

Research Article

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Author for correspondence:

Nilda Roma-Burgos, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, 1366 Fayetteville, AR 72704. (Email: nburgos@uark.edu)

Resistance of Palmer amaranth (*Amaranthus palmeri*) to S-metolachlor in the midsouthern United States

Koffi Badou Jeremie Kouame¹, Matthew B. Bertucci² , Mary C. Savin³ , Taghi Bararpour⁴, Lawrence E. Steckel⁵ , Thomas R. Butts⁶ , Cammy D. Willett⁷ , Fellipe G. Machado⁸  and Nilda Roma-Burgos³ 

¹Graduate Student, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville, AR, USA; ²Assistant Professor, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville, AR, USA; ³Professor, Department of Crop, Soil, and Environmental Sciences, University of Arkansas, Fayetteville, AR, USA; ⁴Assistant Extension/Research Professor, Department of Plant and Soil Sciences, Mississippi State University, Stoneville, MS, USA; ⁵Professor and Extension Weed Scientist, Department of Plant Sciences, University of Tennessee, TN, USA; ⁶Assistant Professor and Extension Weed Scientist, University of Arkansas System Division of Agriculture, Lonoke, AR, USA; ⁷Research Soil and Environmental Scientist, University of Missouri, Division of Applied Social Sciences, Columbia, MO, USA and ⁸Graduate Student, Departamento de Agronomia, Universidade Estadual de Maringá, Maringá (PR), Brazil

Abstract

Palmer amaranth (*Amaranthus palmeri* S. Watson) is one of the most problematic weeds in many cropping systems in the midsouthern United States because of its multiple weedy traits and its propensity to evolve resistance to many herbicides with different mechanisms of action. In Arkansas, *A. palmeri* has evolved metabolic resistance to S-metolachlor, compromising the effectiveness of an important weed management tool. Greenhouse studies were conducted to evaluate the differential response of *A. palmeri* accessions from three states (Arkansas, Mississippi, and Tennessee) to (1) assess the occurrence of resistance to S-metolachlor among *A. palmeri* populations, (2) evaluate the resistance level in selected accessions and their resistant progeny, (3) and determine the susceptibility of most resistant accessions to other soil-applied herbicides. Seeds were collected from 168 crop fields between 2017 and 2019. One hundred seeds per accession were planted in silt loam soil without herbicide for >20 yr and sprayed with the labeled rate of S-metolachlor (1,120 g ai ha⁻¹). Six accessions (four from Arkansas and two from Mississippi) were classified resistant to S-metolachlor. The effective doses (LD₅₀) to control the parent accessions ranged between 73 and 443 g ha⁻¹, and those of F₁ progeny of survivors were 73 to 577 g ha⁻¹. The resistance level was generally greater among progeny of surviving plants than among resistant field populations. The resistant field populations required 2.2 to 7.0 times more S-metolachlor to reduce seedling emergence 50%, while the F₁ of survivors needed up to 9.2 times more herbicide to reduce emergence 50% compared with the susceptible standard.

Introduction

Palmer amaranth (*Amaranthus palmeri* S. Watson) is one of the most common, problematic, and economically detrimental weeds throughout the southern United States (Ward et al. 2013). It is one of the two most troublesome weeds in Arkansas, Louisiana, Mississippi, and Tennessee (Riar et al. 2013). Glyphosate-resistant *A. palmeri* infestations occurred in 16% of scouted areas in Louisiana and in 54% of scouted areas in Mississippi, Tennessee, and Arkansas (Riar et al. 2013). The average cost of hand weeding *A. palmeri* was US\$59 ha⁻¹ (Riar et al. 2013). *Amaranthus palmeri* emerges continuously from late spring to late summer as long as the soil temperature is favorable (between 22 and 32 °C; Chahal et al. 2021; Keeley et al. 1987).

The propensity of *A. palmeri* to evolve resistance to many herbicides has made it difficult to control. To date, it is resistant to 5-enolpyruvyl-shikimate-3-phosphate synthase-inhibiting herbicides (Culpepper et al. 2006; Norsworthy et al. 2008), acetolactate synthase (ALS)-inhibiting herbicides (Burgos et al. 2001; Gaedert et al. 1997; Horak and Peterson 1995), microtubule-inhibiting herbicides (Gossett et al. 1992), 4-hydroxyphenylpyruvate dioxygenase-inhibiting herbicides (Jhala et al. 2014; Nakka et al. 2017b), photosystem II (PSII)-inhibiting herbicides (Nakka et al. 2017a), protoporphyrinogen oxidase (PPO)-inhibiting herbicides (Salas et al. 2016; Salas-Perez et al. 2017; Varanasi et al. 2018a, 2018b), and auxin mimic- and glutamine synthetase-inhibiting herbicides (Heap 2021). *Amaranthus palmeri* has also evolved resistance to very-long-chain fatty acid (VLCFA)-inhibiting herbicides in Arkansas (Brabham et al. 2019; Rangani et al. 2021).

VLCFAs are important components of lipids such as triacylglycerols (accumulated in seeds), some sphingolipids and phospholipids found in cell membranes, and cuticular waxes on plant

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Table 1. Weed species that evolved resistance to very-long-chain fatty-acid-inhibiting herbicides globally, between 1982 and 2020.^a

| Species | Herbicide | Country | References |
|--------------------------------|---|--|---|
| <i>Lolium rigidum</i> | Pyroxasulfone | Australia | Brunton et al. 2018; Busi and Powles 2013, 2016; Busi et al. 2014, 2018 |
| <i>Lolium rigidum</i> | S-metolachlor, metazachlor, pyroxasulfone | Australia | Brunton et al. 2019 |
| <i>Lolium multiflorum</i> | Flufenacet | France, United Kingdom, Australia, United States | Ducker et al. 2019a |
| <i>Alopecurus myosuroides</i> | Flufenacet | France, United Kingdom, Germany | Ducker et al. 2019b, 2020 |
| <i>Echinochloa crus-galli</i> | Butachlor | Philippines, China, Thailand | Heap 2021; Juliano et al. 2010 |
| <i>Avena fatua</i> | Pyroxasulfone | Canada | Heap 2021 |
| <i>Amaranthus tuberculatus</i> | S-metolachlor | United States | Strom et al. 2020 |
| <i>Amaranthus palmeri</i> | S-metolachlor | United States | Brabham et al. 2019 |
| <i>Raphanus raphanistrum</i> | pyroxasulfone | Australia | Heap 2021 |

^aTime span of resistance recorded by Heap (2021).

aerial surfaces (Trenkamp et al. 2004). Therefore, VLCFAs are major components of hydrophobic polymers on the leaf surface, playing an important role in preventing desiccation (Trenkamp et al. 2004). Sphingolipids and phospholipids are required for cell division, polarity, and differentiation (Lechelt-Kunze et al. 2003). Herbicides that inhibit the VLCFAs target the condensing enzyme 3-ketoacyl-CoA synthase FAE1 within the elongase enzymatic complex bound to the endoplasmic reticulum (Boger 2003; Busi 2014; Matthes et al. 1998; Millar and Kunst 1997). By provoking a disruption of VLCFA levels in plants, these herbicides can inhibit growth or cause embryonic mortality (Du Granrut and Cacas 2016). Herbicides that inhibit VLCFAs have been used for more than 60 yr (Busi 2014). Important VLCFA-inhibiting herbicides include pyroxasulfone, dimethenamid-P, acetochlor, and S-metolachlor, with S-metolachlor labeled for use in more than 70 crops (O'Connell et al. 1998). S-metolachlor effectively suppresses yellow nutsedge (*Cyperus esculentus* L.), annual grasses, and small-seeded broadleaf species, including *A. palmeri* (Barber et al. 2021). Despite the prevalent use of VLCFA-inhibiting herbicides, only five grasses had evolved resistance to them before resistance among *Amaranthus* species was reported (Busi 2014; Heap 2021) (Table 1).

Weed resistance to herbicides is a major concern in modern agriculture, as it compromises producers' efforts to sustainably manage crop production. Weeds generally cause greater yield reductions than other pests; therefore, weed management is mandatory in crop production (Oerke 2006). The use of synthetic herbicides has permitted simple and effective management of weeds in many cropping systems (Busi et al. 2018). However, resistance evolution in many weed species worldwide is reducing the effectiveness of chemical weed control (Beckie and Tardif 2012; Busi et al. 2018; Powles and Yu 2010; Roma-Burgos et al. 2019). Therefore, herbicide resistance is a key factor that spurs the search for new herbicide targets and intervention technologies (Burgos

2015) and the promotion of best management practices (Burgos 2015; Norsworthy et al. 2012). The loss of crucial herbicides and the need for immediate answers to growers' needs require extensive research on weed resistance to enable proactive management of herbicide-resistant weeds (Burgos et al. 2013).

For a comprehensive assessment of the resistance problem, other soil-applied herbicides need to be tested on populations deemed resistant to S-metolachlor. PPO-inhibiting herbicides such as fomesafen, flumioxazin, saflufenacil, and sulfentrazone have been extensively used as alternative herbicides to manage resistance to other herbicide modes of action (Umphres et al. 2018). They can be applied either preemergence or postemergence. Flumioxazin and fomesafen are effective on major weeds in field crop production such as common lambsquarters (*Chenopodium album* L.), common ragweed (*Ambrosia artemisiifolia* L.), *A. palmeri*, and morningglory species (*Ipomoea* spp.) (Askew et al. 1999, 2002; Clewis et al. 2007; Niekamp et al. 1999; Umphres et al. 2018). Flumioxazin can be applied with nonselective preplant burndown herbicides, preemergence alone or tank-mixed with other pre-emergence herbicides (Umphres et al. 2018). It is effective on glyphosate-resistant *A. palmeri* (Whitaker et al. 2010) or species resistant to ALS inhibitors or atrazine (Taylor-Lovell et al. 2002). Fomesafen, in combination with S-metolachlor or pendimethalin, can control glyphosate-resistant *A. palmeri* (Nandula et al. 2013). PSII-inhibiting herbicides are widely used for weed control in corn (*Zea mays* L.) and sorghum [*Sorghum bicolor* (L.) Moench] production (Norsworthy et al. 2020). Many PSII-inhibiting herbicides have soil and foliar activity. Among the oldest PSII inhibitors with the broadest weed spectrum is atrazine (Senseman 2007). Together, the VLCFA, PPO, and PSII inhibitors comprise the most important groups of herbicides used in several production systems.

The extent of *A. palmeri* resistance to S-metolachlor in the mid-southern United States has not been investigated. The response of S-metolachlor-resistant populations to other soil-applied herbicides needs to be assessed to determine effective alternative chemical tools. The objectives of this research were to (1) evaluate the extent of *A. palmeri* resistance to S-metolachlor in the mid-southern United States, (2) determine the resistance level of accessions classified as resistant, (3) determine the change in resistance level from original populations to their progeny, and (4) investigate alternative pre-emergence herbicides for the control of resistant populations.

Materials and Methods

Amaranthus palmeri Seed Collection

Amaranthus palmeri seeds were collected in soybean [*Glycine max* (L.) Merr.] and cotton [*Gossypium hirsutum* L.] fields in 2017, 2018, and 2019 from mid-southern U.S. states Arkansas, Mississippi, and Tennessee (Figure 1). In Arkansas, samples were collected from 61 crop fields (15 counties) in 2017 and 35 crop fields (14 counties) in 2018. In Mississippi, samples were collected from 54 fields (17 counties) in 2017. In Tennessee, samples were collected from a total of 18 fields (10 counties) between 2018 and 2019. Samples were collected according to standard procedures (Burgos 2015) from fields reported by growers to university Extension agents as having a history of S-metolachlor use and *A. palmeri* at the end of the season. Inflorescences were harvested from at least 10 female plants and bagged to make one composite sample per field. The inflorescences were air-dried and threshed, and the seeds were cleaned. Seeds were stored at room temperature.

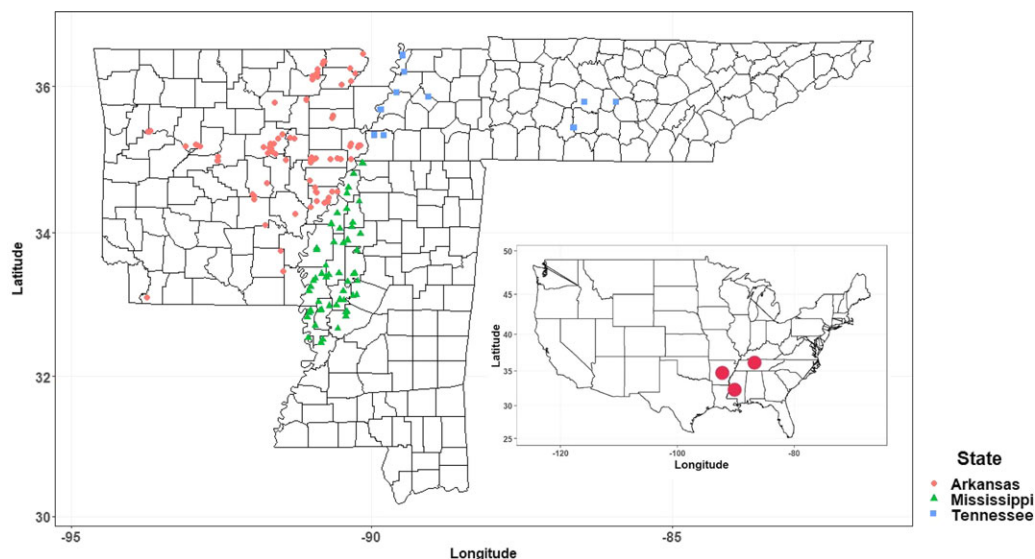


Figure 1. *Amaranthus palmeri* sampling sites in Arkansas, Mississippi, and Tennessee, USA, from 2017 to 2019.

During fall 2019, county Extension agents collected additional seeds from fields with accessions that were the most difficult to control among the 2018 collection (18CRI-D, 18PHI-C, and 18WOO-B). Accessions from these fields had high frequency of survivors in the resistance test (see “Results and Discussion”). The 2019 accessions were labeled 19CRI-D, 19PHI-C, and 19WOO-B, respectively, and included in subsequent dose–response studies.

Resistance Testing

A large-scale test for resistance was conducted in the greenhouse at the Milo J. Shult Agricultural Research & Extension Center (SAREC), University of Arkansas System Division of Agriculture, Fayetteville, AR, USA. Field soil (Roxana silt loam; coarse-silty, mixed, superactive, nonacid, thermic Typic Udifluvents), with no herbicide-use history, was collected from the Vegetable Research Station, Kibler, AR, USA. Greenhouse conditions for the study were 35/23 C day/night temperature and a 14-h photoperiod. Soil was air-dried and sieved. A subsample was submitted to the Agricultural Diagnostic Laboratory, MSAREC, Fayetteville, AR, USA, for analysis (Table 2). Soil pH and electrical conductivity (EC) were measured in a 1:2 soil:water mixture (Sikora and Kissel 2014), and total nitrogen (N) was measured by thermal combustion analysis (Provin 2014). Soil nutrients were analyzed using the Mehlich-3 method (Zhang et al. 2014).

The experimental units (flats) were arranged in a completely randomized design with three replicates, and the resistance test was repeated in time. The flats (12.2 cm by 9.5 cm by 5.7 cm; Insert TO standard, Hummert International, Earth City, MO, USA) were filled with 700 g of soil. The soil-filled flats were saturated with tap water the day before seeding and herbicide application and allowed to drain overnight to obtain uniform, water-holding capacity soil moisture. One hundred seeds were spread uniformly on the soil surface of each tray and were covered with a thin layer of soil. The assay had two treatments per accession (treated and nontreated). *S*-metolachlor (Dual II Magnum®, Syngenta Crop Protection, Greensboro, NC, USA) was applied at the field-labeled rate for soybean (1,120 g ai ha⁻¹) in a spray chamber equipped with a motorized boom sprayer fitted with TeeJet® 1100067 nozzles (Spraying

Systems, Wheaton, IL, USA) calibrated to deliver 187 L ha⁻¹ at a pressure of 276 kPa in one pass and traveling at 0.45 m s⁻¹. *S*-metolachlor was activated shortly after herbicide spraying by misting approximately 0.8 cm of water over the surface. The flats were misted overhead twice a day for the first week, after which the flats were subirrigated for the remainder of the study. Survivors of the labeled rate from the first resistance test (conducted during fall 2018) were grown, isolated within cages by accession, and allowed to interbreed for seed production to evaluate progression of herbicide resistance from parents to progeny. Two lines of progeny were produced (18PHI-C-F₁ and 18WOO-B-F₁).

S-Metolachlor Dose–Response Bioassays

Accessions with the least susceptibility to *S*-metolachlor, controlled less than 88% during the large-scale test, were subjected to a follow-up dose–response study. In 2019 and 2020, dose–response studies were conducted using nine rates of *S*-metolachlor (0, 0.125, 0.25×, 0.5×, 0.75×, 1×, 1.5×, 2×, 2.5×) for the putative resistant accessions, with the 1× rate being 1,120 g ha⁻¹. A susceptible standard (SS), collected from an organic field in Woodruff County (AR, USA), was used as reference and treated with eight rates of *S*-metolachlor (0, 0.03125×, 0.125×, 0.25×, 0.5×, 0.75×, 1×, 1.5×). Overall, seven parent accessions were evaluated: five from Arkansas (17PRA-A, 17RAN-A, 18CRI-D, 18PHI-C, and 18WOO-B) and two from Mississippi (17TUN-A and 17TUN-D). The planting medium, seeding rate, herbicide application volume, watering, and plant maintenance were as described in “Resistance Testing.”

The “second-year” accessions—19CRI-D, 19PHI-C, and 19WOO-B—were included in the dose–response assay with the corresponding accessions collected from the same fields in 2018 and the respective progeny of survivors. The intent was to compare resistance levels between the 2018 and 2019 populations from the same fields and compare resistance levels between field-collected parents in 2018 and the progeny of plants surviving herbicide treatment in the greenhouse. Survivors of 18CRI-D did not produce enough seeds for a dose–response study of its progeny, so only field populations (18CRI-D and 19CRI-D) were studied. The dose–response rate structures were the same as those for the first year.

Table 2. Chemical and physical characteristics of soil used for the greenhouse experiments conducted in 2018 to 2020 at the Shult Agricultural Research & Extension Center, University of Arkansas, Fayetteville, AR, USA.^a

| pH ^c | EC ^c | Mehlich-3 extractable soil nutrients ^b | | | | | | | | | | | | | Sand | Silt | Clay |
|-----------------|-----------------|---|---------|-----|-----|------|-----|-----|------|-------|-----|------|------|------|------|------|------|
| | | Total N ^d | Total C | P | K | Ca | Mg | S | Na | Fe | Mn | Zn | Cu | B | | | |
| 7.3 | 112 | 0.04 | 0.4 | 111 | 164 | 1308 | 237 | 5.0 | 17.1 | 232.8 | 103 | 3.39 | 1.59 | 0.42 | 18.8 | 68.2 | 12.9 |

^aRoxana silt loam soil from the Vegetable Research Station of the University of Arkansas, Kibler, AR, USA.

^bExtracted using Mehlich-3 method.

^cSoil pH and electrical conductivity (EC) measured in a 1:2 soil:water mixture.

^dMeasured by thermal combustion analysis.

Table 3. Herbicides used in resistance testing of *Amaranthus palmeri* from the midsouthern United States (Arkansas, Mississippi, Tennessee) in the greenhouse at the Shult Agricultural Research & Extension Center, University of Arkansas, Fayetteville, AR, USA.

| Herbicide | Product and manufacturer | Family | MOA ^a | Chemical name ^b | Labeled rate |
|----------------|---|---------------------|------------------|--|--------------------------------|
| S-metolachlor | Dual II Magnum®, Syngenta Crop Protection, LLC, Greensboro, NC, USA | Chloroacetamide | VLCFA inhibitor | 2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl)acetamide | g ai ha ⁻¹ 1,120 |
| Pyroxasulfone | Zidua® SC, BASF Corporation, Research Triangle Park, NC, USA | Pyrazole | VLCFA inhibitor | 3-[[[5-(difluoromethoxy)-1-methyl-3-(trifluoromethyl)-1H-pyrazol-4-yl]methyl]sulfonyl]-4,5-dihydro-5,5-dimethylisoxazole | 120 |
| Dimethenamid-P | Outlook®, BASF Corporation, Research Triangle Park, NC, USA | Chloroacetamide | VLCFA inhibitor | (RS) 2-chloro-N-(2,4-dimethyl-3-thienyl)-N-(2-methoxy-1-methylethyl)acetamide | 631 |
| Atrazine | AAtrex® 4L, Syngenta Crop Protection, LLC, Greensboro, NC, USA | Triazine | PSII inhibitor | 6-chloro-N-ethyl-N9-(1-methylethyl)-1,3,5-triazine-2,4-diamine | 2,240 |
| Fomesafen | Flexstar®, Syngenta Crop Protection, LLC, Greensboro, NC, USA | Diphenylether | PPO inhibitor | 5-[2-chloro-4-(trifluoromethyl)phenoxy]-N-(methylsulfonyl)-2-nitrobenzamide | 280 |
| Flumioxazin | Valor® SX, Valent U.S.A. Corporation, Walnut Creek, CA, USA | N-phenylphthalimide | PPO inhibitor | 2-[7-fluoro-3,4-dihydro-3-oxo-4-(2-propynyl)-2H-1,4-benzoxazin-6-yl]-4,5,6,7-tetrahydro-1H-isoindole-1,3(2H)-dione | 70 |

^aMOA, mechanism of action; PSII, photosystem II; PPO, protoporphyrinogen; VLCFA, very-long-chain fatty acid.

^bChemical names from Ransom (2013).

The experimental design, plant establishment, and herbicide application details were as described in “Resistance Testing.” The assays were repeated in time.

Response of S-Metolachlor-Resistant Accessions to Other Soil-applied Herbicides

The response of the four accessions most resistant to S-metolachlor from dose–response assays (18CRI-D, 18WOO-B, 17TUN-A, and 17TUN-D) and one SS to five alternative residual herbicides representing three mechanisms of action (Table 3) was evaluated. These accessions (100 seeds per accession) were planted and treated with dimethenamid-P, pyroxasulfone, flumioxazin, fomesafen, and atrazine. Herbicides were applied at their respective field-use rates for soybean (dimethenamid-P, pyroxasulfone, flumioxazin, fomesafen) and corn (atrazine). Each accession had a nontreated control. The experiment was arranged in a completely randomized design with three replicates and was repeated in two greenhouses. Plant establishment and herbicide application details were as described earlier.

Data Collection and Analysis

All bioassays were evaluated at 21 d after treatment (DAT). In each case, live plants were counted, and the data were converted to percent survival based on the number of live plants in the respective

nontreated control. For the responses of S-metolachlor-resistant accessions to other soil-applied herbicides, survival rates were also evaluated at 14 DAT. The interaction between treatments and runs was not significant ($P > 0.05$); therefore, dose–response data were pooled across runs. *Amaranthus palmeri* percent survival in response to increasing rates of S-metolachlor, for parents and F₁ progeny, were analyzed using a nonlinear regression equation. A three-parameter log-logistic model (Equation 1) was used to relate *A. palmeri* percent survival to S-metolachlor rates using nonlinear least-squares regression (nls) in R v. 4.0.0 (R Core Team 2020):

$$Y = \frac{d}{1 + \exp[b(\log(x) - \log e)]} \quad [1]$$

where Y is *A. palmeri* percent survival, d is the upper asymptotic value of Y , b is the slope of the curve, e is the rate of the herbicide required to reduce seedling emergence 50% (LD₅₀), and x is the S-metolachlor dose.

For the resistance-profiling bioassay, *A. palmeri* percent control was subjected to ANOVA using the GLIMMIX procedure in SAS 9.4 (SAS Institute, Cary, NC, USA) assuming a beta distribution (Gbur et al. 2012). Greenhouses were considered random effects, while herbicides and accessions were considered fixed effects. Treatment means were separated at $P \leq 0.05$ using Tukey’s honestly significant difference (HSD) adjustment.

Results and Discussion

Differential Responses to S-Metolachlor of Amaranthus palmeri from the Midsouthern United States

This research included 168 accessions covering 24, 17, and 10 counties in Arkansas (57% of accessions), Mississippi (32% of accessions), and Tennessee (11% of accessions), respectively. Out of 61 accessions from Arkansas in 2017, 3.3% were controlled less than 90%, 10% were controlled between 90% and 95%, and 87% were controlled 95% or more (Figure 2). Among 35 accessions collected in Arkansas in 2018, 23% were controlled less than 90%, 17% were controlled between 90% and 95% and 60% were controlled 95% or more. Of the 54 accessions from Mississippi in 2017, 4% were controlled less than 90%; the rest were controlled 90% or more. No accession from Tennessee was controlled less than 90%. Of the 18 Tennessee accessions evaluated, 6% were controlled between 90% and 95%. From experience, 5% to 10% escape is enough to start a cohort of resistant plants if some of these escapes carry a resistance trait (Salas et al. 2016).

It is commonly understood that weed populations have differential tolerance to herbicides due to genetic background variation within and among populations (Radosevich et al. 2007). The labeled rates of herbicides are set to ensure that the most-tolerant individuals, or populations of target species, are controlled 100% as consistently as possible across environments. In crop production, weed control $\geq 90\%$ is considered excellent (Barber et al. 2021). Differential tolerance to labeled rate of herbicides has been documented among older (collected between 2008 and 2016) susceptible *A. palmeri* populations from Arkansas, for example, with respect to fomesafen (Salas et al. 2016), glufosinate (Salas-Perez et al. 2018), mesotrione (Singh et al. 2018), and ALS-inhibiting herbicides (Bond et al. 2006; Burgos et al. 2001). Significant variations in background response to herbicides were also documented among populations from Kansas with respect to glyphosate, 2,4-D, atrazine, and mesotrione (Kumar et al. 2020). In Arkansas, 34% of *A. palmeri* surveyed survived mesotrione applications with injury ranging from 61% to 90% (Singh et al. 2018).

When a population starts having an increasing number of individuals surviving the labeled rate, this is an indication of evolving resistance, as was observed with *A. palmeri* populations resistant to PPO-inhibiting herbicides (Salas et al. 2016). The fact that a number of recent populations showed less than 90% control with the labeled rate of S-metolachlor indicates possible evolving resistance in those populations. The occurrence of resistance to S-metolachlor has already been confirmed in a few *A. palmeri* populations (Brabham et al. 2019; Rangani et al. 2021). The current survey indicated that additional populations might have also evolved resistance to S-metolachlor.

Resistance Level to S-Metolachlor

The resistance level to S-metolachlor was evaluated for accessions that were controlled less than 88% during the large-scale test for resistance. In total, seven accessions were used for the dose-response studies: two accessions from Arkansas in 2017 (17PRA-A and 17RAN-A), three accessions from Arkansas in 2018 (18CRI-D, 18PHI-C, and 18WOO-B), and two accessions from Mississippi in 2017 (17TUN-A and 17TUN-D). The LD₅₀ values (*e*) ranged between 73 and 443 g ha⁻¹ for field populations of all seven accessions evaluated. The SS required 63 ± 16 g ha⁻¹, while resistant accessions required 443 ± 36, 289 ± 12, 156 ± 16, 140 ± 11, 73 ± 21, 313 ± 54, and 242 ± 32 g ha⁻¹ to reduce seedling

emergence 50% for 18WOO-B, 18CRI-D, 17PRA-A, 17RAN-A, 18PHI-C, 17TUN-A, and 17TUN-D, respectively (Table 4; Figure 3; Supplemental Figure 1). The levels of resistance of 18WOO-B, 18CRI-D, 17RAN-A, 17PRA-A, 18PHI-C, 17TUN-A, and 17TUN-D to S-metolachlor were 7.0-, 4.6-, 2.2-, 2.5-, 1.2-, 5.0-, and 3.8-fold, respectively. Accession 18PHI-C was susceptible, while the rest were resistant to S-metolachlor. This survey confirmed resistance to S-metolachlor in four counties in Arkansas (Randolph, Prairie, Crittenden, Woodruff) and one county in Mississippi (Tunica). Brabham et al. (2019) had also reported two resistant populations from Marion and Crawfordsville (Crittenden County), while Rangani et al. (2021) reported resistant populations in Crittenden, Woodruff, and Mississippi counties in 2014 and 2015. Resistant accessions reported by Brabham et al. (2019) required 156 and 133 g ai ha⁻¹ S-metolachlor to attain 50% control and were 9.8 and 8.3 times less responsive to S-metolachlor than the susceptible standards. In a previous study, the LD₅₀ values of resistant accessions were between 88 and 785 g ai ha⁻¹ (Rangani et al. 2021), which equated to resistance levels between 3- and 29-fold. Results from this research documented, for the first time, S-metolachlor resistance in accessions collected from two crop fields in Tunica County, MS, USA. The dose-response studies produced survivors at a 2× rate of S-metolachlor. Should these types of individuals be allowed to produce seeds in the field owing to insufficient supplemental control measures, failure of the herbicide would be expected in a few years.

Resistance Progression in the Progeny

The progeny of surviving plants from 18WOO-B (18WOO-B-F₁) had the highest level of resistance to S-metolachlor at 9.2-fold compared with the SS (Figure 3), requiring 577 ± 52 g ha⁻¹ of the herbicide to reduce seedling emergence 50%. The second F₁ progeny (18PHI-C-F₁) was only 2-fold resistant compared with SS. Therefore, the progression in resistance level from one cycle to the next is not always large. This most likely depends on the frequency and vigor of resistant plants in the field population. Vigorous resistant plants will produce more seed, and their seed will compose a large fraction of F₁ seed, resulting in an increase in the resistance level of the F₁ generation (Radosevich et al. 2007). Accessions 19CRI-D and 19WOO-B required 327 ± 47 and 520 ± 64 g ha⁻¹ to reduce seedling emergence 50%. Based on LD₅₀ values, these populations were 5 and 8 times less sensitive to S-metolachlor compared with the SS (Figure 4). In both cases, the resistance level of the field population in the second year of sampling was the same as that of the same field in the first year. This indicates that whereas resistance level increases significantly after one cycle of “purification” in the greenhouse, the resistance progression could be slower in the field. One reason for this is the supplemental weed management measures done across seasons in the field. Accession 19PHI-C required 73 ± 19 g ha⁻¹ to reduce seedling emergence 50% and was as sensitive as the SS.

Resistance to VLCFA-inhibiting herbicides evolved more slowly compared with herbicides that target other sites of action (Heap 2021), despite the extensive use of VLCFA-inhibiting herbicides in numerous crops and millions of hectares for decades. Several factors may explain the slower evolution of weed resistance to VLCFA-inhibiting herbicides, including the infrequent mutations in the condensing enzyme (Boger et al. 2000; Busi 2014); the requirement of highly improbable simultaneous changes in several different targets to deliver resistance to VLCFA-inhibiting herbicides due to the interaction of these herbicides with multiple

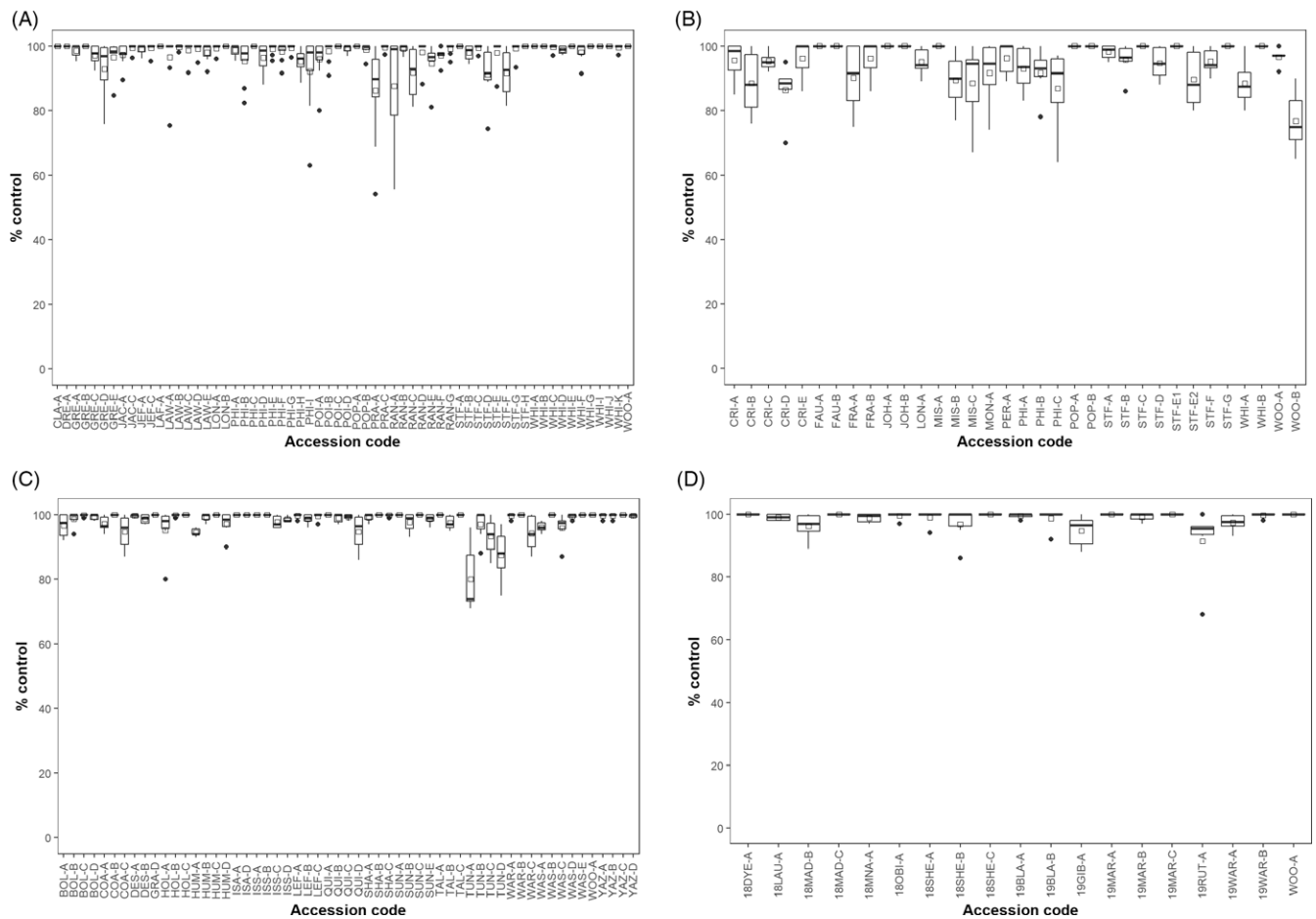


Figure 2. Response of *Amaranthus palmeri* accessions to 1,120 g ha⁻¹ S-metolachlor in the greenhouse, Milo J. Shult Agricultural Research & Extension Center (University of Arkansas, Fayetteville, AR, USA). (A) Arkansas 2017, (B) Arkansas 2018, (C) Mississippi 2017, and (D) Tennessee 2018 and 2019.

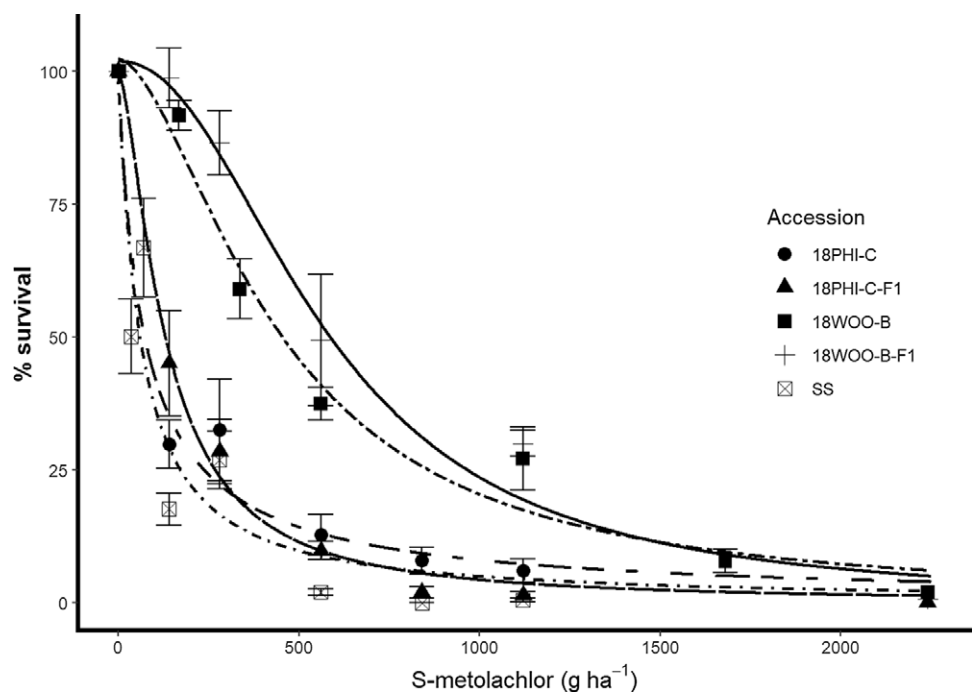


Figure 3. Dose–response studies of parental *Amaranthus palmeri* accessions collected in Arkansas (in 2018) and F₁ progeny obtained in the greenhouse at the Milo J. Shult Agricultural Research & Extension Center (University of Arkansas, Fayetteville, AR, USA). Data were fit using a three-parameter log-logistic equation. Error bars represent *A. palmeri* % survival– associated standard errors.

Table 4. Resistance levels of *A. palmeri* populations to S-metolachlor in greenhouse experiments conducted at the Milo J. Shult Agricultural Research & Extension Center, University of Arkansas, Fayetteville, AR, USA.

| Population | LD ₅₀ ^a g ai ha ⁻¹ | R/S ^b |
|------------------------|--|------------------|
| 18WOO-B | 443 (36) | 7.0 |
| 19WOO-B | 520 (64) | 8.3 |
| 18WOO-B-F ₁ | 577 (52) | 9.2 |
| 18CRI-D | 289 (12) | 4.6 |
| 19CRI-D | 327 (47) | 5.2 |
| 17TUN-A | 313 (54) | 5.0 |
| 17TUN-D | 242 (32) | 3.8 |
| 17PRA-A | 156 (16) | 2.5 |
| 17RAN-A | 140 (11) | 2.2 |
| 18PHI-C | 73 (21) | 1.2 |
| 19PHI-C | 73 (19) | 1.2 |
| 18PHI-C-F ₁ | 130 (15) | 2.1 |
| SS | 63 (16) | 1.0 |

^aLD₅₀, S-metolachlor rate that reduced seedling emergence by 50%. Values in parenthesis are standard errors of the mean.

^bR/S, resistance index, ratio between the LD₅₀ value of the S-metolachlor-resistant accessions and the LD₅₀ value of the susceptible accession.

Table 5. The *F*- and *P*-values for *Amaranthus palmeri* control (%) at 21 d after herbicide application (DAT) in a greenhouse experiment in Fayetteville, AR, USA.

| Effect | 21 DAT | |
|--------------------------------|-----------------|---------------------|
| | <i>F</i> -value | <i>P</i> > <i>F</i> |
| Greenhouse | 2.45 | 0.1260 |
| Accession | 1.63 | 0.1728 |
| Greenhouse*accession | 0.85 | 0.4939 |
| Herbicide | 7.91 | <.0001 |
| Greenhouse*herbicide | 0.72 | 0.5772 |
| Accession*herbicide | 1.41 | 0.1522 |
| Greenhouse*accession*herbicide | 0.86 | 0.6196 |

targets (Busi 2014; Tanetani et al. 2009; Trenkamp et al. 2004); and the low proportion of survivors of these herbicides that grow to maturity and produce seeds because of postemergence applications of herbicides with different modes of action (Busi 2014). However, the occurrence of resistance to VLCFA-inhibiting herbicides has been increasing in recent years with five grasses: rigid ryegrass (*Lolium rigidum* Gaudin) (Busi et al. 2018), Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot] (Ducker et al. 2019a), slender meadow foxtail (*Alopecurus myosuroides* Huds.) (Ducker et al. 2019b), barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.] (Juliano et al. 2010), wild oat (*Avena fatua* L.) (Heap 2021); and some broadleaf species, including wild radish (*Raphanus raphanistrum* L.) (Heap 2021), waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer], and *A. palmeri*] (Brabham et al. 2019; Rangani et al. 2021; Strom et al. 2020) reported to date.

Efficacy of Other Soil-applied Herbicides on *Amaranthus palmeri* Resistant to S-Metolachlor

Four S-metolachlor-resistant accessions (18CRI-D, 18WOO-B, 17TUN-A, and 17TUN-D) were evaluated. The three-way greenhouse-by-accession-by-herbicide interaction was not significant at 14 and 21 (*P* > 0.05) DAT. The two-way greenhouse-by-accession, greenhouse-by-herbicide, and accession-by-herbicide interactions were not significant at 14 and 21 DAT (*P* > 0.05) (Table 5). At full labeled rates, all soil-applied herbicides tested provided excellent

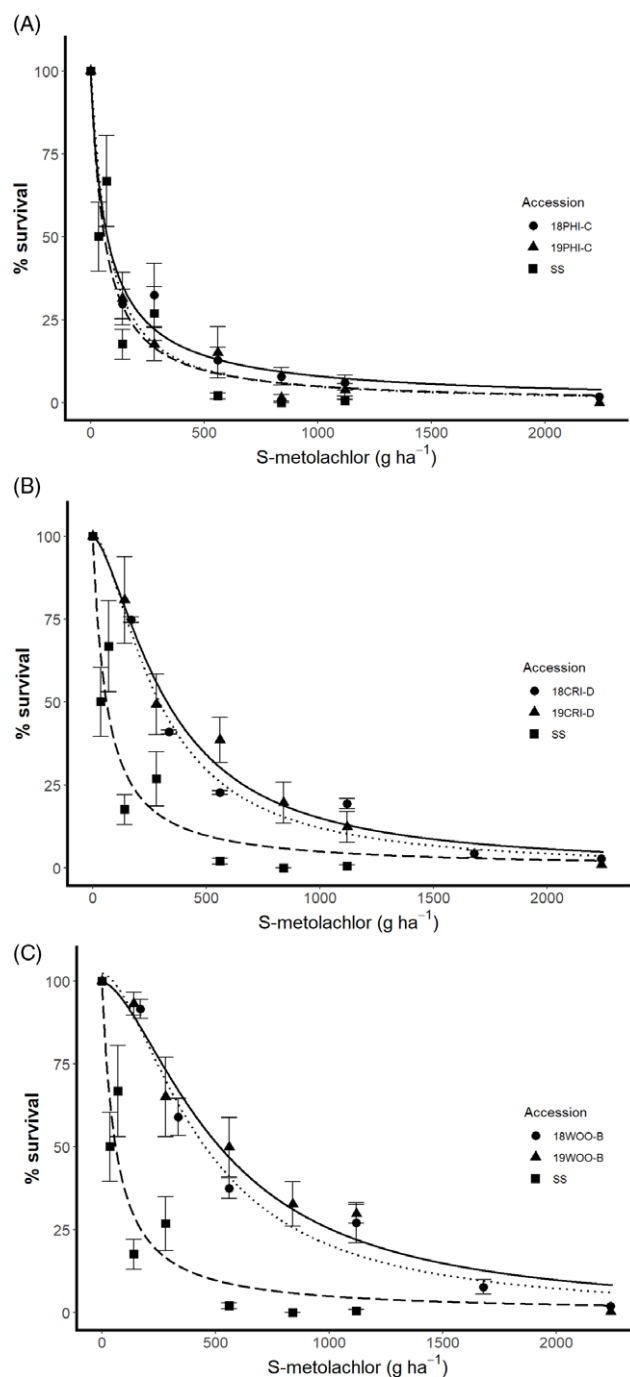


Figure 4. Dose-response studies of parental *Amaranthus palmeri* accessions collected in Arkansas (in 2018) and accessions collected from the same fields in 2019: PHI-C (A), CRI-D (B), and WOO-B (C). The test was conducted in the greenhouse at the Milo J. Shult Agricultural Research & Extension Center (University of Arkansas, Fayetteville, AR, USA). Data were fit using a three-parameter log-logistic equation. Error bars represent *A. palmeri* % survival-associated standard errors.

control of S-metolachlor-resistant *A. palmeri* ($\geq 90\%$), except for fomesafen, which had 89% control of 18WOO-B (Table 6). This level of control cannot be classified as resistant, but it is possible that resistance to soil-applied fomesafen is evolving in this population, just as had been discovered previously by Salas et al. (2016) in other populations. The efficacy of soil-applied herbicides tested on the S-metolachlor-resistant accessions was the same as

Table 6. Efficacy of other soil-applied herbicides on *S*-metolachlor-resistant *Amaranthus palmeri* accessions from Arkansas and Mississippi, USA.

| Herbicide | WSSA Group | <i>A. palmeri</i> control, 21 d after treatment ^a | | | | | Herbicide mean ^b |
|-----------------------------|------------|--|---------|---------|---------|----|-----------------------------|
| | | 17TUN-A | 17TUN-D | 18CRI-D | 18WOO-B | SS | |
| | | % | | | | | |
| Atrazine | 5 | 93 | 93 | 93 | 93 | 93 | 93 a |
| Dimethenamid-P | 15 | 93 | 92 | 93 | 93 | 93 | 93 a |
| Flumioxazin | 14 | 93 | 93 | 92 | 91 | 93 | 92 a |
| Fomesafen | 14 | 93 | 92 | 91 | 89 | 93 | 91 b |
| Pyroxasulfone | 15 | 91 | 92 | 91 | 91 | 91 | 91 b |
| Accession mean ^c | | 93 | 92 | 92 | 91 | 93 | |

^aPooled over two runs.

^bHerbicide means within a column followed by the same letter are not significantly different based on Tukey's honestly significant difference (HSD) test at $\alpha = 0.05$.

^cAccession means are not different based on Tukey's HSD test at $\alpha = 0.05$; the interaction effect between herbicide and accession was not significant.

that on the SS. These results are consistent with previous research (Brabham et al. 2019; Gonzalez-Torralva et al. 2020; Umphres et al. 2018). All five herbicides are viable options for the control of *S*-metolachlor-resistant *A. palmeri*, with a caveat that survivors of preemergence herbicides be controlled with follow-up herbicide applications and cultural management operations. Cross-resistance to other VLCFA inhibitors is possible. Brabham et al. (2019) reported reduced sensitivity of *S*-metolachlor-resistant accessions to dimethenamid-P, although the survivors were severely stunted at 0.25× the rate of dimethenamid-P. Still, the *S*-metolachlor-susceptible accessions were killed 100% at this rate of dimethenamid-P. All accessions were susceptible to other VLCFA inhibitors, but the reduced sensitivity to another herbicide in this MOA group, reported by Brabham et al. (2019) is noteworthy for planning resistance mitigation measures.

In a larger survey of *A. palmeri* populations, atrazine remains an effective option for most *A. palmeri* accessions from Arkansas (Gonzalez-Torralva et al. 2020), likely aided by the small acreage of corn and grain sorghum produced in the state. Increasing the frequency of corn and grain sorghum in crop rotations would be a good strategy for delaying *S*-metolachlor resistance evolution in the midsouthern United States.

Umphres et al. (2018) reported more than 90% control of *A. palmeri* by flumioxazin in a greenhouse study in Tennessee. Fomesafen and flumioxazin have both foliar and soil activity, but the former is primarily used as a postemergence herbicide (Senseman 2007), while the latter is primarily used as a preemergence herbicide (Senseman 2007; Umphres et al. 2018). In Arkansas, *A. palmeri* resistance to PPO-inhibiting herbicides has been documented in all major row crop-producing counties (Butts et al. 2019; Salas et al. 2016; Varanasi et al. 2018b). A foliar application of fomesafen to a fomesafen-resistant accession resulted in 55% survival (Varanasi et al. 2018a), and 16% of 227 accessions collected throughout Arkansas had mortality ratings <90% (Varanasi et al. 2018b). Given the prevalence of *A. palmeri* resistance to PPO inhibitors in the U.S. Midsouth (Noguera et al. 2021), it can be assumed that some of these *S*-metolachlor-resistant populations are also resistant to PPO-inhibiting herbicides. However, resistance to foliar-applied fomesafen does not necessarily translate to loss of efficacy when it is applied preemergence. In the present study, flumioxazin applied preemergence provided >90% control of all accessions. Multiple factors could contribute to obtaining excellent control with soil-applied PPO herbicides, even if such accessions were resistant to foliar-applied PPO herbicides. Germinating seedlings have weak protective barriers (cuticular waxes) compared with seedlings used in foliar tests. Germinating seedlings are expected to absorb and accumulate

more herbicide. Because seedlings do not have fully functional or sufficient level of protection mechanisms, it would take less herbicide to kill germinating seeds than fully developed (i.e., 4-leaf) seedlings.

Because *A. palmeri* resistance evolution to *S*-metolachlor is recent in the midsouthern United States, adoption of best management practices is critical for slowing the spread of resistance evolution. Adopting an integrated weed management program that involves the use of cultural and mechanical methods (Norsworthy et al. 2012), herbicide tank mixtures, sequential herbicide applications (preemergence followed by postemergence), and rotation of herbicides and crop traits will be beneficial for controlling *S*-metolachlor-resistant *A. palmeri* populations. For example, growing corn or grain sorghum in rotation with soybean/cotton will allow the use of atrazine, which continues to control *S*-metolachlor-resistant *A. palmeri* populations from the U.S. Midsouth. Because *S*-metolachlor resistance reported in Arkansas is metabolism based (Rangani et al. 2021), the addition of glutathione *S*-transferase inhibitors may help reverse resistance in these populations, a potential strategy to delay *S*-metolachlor resistance in *A. palmeri*. However, research is needed to validate this theory.

This research has documented resistance of *A. palmeri* to *S*-metolachlor in four counties in Arkansas and in one county in Mississippi. This evolving resistance is expected to increase weed management problems. The majority of populations in the U.S. Midsouth are currently susceptible to *S*-metolachlor, and the resistant ones exhibit resistance levels up to 7-fold. The level and frequency of resistance generally increased from parents to the first generation of progeny. The resistant populations reported here are not cross-resistant to other VLCFA inhibitors tested (dimethenamid-P and pyroxasulfone). These populations can also be controlled with soil-applied Group 14 herbicides tested here (flumioxazin and fomesafen) and atrazine. For now, there are effective herbicide options to manage *S*-metolachlor-resistant *A. palmeri* in various crops that could be grown in rotation.

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/wsc.2022.37>

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