFNC Palmer amaranth. Palmer amaranth surviving glufosinate were as fecund as the WFIC Palmer amaranth in both experiments for soybean. The results prove that despite the significant vegetative growth rate decrease of Palmer amaranth surviving glufosinate, plants can be fecund as non-treated plants in soybean. The trends of growth and fecundity of Palmer amaranth surviving 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 surviving glufosinate.

Nomenclature: glufosinate; Palmer amaranth, *Amaranthus palmeri* S. Watson; soybean, *Glycine max* L.

Keywords: competition, fitness, weed management

Introduction

Palmer amaranth is a pervasive and ubiquitous weed across the Southeast United States its biology and the widespread evolution of herbicide resistance in this species (Webster and Grey 2015; Webster and Nichols 2012). Palmer amaranth can grow 0.5 to 2.5 cm day^{-1} and produce 250,000 to 500,000 seeds $plant^{-1}$, on average (Mahoney et al. 2021; Sellers et al. 2003a). Since Palmer amaranth is an obligate outcrosser, offspring will be genetically diverse, which can facilitate rapid adaption 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 yield 14 to 68% in soybean (Basinger et al. 2019; Klingaman and Oliver 1994). Only a few postemergence herbicides remain effective for Palmer amaranth control in soybean grown in the Southeast United States.

Glufosinate is an effective, non-selective, fast-acting contact herbicide that inhibits glutamine synthetase (EC 6.3.1.2; WSSA Group 10), 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 greater than 10 cm in height, reflecting the importance of spray coverage (Steckel et al. 1997; Jones et al. 2022). While glufosinate is efficacious, overreliance has led to the evolution of several isolated glufosinate-resistant Palmer amaranth populations (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 sub-lethal herbicide dose, but a sub-lethal herbicide dose can also stimulate growth (Belz 2018; Cedergreen 2008). Previous research reported weed growth is not hormetic after surviving glufosinate or a related herbicide (i.e., cell membrane disruptor) (Cedergreen 2008; Haarmann et al. 2021). Quantifying the growth of Palmer amaranth surviving glufosinate is important to determine putative yield loss if plants are allowed to interfere with the crop (Everman et al. 2008; Page et al. 2012). For example, Palmer amaranth exhibiting 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 to the fecundity of plants in the weedy non-treated controls, which may not be a true representation of the fecundity reduction due to the high levels of inter- and intra-specific competition. Additionally, the research reporting the fecundity of Palmer amaranth in the vegetative stage surviving glufosinate did not control grass weeds or later emerging weeds, while other research reporting the fecundity of surviving Palmer amaranth in the reproductive stage controlled other weeds before applying glufosinate (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 surviving glufosinate with and without grass competition have not been documented in soybean. Thus, the objectives of the research were to quantify the growth and fecundity of Palmer amaranth surviving glufosinate with and without grass competition compared to weedy—and weed-free-non-treated Palmer amaranth in soybean.

Materials and methods

Two separate field experiments were each conducted in 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, Edgecombe County (35.89 N, 77.68 W [Rocky Mount] and Johnston County (35.66 N, 78.51 W [Clayton]), North Carolina, during the 2020 growing season. The Rocky Mount site has a 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 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) soils. 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 9th and 10th, 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 ([EPOST] 5 cm Palmer amaranth), mid postemergence ([MPOST] 7 to 10 cm Palmer amaranth), late postemergence ([LPOST] >10 cm Palmer amaranth and at orthogonal combinations of those timings. The three application timings were separated by seven days. Three additional treatments were included in the experiments for comparison: weedy non-treated in-crop control (NTC), weed-free in-crop (WFIC), and weed-free no-crop (WFNC) for a total of ten treatments. The WFIC and WFNC plots were sprayed with glufosinate at the EPOST timing, but ten 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 flat-fan nozzles (XR110002 TeeJet nozzles, TeeJet technologies, Wheaton, 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 2 ± hours 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 (1071 g ai ha^{-1}) was applied to the entirety of the study using the described application methods three d after the LPOST application to control later emerging weeds and mitigate confounding effects of inter- and intraspecific competition on growth and fecundity not attributable to plants surviving glufosinate in both experiments. In the ‘No Grass Competition’ experiment, clethodim (280 g ai ha^{-1}) was applied to control grass species to the entirety of the study using the described application methods 10 d after the LPOST application to avoid control antagonism (Burke et al. 2005). Palmer amaranth control was visually estimated using a 0-100 scale, where 0 equals no control, and 100 equals complete control 35 d after treatment (DAT), respectively. Palmer amaranth plants emerging after glufosinate applications were not rated as glufosinate has no soil residual activity (Krausz et al. 1999). Density counts (plants 0.25 m^{-2}) by species were recorded at 35 DAT, respectively, in both experiments.

Palmer amaranth plants surviving glufosinate were marked with a flag (ten plants $plot^{-1}$) seven days 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 one until six wk after the last treatment (WAT). Circumference was measured as a metric for apical dominance (Cline 1997). At the end of the season, if present, three surviving female Palmer amaranth plants 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 elucidated surviving a glufosinate application. Harvested plants were placed in a drier at 60 C for 72 hours. 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 non-viable (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 remove plant residue further. The total number of seeds produced by each female plant was extrapolated by determining the mass of five 100-seed sub-samples for each treatment (Sellers et al. 2003a). The total number of seeds produced was calculated using the 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 sub-samples, and *T* equals the calculated number of seeds produced.

After female Palmer amaranth plants were harvested and soybean reached physiological maturity, soybean were 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 non-

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treated 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 an analysis of variance using the GLIMMIX procedure in SAS 9.4 (Statistical Analysis Solutions, Cary, NC), where $\alpha = 0.05$. Location, treatment, and their interactions were considered the main effects, while replication was considered random. Palmer amaranth biomass, control, and fecundity means were separated using Tukey's honest significant difference ($p \leq 0.05$). Palmer amaranth control data from nontreated plots and treatments that incurred complete control (e.g., 100% control) were excluded from statistical analysis as not to violate the constant variance assumption of analysis of variance. Ninety-five percent confidence intervals were calculated to determine if any treatment was similar to the treatments excluded from the analysis.

Palmer amaranth apical and circumference growth throughout the growing season was modeled using a four-parameter Gompertz equation in Sigmaplot 14.0 (Systat Software, San Jose, CA) [2]:

$$y = y0 + a^{\left(-\frac{(x-x0)}{b}\right)} \text{ [2]}$$

where *y* equals growth, *y0* equals the y-intercept, *a* equals an upper asymptote, *x* equals the time in wk, *x0* equals the x-intercept, and *b* equals the slope at *x*. If apical or circumference growth did not fit the four-parameter Gompertz equation, the growth was modeled with a linear equation in Sigmplot 14.0 [3]:

$$y = y0 + a * x \text{ [3]}$$

Where *y* equals growth rate, *y0* equals the y-intercept, *a* equals the slope, *x* equals time in wks. Regression parameters for the apical and circumference growth are provided in Tables 1 and 2.

Results and Discussion

<u>Palmer amaranth control following glufosinate application timings</u>

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 EPOST and sequential applications was greater than 90%; however, surviving plants were observed following the

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EPOST application at Clayton (Table 3). Control was reduced when glufosinate applications were made at the MPOST and LPOST timings and were less effective than the EPOST 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 not controlled by glufosinate as demonstrated by no plants in the treated plots (Table 3).

Grass Competition Experiment

Grass weed composition differed between Clayton and Rocky Mount: 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, while the MPOST and LPOST applications on larger Palmer amaranth were less effective (Table 3). These results align with 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 MPOST and LPOST 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-applied EPOST at Rocky Mount; 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 circumference growth were analyzed by location and treatment.

Apical growth. Across locations, the Palmer amaranth plants growing under WFIC and WFNC conditions exhibited the greatest growth rate followed by the plants under NTC conditions and Palmer amaranth surviving glufosinate (Figure 1; Table 5). The differential apical growth between Palmer amaranth plants growing under WFNC and WFIC 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 surviving the MPOST application exhibited a greater growth rate than plants surviving the EPOST and LPOST applications at Clayton (Figure 1; Table 5). Regardless of timing, Palmer amaranth plants surviving glufosinate at Clayton did not resume apical growth until 1 WAT (Figure 1). At Rocky Mount, the growth rate of Palmer amaranth plants surviving the MPOST application was higher than plants surviving the LPOST application (Figure 1; Table 5). Palmer amaranth plants surviving glufosinate-applied MPOST and LPOST at Rocky Mount did not resume apical growth until 4 and 3 WAT, respectively (Figure 1). Average final height reductions for Palmer amaranth surviving glufosinate at Clayton were more than 40% and 58% when compared to the Palmer amaranth plants under WFIC and WFNC conditions, respectively, while reductions for Palmer amaranth surviving glufosinate at Rocky Mounty were more than 69% and 76% when compared to Palmer amaranth plants under WFIC and WFNC conditions, respectively (Figure 1).

Canopy circumference growth. Palmer amaranth plants at Clayton and Rocky Mount growing under WFNC conditions exhibited the greatest growth rate, with decreasing values for those grown under WFIC, NTC, and surviving glufosinate (Figure 2; Table 5). This result suggests soybean competition significantly affects vegetative growth in the absence of other species' competition. Palmer amaranth plants surviving glufosinate at Clayton and Rocky Mount did not resume circumference growth until 1 and 2 WAT, respectively (Figure 2). Average final circumference reductions of Palmer amaranth surviving glufosinate were 75 and 82% compared to the Palmer amaranth plants under WFIC and WFNC conditions, respectively, at Clayton (Figure 2). Average circumference reductions of the Palmer amaranth surviving glufosinate at Rocky Mount were 78% compared to the Palmer amaranth plants under WFNC conditions (Figure 2).

Accumulated female biomass. Palmer amaranth female biomass 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 resulted in greater biomass at Rocky Mount (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 growing in the WFIC were not significantly different from those surviving glufosinate or under NTC conditions (Table 6). Average biomass reductions of Palmer amaranth surviving glufosinate were 92% and 96% at Clayton and Rocky Mount compared to the Palmer amaranth plants under WFIC (Clayton-only) and WFNC conditions, respectively.

Fecundity. Palmer amaranth fecundity was affected by application timing ($p < 0.0001$) but not the location ($p = 0.84$). While the interaction was non-significant ($p = 0.89$); fecundity data were analyzed by treatment and location since Palmer amaranth only survived the EPOST application at Clayton.

The seed mass was the greatest for Palmer amaranth plants under WFIC and WFNC conditions as well as Palmer amaranth surviving glufosinate applied MPOST and LPOST at Clayton (Table 7). Seeds were the smallest for Palmer amaranth plants under NTC conditions followed by Palmer amaranth surviving the EPOST and MPOST application at Clayton (Table 7). Seed size was not different across treatments at Rocky Mount (Table 7). The Palmer amaranth under WFNC conditions were the most fecund, followed by plants under WFIC and NTC conditions, and Palmer amaranth survived glufosinate at both locations (Table 7). The Palmer amaranth fecundity under WFIC conditions being no different from plants under NTC conditions or Palmer amaranth surviving glufosinate is likely a function of intra-specific competition. The fecundity of Palmer amaranth surviving glufosinate did not differ across 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 surviving glufosinate were 87% and 97% compared to Palmer amaranth under WFNC conditions at Clayton and Rocky Mounty, 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 EPOST at Clayton but not Rocky Mount; thus, the growth and fecundity for this treatment cannot be reported with no surviving plants at Rocky Mount. Significant main effects and interactions ($p < 0.0001$) were detected; thus, apical and circumference growth were analyzed by location and treatment.

Apical growth. The Palmer amaranth plants under WFIC and WFNC conditions exhibited the greatest growth rate followed by the plants under NTC conditions and Palmer amaranth

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surviving glufosinate at Clayton (Figure 3; Table 5). The Palmer amaranth plants under WFNC conditions exhibited the greatest growth rate, followed by the plants under WFNC conditions, then plants under NTC conditions and surviving glufosinate at the MPOST application timing, then finally, plants surviving glufosinate at the LPOST application timing at Rocky Mount (Figure 3; Table 5). The differential apical growth between Palmer amaranth plants growing under WFNC and WFIC at both locations suggests that the apical growth of Palmer amaranth is affected by environmental conditions and soybean competition. Palmer amaranth surviving the MPOST application exhibited a greater growth rate than the Palmer amaranth surviving the LPOST application at Rocky Mount (Figure 3; Table 5). Palmer amaranth plants surviving glufosinate at Clayton did not resume apical growth until 1 WAT, while the plants surviving glufosinate resumed apical growth 2 WAT at Rocky Mount (Figure 3). Average height reductions for Palmer amaranth surviving glufosinate were 52-64% when compared to the Palmer amaranth plants under WFIC and WFNC conditions at Clayton (Figure 3). Average final height reductions for Palmer amaranth surviving glufosinate were 50 to 76% and 60 to 80% compared to the Palmer amaranth plants under WFIC and WFNC conditions at Rocky Mount, respectively (Figure 3).

Canopy circumference growth. The Palmer amaranth plants under WFNC conditions exhibited the greatest growth rate, followed by those under WFIC and NTC conditions and plants surviving glufosinate at both locations (Figure 4; Table 5). Palmer amaranth surviving the EPOST, MPOST, and LPOST applications did not resume apical growth until 2, 1, and 0.25 WAT at Clayton, respectively (Figure 4). Palmer amaranth surviving the MPOST and LPOST applications did not resume apical growth until 1 and 3 WAT at Rocky Mount, respectively (Figure 4). Average final circumference reductions for Palmer amaranth surviving glufosinate were 63 to 71% and 73 to 79% compared to the Palmer amaranth plants under WFIC and WFNC conditions at Clayton, respectively, and the circumference reductions realized at Rocky Mount were similar (Figure 4).

Accumulated female biomass. Palmer amaranth female biomass 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 the No Grass Competition experiment as described above (Table 6). Average biomass reductions of Palmer amaranth surviving

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glufosinate were 94% compared to the Palmer amaranth plants under WFIC/WFNC and WFNC conditions at Clayton and Rocky Mount, respectively (Table 6).

Fecundity. 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 for Palmer amaranth subjected to less competition (WFNC and WFIC) compared to Palmer amaranth subjected to greater competition or herbicide treatment (NTC, MPOST, and LPOST-treated) at Clayton (Tables 4 and 7). The Palmer amaranth surviving the EPOST application exhibited an intermediate seed size at Clayton (Table 7). Seed size followed a dissimilar trend at Rocky Mount. Seeds from Palmer amaranth plants under NTC conditions were the smallest, while the seeds from plants under WFIC conditions and POST-treated plants were the largest (Table 7). The seeds from the plants under WFNC conditions and LPOST-treated plants exhibited an intermediate seed size at Rocky Mount (Table 7). The fecundity of Palmer amaranth surviving glufosinate did not differ across application timing 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 surviving glufosinate was 84% and 87% compared to the Palmer amaranth plants under WFNC conditions at Clayton and Rocky Mount, 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 data were analyzed across location and glufosinate application. On average, soybean yield was higher at Clayton (4433 kg ha-1) than Rocky Mounty (3188 kg ha-1). Lesser soybean yields were incurred with MPOST and LPOST applications at Clayton; no difference in soybean yield was detected between the EPOST 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 research (Fickett et al. 2013; Johnson and Hoverstad 2002). No difference in soybean yield was detected in applications at Rocky Mount (Table 8).

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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 (4509 kg ha^{-1}) than Rocky Mount (3502 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 surviving glufosinate is reduced when growing with or without intraspecific grass weed competition when compared to Palmer amaranth plants under WFIC and WFNC conditions. The apical and circumference growth of Palmer amaranth plants surviving glufosinate will resume reduced growth after treatment regardless of inter- and intra-specific competition and continue to interfere with the crop. The loss of apical dominance or increased circumference growth was not realized with Palmer amaranth plants surviving 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* spp. (Jones et al. 2019; Mahoney et al. 2021).

Since the collected female Palmer amaranth surviving glufosinate from all experiments produced seed, the Palmer amaranth surviving glufosinate produced viable ovules (stigmas). Previous research has shown non-treated Palmer amaranth grown in weed-free soybean to produce 40,000-550,000 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 intra-specific competition levels (Bensch et al. 2003; Webster and Gray 2015). While the plants under WFIC conditions in these experiments produced less seed compared to NTC, the fact that Palmer amaranth surviving glufosinate has the plasticity to overcome herbicide injury to produce the same number of seed of a weed-free non-treated plant is noteworthy. While noteworthy, it is also important to highlight the differential densities in each treatment that would

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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 surviving glufosinate, which highlights the importance of crop competition (Swanton and Weise 1991). Palmer amaranth in the vegetative stage surviving glufosinate in these experiments were more fecund than the reproductive stage Palmer amaranth surviving glufosinate and related herbicides (de Sanctis et al. 2021; Jha and Norsworthy 2012; Scruggs et al. 2020). While the Palmer amaranth in the reproductive stage surviving glufosinate investigated by Jha and Norsworthy (2012) and Scruggs et al. (2020) produced less seeds, the glufosinate rate (656 to 820 g ai ha^{-1}) was significantly higher than used in this research (590 g ai ha^{-1}), suggesting fecundity of Palmer amaranth surviving glufosinate may be rate-dependent. Additionally, these previously mentioned experiments were conducted under 76 cm row spacing, while the presented experiments were conducted under 91 cm row spacing, suggesting that row spacing could be an effective tactic to reduce seed production.

While direct comparisons cannot be made across experiments, Palmer amaranth surviving glufosinate with and without grass competition exhibited similar growth and fecundity. Future research should determine the growth and fecundity of Palmer amaranth surviving glufosinate in other glufosinate-tolerant crops due to the different vegetative architecture compared to soybean (Hartzler et al. 2004; Nordby and Hartzler 2004). While 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 to grass weeds treated with a herbicide with no grass control (i.e., dicamba) (Terra et al. 2007). While farmers would likely apply glyphosate or an acetyl CoA carboxylase (EC 6.4.1.2; 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 surviving 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 bolsters applying glufosinate to small Palmer amaranth plants, resulting in greater control. Sequential applications of glufosinate eliminated Palmer amaranth survivors, but other tactics (chemical and non-chemical) should be implemented to reduce

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selection pressure on resistant plants. Palmer amaranth surviving glufosinate exhibited reduced growth but yield loss is likely attributable to early season competition. While 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 surviving glufosinate will produce seed (approximately 3800 to 25,000 seeds $plant^{-1}$) equivalent to non-treated plants growing with soybean. This result is very important as any Palmer amaranth escape adds a substantial number of seed to soil to be controlled in subsequent growing seasons. This result should provide caution of only using a single glufosinate application as even 5 cm plants survived and produced several thousand seeds.

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Competing interest

No competing interests have been declared.

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Table 1. No Grass Competition experiment regression parameters from the four-parameter Gompertz equation to model apical and canopy circumference growth of Palmer amaranth treated with glufosinate conducted in soybean at Clayton and Rocky Mount, North Carolina.[a]

		Apical					Canopy circumference				
		Regression parameters					Regression parameters				
Location	Treatment	a	b	x0	y0	r^2	a	b	x0	y0	r^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	-[b]	-	-	-	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	-[b]	-	-	-	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

[a] Abbreviations: NTC, non-treated; WFNC, weed-free non-treated no-crop; WFIC, weed-free non-treated in-crop; EPOST, early postemergence (5 cm Palmer amaranth height); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by; NS, no survivors.

[b] Growth was best modeled with a linear equation. Apical growth:; Palmer amaranth under NTC conditions in soybean at Rocky Mount: y=-2.2+7.9*x. Circumference growth:; Palmer amaranth under WFIC conditions in soybean at Rocky Mount y=33.7+7.8*x.

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Table 2. Grass Competition experiment egression parameters from the four-parameter Gompertz equation to model apical and canopy circumference growth of Palmer amaranth treated with glufosinate conducted in soybean at Clayton and Rocky Mount, North Carolina.

		Apical					Canopy circumference				
		Regression parameters					Regression parameters				
Location	Treatment	a	b	x0	y0	r^2	a	b	x0	y0	r^2
Clayton	NTC[a]	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	-[b]	-	-	-	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

[a] Abbreviations: NTC, non-treated; WFNC, weed-free non-treated no-crop; WFIC, weed-free non-treated in-crop; EPOST, early postemergence (5 cm Palmer amaranth height); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by; NS, no survivors.

[b] Growth was best modeled with a linear equation. Apical growth: Palmer amaranth under NTC conditions at Rocky Mount: y=-4.3+10.6*x.

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Table 3. Palmer amaranth control with glufosinate (590 g ai ha^{-1}) from the No Grass and Grass Competition experiments conducted in soybean at Clayton and Rocky Mount, North Carolina 35 days after treatment.

Treatment	No Grass Competition				Grass Competition[a]	
	Clayton		Rocky Mount			
	% (SE)					
EPOST[b]	95 (4)	a[c,d]	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

[a] Due to the lack of an interaction between location and application timing for the Grass Competition experiment, data were pooled across location.

[b] Abbreviations: EPOST, early postemergence (5 cm Palmer amaranth height); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by.

[c] Similar letters within columns are not different according to Tukey's honest significant differences ($p \leq 0.05$).[d] Treatments that violated the constant variance assumption were not included in the analysis but 95% confidence intervals were used to determine if values were similar.

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Table 4. Weed species density with various glufosinate treatments from the No Grass and Grass Competition experiments conducted in soybean at Clayton and Rocky Mount, North Carolina 35 days after treatment.[a]

Location	Treatment	AMAPA	BRAAP	DIGSA	ELEIN	PANDI
		plants 0.25 m^{-2}				
No Grass Competition						
Clayton	NTC	50	-[b]	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

[a] Abbreviations: AMAPA, Palmer amaranth; BRAAP, bermudagrass; DIGSA, large crabgrass; ELEIN, goosegrass; PANTE, Texas panicum; NTC, non-treated control; EPOST, early postemergence (5 cm Palmer amaranth height); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm)

[b] Species was not present.

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Table 5. Apical and canopy circumference growth rate of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments conducted in soybean at Clayton and Rocky Mount, North Carolina.

Treatment	Apical growth				Circumference growth			
	Clayton		Rocky Mount		Clayton		Rocky Mount	
	------------------ cm week^{-1} (±SE) -----------------------							
No Grass Competition								
NTC[a]	15 (0.2)	c[b]	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[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	

[a] Abbreviations: NTC, non-treated; WFNC, weed-free non-treated no-crop; WFIC, weed-free non-treated in-crop; EPOST, early postemergence (5 cm); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by; NS, no survivors.

[b] Similar letters within columns for the No Grass and Grass Competition experiments are not different according to Tukey's honest significant differences ($\alpha \leq 0.05$).

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Table 6. Biomass of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments conducted in soybean at Clayton and Rocky Mount, North Carolina.

Treatment	No Grass Competition				Grass Competition			
	Clayton		Rocky Mount		Clayton		Rocky Mount	
	------------------------- g plant^{-1} (±SE) --------------------------							
NTC[a]	50 (6)	b[b]	19 (5)	b	32 (7)	b[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	

[a] Abbreviations: NTC, non-treated; WFNC, weed-free non-treated no-crop; WFIC, weed-free non-treated in-crop; EPOST, early postemergence (5 cm); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by; NS, no survivors.

[b] Similar letters within columns are not different according to Tukey's honest significant differences ($\alpha \leq 0.05$).

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Table 7. Seed mass and fecundity of Palmer amaranth treated with glufosinate from the No Grass and Grass Competition experiments conducted in soybean at Clayton and Rocky Mount, North Carolina.

Treatment	Seed mass				Fecundity			
	Clayton		Rocky Mount		Clayton		Rocky Mount	
	--------- g 100 seeds^{-1} (±SE) ----------				------- seeds plant^{-1} (±SE) ----------			
No Grass Competition								
NTC[a]	0.027 (0.0006)	c[b]	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

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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	

Table 7 (Continued) [a] Abbreviations: NTC, non-treated; WFNC, weed-free non-treated no-crop; WFIC, weed-free non-treated in-crop; EPOST, early postemergence (5 cm); POST, postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by; NS, no survivors.

[b] Similar letters within columns for the No Grass and Grass Competition experiments are not different according to Tukey's honest significant differences ($\alpha \leq 0.05$).

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Table 8. Soybean yield with various glufosinate treatments from the No Grass Competition experiments conducted in Clayton and Rocky Mount, North Carolina.

Treatment	Clayton		Rocky Mount
	--------- kg ha^{-1} (±SE) -------------		
EPOST[a]	4653 (242)	a[b]	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)

[a] Abbreviations: EPOST, early postemergence (5 cm); MPOST, mid postemergence (7-10 cm); LPOST, late postemergence (>10 cm); fb, followed by

[b] Similar letters within column are not different according to Tukey's honest significant differences ($p \leq 0.05$).

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Fig. 1A

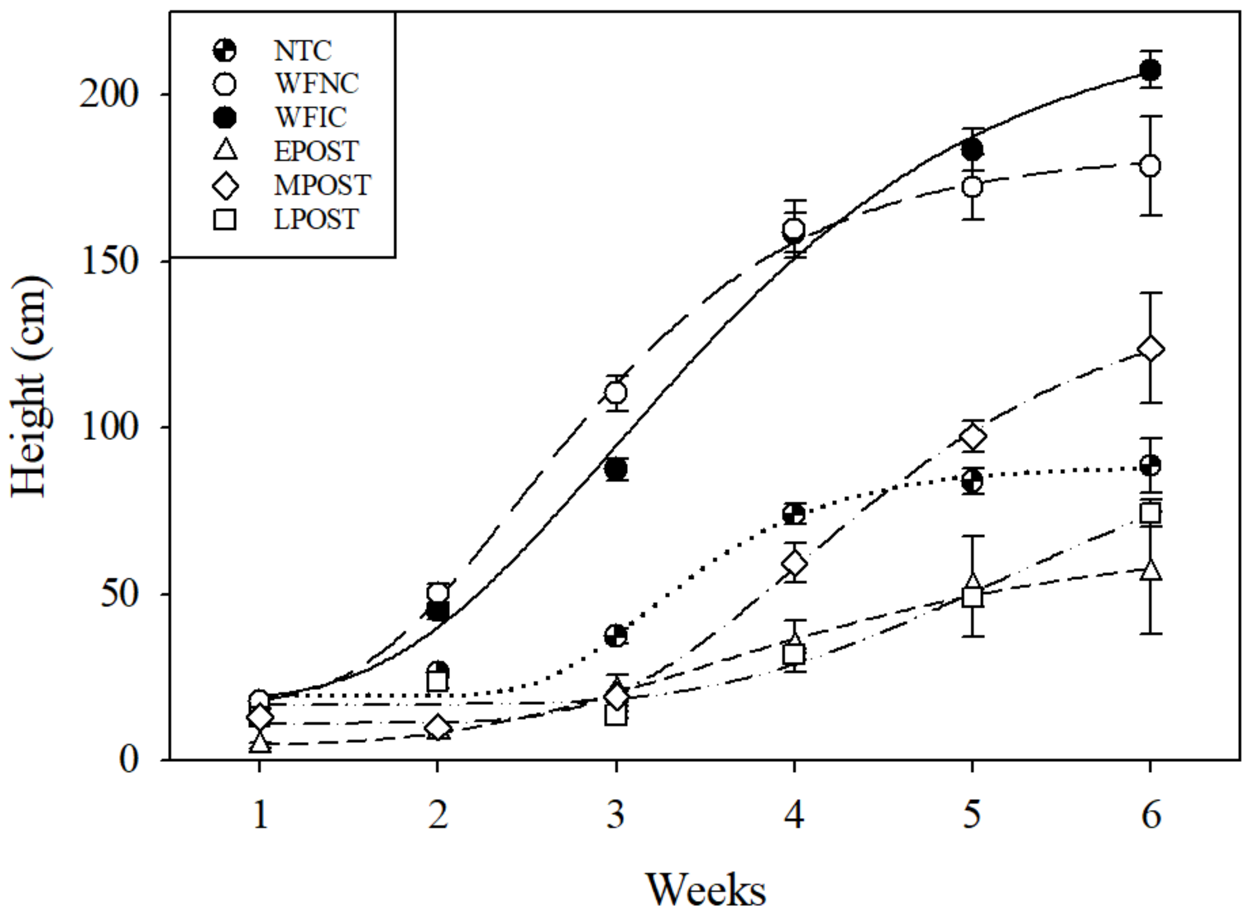

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Fig. 1B

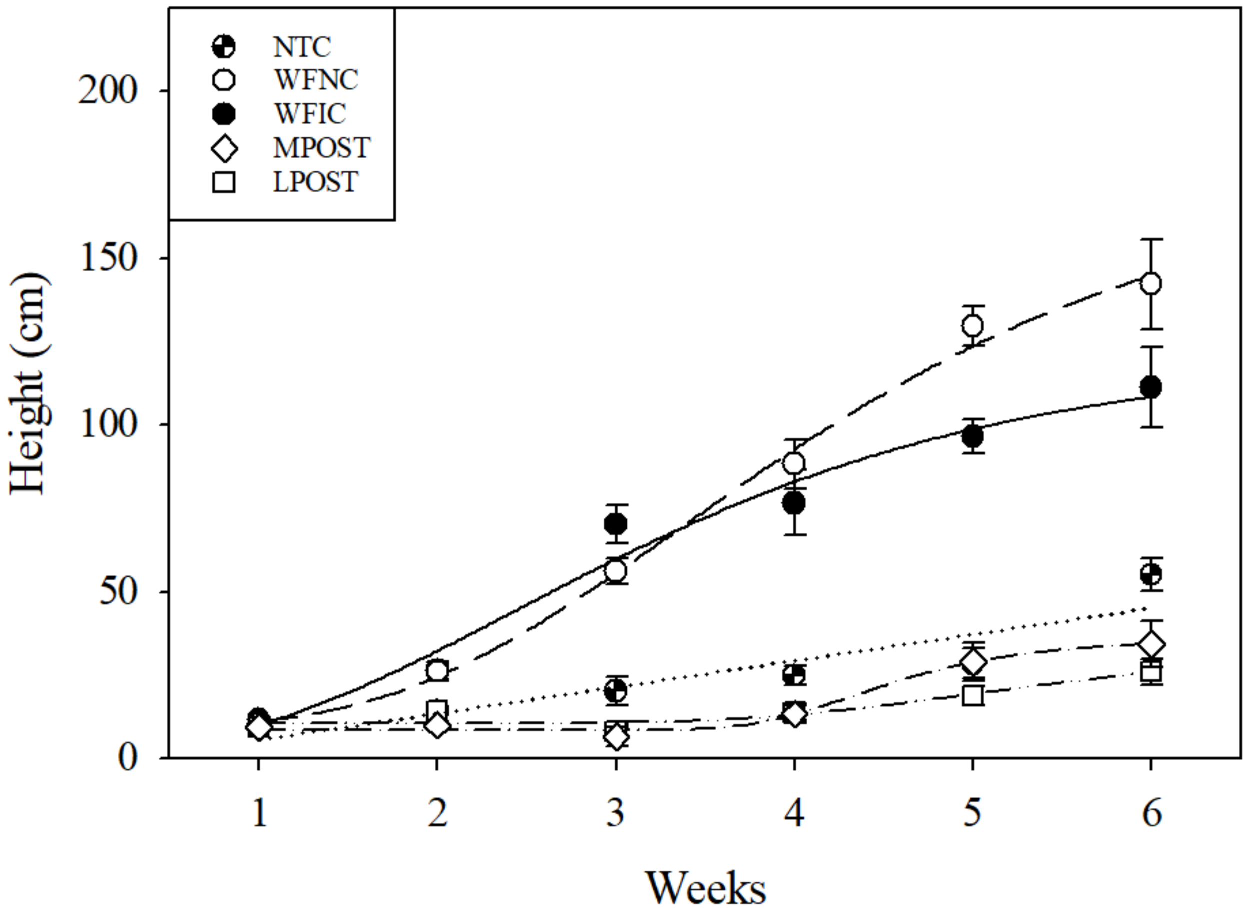

Figure 1. Plant height of Palmer amaranth plants treated with glufosinate from the No Grass Competition experiments conducted in soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began one week after the first application. Apical growth was modeled with a four-parameter Gompertz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

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Fig. 2A

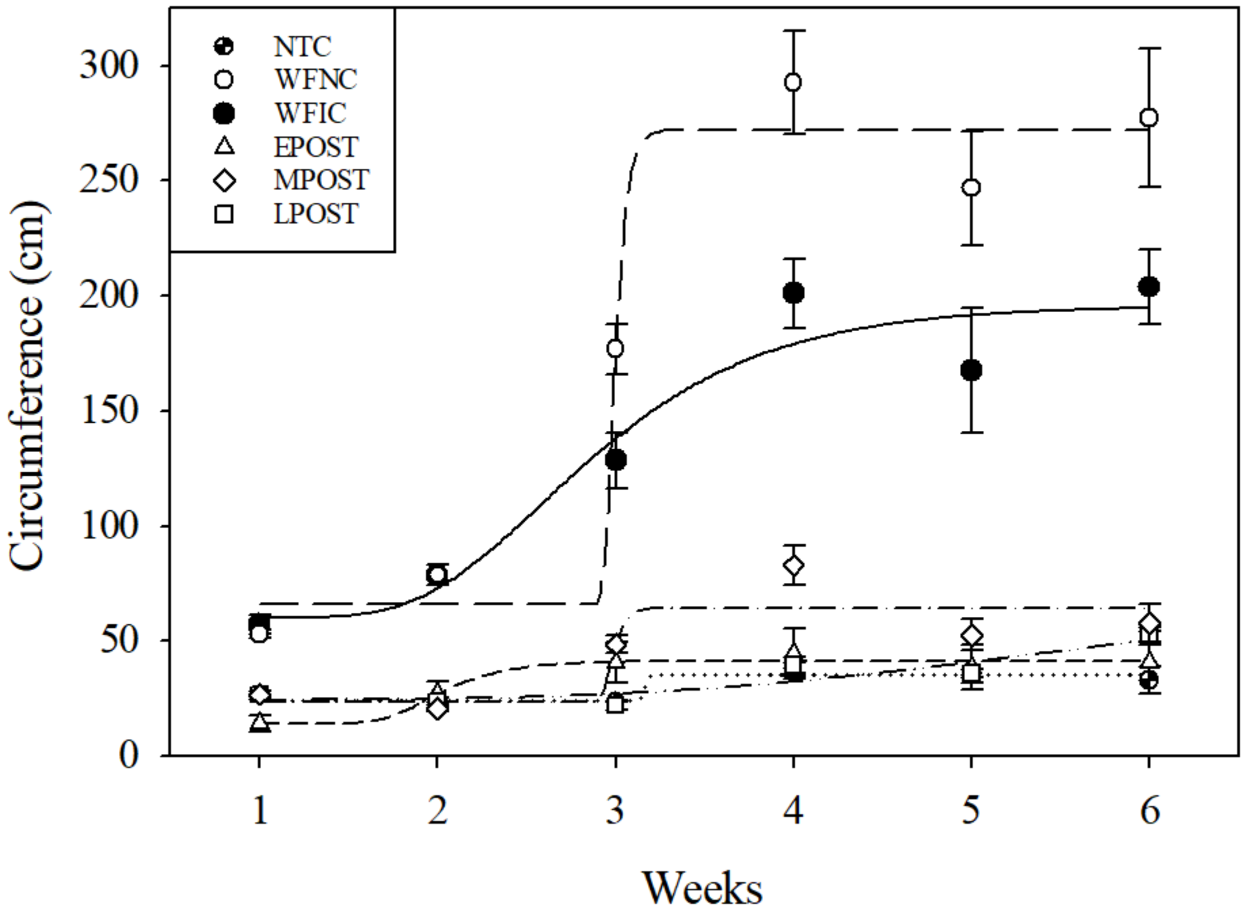

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Fig. 2B

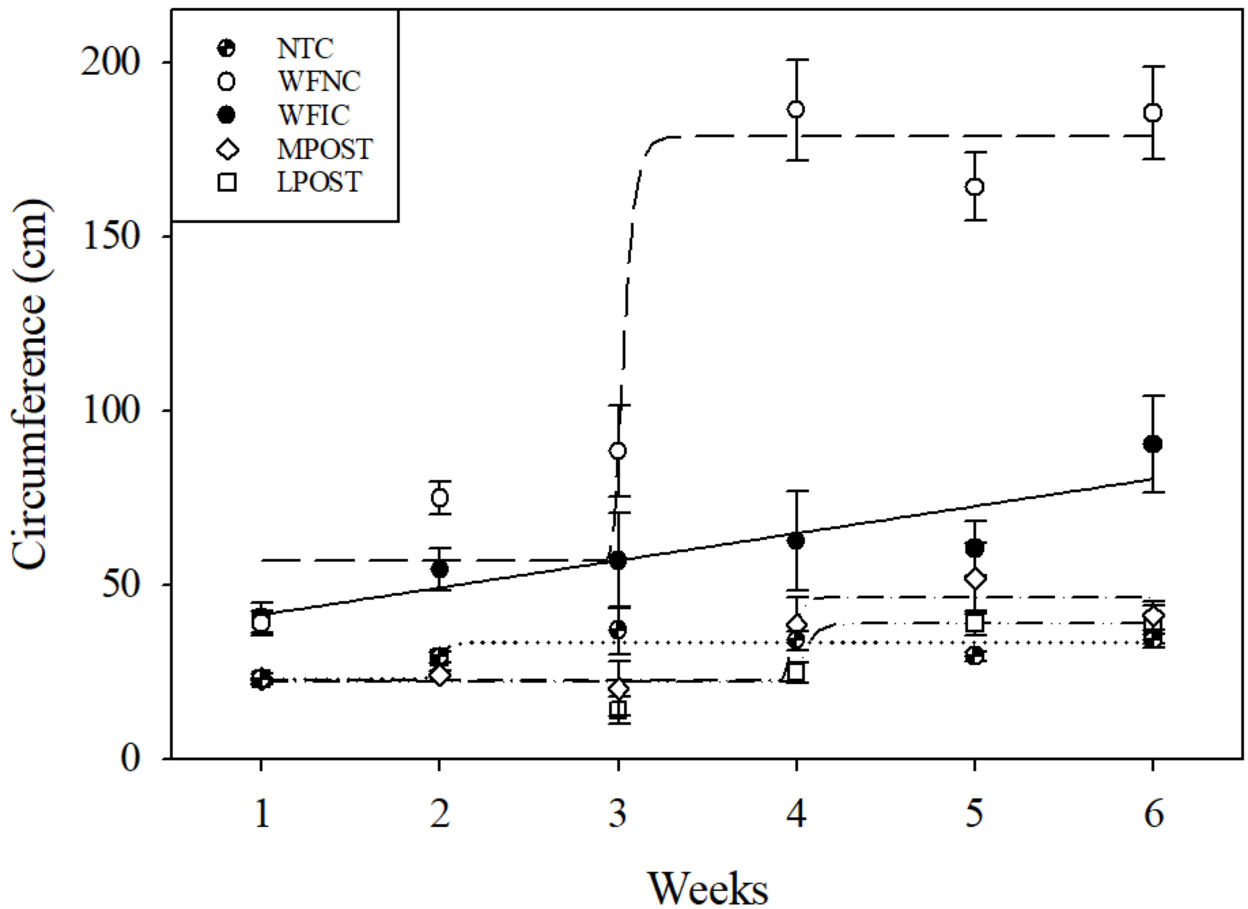

Figure 2. Canopy circumference of Palmer amaranth plants treated with glufosinate from the No Grass Competition experiments conducted in soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began one week after the first application. Circumference growth was modeled with a four-parameter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

Fig. 3A

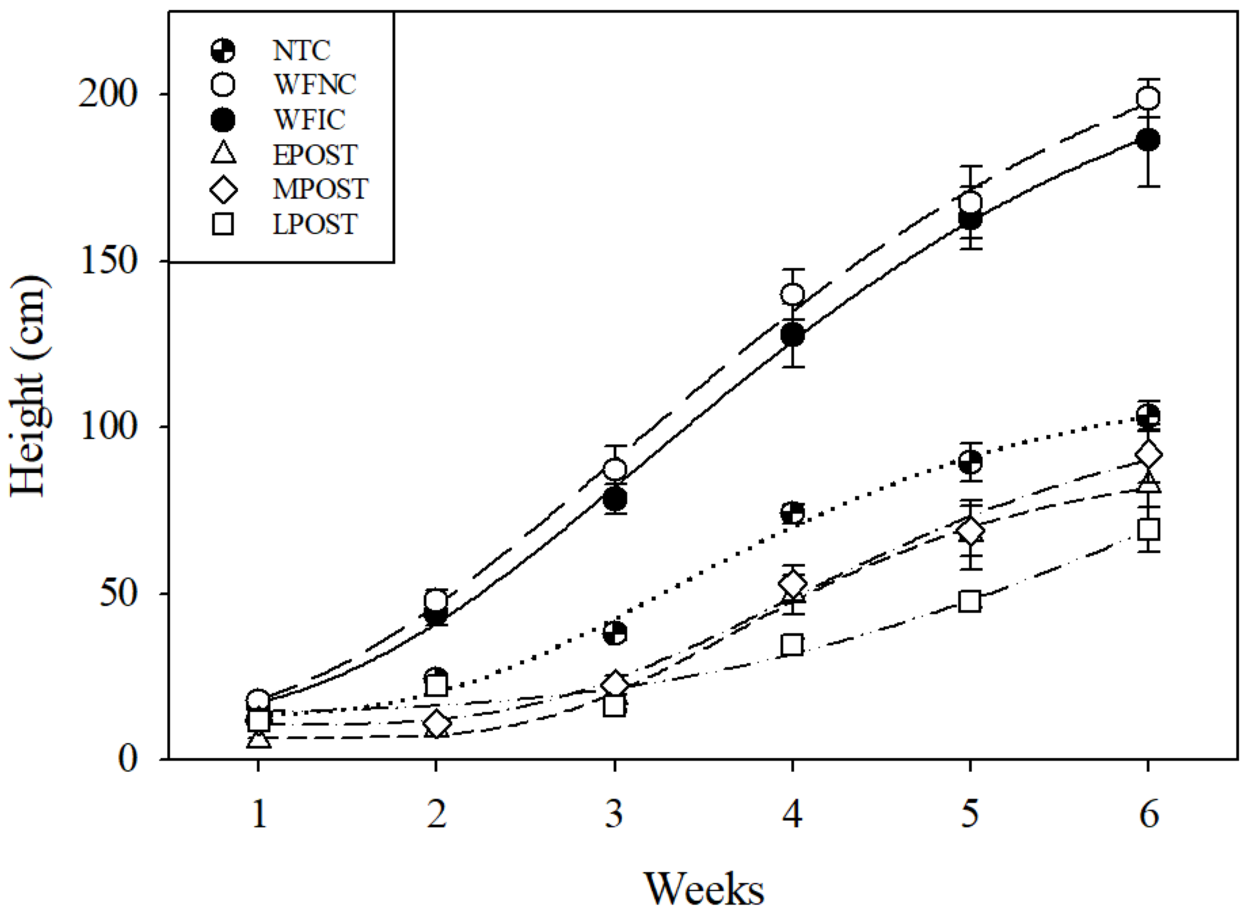

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Fig. 3B

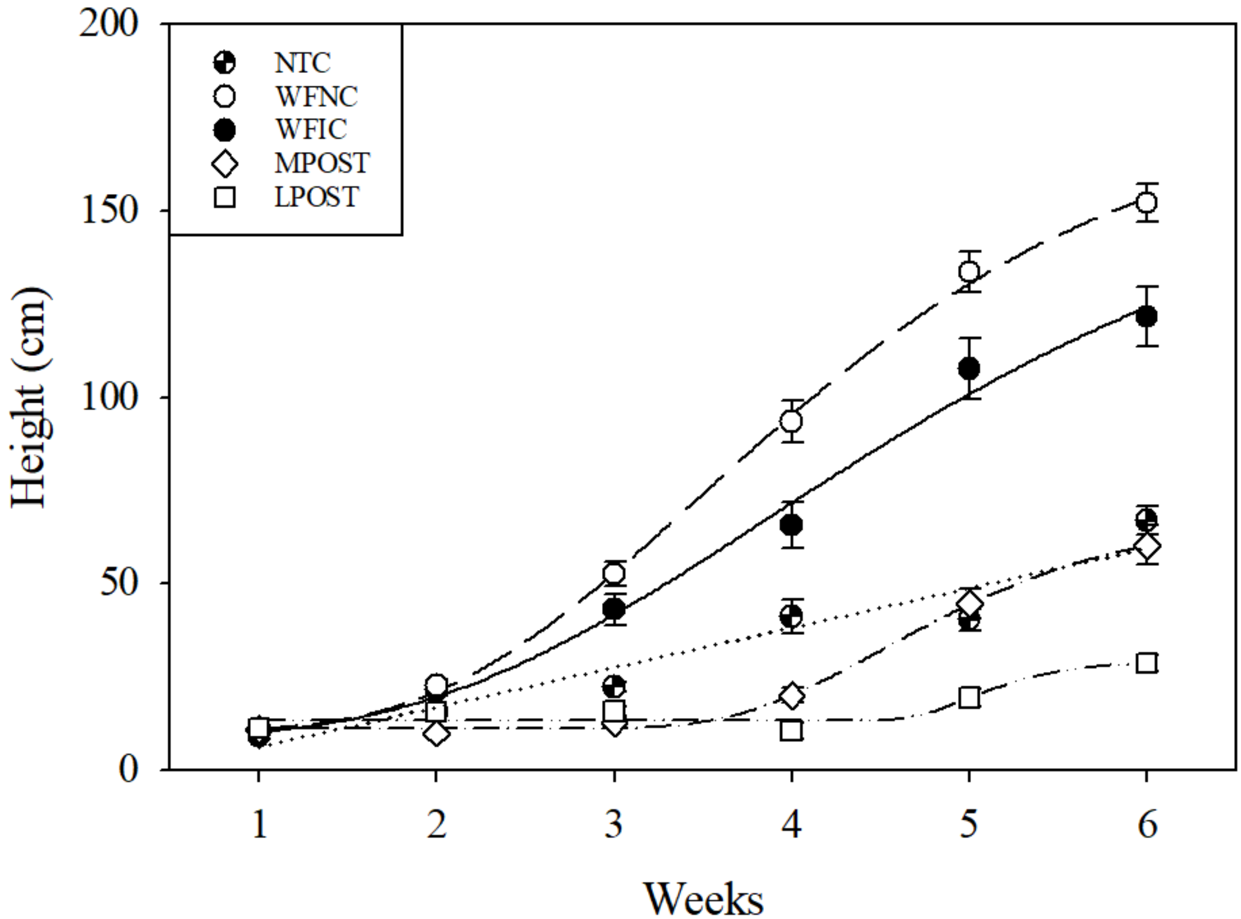

Figure 3. Plant height of Palmer amaranth plants treated with glufosinate from the Grass Competition experiments conducted in soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began one week after the first application. Apical growth was modeled with a four-parameter Gompertz equation except for the Palmer amaranth plants under NTC conditions at Rocky Mount which were modeled with a linear equation. Abbreviations: NTC, non-treated; NC, non-treated no-crop; IC, non-treated in-crop; EPOST, early postemergence (5 cm Palmer amaranth height); POST, postemergence (7-10 cm); LPOST, late postemergence (>10 cm).

Fig. 4A

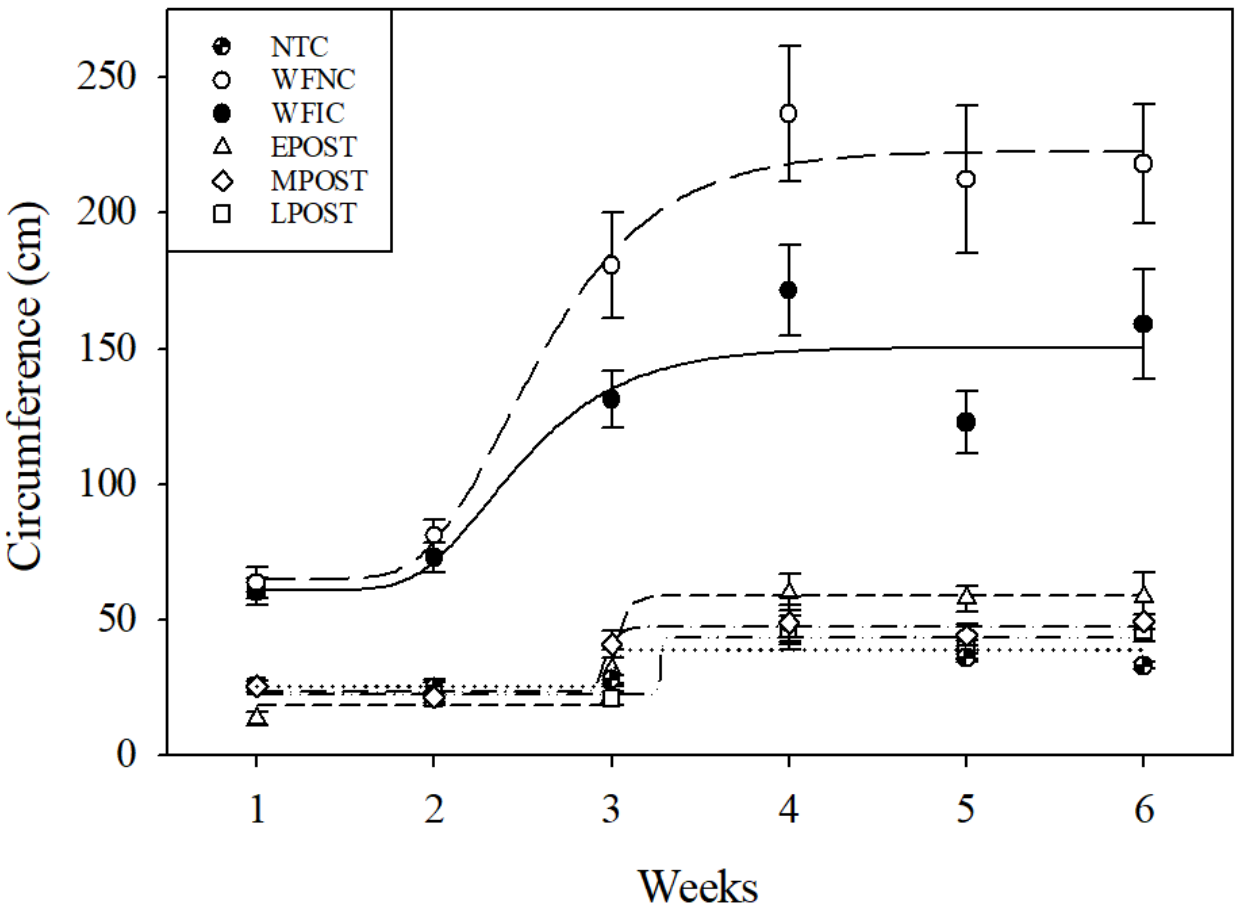

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Fig. 4B

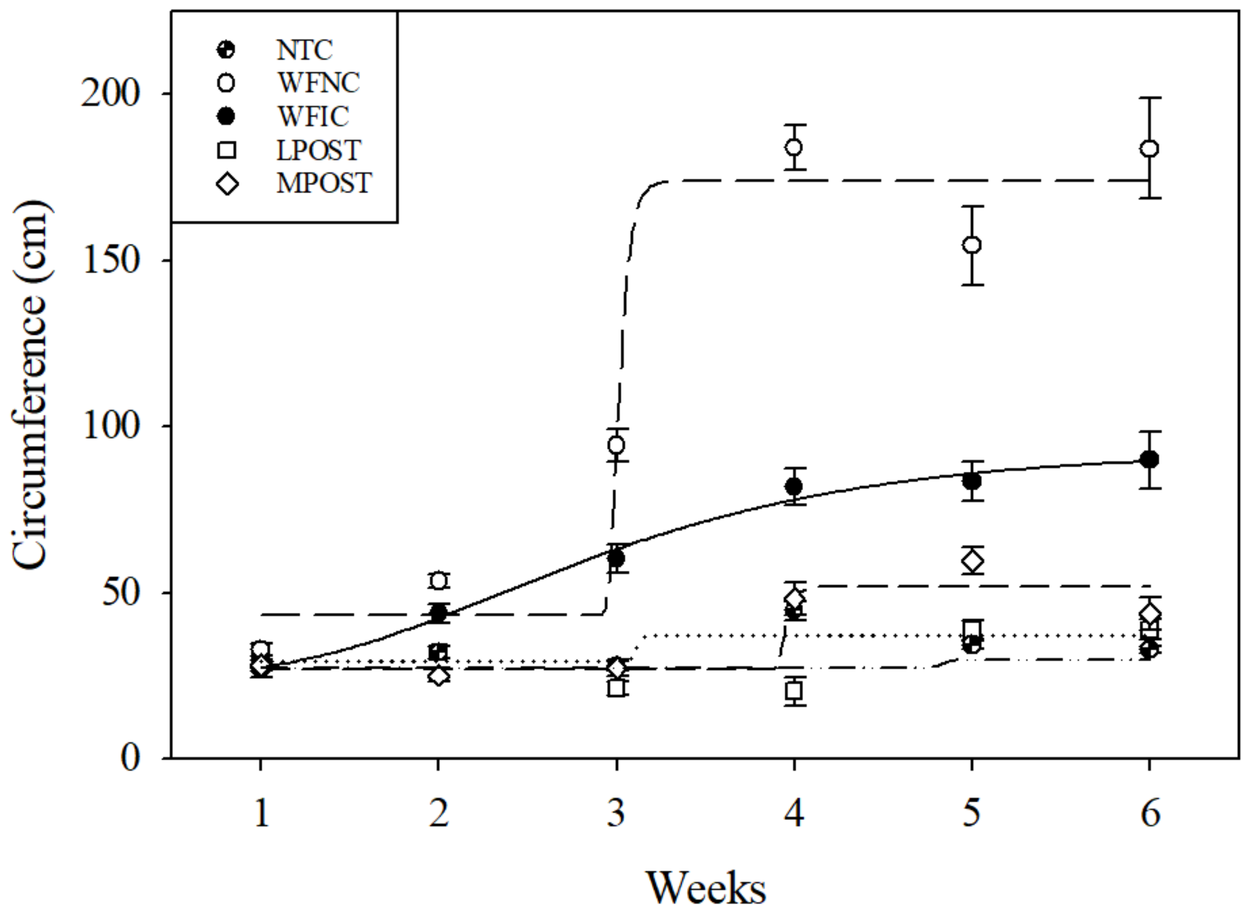

Figure 4. Canopy circumference growth of Palmer amaranth plants treated with glufosinate from the Grass Competition experiments conducted in soybean at Clayton (A) and Rocky Mount (B), North Carolina. Evaluation began one week after the first application. Circumference growth was modeled with a four-parameter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

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