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Interference and Control of Glyphosate-Resistant and -Susceptible Palmer Amaranth (*Amaranthus palmeri*) Populations under Greenhouse Conditions

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Interference for 40 d after emergence (DAE) of corn, cotton, peanut, and snap bean by four glyphosate-resistant (GR) and four glyphosate-susceptible (GS) Palmer amaranth populations from Georgia and North Carolina was compared in the greenhouse. Greater interference from Palmer amaranth, measured as crop height and fresh weight reduction, was noted in cotton and peanut compared with corn or snap bean. Crop height 15 to 40 DAE was reduced similarly by GR and GS populations. Crop fresh weight, however, was reduced 25 and 19% in the presence of GS and GR populations, respectively. Measured as percent reduction in fresh weight, GR and GS populations of Palmer amaranth were controlled similarly by glufosinate, lactofen, paraquat, and trifloxysulfuron applied POST. Atrazine and dicamba controlled GR populations more effectively than GS populations.

Nomenclature: Atrazine; dicamba; glufosinate; glyphosate; lactofen; paraquat; trifloxysulfuron; Palmer amaranth, *Amaranthus palmeri* S. Wats.; corn, *Zea mays* L.; cotton, *Gossypium hirsutum* L.; peanut, *Arachis hypogaea* L.; snap bean, *Phaseolus vulgaris* L.

Key words: Population response to herbicides, weed interference.

Palmer amaranth is among the most troublesome weeds of agronomic crops in southern cropping systems, including corn, cotton, and soybean [*Glycine max* (L.) Merr.] (Webster 2004, 2005; Webster and Coble 1997), because of its competitive ability, C_4 photosynthesis, higher water use efficiency and drought tolerance, rapid growth rate, and prolific seed production (Bensch et al. 2003; Black et al. 1969; Burke et al. 2007; Ehleringer 1983; Horak and Loughin 2000; Place et al. 2008; Sellers et al. 2003; Wright et al. 1999). Palmer amaranth is also resistant to herbicides representing different modes of action, including 5-enolpyruvylshikimate-3-phosphate synthase inhibitors, mitotic inhibitors, acetolactate synthase (ALS) inhibitors, and photosynthetic inhibitors (Heap 2012).

Yield reduction due to interference from Palmer amaranth varies by crop. Interference with Palmer amaranth at a density of 10 plants m^{-1} of row reduced soybean yield up to 68%, whereas reduction of up to 92% in cotton lint yield was reported at 0.9 plants m^{-1} of row (Klingaman and Oliver 1994; Rowland et al. 1999). Palmer amaranth reduced corn leaf area index and corn grain yield from 11 to 91% as density increased from 0.5 to 8 plants m^{-2} (Massinga and Curie 2002; Massinga et al. 2001). Although a linear decrease in cotton yield was observed from 13 to 54% with an increase in Palmer amaranth density from 1 to 10 plants m^{-2}, volume and biomass of Palmer amaranth remained unaffected by intraspecific competition at any of these densities (Morgan et al. 2001). Increasing weed density decreased grain sorghum [*Sorghum biclor* (L.) Moench] yield by reducing the number of grains produced per panicle (Moore et al. 2004). Season-long Palmer amaranth interference in peanut reduced peanut canopy diameter and 1 plant m^{-1} of row resulted in a predicted yield loss of up to 28% (Burke et al. 2007).

Biotypes of Palmer amaranth resistant to glyphosate have been reported in 12 states (Heap 2012). Herbicide-resistant weed biotypes sometimes have a fitness penalty compared with nonresistant wild types (Holt 1996; Jasieniuk et al. 1996; Jordan 1996, 1999; Preston and Wakelin 2008; Wakelin and Preston 2006; Warwick 1991). A fitness penalty is usually associated with triazine herbicide resistance, making resistant weed biotypes less competitive than wild types (Ahrens and Stoller 1983; Conrad and Radosevich 1979; Jordan 1996, 1999). Evolved resistance in Powell's amaranth [*Amaranthus powellii* (S.) Wats.] to ALS-inhibiting herbicide resulted in thinner roots and stem and reduced leaf area causing 67% reduction in aboveground vegetative mass and reduction in seed production (Tardif and Powels 2006). An acetyl coenzyme A carboxylase inhibitor–resistant mutant of black-grass (*Alopecurus myosuroides* Huds.) had reduction in height and vegetative and reproductive biomass as compared to wild biotype (Menchari et al. 2008). Proportion of resistant individuals in a segregating F_2 populations of rigid ryegrass (*Lolium rigidum* Gaudin) decreased as compared to susceptible individuals over a period of 4 yr (Preston and Wakelin 2008; Wakelin and Preston 2006). Baucom and Mauricio (2004) reported a high fitness cost of glyphosate tolerance in tall morningglory [*Ipomoea purpurea* (L.) Roth].

One component of weed management strategies designed to control herbicide-resistant Palmer amaranth is rotation of herbicides having different modes of action and use of multiple herbicides with different modes of action applied in combination or sequentially (Bond et al. 2006; Culpepper et al. 2008a,c). Differences in weed biotype response to herbicides have been reported previously even with biotypes considered susceptible to the herbicide in question (Bond et al. 2006; Li et al. 2004; Padzolt et al. 2002). Palmer amaranth control ranged from 20 to 94% 21 d after treatment (DAT) with pyrithiobac, depending on the accession (Bond et al. 2006). Differential response was observed among common waterhemp (*Amaranthus rudis* Sauer.) and tall waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer] accessions for control

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by atrazine, glyphosate, and imazethapyr (Padzoldt et al. 2002). However, there was no difference in response of accessions to fomesafen. Common waterhemp control in soybean by POST-applied ALS inhibitors varied from 24 to 95% among biotypes whereas control varied from 23 to 99% among four *Amaranthus* species (Sweat et al. 1998). Differential response to glyphosate and quizalofop-P was also observed in quackgrass [*Elymus repens* (L.) Gould] biotypes (Tardif and Leroux 1991). Red rice (*Oryza sativa* L.) ecotypes from Arkansas, Kansas, Louisiana, Mississippi, and Texas exhibited variable sensitivity to soil- and foliar-applied herbicides (Noldin et al. 1999). Differences in LD_{50} values for glyphosate in four giant ragweed (*Ambrosia trifida* L.) accessions from Arkansas were reported by Norsworthy et al. (2011).

Determining relative differences in early season interference of Palmer amaranth populations with crops and control with POST herbicides other than glyphosate could be of benefit in formulation of weed management strategies. Therefore, greenhouse research was conducted to compare the effects of interference from GR and GS populations of Palmer amaranth on early season vegetative growth of corn, cotton, peanut, and snap bean. Research was also conducted to compare response of these Palmer amaranth populations to atrazine, dicamba, glufosinate, glyphosate, lactofen, paraquat, and trifloxysulfuron applied POST.

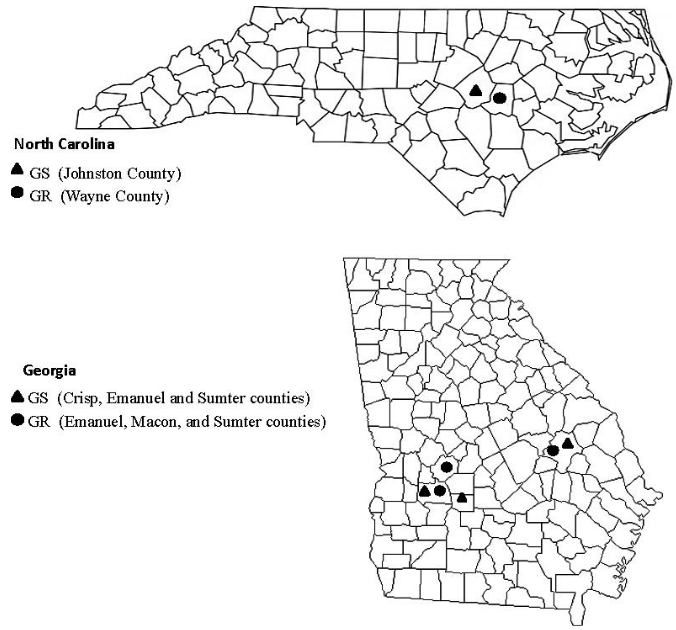

Figure 1. Location of North Carolina and Georgia populations used in the study.

Materials and Methods

Experiment 1. Interference of GR and GS Palmer Amaranth Populations with Selected Crops. Seeds of eight Palmer amaranth populations (Culpepper et al. 2008b) collected from fields in Georgia and North Carolina during fall 2005 were grown with corn hybrid '31G71' (Pioneer Hi-Bred, Johnston, IA 50131), cotton cultivar 'DP 424 BGRR' (Monsanto Company, St. Louis, MO 63167), peanut cultivar 'VA 98R' (Mozingo et al. 2000), or snap bean cultivar 'Kentucky Wonder' (Wyatt-Quarles Seed Company, Garner NC 27529) in 15-cm round plastic pots (ITML green standard pots, Myers Industries Lawn & Garden Group, Middlefield, OH 44062) containing commercial potting soil (Fafard 4P potting mix, Conrad Fafard Inc., Agawam, MA 01001). Four Palmer amaranth populations were GS (one from North Carolina and three from Georgia) and four were GR (one from North Carolina and three from Georgia) (Figure 1). Approximately six crop seeds and 25 Palmer amaranth seeds were planted in each pot in two parallel rows spaced 2.5 cm apart and seedlings were thinned to one crop and one Palmer amaranth plant per pot 10 DAE. A single crop plant per pot and a single Palmer amaranth plant per pot were planted as controls. Plants were fertilized (Scotts Starter Fertilizer, The Scotts Company LLC, Marysville, OH 43041) every 10 d with 25 ml of a 4.6 g L^{-1} fertilizer solution per pot to ensure optimum plant growth. Plants were irrigated daily using an overhead sprinkler system. The greenhouse was maintained at 35 $\pm$ 5 C, and natural illumination was supplemented for 14 h each day with metal halide lighting (400 μmol $m^{-2}s^{-1}$) (Hubbell Lighting, Inc., Greenville, SC 29607). The experimental design was a randomized complete block with treatments replicated 10 times. The experiment was conducted twice. Due to lack of interaction data were pooled over the two runs of the experiment.

Height of the Palmer amaranth and crop plants was determined 15, 20, 25, 30, 35, and 40 DAE. Plant height was measured from the soil surface to the point of attachment of the upper-most fully expanded leaf for all crops and Palmer amaranth plants. At 40 DAE, Palmer amaranth and crop plants were severed at the soil surface and fresh weight was determined.

Data for percent reduction in plant height and percent reduction in fresh weight relative to controls without interference were subjected to ANOVA considering the factorial treatment structure of four levels of crop (corn, cotton, peanut, and snap bean) and eight levels of Palmer amaranth populations. Plant heights and fresh weights of crop and Palmer amaranth controls are presented in Table 1. Percent reduction in these parameters was used to allow statistical comparisons of crops and Palmer amaranth populations that varied considerably in actual plant height and fresh weight. In a separate analysis, data were grouped for populations expressing resistance or susceptibility to glyphosate and subjected to ANOVA for a four (crops) by two (GR and GS population groupings) factorial treatment structure. Means of significant main effects and interactions were separated using Fisher's Protected LSD test at $P \leq 0.05$. Percent reduction in heights of crops and Palmer amaranth populations were regressed against DAE based on results of ANOVA to fit linear ($y = a + bx$) and quadratic ($y = a + bx + cx^2$) curves, respectively, where a, b, and c are constants, x = days at evaluation, and y = percent reduction in height.

Experiment 2. Efficacy of Herbicides against Palmer Amaranth Populations. Seeds from the eight Palmer amaranth populations described previously were planted in excess in 10-cm square pots containing the commercial soil medium described earlier and thinned to four plants prior to POST herbicide application. Atrazine (AAtrex herbicide®, Syngenta Crop Protection, Greensboro, NC 27419) at 560 and 1680 g ai ha^{-1}, the diglycolamine salt of dicamba (Clarity herbicide®, BASF Corp., Research Triangle Park, NC 27709) at 70 and 210 g ae ha^{-1}, the potassium salt of glyphosate (Roundup Weathermax, Monsanto Company) at 210 and

Table 1. Height and fresh weight of crop and Palmer amaranth controls. Experiment 1.[a]

Palmer amaranth population or crop	Plant height						Fresh weight
	15	20	25	30	35	40	40
	cm						g $plant^{-1}$
Individual Palmer amaranth populations[b]							
Emanuel (GR)	10.2	15.2	22.9	35.6	48.3	73.7	39.7
Macon (GR)	10.2	15.2	22.9	38.1	53.3	81.3	49.2
Sumter (GR)	12.7	17.8	25.4	40.6	55.9	81.3	54.8
Wayne (GR)	12.7	17.8	22.9	40.6	55.9	78.7	49.0
Crisp (GS)	15.2	20.3	27.9	48.3	66.0	91.4	55.0
Emanuel (GS)	17.8	25.4	33.0	53.3	71.1	94.0	62.0
Johnston (GS)	17.8	25.4	33.0	53.3	68.6	94.0	60.1
Sumter (GS)	12.7	20.3	27.9	43.2	58.4	86.4	51.5
Palmer amaranth population grouped by response to glyphosate[c]							
Resistant (GR)	10.2	17.8	22.9	38.1	53.3	78.7	48.2
Susceptible (GS)	15.2	22.9	30.5	48.3	66.0	91.4	57.1
Crop							
Corn	30.5	35.6	40.6	50.8	58.4	66.0	159.1
Cotton	20.3	27.9	30.5	40.6	45.7	53.3	22.4
Peanut	12.7	15.2	17.8	25.4	30.5	33.0	88.1
Snap bean	30.5	35.6	40.6	55.9	63.5	66.0	17.5

[a] Abbreviations: GR, glyphosate-resistant; GS, glyphosate-susceptible.
[b] Consists of eight Palmer amaranth populations.
[c] Consists of a group of four GR populations and a group of four GS populations.

630 g ae ha^{-1}, glufosinate ammonium salt (Ignite herbicide®, Bayer Crop Science, Research Triangle Park, NC 27709) at 118 and 353 g ae ha^{-1}, lactofen (Cobra 2EC herbicide®, Valent USA Corporation, Walnut Creek, CA 94596) at 70 and 210 g ai ha^{-1}), the dichloride salt of paraquat (Gramoxone Inteon herbicide®, Syngenta Crop Protection, Greensboro, NC 27419) at 35 and 105 g ae ha^{-1}, and trifloxysulfuron-sodium (Envoke herbicide®, Syngenta Crop Protection) at 1.25 and 3.75 g ai ha^{-1}) were applied to Palmer amaranth 10 to 12 cm tall with four to five leaves. Application rates were equivalent to 0.25X and 0.75X, where X is the manufacturer's suggested use rate. Nonionic surfactant (Induce® nonionic surfactant, Helena Chemical Company, Collierville, TN 38107) was included with dicamba, lactofen, paraquat, and trifloxysulfuron. Crop oil concentrate (Agri-Dex® spray adjuvant, Helena Chemical Company, Collierville, TN 38107) was included with atrazine. No adjuvant was included with glyphosate and glufosinate. A nontreated control was included. Plants were fertilized every 10 d as described previously to ensure optimum plant growth. Temperature in the greenhouse was maintained as described previously. The experimental design was a split plot with herbicide and herbicide rate combinations serving as whole plot units and Palmer amaranth populations serving as subplot units. Treatments were replicated four times, and the experiment was conducted twice. Due to lack of interaction, data were pooled over the two runs of the experiment.

Palmer amaranth and crop plants were severed at the soil surface to determine shoot fresh weight 21 DAT. Percent reduction in fresh weight was calculated with respect to the nontreated control for each Palmer amaranth population. Data for percent reduction in fresh weight were subjected to ANOVA appropriate for a seven (herbicides) by two (herbicide rates) by eight (Palmer amaranth populations) factorial treatment arrangement. In a separate analysis, data were grouped for populations expressing resistance or susceptibility to glyphosate and subjected to ANOVA for a seven (herbicides) by two (herbicide rates) by two (GR and GS population groupings) factorial treatment structure. Means of significant main effects and interactions were separated using Fisher's Protect LSD test at $P \leq 0.05$.

Results and Discussion

Experiment 1. Interference of GR and GS Palmer Amaranth Populations with Selected Crops. The interaction of crop type by Palmer amaranth population was not significant for percent reduction in crop height ($P > 0.05$) and crop fresh weight ($P = 0.9797$), but the main effect of crop was significant for both of these parameters ($P < 0.0001$). Reduction in crop height and fresh weight was greater for cotton and peanut than for corn and snap bean (Table 2; Figure 2). Differential reduction in crop growth in the presence of competing weeds was expected given inherent variation in interference by crops (Burke et al. 2007; Massinga et al. 2001; Morgan et al. 2001; van Heemst 1995). A decrease in plant height reduction was observed for all crops from 15 to 40 DAE (Figure 2). The steepest reduction in crop height (% reduction d^{-1}) was noted for corn ($slope_{corn} = -0.31$, $P = 0.0002$, $LSD = 0.12$) which was indicative of its increasing competitive ability from 15 to 45 DAE as compared to cotton, peanut, and snap bean. The rate of reduction in height did not differ for cotton, peanut, and snap

Table 2. Percent reduction in crop fresh weight 40 d after emergence. Experiment 1.[a]

Crop	Fresh weight reduction
	%
Corn	11 b
Cotton	35 a
Peanut	32 a
Snap bean	10 b

[a] Means within a column followed by the same letter are not significantly different according to Fisher's Protected LSD test at $P \leq 0.05$. Data are pooled over Palmer amaranth populations and experiments.

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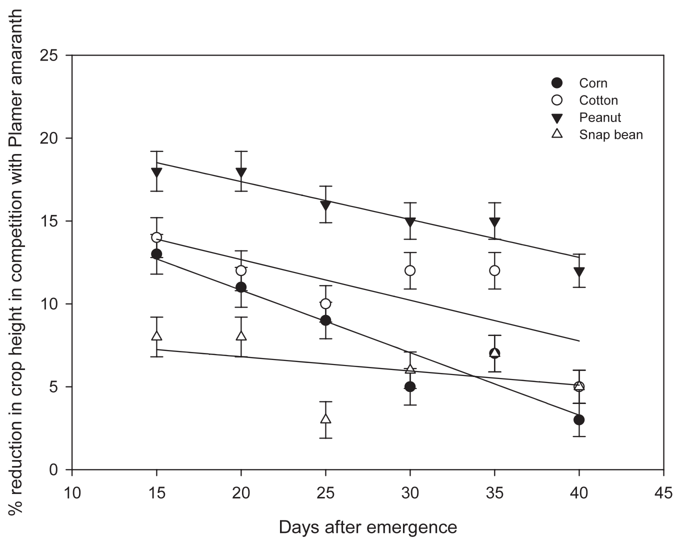

Figure 2. Percent reduction in crop height at 15, 20, 25, 30, 35, and 40 days after emergence pooled over Palmer amaranth populations. Regression equations are as follows: cotton, $y = 17.6 - 0.2x$, $r^2 = 0.54$; corn, $y = 18.3 - 0.4x$, $r^2 = 0.90$; peanut, $y = 22.0 - 0.2x$, $r^2 = 0.90$; snap bean, $y = 8.5 - 0.1x$, $r^2 = 0.20$. Points are means ± SE.

Table 3. Percent reduction in crop fresh weight as influenced by Palmer amaranth populations 40 d after emergence. Experiment 1.[a,b]

Palmer amaranth population	Fresh weight reduction
Individual Palmer amaranth populations[c]	%
Emanuel (GR)	17 c
Macon (GR)	20 bc
Sumter (GR)	20 bc
Wayne (GR)	21 abc
Crisp (GS)	22 abc
Emanual (GS)	26 a
Johnston (GS)	26 a
Sumter (GS)	25 ab
Palmer amaranth populations grouped by response to glyphosate[d]	
Resistant (GR grouping)	19
Susceptible (GS grouping)	25*

[a] Means within a column followed by the same letter are not different according to Fisher's Protected LSD test at $P \leq 0.05$. Data are pooled over crops and experiments.
[b] Abbreviations: GR, glyphosate-resistant; GS, glyphosate-susceptible.
[c] Consists of eight Palmer amaranth populations.
[d] Consists of a group of four GR populations and a group of four GS populations.
* Indicates significance at $P \leq 0.05$ for Palmer amaranth populations grouped by response to glyphosate.

bean throughout their growth from 10 to 45 DAE ($slope_{cotton} = -0.03$, $slope_{snap\ bean} = -0.04$, and $slope_{peanut} = -0.14$). The main effect of Palmer amaranth population was significant for percent reduction in crop height at 20, 25, and 30 DAE ($P \leq 0.05$) and for percent crop fresh weight reduction ($P = 0.0252$). The significant main effect of populations indicates differential early season competitiveness among populations, and the lack of a crop by population interaction indicates the differential competitiveness was independent of the crop. Averaged over crops, Palmer amaranth populations were less effective in reducing crop height from 15 to 40 DAE; however, differences among individual plants were observed (Figure 3). Plants from Sumter (GR) and Crisp (GS) counties generally reduced crop height less than the plants from other populations.

When populations were grouped according to response to glyphosate (GR population grouping and GS population grouping), no differences were noted in crop height reduction for the GR and GS groupings ($P > 0.05$). In contrast, the individual GS Palmer amaranth populations generally reduced crop fresh weight more than the GR populations (Table 3). Overall, the GR population grouping reduced crop fresh weight 19% compared with 25% reduction by GS population grouping.

The interaction of crop by Palmer amaranth population was noted for Palmer amaranth height only at 25 and 30 DAE ($P \leq 0.05$) and for Palmer amaranth fresh weight reduction ($P = 0.0471$). The main effect of crop was significant for Palmer amaranth height reduction at each period between 15 and 40 DAE as well as reduction in shoot fresh weight ($P < 0.0001$). Corn and snap bean reduced Palmer amaranth height and fresh weight more than cotton or peanut (Table 4; Figure 4). Palmer amaranth height was reduced similarly by cotton and peanut from 15 to 40 DAE; however, reduction in height increased continuously as result of interference from corn and snap bean. Pooled over crops, there was linear reduction in Palmer amaranth height from 15 to 40 DAE

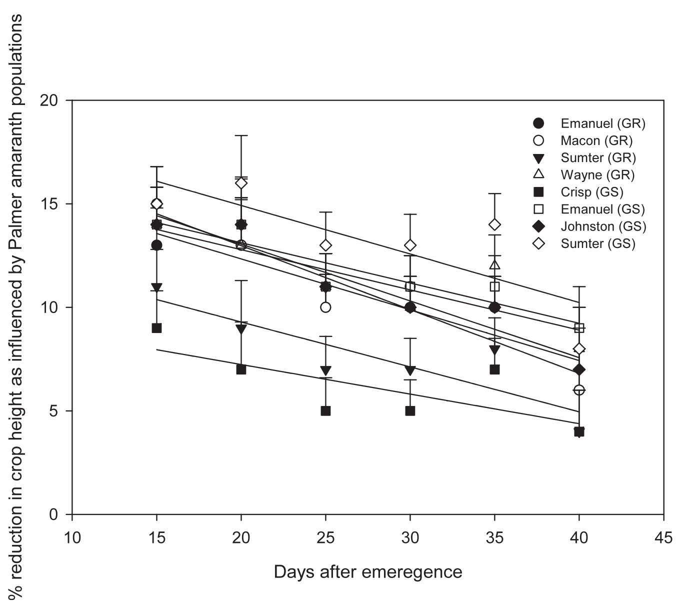

Figure 3. Percent reduction in crop height at 15, 20, 25, 30, 35, and 40 days after emergence (DAE) pooled over crops as influenced by eight Palmer amaranth populations. Regression equations are as follows: Emanuel (GR), $y = 17.3 - 0.2x$, $r^2 = 0.80$; Macon (GR), $y = 19.1 - 0.3x$, $r^2 = 0.90$; Sumter (GR), $y = 13.6 - 0.2x$, $r^2 = 0.80$; Wayne (GR), $y = 16.7 - 0.2x$, $r^2 = 0.71$; Crisp (GS), $y = 10.1 - 0.1x$, $r^2 = 0.60$; Emanuel (GS), $y = 17.0 - 0.2x$, $r^2 = 0.90$; Johnston (GS), $y = 18.5 - 0.3x$, $r^2 = 0.91$; Sumter (GS), $y = 19.6 - 0.2x$, $r^2 = 0.61$. Points are means + SE.

Table 4. Percent reduction in Palmer amaranth fresh weight as influenced by crops 40 days after emergence. Experiment 1.[a]

Crop	Fresh weight reduction
	%
Corn	88 a
Cotton	34 b
Peanut	20 c
Snap bean	86 a

[a] Means within a column followed by the same letter are not different according to Fisher's Protected LSD test at $P \leq 0.05$. Data are pooled Palmer amaranth populations and experiments.

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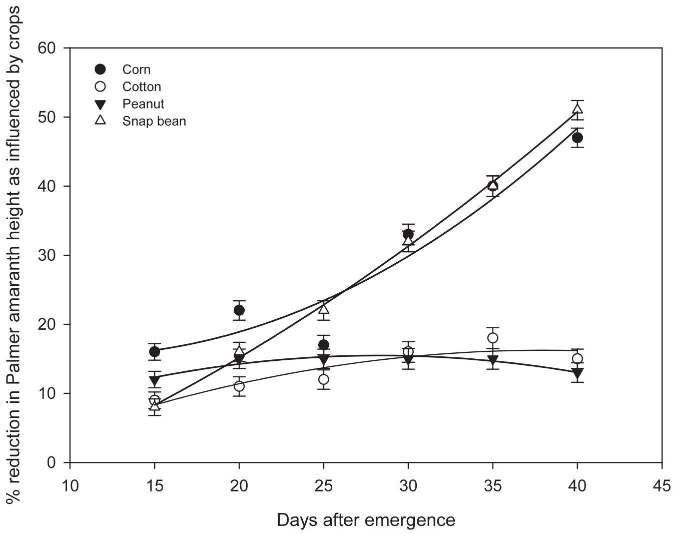

Figure 4. Percent reduction in Palmer amaranth height at 15, 20, 25, 30, 35, and 40 days after emergence (DAE) pooled over Palmer amaranth populations as influenced by four crops. Regression equations are as follows: cotton, $y = -5.3 - 1.1x - 0.02x^2$, $r^2 = 0.84$; corn, $y = 19.7 - 0.8x - 0.04x^2$, $r^2 = 0.92$; peanut, $y = 1.2 + 1.0x - 0.02x^2$, $r^2 = 0.88$; snap bean, $y = -7.3 + 0.8x - 0.02x^2$, $r^2 = 0.99$. Points are means ± SE.

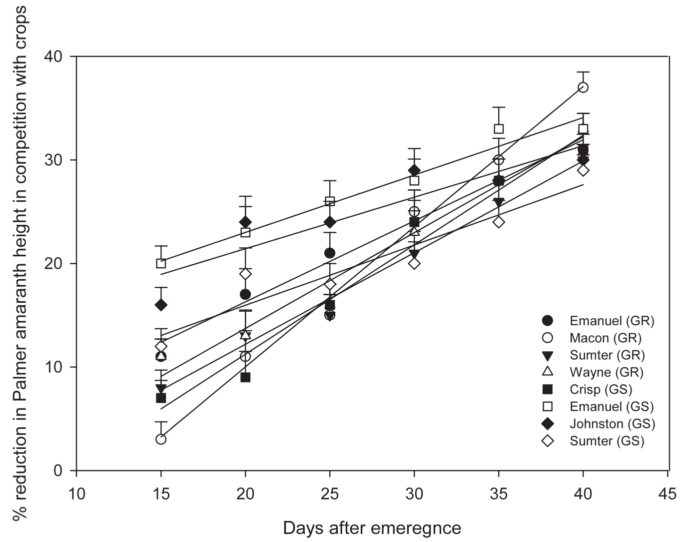

Figure 5. Percent reduction in Palmer amaranth height at 15, 20, 25, 30, 35, and 40 days after emergence (DAE) pooled over crops. Regressions equations are as follows: Emanuel (GR), $y = 0.6 + 0.8x$, $r^2 = 0.98$; Macon (GR), $y = -17.1 + 1.4$, $r^2 = 0.99$; Sumter (GR), $y = -5.5 + 0.9x$, $r^2 = 0.99$; Wayne (GR), $y = -4.8 + 0.9x$, $r^2 = 0.97$; Crisp (GS), $y = -9.9 + 1.1x$, $r^2 = 0.97$; Emanuel (GS), $y = 11.9 + 0.6x$, $r^2 = 0.97$; Johnston (GS), $y = 11.5 + 0.5x$, $r^2 = 0.81$; Sumter (GS), $y = 4.3 + 0.6x$, $r^2 = 0.90$. Points are means + SE.

(Figure 5). Among the GS populations, height of plants from Emanuel and Johnston counties was generally reduced more than plants from Crisp and Sumter counties. With the GR populations, height of Macon County plants was reduced less at 15 DAE, but differences were less obvious at later periods. When grouped according to glyphosate resistance, greater height reduction in the GS population grouping due to crop interference was noted early in the study (< 25 DAE), but not later (data not shown). Also, there was no difference between population groupings for Palmer amaranth fresh weight reduction due to crop interference ($P = 0.1209$).

Experiment 2. Efficacy of Herbicides against Palmer Amaranth Populations. Palmer amaranth control by paraquat was complete regardless of population or herbicide rate (data not shown). Similar control of GR and GS populations of Palmer amaranth by paraquat was reported by Norsworthy et al. (2008). Gossett et al. (1992) reported complete control of dinitroaniline-resistant Palmer amaranth by paraquat.

The interaction of herbicide rate by population for Palmer amaranth fresh weight reduction was significant for atrazine ($P < 0.0001$) and glyphosate ($P = 0.0483$). Atrazine at 75% of the manufacturer's suggested use rate reduced fresh weight of all populations at least 95%, with no differences among populations (Table 5). Fresh weight reduction by atrazine at the lower rate was similar to that with the higher rate for five of the eight populations. However, a rate response to atrazine was noted with three of the four GS populations (Emanuel, Johnston, and Sumter counties), where atrazine at the lower rate reduced fresh weight 47 to 86%. When populations were grouped according to response to glyphosate, the atrazine rate by population grouping interaction was noted ($P < 0.0002$). Fresh weight of both population groupings was reduced 99 to 100% by atrazine at the higher rate (Table 5). Atrazine at the lower rate reduced fresh weight of the GR and GS groupings 97 and 76%, respectively. These results indicate that presence of glyphosate resistance may be associated with greater susceptibility to atrazine.

For most populations, fresh weight reduction was similar with the two rates of glyphosate (Table 5). The exception was the GS population from Sumter County, where glyphosate at the higher rate reduced fresh weight nearly 40% more than the lower rate. When Palmer amaranth populations were grouped according to response to glyphosate, a rate by population interaction was not observed, but main effects of glyphosate rate ($P = 0.0117$) and population grouping ($P < 0.0001$) were significant. Glyphosate at 0.25 and 0.75 times the manufacturer's suggested use rate reduced fresh weight 45 and 56%, respectively (data not shown). As expected, fresh weight reduction of GR populations was much less than the reduction of GS populations. Fresh weight of the GS population grouping was reduced 80% compared with only 19% reduction for the GR population grouping (data not shown).

A significant main effect of herbicide rate on percent fresh weight reduction was noted with dicamba, glufosinate, and lactofen ($P < 0.0001$) for individual Palmer amaranth populations as well as population groupings. Fresh weight reduction was 33, 37, and 25% greater with the higher rate of dicamba, glufosinate, and lactofen, respectively (Table 6). The main effect of trifloxysulfuron rate was not significant ($P = 0.0575$), and trifloxysulfuron at the higher rate reduced Palmer amaranth fresh weight only 25%. Trifloxysulfuron is typically effective on Palmer amaranth (Branson et al. 2005; Porterfield et al. 2003), but the populations used in this experiment were likely resistant to ALS-inhibiting herbicides, such as trifloxysulfuron. Earlier research has shown that trifloxysulfuron was not effective in controlling GR and GS Palmer amaranth accessions from Arkansas when applied at manufacturer's suggested field rate (Norsworthy et al. 2008). Palmer amaranth resistant to ALS inhibitors is common in Georgia and North Carolina (Whitaker 2009; Wise et al. 2009).

The main effect of Palmer amaranth populations was significant for dicamba, glufosinate, and trifloxysulfuron

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Table 5. Percent reduction in Palmer amaranth fresh weight as influenced by the interaction of POST herbicide rate and population 21 d after treatment. Experiment 2.[a–c]

Palmer amaranth population	Atrazine		Glyphosate	
	0.25X	0.75X	0.25X	0.75X
	%			
Individual Palmer amaranth populations[d]				
Emanuel (GR)	96 ab	100 a	8 f	18 f
Macon (GR)	100 a	100 a	23 f	32 ef
Sumter (GR)	96 ab	100 a	13 f	32 ef
Wayne (GR)	95 ab	100 a	13 f	16 f
Crisp (GS)	98 a	100 a	88 ab	85 ab
Emanuel (GS)	86 b	100 a	69 b	86 ab
Johnston (GS)	47 d	95 a	82 ab	87 ab
Sumter (GS)	72 c	100 a	52 de	91 a
Palmer amaranth populations grouped by response to glyphosate[e]				
Resistant (GR grouping)	97	100	17	22
Susceptible (GS grouping)	76*	99	73	87

[a] Means within an herbicide followed by the same letter are not different according to Fisher's Protected LSD test at $P \leq 0.05$. Data are pooled over experiments.
[b] Abbreviations: GR, glyphosate-resistant; GS, glyphosate-susceptible.
[c] Herbicides were applied at 0.25X and 0.75X, where X is manufacturer's suggested use rate. Herbicide rates corresponding to 0.25X and 0.75X are atrazine at 560 and 1680 g ha^{-1} and glyphosate at 210 and 630 g ha^{-1}.
[d] Consists of eight Palmer amaranth populations.
[e] Consists of a group of four GR populations and a group of four GS populations.
* Indicates significance at $P \leq 0.05$ within atrazine for Palmer amaranth populations grouped by response to glyphosate.

($P < 0.0001$), but not lactofen ($P = 0.6419$). Palmer amaranth populations from Wayne (GR), Johnston (GS), and Sumter (GR) counties generally had less fresh weight reduction for each of dicamba, glufosinate, and trifloxysulfuron while the Macon (GR) County population had greater fresh weight reduction from those three herbicides (Table 7). Relative responses of Crisp (GS), Emanuel (GR), Emanuel (GS), and Sumter (GS) counties varied among the three herbicides. When populations were grouped according to glyphosate resistance, herbicide rate by population interaction was not observed with dicamba ($P = 0.5606$), glufosinate ($P = 0.4367$), lactofen ($P = 0.8712$), or trifloxysulfuron ($P = 0.4738$). The GR and GS population groupings responded similarly to glufosinate, lactofen, and trifloxysulfuron (Table 7). Dicamba reduced fresh weight of GR populations more that GS populations.

These results indicate that interference can vary among Palmer amaranth populations. Genetic variability in Palmer amaranth populations has not been reported previously. Genetic variation in the Palmer amaranth populations used in the present study was assessed in another experiment using amplified fragment length polymorphisms (Chandi et al. 2013). Pair-wise genetic similarity values were found to be relatively low, averaging 0.34. It could be possible that a high degree of genetic variability might be responsible for the observed differences in interference.

When pooled over crops, reduction in crop fresh weight was less for GR populations than for GS populations of Palmer amaranth (Table 3). Fresh weight reduction of crops was 19% in the presence of GR populations compared to 25% in the presence of GS populations. Fitness costs associated with glyphosate resistance have been reported in other weed species (Baucom and Mauricio 2004; Pederson et al. 2007; Preston and Wakelin 2008; Wakelin and Preston 2006). Fitness penalty for glyphosate resistance in Palmer amaranth has not been reported. Although these results indicated a possible advantage of GS Palmer amaranth populations in terms of their competitive ability with crops, these results could also be associated with natural variability in populations selected for this study. The variation among GR and GS population groupings used in this study was found to be less than the overall variability present within all the individual populations used in the study (Chandi et al. 2013). Although data suggest that there may be a disadvantage due to

Table 6. Percent reduction in Palmer amaranth fresh weight as influenced by POST herbicide rate 21 d after treatment. Experiment 2.

Herbicide rate[a]	Dicamba	Glufosinate	Lactofen	Trifloxysulfuron
	%			
Individual Palmer amaranth populations[b]				
0.25X	38	53	67	19
0.75X	71*	90*	92*	25
Palmer amaranth populations grouped by response to glyphosate[c]				
0.25X	38	56	78	19
0.75X	72*	90*	92*	25

[a] Herbicides were applied at 0.25 X and 0.75 X, where X is manufacturer's suggested use rate. Herbicide rates corresponding to 0.25X and 0.75X are: dicamba, 70 and 210 g ha^{-1}; glufosinate, 118 and 353 g ha^{-1}; lactofen, 70 and 210 g ha^{-1}; and trifloxysulfuron, 1.25 and 3.75 g ha^{-1}.
[b] Consists of eight Palmer amaranth populations.
[c] Consists of a group of four glyphosate-resistant populations and a group of four glyphosate-susceptible populations.
* Indicates significance at $p \leq 0.05$ within a Palmer amaranth grouping (individual populations versus grouping by response to glyphosate) and within an herbicide. Data are pooled over Palmer amaranth populations and experiments.

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Table 7. Percent reduction in Palmer amaranth fresh weight as influenced by population and POST herbicides 21 d after treatment. Experiment 2.[a,b]

Palmer amaranth population	Dicamba	Glufosinate	Lactofen	Trifloxysulfuron
	%			
Individual Palmer amaranth populations[c]				
Emanuel (GR)	68 ab	79 ab	74 a	20 bc
Macon (GR)	77 a	87 a	75 a	39 a
Sumter (GR)	43 d	67 bcd	84 a	18 bcd
Wayne (GR)	50 cd	64 cd	75 a	11 cd
Crisp (GS)	53 cd	80 a	79 a	17 bcd
Emanuel (GS)	59 bc	66 bcd	90 a	35 a
Johnston (GS)	42 d	56 d	80 a	7 d
Sumter (GS)	44 d	74 abc	77 a	29 ab
Palmer amaranth populations grouped by response to glyphosate[d]				
Resistant (GR grouping)	61	74	85	22
Susceptible (GS grouping)	49*	72	85	22

[a] Means within an herbicide followed by the same letter are not different according to Fisher's Protected LSD test at $P \leq 0.05$ for individual Palmer amaranth populations. Data are pooled over herbicide rates and experiments.
[b] Abbreviations: GR, glyphosate-resistant; GS, glyphosate-susceptible.
[c] Consists of eight Palmer amaranth populations.
[d] Consists of a group of four GR populations and a group of four GS populations.
* Indicates significance at $P \leq 0.05$ within an herbicide for Palmer amaranth populations grouped by response to glyphosate. Data are pooled over herbicide rates and experiments.

the GR trait in terms of competitive ability and control with POST herbicides, including a higher number of both GR and GS populations that represent an even larger geographical distribution, would improve understanding the involvement of the resistance trait toward fitness.

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Literature Cited

Ahrens, W. H. and E. W. Stoller. 1983. Competition, growth rate, and CO_2 fixation in triazine- susceptible and -resistant smooth pigweed (*Amaranthus hybridus*). Weed Sci. 31:438–444.

Baucom, R. S. and R. Mauricio. 2004. Fitness costs and benefits of novel herbicide tolerance in a noxious weed. Proc. Natl. Acad. Sci. U. S. A. 101:13386–13390.

Bensch, C. N., M. J. Horak, and D. Peterson. 2003. Interference of redroot pigweed (*Amaranthus retroflexus*), Palmer amaranth (*A. palmeri*), and common waterhemp (*A. rudis*) in soybean. Weed Sci. 51:37–43.

Black, C. C., T. M. Chen, and R. H. Brown. 1969. Biochemical basis for plant competition. Weed Sci. 17:338–344.

Bond, J. A., L. R. Oliver, and D. O. Stephenson IV. 2006. Response of Palmer amaranth (*Amaranthus palmeri*) accessions to glyphosate, fomesafen, and pyrithiobac. Weed Technol. 20:885–892.

Branson, J. W., K. L. Smith, and J. L. Barrentine. 2005. Comparison of trifloxysulfuron and pyrithiobac in glyphosate-resistant and bromoxynil-resistant cotton. Weed Technol. 19:404–410.

Burke, I. C., M. Schroeder, W. E. Thomas, and J. W. Wilcut. 2007. Palmer amaranth interference and seed production in peanut. Weed Technol. 21:367–371.

Chandi, A., S. R. Milla-Lewis, D. L. Jordan, A. C. York, J. D. Burton, M. C. Zuleta, J. R. Whitaker, and A. S. Culpepper. 2013. Use of AFLP markers to assess genetic diversity in Palmer amaranth (*Amaranthus palmeri*) populations from North Carolina and Georgia. Weed Sci. 61:136–145.

Conrad, S. G. and S. R. Radosevich. 1979. Ecological fitness of *Senecio vulgaris* and *Amaranthus retroflexus* biotypes susceptible or resistant to atrazine. J. Appl. Ecol. 16:171–177.

Culpepper, A. S., A. W. MacRae, A. C. York, and J. R. Whitaker. 2008a. Managing glyphosate-resistant Palmer amaranth in conventional and strip-till Roundup Ready cotton. Proc. South. Weed Sci. Soc. 61:62.

Culpepper, A. S., J. R. Whitaker, A. W. MacRae, and A. C. York. 2008b. Distribution of glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) in Georgia and North Carolina during 2005 and 2006. J. Cotton Sci. 12:306–310.

Culpepper, A. S., A. C. York, and J. Kichler. 2008c. University of Georgia Herbicide Programs for Controlling Glyphosate-Resistant Palmer Amaranth in 2008 Cotton. Tifton, GA: Georgia Coop. Ext. Serv. Circular 924. http://www.gaweed.com/HomepageFiles/Palmer2008.pdf. Accessed: April 9, 2012.

Ehleringer, J. 1983. Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. Oecologia. 57:107–112.

Gossett, B. J., E. C. Murdock, and J. E. Toler. 1992. Resistance of Palmer amaranth (*Amaranthus palmeri*) to the dinitroaniline herbicides. Weed Technol. 6:587–591.

Heap, I. 2012. The International Survey of Herbicide Resistant Weeds. http://www.weedscience.org. Accessed: March 24, 2012.

Holt, J. S. 1996. Ecological fitness of herbicide-resistant weeds. Pages 387–392 *in* Proceedings of the Second International Weed Control Congress, Copenhagen, Denmark: Department of Weed Control and Pesticide Ecology.

Horak, M. J. and T. M. Loughin. 2000. Growth analysis of four *Amaranthus* species. Weed Sci. 48:347–355.

Jasieniuk, M. A., A. L. Brûlé-Babel, and I. N. Morrison. 1996. The evolution and genetics of herbicide resistance in weeds. Weed Sci. 44:176–193.

Jordan, N. 1996. Effects of triazine-resistance mutation in fitness in *Amaranthus hybridus* (smooth pigweed). J. Appl. Ecol. 33:141–150.

Jordan, N. 1999. Fitness effects of the triazine resistance mutation in *Amaranthus hybridus*: relative fitness in maize and soybean crops. Weed Res. 39:493–505.

Klingaman, T. E. and L. R. Oliver. 1994. Palmer amaranth (*Amaranthus palmeri*) interference in soybeans (*Glycine max*). Weed Sci. 42:523–527.

Li, J., R. J. Smeda, and J. D. Wait. 2004. Population difference in waterhemp treated with glyphosate and lactofen. Weed Sci. Soc. Am. Abstr. 44:53.

Massinga, R. A. and R. S. Curie. 2002. Impact of Palmer amaranth (*Amaranthus palmeri*) on corn (*Zea mays*) grain yield and quality of forage. Weed Technol. 16:532–536.

Massinga, R. A., R. S. Curie, M. J. Horak, and J. Boyer, Jr. 2001. Interference of Palmer amaranth in corn. Weed Sci. 49:202–208.

Menchari, Y., B. Chauvel, H. Darmency, and C. Delye. 2008. Fitness costs associated with three mutant acetyl-coenzyme A carboxylase alleles endowing herbicide resistance in black-grass (*Alopecurus myosuroides*). J. Appl. Ecol. 45:939–947.

Moore, J. W., D. S. Murray, and R. B. Westerman. 2004. Palmer amaranth (*Amaranthus palmeri*) effects on the harvest and yield of grain sorghum (*Sorghum bicolor*). Weed Technol. 18:23–29.

Morgan, G. D., P. A. Baumann, and J. M. Chandler. 2001. Competitive impact of Palmer amaranth (*Amaranthus palmeri*) on cotton (*Gossypium hirsutum*) development and yield. Weed Technol. 15:408–412.

Mozingo, R. W., T. A. Coffelt, and T. G. Isleib. 2000. Registration of 'VA 98R' peanut. Crop Sci. 40:1201–1203.

Noldin, J. A., J. M. Chandler, M. L. Ketchersid, and G. N. McCauley. 1999. Red rice (*Oryza sativa*) biology. II. Ecotype sensitivity to herbicides. Weed Technol. 13:19–24.

https://doi.org/10.1614/WS-D-12-00063.1 Published online by Cambridge University Press

Norsworthy, J. K., G. M. Griffith, R. C. Scott, K. L. Smith, and L. R. Oliver. 2008. Confirmation and control of glyphosate-resistant Palmer amaranth (*Amaranthus palmeri*) in Arkansas. Weed Technol. 22:108–113.

Norsworthy, J. K., D. Riar, P. Jha, and R. C. Scott. 2011. Confirmation, control, and physiology of glyphosate resistant giant ragweed (*Ambrosia trifida*) in Arkansas. Weed Technol. 25:430–435.

Padzoldt, W. L., P. J. Tranel, and A. G. Hager. 2002. Variable herbicide response among Illinois waterhemp (*Amaranthus rudis* and *A. tuberculatus*) populations. Crop Prot. 21:707–712.

Pederson, M. B., P. Neve, C. Andreasen, and S. B. Powles. 2007. Ecological fitness of a glyphosate-resistant *Lolium rigidum* population: growth and seed production along competition gradient. Basic Appl. Ecol. 8:258–268.

Place, G., D. Bowman, M. Burton, and T. Rufty. 2008. Root penetration through a high bulk density soil layer: differential response of a crop and weed species. Plant Soil 307:179–190.

Porterfield, D., J. W. Wilcut, J. W. Wells, and S. B. Clewis. 2003. Weed management with CGA-362622 in transgenic and nontransgenic cotton. Weed Sci. 51:1002–1009.

Preston, C. and A. M. Wakelin. 2008. Resistance to glyphosate from altered herbicide translocation patterns. Pest Manag. Sci. 64:372–376.

Rowland, M. W., D. S. Murray, and L. M. Verhalen. 1999. Full-season Palmer amaranth (*Amaranthus palmeri*) interference with cotton (*Gossypium hirsutum*). Weed Sci. 47:305–309.

Sellers, B. A., R. J. Smeda, W. G. Johnson, J. A. Kendig, and M. R. Ellersieck. 2003. Comparative growth of six *Amaranthus* species in Missouri. Weed Sci. 51:329–333.

Sweat, J. K., M. J. Horak, D. E. Peterson, R. W. Lloyd, and J. E. Boyer. 1998. Herbicide efficacy of four *Amaranthus* species in soybean (*Glycine max*). Weed Technol. 12:315–321.

Tardif, F. J. and G. D. Leroux. 1991. Response of quackgrass biotypes to glyphosate and quazalofop. Can. J. Plant Sci. 71:803–810.

Tardif, F. J. and S. B. Powels. 2006. A mutation in the herbicide target site acetohydoxyacid synthase produces morphological and structural alterations and reduces fitness in *Amaranthus powellii*. New Phytol. 169:25–264.

van Heemst, H.D.J. 1985. The influence of weed competition on crop yield. Agric. Systems 18:81–93.

Wakelin, A. M. and C. Preston. 2006. The cost of glyphosate resistance: is there a fitness penalty associated with glyphosate resistance in annual ryegrass? Pages 515–518 in Proc. of the 15th Australian Weeds Conference. Adelaide, Australia, Weed Management Society of South Australia, Incorporated.

Warwick, S. I. 1991. Herbicide resistance in weedy plants: physiology and population biology. Ann. Rev. Ecol. Syst. 22:95–114.

Webster, T. M. 2004. Weed survey—southern states. Proc. South. Weed Sci. Soc. 57:404–426.

Webster, T. M. 2005. Weed survey—southern states. Proc. South. Weed Sci. Soc. 58:291–06.

Webster, T. M. and H. D. Coble. 1997. Changes in the weed species composition of the southern United States: 1974–1995. Weed Technol. 11:308–317.

Whitaker, J. R. 2009. Distribution, Biology, and Management of Glyphosate-Resistant Palmer Amaranth. Ph.D dissertation. Raleigh, NC: North Carolina State University. 231 p.

Wise, A. M., T. L. Grey, E. P. Prostko, W. K. Vencill, and T. M. Webster. 2009. Establishing the geographical distribution and level of acetolactate synthase resistance in Palmer amaranth (*Amaranthus palmeri*) accessions in Georgia. Weed Technol. 23:214–200.

Wright, S. R., M. W. Jennette, H. D. Coble, and T. W. Rufty. 1999. Root morphology of young *Glycine max*, *Senna obtusifolia*, and *Amaranthus palmeri*. Weed Sci. 47:706–711.

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