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CGA-43089 Effects on Metolachlor Uptake and Membrane Permeability in Grain Sorghum (*Sorghum bicolor*)*

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Abstract. Phytotoxicity of metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide] toward grain sorghum [*Sorghum bicolor* (L.) Moench] increased as soil moisture increased. This was found with both unprotected sorghum and sorghum protected with 1.25 g CGA-43089 [α([cyanomethoxy]imino)benzeneacetonitrile] per kg of seed. However, under all conditions, metolachlor was less phytotoxic to protected sorghum than to unprotected sorghum. Metolachlor in sorghum coleoptiles increased as soil water increased. The rate of absorption of metolachlor and the total amount accumulated by excised sorghum coleoptiles was decreased by CGA-43089. Initial uptake of leucine by excised sorghum coleoptiles was decreased by metolachlor or metolachlor plus CGA-43089 but, after 24 h, uptake of leucine was increased by these treatments. Leucine incorporation into protein by coleoptiles was increased after 24 h treatment with CGA-43089. The apparent competitive effect of CGA-43089 on the absorption of metolachlor was most evident in the roots. Leakage of photosynthate from roots was highest following treatment with both CGA-43089 and metolachlor. Metolachlor did not increase leakage of labeled carbon from roots as compared with the control. These data indicate that the decreased rate of uptake of metolachlor in the presence of CGA-43089 was not a direct effect on cell permeability.

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Although metolachlor selectively controls annual grasses in corn (*Zea mays* L.) and a number of other crops, phytotoxicity prevents comparable selective control of annual grassy weeds in grain sorghum. Responses to metolachlor, including increased permeability of cell membranes and stimulated plant respiration, have provided evidence for a possible mode of action. Both plasmalemma and organelle membranes have been affected by the herbicide (Ebert 1980). An increased leakage of ^{32}P from roots has provided quantitative evidence of metolachlor-induced membrane damage (Pillai et al. 1977). Metolachlor treatment has increased respiration in chlorella and mitochondrial preparations (Pillai and Davis 1975) and stimulated respiration of sorghum seedlings.[1]

Resistance of corn to the chloroacetamides has been attributed to reduced uptake or to rapid detoxification of the herbicide (Hamill and Penner 1973, Jaworski 1975). Yellow nutsedge (*Cyperus esculentus* L.) (Armstrong et al. 1973) and barley (*Hordeum vulgare* L.) (Hamill and Penner 1973) also rapidly metabolize the chloroacetamide alachlor [2-chloro-2',6'-diethyl-*N*-(methoxymethyl) acetanilide]. Dehalogenation of the α-chlorine of metolachlor represents a relatively simple, early metabolic step that could explain herbicide inactivation in the resistant plants (Hamm 1974, Jaworski 1975).

Chandler et al. (1974) found that excised coleoptile and leaf tissue of wheat (*Triticum aestivum* L.) continued to absorb alachlor for more than 30 h. Winkle et al. (1980) reported that even in susceptible plants, rapid metabolism of metolachlor generally occurs. A glutathione conjugate is the major metabolite of metolachlor found in treated plants (Winkle et al. 1980). A direct relationship between metolachlor phytotoxicity and soil moisture has been attributed to soil moisture enhancement of herbicide uptake (Ketchersid et al. 1981).

Seed treatment using CGA-43089 has effectively protected sorghum against metolachlor and made selective annual grass control with metolachlor possible (Ellis et al. 1980). Although the mode of action of CGA-43089 has not been determined, it has been shown to stunt early growth and reduce respiration of sorghum seedlings (Ketchersid et al. 1981). CGA-43089 did not decrease the total uptake of alachlor by seedling grain sorghum exposed to concentrations of 0.6 or 1.2 ppm, if the first sampling did not occur until 2 days after treatment (Winkle et al. 1980).

The objective of this research was to study the effects of CGA-43089 on the response of sorghum seedlings to metolachlor with emphasis on the effects of the protectant on herbicide uptake and on membrane permeability.

Materials and Methods

Metolachlor Content of Sorghum Emerging from Treated Soil

Sorghum was grown at three moisture levels in Ship's clay (very fine, mixed, thermic, Udic Chromusterts) [16% sand, 28% silt and 56% clay; 1.7% organic matter and a field capacity (FC) of

[1] Ketchersid, ML Unpublished data.

37% (w/w)]. To prepare 250-ml-capacity Styrofoam cups for seeding, 100 g of dry soil were placed in each cup and watered to field capacity. Both unprotected seed and seed protected with 1.25 g CGA-43089/kg seed were planted 20 per cup. Seed were covered with a 50-g layer of soil and the soil watered to field capacity. One g of charcoal was spread on top of the soil and a 50-g layer of soil containing 20 ppmw of metolachlor was added from which the coleoptile could absorb the herbicide. Treated soil was left dry or moistened to 85 or 105% FC. The treated soil layer was then covered with 50 g of coarse sand. In duplicate experiments, each treatment was replicated four times for residue analysis and four times for growth measurements taken 8 days after emergence.

Coleoptiles were collected as they emerged from the sand, approximately 60 h after planting. Shoots were cut at the interface between treated and untreated soil, washed in running distilled water, and weighed. Shoot samples were homogenized with 4 ml 80% (v/v) acetone:water using a tissue homogenizer. The homogenate was then shaken with 5 ml benzene and 5 ml water and allowed to partition between aqueous and benzene layers.

The metolachlor and/or CGA-43089 content of the benzene fraction was determined with a Ni^{63} electron-capture, gas-liquid chromatograph with injector, column, and detector temperatures of 250, 190, and 300°C, respectively. The carrier gas was prepurified nitrogen at a flow rate of 50 ml/min. The glass column had an inside diameter of 4 mm, was 1.8 m long, and was packed with 3% OV-1 on 100–120 mesh chromosorb W.

Uptake of Metolachlor and/or CGA-43089 by Excised Sorghum Coleoptiles

Sorghum seed were surface sterilized with 0.5% commercial bleach, planted in sterile vermiculite, and incubated in the dark at 30°C for 4 days. Epicotyl sections, 2 cm in length, consisting of the coleoptile with enclosed leaves and meristem plus some mesocotyl tissue, were cut from the germinated seedlings and immediately transferred to 500 ml of cold, 5 mM KH_2PO_4-KOH buffer (pH 6.5) containing 50 ppm chloramphenicol. Treatment solutions [5 mM KH_2PO_4-KOH buffer (pH 6.5) containing 1% (w/v) sucrose] were prepared. Metolachlor or CGA-43089 was added to the treatment solutions so that the final concentrations were 0 or 20 ppm metolachlor and 0 or 15 ppm CGA-43089. After all of the coleoptile sections had been harvested, 15 sections were randomly placed into 25-ml side-arm vacuum flasks containing 15 ml of treatment solution.

Coleoptiles were incubated on a shaker in a growth chamber having a photosynthetic photon flux density of 185 $\mu E\ m^{-2}\ s^{-1}$ supplied by mixed incandescent and fluorescent lamps. The tops of the flasks were covered with plastic wrap, but the side arms were left open to provide an air supply. Temperatures of 25, 30, or 35°C were maintained in separate experiments. All experiments included two sets of controls, which consisted of flasks containing only the treating solution or flasks containing the treating solution plus coleoptiles that had been killed.

Samples (0.5 ml) of the treatment solutions were removed 0, 1, 2, 4, 8, 16, 24, 32, and 48 h after the coleoptile sections had been added. The sample was mixed with 0.5 ml acetone and extracted with 10 ml benzene, and the metolachlor and/or CGA-43089 concentration was determined by gas chromatographic analysis. After each sample was removed, 0.5 ml of treatment solution was added to the flasks to replace the volume removed. Uptake was determined by calculating the difference in concentration between controls and samples containing living coleoptiles. After 48 h, coleoptiles were washed, extracted, and assayed for metolachlor and CGA-43089 as described previously. Numerous experiments were conducted following this protocol. Data reported represent repeated studies with five replications per treatment.

^{3}H-leucine Uptake and Incorporation

Metolachlor has been reported to affect membrane permeability (Truelove et al. 1979). Uptake of ^{3}H-leucine by sorghum coleoptiles was studied as an indicator of changes in cell permeability. Flasks were prepared as in the previous study, but a 3-h pulse treatment with 0.5 μCi ^{3}H-leucine (1 μCi/μg) was given to each flask after either 0 or 24 h. Metolachlor concentration in the treatment solution

was either 0 or 20 ppm and the CGA-43089 concentration was either 0 or 15 ppm. The chemicals were used alone or in combination. After the pulse-labeling period, the solution was sampled for radioactivity by scintillation spectrometry. Effects of the treatments on ^{3}H-leucine uptake and incorporation into protein by the coleoptile sections were determined essentially as described by Gruenhagen and Moreland (1977). Incorporation was expressed on a specific activity basis (amount of radioactivity per unit protein). Protein content was determined as described by Lowry et al. (1951). The experiment was repeated and each treatment had four replications.

Uptake of Metolachlor and/or CGA-43089 and ^{14}C-carbohydrate Leakage from Roots

Sorghum seedlings were grown axenically in an autoclavable apparatus consisting of two 18-mm inside diameter by 15-cm-long test tubes joined by a #2 rubber stopper through which a 1-cm inside diameter by 5-cm-long glass tube had been inserted. A layer of cheesecloth was stretched over the basal end of the glass tube and stopper during insertion into the test tube filled with nutrient solution (Hoagland and Arnon 1950). The glass tubing projecting from the rubber stopper was wrapped in cotton to vertically support and fill the open end of the other inverted test tube.

Seed were germinated on nutrient–agar plates following surface sterilization in equal volumes of sodium hypochlorite and citrate buffer (Abdul-Baki 1979). After the apparatus was autoclaved, sterile seedlings were aseptically transferred into the glass tube and the primary root was inserted through the cheesecloth into the nutrient solution. After coleoptile emergence from the glass tube in darkness, the inverted test tube was removed and sterile cotton was inserted around the base of the coleoptile.

The sorghum seedlings were placed in a growth chamber with a 28/25°C, day/night temperature under metal-halide lamps (600 μE m^{-2} s^{-1}). Aluminum sleeves around the test tube excluded light from the nutrient medium. Photosynthate was pulse-labeled simultaneously for all seedlings 5 days after transplanting (three-leaf stage) via photosynthetic assimilation of $^{14}CO_2$ in a closed, illuminated system containing 175–200 μCi of $^{14}CO_2$. Sterile metolachlor and/or CGA-43089 solution were added to the nutrient solution immediately following pulse-labeling. The five treatments imposed on the pulse-labeled seedlings were 20 ppm metolachlor, 20 ppm CGA-43089, 20 ppm and 10 ppm mixtures of metolachlor and CGA-43089, and a control. Seven seedlings comprised each treatment. Seedlings were maintained under metal-halide lamps in a growth chamber (1000 μE m^{-2} s^{-1}, 35/25°C day/night).

Seedlings were removed from the nutrient medium 48 h after pulse-labeling and separated into the shoot and root prior to drying at 70°C. One milliliter samples from the nutrient medium were acidified and placed under vacuum for 30 min to remove $^{14}CO_2$. The acidified samples were assayed by scintillation spectrometry. One-half-milliliter samples were also taken and plated on nutrient agar to determine whether the rooting medium had remained sterile.

Radioactivity in shoots and roots was determined by combustion in oxygen at 680°C and trapping the combustion products in 5 ml of a phenethylamine solution (phenethylamine:methanol:toluene, 1:2:1/v:v:v). This solution was then mixed with 10 ml of scintillation fluid and assayed by scintillation spectrometry. The ^{14}C-labeled organic compounds present in the nutrient medium of each seedling were expressed as a percent of the total radioactivity recovered from the shoot, root, and rooting medium.

The amount of metolachlor and/or CGA-43089 remaining in the rooting solution after seedling harvest was determined by electron-capture gas chromatography.

Statistical Analyses

For all studies, combined results from duplicate experiments were analyzed using analysis of variance followed by Duncan's Multiple Range Test on data presented in tabular form or Tukey's *W* procedure to determine LSD values for figures.

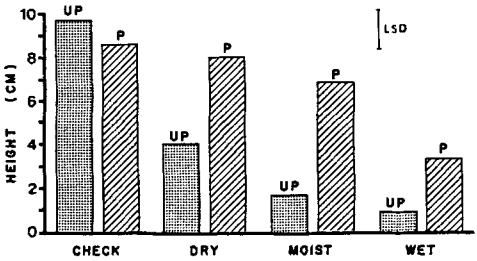

Fig. 1. Height of 8-day-old sorghum after emergence through 20 ppmw metolachlor. UP = unprotected and P = protected by CGA-43089 (1.25 g/kg). Surface soil moisture levels are dry, moist (85% FC) and wet (105% FC). Check height is the average for all moisture levels with no metolachlor treatment. LSD was determined using Tukey's *W* procedure.

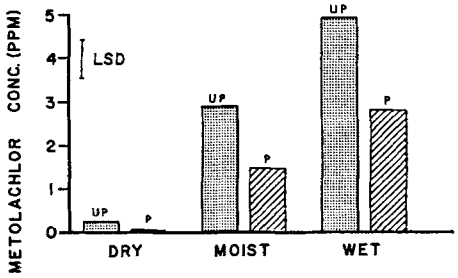

Fig. 2. Metolachlor in sorghum coleoptiles emerging through 20 ppmw metolachlor 60 h after planting. UP = unprotected and P = protected by CGA-43089 (1.25 g/kg). Surface soil moisture levels are dry, moist (85% FC) and wet (105% FC). LSD was determined using Tukey's *W* procedure.

Results and Discussion

Metolachlor Content of Sorghum Emerging from Treated Soil

In all soils treated with metolachlor, plants from seed treated with CGA-43089 grew better than plants from unprotected seed (Fig. 1). Sorghum grown from seed treated with CGA-43089 was significantly stunted by metolachlor when soil moisture was continuously above field capacity. The concentration of metolachlor used in this research (20 ppm) in combination with the high moisture conditions would be rare in a field situation but were included as a model system to make the seedlings more responsive to treatments and the herbicide more available during emergence. As expected, residues of metolachlor increased with increased soil moisture in both protected and unprotected seedlings but were highest in coleoptiles of unprotected sorghum (Fig. 2); thus CGA-43089 either reduced uptake or facilitated degradation of the metolachlor. Resistant plants have been reported to degrade other chloroacetamide herbicides rapidly (Armstrong et al. 1973, Hamill and Penner 1973, Hamm 1974, Jaworski 1969, 1975). At the time of analysis, there was no detectable CGA-43089 in any of the coleoptiles.

Additional samples taken after the coleoptilar node had emerged contained

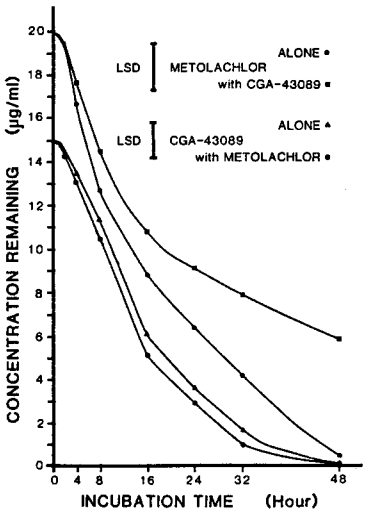

Fig. 3. Uptake of metolachlor and CGA-43089 from solution by excised sorghum coleoptiles at 30°C. LSD was determined using Tukey's *W* procedure.

40% or less of the herbicide detected at the first sampling on a µg/shoot basis, and severely damaged sorghum sampled two weeks after planting had only a trace of metolachlor remaining (data not shown). Clearly, grain sorghum metabolized and degraded metolachlor with or without the CGA-43089 treatment.

Uptake of Metolachlor and/or CGA-43089 by Excised Sorghum Shoots

Experiments were designed to quantitate uptake of metolachlor and CGA-43089 by excised sorghum shoots by measuring disappearance of the metolachlor and/or CGA-43089 from solution. In preliminary tests, conducted with aqueous solutions, CGA-43089 was found to inhibit growth more than metolachlor at the same concentration. Consequently, 15 µg of CGA-43089/ml and/or 20 µg of metolachlor/ml were used in later studies. Concentrations of CGA-43089 above 15 µg/ml were too toxic and caused plant death before the end of the 48-h test period, while lower concentrations were metabolized too rapidly to observe any effect of CGA-43089 on uptake of metolachlor. The 20 µg of metolachlor per ml of solution closely approximated the 20 ppm soil treatment. The uptake of CGA-43089 by excised sorghum shoots at 30°C was not affected significantly by the presence of metolachlor (Fig. 3). However, at the same temperature, metolachlor was absorbed more slowly in the presence than in the absence of CGA-43089 (Fig. 3). The difference was significant by 24 h and increased thereafter.

Similar results were found at 25°C and 35°C, except that uptake of metolachlor was slower at 25°C. This could be due to slower partitioning of the lipid soluble herbicide into cellular membranes (Morrod 1976). The change in solution concentration must be due to uptake by the coleoptiles, because the concentrations of metolachlor and/or CGA-43089 in solution did not change

Table 1. Comparison of ^{3}H-leucine uptake and incorporation into protein by excised sorghum coleoptile sections after 0 and 24 h treatment with metolachlor and CGA-43089 and combinations.[a]

Treatment[b] CGA	MET	^{3}H-leucine absorbed	^{3}H-leucine incorporated	$\frac{\text{Incorporated}}{\text{absorbed}} \times 100$
ppm	ppm	dpm/mg tissue protein		%
		Leucine supplied at 0 h		
0	0	1481 a	915 a	62 a
15	0	1491 a	882 a	59 a
0	20	1156 b	680 b	59 a
15	20	1081 b	573 b	53 b
		Leucine supplied at 24 h		
0	0	1957 c	1342 c	69 b
15	0	2009 c	1816 b	90 a
0	20	2851 a	2074 a	73 b
15	20	2314 b	1646 b	71 b

[a] Data within columns for each time followed by different letters are significantly different at the 5% level as determined by Duncan's Multiple Range Test.
[b] CGA = CGA-43089 and MET = metolachlor.

during incubation in the presence of dead coleoptiles but decreased rapidly with living tissue. Metolachlor was detected in only trace amounts in coleoptile sections analyzed after 48 h of incubation. Additional coleoptile sections were analyzed after 40 h of incubation at 30°C. Metolachlor content was 1.4% of the total supplied when exposed to metolachlor alone compared with 0.2% when exposed to metolachlor in combination with CGA-43089. The amount of metolachlor remaining in solution at 40 h was 14% without CGA-43089 and 38% with CGA-43089.

^{3}H-leucine Uptake and Incorporation

Cell permeability can be studied using a variety of organic molecules. Leucine uptake was presumed to be passive in this study because only 20% of the 0.5 μg added was absorbed by the plant tissue. At zero time or 24 h after treatment with CGA-43089 and/or metolachlor, shoots were pulse-labeled for 3 h with ^{3}H-leucine (Table 1). If the pulse-labeling occurred simultaneously with exposure to metolachlor, the herbicide reduced the amount of ^{3}H-leucine absorbed and incorporated into protein, even in the presence of CGA-43089. Pillai et al. (1977) also reported that leucine uptake by root tips was decreased by 10^{-4} and 10^{-5} M metolachlor.

If pulse-labeling occurred 24 h after exposure of the coleoptiles to metolachlor or CGA-43089, CGA-43089 alone had no effect on leucine uptake. However, metolachlor alone increased leucine absorption significantly, and when CGA-43089 was present with metolachlor, absorption was intermediate between the check and metolachlor treatment values. Also, at this time, the ratio of leucine incorporated into protein to leucine absorbed was near 70% for all treatments, except for CGA-43089 supplied alone, where incorporation was 90%. As in the metolachlor uptake study, there was more metolachlor remain-

Table 2. Absorption of CGA-43089 and metolachlor and their effects on sorghum growth and loss of fixed carbon in root exudates 48 h after pulse-labeling with $^{14}CO_2$.[a]

Treatment[b]		CGA-43089	Metolachlor	Weight		^{14}C in
CGA	MET	absorbed	absorbed	Shoot	Root	Exudate[c]
ppm	ppm	%	%	mg	mg	%
0	0	—	—	54 a	18 a	1.0 d
20	0	81 b	—	55 a	11 bc	2.9 b
0	20	—	59 c	52 a	13 b	1.4 d
20	20	75 a	41 a	51 a	9 c	4.3 a
10	10	79 ab	49 b	52 a	10 c	2.2 c

[a] Data within columns followed by different letters are significantly different at the 5% level as determined by Duncan's Multiple Range Test.
[b] CGA = CGA-43089 and MET = metolachlor.
[c] Total $^{14}CO_2$ fixed average 2.9 μCi per plant and an average of 20% of the total $^{14}CO_2$ fixed was translocated to the root. There were no significant differences due to CGA-43089 or metolachlor treatments. ^{14}C in the exudate is expressed as the % of the total μCi detected per plant.

ing in the solution at the end of the study when CGA-43089 was present than when CGA-43089 was not added.

Uptake of Metolachlor and/or CGA-43089 and ^{14}C-carbohydrate Leakage from Roots

The effect of chloroacetamide herbicides on cell permeability has been determined by monitoring both leucine uptake by root tips and mineral nutrient uptake or efflux after preloading intact root systems (Pillai et al. 1979, 1977). Excised root tips are generally more sensitive to the herbicide than other plant parts when treated in solution (Pillai et al. 1979).

All sorghum seedlings assimilated nearly equal amounts of $^{14}CO_2$ (2.9 ± 0.2 μCi/plant). During the 48-h period following pulse-labeling, 20% of the ^{14}C-labeled photosynthate was recovered from the roots plus nutrient solution of all five treatments (data not shown). Although leakage of ^{14}C-labeled photosynthate was expected to be greatest for the roots treated with metolachlor, the CGA-43089 and CGA-43089 plus metolachlor treatments resulted in the greatest percent release of ^{14}C-labeled compounds from the roots (Table 2). The highest level of leakage was associated with the highest degree of root stunting. Balke (1980) found that alachlor did not directly alter membrane permeability but reduced ATP content in the roots, which secondarily affected root permeability. Sucrose is the principal form of carbohydrate transported in the phloem to the roots. A number of mechanisms for unloading sucrose from the phloem have been presented (Keener et al. 1979). These include both active (Dick and apRees 1975) and concentration-dependent (Goeschl et al. 1976) unloading processes, which may vary within the root system depending on the age and the stage of development of the root tissue involved. Since near equal amounts of pulse-labeled carbohydrate were moved to all roots, there should potentially be similar amounts of phloem unloading. When growth processes in the sink cells

are inhibited, some of the sugar can diffuse into the root medium. The low level of leakage from control roots could be due to rapid use of the carbohydrate in the actively growing sink cells. Apparently, loss of carbohydrate is controlled by a different mechanism from the uptake of metolachlor, and a change in cellular permeability per se is not the major controlling factor. The competitive effect on absorption between CGA-43089 and metolachlor by sorghum roots was significant (Table 2). As in preceding experiments, uptake of metolachlor by sorghum roots was reduced when CGA-43089 was present. In addition, uptake of CGA-43089 was reduced when metolachlor was present.

Data indicate that metolachlor and CGA-43089 are readily absorbed and metabolized by grain sorghum. CGA-43089 decreased the amount of metolachlor absorbed by sorghum coleoptiles and roots in 48 h (Fig. 3 and Table 2). This decrease in rate of uptake corresponded to a decrease in phytotoxic symptoms and apparently was sufficient to allow the grain sorghum to deactivate the herbicide, thus preventing a toxic dose from accumulating at the site or sites of action.

The mechanism affecting uptake of metolachlor is still unknown, but it does not appear to be a simple change in cell permeability. The increased incorporation of leucine into protein in sorghum coleoptiles treated with CGA-43089 could indicate increased enzyme production used in metabolic or repair processes. The combination of slower uptake and more rapid degradation of the metolachlor absorbed could protect seedling grain sorghum during the 2- to 3-day critical time period in which the coleoptile is in contact with the herbicide.

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