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A CHEMICAL BASIS FOR DIFFERENTIAL ALLELOPATHIC POTENTIAL OF SORGHUM HYBRIDS ON WHEAT[1]

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Abstract—The basis for differential allelopathic potentials among sorghum (*Sorghum bicolor* L. Moench) hybrids was investigated by conducting quantitative and qualitative studies of their phenolic contents. Total phenolic content in sorghum plant parts varied within hybrids, among hybrids, and between growing seasons. Inhibition of wheat (*Triticum aestivum* L.) radicle growth was positively associated ($r = 0.66$) with concentrations of total phenolics contained in plant parts. Extracts from culms contributed the highest proportion of toxicity from sorghum plants, inhibiting radicle growth up to 74.7%. Concentrations of five phenolic acids, *p*-hydroxybenzoic (POH), vanillic (VAN), syringic (SYR), *p*-coumaric (PCO), and ferulic (FER), differed in all plant parts of the three sorghum hybrids. Concentrations of POH, VAN, and SYR were consistently higher than PCO and FER. PCO and FER were absent from some plant parts, with FER being the most frequently missing. Inhibition of wheat radicle growth was found to be positively associated with the concentration of each phenolic acid. Vanillic acid was most highly associated ($r = 0.44$) with inhibition. Thus, above-ground sorghum tissues contained phenolic acids that contributed to allelopathic potential. Additionally, sorghum roots exuded POH, VAN, and SYR that may enhance the overall allelopathic potential of sorghum during growth and after harvest when residues remain on the soil surface or are incorporated prior to planting a subsequent crop.

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INTRODUCTION

Plants produce a large variety of secondary products containing hydroxylated aromatic rings. These substances are classified as phenolic compounds, most of which are synthesized from phenylalanine, a product of the shikimic acid pathway (Taiz and Zeiger, 1991). Sorghum (*Sorghum bicolor* L. Moench) contains phenolic compounds at all stages of growth, with higher levels in leaves and glumes compared to culms and caryopses (Waniska et al., 1988). Within the same plant part, bird-resistant hybrids contain more soluble phenolics than non-bird-resistant hybrids (Reed and Tedla, 1987). In four sorghum genotypes, phenolics such as coumaric and ferulic acids were found to be more concentrated in culms than in leaf blades or leaf sheaths (Cherney et al., 1991).

Plant polyphenols known as tannins are important in the defense mechanisms that plants develop to resist predators. This is largely due to the ability of tannins to bind proteins, which is characterized in the mouth of herbivores as a feeling of constriction, dryness, and roughness (Haslam, 1988). Levels of phenolic acids in healthy plants of sorghum differ considerably among cultivars and always decrease as the plants mature. However, attack by insects and pathogenic fungi increases the phenolic content of plants by varying degrees depending on cultivar and stage of growth (Woodhead, 1981). Sorghum contains a mixture of hydrolases that can transform "inactive" phenolic esters and glycosides into "active" phenolic acids at concentrations high enough to significantly reduce feeding by *Locusta migratoria* (Woodhead and Cooper-Driver, 1979).

In addition to phenolic acids in aerial plant parts, roots of allelopathic crops actively exude phenolics (Abdul-Rahman and Habib, 1989; Alsaadawi et al., 1986; Einhellig and Souza, 1992; Tang and Young, 1982). Caffeic, chlorogenic, isochlorogenic, *p*-coumaric, *p*-OH-benzoic, and ferulic acids were detected in alfalfa root exudates and vegetative residues (Abdul-Rahman and Habib, 1989). Bioassays of trapped root exudates of bigalta limpograss (*Hemarthria altissima*), an allelopathic tropical forage, showed that the inhibitors were mainly phenolic compounds (Tang and Young, 1982). Root exudates of sorghum consist primarily of sorgoleone, a hydroquinone that is quickly oxidized to a benzoquinone, which at extremely low concentrations (0.01–0.125 mM) can potentially inhibit weed growth, suggesting a strong contribution to sorghum allelopathy (Einhellig and Souza, 1992). Water extracts from decaying residues of four sorghum cultivars revealed that all cultivars significantly reduced redroot pigweed (*Amaranthus retroflexus* L.) growth, with greatest inhibition achieved by cultivars having toxic root exudates (Alsaadawi et al., 1986).

The realistic concentrations of phenolics necessary for inhibitory action under field conditions are estimated to be 3.3 mM for ferulic, *p*-coumaric, and vanillic acids. At this concentration, a synergistic effect on germination of sorghum has been reported (Rasmussen and Einhellig, 1979). Phenolic compounds such as *p*-hydroxybenzoic, vanillic, *p*-coumaric, and ferulic acids were found in the soil solution at 0.003–0.39 mM. These compounds are produced by decomposing straw or degradation of humic acids (Whitehead, 1964). Analysis of sorghum residues revealed that *p*-coumaric acid was present in the highest concentration followed by ferulic, syringic, vanillic, and *p*-hydroxybenzoic acids at variable concentrations. Under ideal conditions for decomposition, *p*-coumaric acid could be released in sufficient quantities in localized soil microsites to affect plant growth (Guenzi and McCalla, 1966).

At a concentration of 1.0 mM, *p*-coumaric, ferulic, and vanillic acids significantly reduced dry matter production, leaf expansion, leaf production, height, and net assimilation rate of soybean [*Glycine max* (L) Merr.]. Furthermore, net photosynthetic rate and stomatal conductance were severely reduced, and marked losses of chlorophyll were registered (Patterson, 1989). Leaf diffusive resistance of sorghum seedlings increased and water potential decreased following treatments with ferulic acid, *p*-coumaric acid, and extracts from several allelopathic weeds. Water potential changes resulted from reduction of both osmotic potential and turgor pressure (Einhellig et al., 1985). Treatments with 0.25 mM ferulic acid reduced phosphorus content of roots and shoots of 2-week-old sorghum seedlings. Roots of treated plants also had lower concentrations of potassium and magnesium. In some cases, shoot potassium and iron were lower but magnesium and calcium were higher (Kobsa and Einhellig, 1987). Roots of alfalfa inhibited by water extracts of alfalfa shoots had 46% fewer and 54% shorter root hairs compared to the control, but an anatomical study showed no clogging of root xylem vessels of treated plants (Hedge and Miller, 1992).

The objective of this study was to investigate the chemical basis of the differential allelopathic potential among three sorghum hybrids (Asgrow Topaz, Taylor Evans Y-101G, and Warner W-744DR) reported previously (Ben-Hammouda, 1994). Total phenolic content and concentrations of phenolic acids that have been previously implicated in allelopathic activity of sorghum (Guenzi and McCalla, 1966) were determined.

METHODS AND MATERIALS

Collection and Processing of Sorghum Plant Parts

Randomly selected sorghum plants grown at the University of Missouri Agronomy Research Center in 1991 and 1992 were collected intact at harvest

maturity. Sorghum plants collected both years were free of disease and insect infestations. Roots were washed with tap water to remove the soil, and whole plants were stored frozen until analysis. Sorghum hybrids studied included Asgrow Topaz, Taylor Evans Y-101G, and Warner W-744DR and represented the range of suspected allelopathic potential identified in previous field and laboratory studies (Ben-Hammouda, 1994). Briefly, field studies involved planting wheat after sorghum harvest and using wheat grain yield as a measure of response to potential allelopathy. Subsequent laboratory studies relied on the response of wheat seedling radicle growth to extracts of sorghum plant components in agar bioassays.

Extraction

Sorghum plants were washed gently with distilled water, blotted, and separated into heads, leaves, culms, and roots. Heads were hand-threshed and separated into seeds and glumes. Leaves, culms, and roots were chopped into 1-cm-long pieces. All sorghum plant parts were dried at 50°C for 24 hr. A 2.5-g portion of each plant part was placed in 50 ml distilled water and agitated on a rotary shaker for 24 hr at 200 rpm. Extracts were filtered (Whatman No. 2 filter paper) under vacuum, centrifuged at 12,500 rpm for 20 min at 8°C, and filter-sterilized (0.2-μm membrane) under vacuum prior to total phenol analysis.

Soil samples from a controlled study in which one plant of each sorghum hybrid was grown to full maturity in a separate 20-liter container were extracted for total phenol analysis. Soil extraction followed the procedure described by Read and Jensen (1989). Briefly, a sample of 250 g dry soil was extracted in 250 ml of distilled water by shaking for 24 hr at 200 rpm. Soil suspensions were filtered (Whatman No. 2 filter paper) under vacuum prior to total phenol analysis.

Determination of Total Phenolics

The Folin-Denis method was used for total phenol analysis (A.O.A.C., 1990) except that ferulic acid was used as the standard, since it is an allelopathic agent (Haslam, 1988) and has been previously isolated from sorghum residues (Guenzi and McCalla, 1966).

Folin-Denis Reagent. A mixture of 10 g Na_2WO_4, 2 g phosphomolybdic acid, and 5 ml H_3PO_4 in 75 ml distilled water was refluxed for 2 hr, cooled, and diluted to 100 ml with distilled water.

Sodium Carbonate-Saturated Solution. Anhydrous Na_2CO_3 (4 g) was added to 10 ml distilled water and dissolved for 1 hr at 70–80°C, cooled overnight, and filtered through glass wool.

Ferulic Acid Standard Solution. Ferulic acid (10 g) was dissolved in 100 ml distilled water. Aliquots of 0, 0.2, 0.4, 0.6, 0.8, and 1 ml of the standard

ferulic acid solution were dispensed into tubes containing 0.5 ml Folin-Denis reagent and 1 ml saturated Na_2CO_3 solution. The standards were diluted to 10 ml with distilled water and quickly shaken. Absorbance was determined after 30 min at 750 nm (Blum et al., 1991) on a spectrophotometer (Pharmacia Ultrospec III).

Determination of Total Phenolics. Each sorghum or soil water extract (1.0 ml) was prepared by adding Folin-Denis and Na_2CO_3 reagents. Absorbance was determined, and the total phenolic content was obtained using the standard curve. Units of total phenolics were expressed in milligrams of ferulic acid equivalents per milliliter extract. For soil extracts, total phenolics in ferulic acid equivalents per milliliter of extract were expressed on a per gram basis since the ratio of extraction was 1 : 1 (w/w). For sorghum extracts, ferulic acid equivalents were multiplied by 20 based on an extraction ratio of 1 : 20 (w/w).

Determination of Phenolic Acids by HPLC Analysis

Water extracts of sorghum plants and soils used for estimation of total phenolics were analyzed for five individual phenolic acids. The pH of each water extract sample was lowered to 2.6–3.0 with dilute H_3PO_4. An aliquot of 5 ml from each sample was partitioned with an equal volume of diethyl ether two times by shaking the mixture for approximately 1 min and allowing it to stand until diethyl ether partitioning occurred. The pooled partitioned volumes of diethyl ether from each sample were dispensed into a 50-ml Erlenmeyer flask and evaporated to near dryness in a suction chamber. Residues in the flask were dissolved in 2 ml methanol and filtered through a 0.2-μm sterile membrane.

Methanol extracts were analyzed for phenolic acids using a Beckman model 338 HPLC system. The system consisted of two model 110B pumps operated at a 1 ml/min flow rate, a model 507 autosampler with a 100-μl sample loop, and a model 166 variable-wavelength UV detector set at 280 nm. A Beckman octadecyl (C18) reversed-phase column (Ultrasphere ODS, 5 μm) with dimensions at 250 $\times$ 4.6 mm (ID) was used. The mobile phase was methanol–water (30:70, v/v).

Five different phenolic acids (POH, VAN, SYR, PCO, and FER) were identified in the samples by comparing their relative retention times with that of the standard chromatogram. The identified peaks were then quantified by preparing standard curves using peak areas for each phenolic acid.

Bioassay

Potential allelopathic activity of water extracts of sorghum plant parts was assessed using a wheat seedling bioassay (Ben-Hammouda, 1994). Water extracts (2.5 g plant tissue per 50 ml water shaken for 24 hr) were incorporated in 1.0% agar and dispensed into test tubes. Pregerminated Cardinal wheat seeds were

placed on the solidified extract-agar (one pregerminated seed per tube) and incubated in the dark at 28°C for 48 hr. Radicle lengths were measured and compared to controls containing no plant extracts. Each determination consisted of measurements from 10 tubes per treatment, including controls, replicated four times.

Statistical Analyses

Root length data from bioassays were subjected to analysis of variance followed by the LSD test to determine significant differences among mean values at the 0.05 level of probability. Regression and correlation analyses of wheat radicle growth inhibition were conducted with total phenolics, individual phenolic acid (POH, VAN, SYR, PCO, FER) concentrations estimated from sorghum plant parts, and total phenolic content as quantitative variables and the sources of phenolics (hybrid, growing season, plant parts, and plant parts within hybrid) as qualitative variables.

RESULTS AND DISCUSSION

The three sorghum hybrids were presumed to be allelopathic on wheat based on wheat grain yield depression in field tests over two years and on wheat seedling radicle reduction in laboratory bioassays of sorghum extracts. Relative to water controls, extracts of one or more plant parts from each hybrid reduced wheat radicle growth (Table 1). Wheat radicle inhibition was positively correlated ($r = 0.66$) with total phenolic content (Table 2) in individual plant parts (Figure 1). When inhibition of wheat radicle growth was regressed on total phenolics as a quantitative variable and the source of phenolics as qualitative variables, significant factors in the best fitting regression were total phenolics and the plant parts glumes and culms. Parameters in this best fitting equation were: $b_0 = -4.3$, $b_1 = 267.0$, $b_2 = -14.8$, and $b_3 = 28.0$ with $Y =$ inhibition (dependent variable), $x_1 =$ total phenolics, $x_2 =$ glumes, and $x_3 =$ culms (independent variables). Phenolics from glumes reduced the inhibition by an average of 14.8 times more than any other source of phenolics. However, phenolics from culms increased the inhibition 42.8 times more than phenolics from glumes and 28 times more than any other source of phenolics.

Ranges of total phenolics in seeds, glumes, leaves, and roots were small (Table 2) but inhibition varied significantly (Table 1). This suggested that inhibition may be associated with qualitative rather than quantitative components of phenolics.

Three phenolic acids (POH, VAN, SYR) were found in different amounts in all plant parts of the three sorghum hybrids during both growing seasons (Table 3). Concentrations varied among plant parts within and between sorghum

TABLE 1. INHIBITION OF WHEAT RADICLE GROWTH BY WATER EXTRACTS FROM PLANT PARTS OF THREE SORGHUM HYBRIDS

Sorghum hybrid	Inhibition of wheat radicle growth (% of control)[a]				
	Seeds	Glumes	Leaves	Culms	Roots
1991					
Asgrow Topaz	−0.5[b]	12.1	8.9*	25.2*	50.8
Warner W-744DR	13.4*	10.0	66.6*	32.6*	45.5*
Taylor Evans Y-101G	6.7	20.6*	56.5*	74.4*	63.2*
1992					
Asgrow Topaz	5.7	40.2*	70.0*	74.7*	31.4*
Warner W-744DR	4.4	16.7*	68.5*	73.3*	37.0*
Taylor Evans Y-101G	2.7	36.9*	65.9*	65.2*	41.6*

[a]Values within a column within year followed by asterisk (*) differ significantly from the water control (LSD test, $P < 0.005$).
[b]Negative sign indicates increase over control.

TABLE 2. TOTAL PHENOLIC CONTENT IN SORGHUM PLANT PARTS

Sorghum hybrid	Total phenolics (mg ferulic acid equivalents/g)[a]				
	Seeds	Glumes	Leaves	Culms	Roots
1991					
Asgrow Topaz	0.033	0.120	0.217	0.060	0.166
Warner W-744DR	0.074	0.160	0.208	0.105	0.189
Taylor Evans Y-101G	0.035	0.135	0.214	0.202	0.189
1992					
Asgrow Topaz	0.015	0.160	0.239	0.140	0.215
Warner W-744DR	0.051	0.193	0.246	0.122	0.203
Taylor Evans Y-101G	0.007	0.171	0.232	0.132	0.182

[a]Total phenolics determined by Folin-Denis method (A.O.A.C., 1990) expressed as milligrams ferulic acid equivalents per gram sorghum tissue.

hybrids. Of the five phenolic acids analyzed, only PCO or FER was absent from any plant part, with FER absent in 53% of the cases. In 1991, Taylor Evans Y-101G did not have any detectable FER. Wheat radicle inhibition was found positively associated with each of the five phenolic acids, the highest correlation occurring with VAN (Table 4). While significant individually, asso-

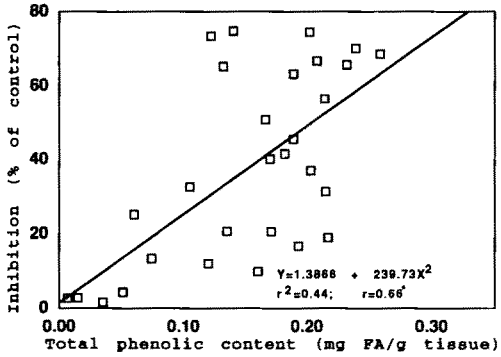

FIG. 1. Relationship of wheat radicle inhibition to total phenolic content in water extracts of plant parts from sorghum hybrids grown in 1991 and 1992. Total phenolic content expressed in ferulic acid equivalents per gram of sorghum tissue.

ciations were small, accounting for less than 20% of the variation in inhibition. Together, the five phenolic acids accounted for 72% of the variability in inhibition of wheat radicle growth due to total phenolics. Plant species are known to contain many phenolic acids in addition to those assayed, and many are phytotoxic (Chou and Patrick, 1976). Total inhibitory effects on sorghum may therefore involve other phenolic compounds and/or allelochemicals of different chemical types. Sampling intensity did not permit detection of statistically significant relationships between total phenolic content or individual phenolic acid levels and inhibition within individual plant parts, hybrids, or years.

Bioassays of water extracts from soils on wheat radicle growth showed that soil with no plants, and soils planted to Warner W-744DR and Asgrow Topaz were relatively equal in allelopathic potential (Ben-Hammouda, 1994). The minimal differences among total phenolic contents in these soils likely account for the low inhibitory activity (Table 5). However, inhibition by soil extracts from Warner W-744DR and Asgrow Topaz were significant ($P \leq 0.05$) compared to control soil, suggesting that allelochemicals other than the detected phenolics were released by sorghum roots. Extracts from Taylor Evans Y-101G soil contained the highest total phenolic content and were significantly higher in allelopathic potential, indicating a relationship between quantity of phenolics released by roots and inhibitory activity, similar to that illustrated for plant extracts (Figure 1). Other phytotoxins exuded from roots have been reported, including sorgoleone from sorghum (Einhellig and Souza, 1992) and phenolic acids from alfalfa roots, a known allelopathic crop (Abdul-Rahman and Habib, 1989; Read and Jensen, 1989). Identification of individual phenolic acids in sorghum root exudates has not been previously reported.

Soil extracts analyzed by HPLC contained only POH, VAN, or SYR (Table

TABLE 3. PHENOLIC ACID CONTENT IN SORGHUM PLANT PARTS

		Phenolic acid content (mg/kg tissue)									
		Seeds		Glumes		Leaves		Culms		Roots	
Sorghum hybrid	Phenolic acid	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
Asgrow Topaz	POH	4.1	4.3	22.5	1.7	88.8	613.2	26.8	104.2	39.8	70.5
	VAN	1.9	0.6	7.4	12.9	22.2	99.8	14.4	9.2	13.7	15.0
	SYR	0.4	1.0	1.0	4.3	1.8	6.8	1.7	2.3	3.8	4.7
	PCO	2.0	0.0	3.7	0.0	6.1	3.9	4.3	0.5	0.0	2.8
	FER	2.0	0.0	1.4	0.0	0.1	3.9	0.0	0.5	1.6	0.0
Warner W-744DR	POH	2.8	5.0	4.6	38.1	20.6	13.7	3.2	1.4	24.8	2.8
	VAN	2.5	2.8	3.7	6.6	60.5	3.4	3.8	10.0	13.4	0.4
	SYR	3.7	0.5	3.0	1.9	83.4	2.6	1.6	1.0	4.3	51.3
	PCO	0.0	0.1	0.5	0.0	0.4	25.6	0.6	0.0	0.0	0.0
	FER	0.0	0.0	0.0	0.7	3.4	0.9	0.0	0.0	0.0	0.8
Taylor Evans	POH	0.4	9.4	0.4	54.5	2.7	278.1	0.3	93.1	0.7	172.1
	VAN	1.9	1.7	0.4	15.7	2.7	49.9	0.3	1.4	0.7	25.7
	SYR	11.2	0.4	10.7	2.3	86.0	22.6	9.4	1.6	23.6	0.4
	PCO	1.5	0.5	2.2	6.0	7.5	13.0	7.5	0.0	1.0	4.5
	FER	0.0	0.0	0.0	0.5	0.0	1.6	0.0	1.4	0.0	2.0

TABLE 4. SIMPLE CORRELATION COEFFICIENTS BETWEEN WHEAT RADICLE GROWTH INHIBITION (% OF CONTROL) AND INDIVIDUAL PHENOLIC ACIDS FROM PLANT PARTS OF THREE SORGHUM HYBRIDS OVER TWO YEARS[a]

Phenolic acid	Correlation coefficient[b]
POH	0.35
VAN	0.44*
SYR	0.32
PCO	0.41*
FER	0.33

[a] $df = 29$.
[b] Values followed by (*) are significant at $P < 0.05$; remaining values are significant at $P < 0.10$.

TABLE 5. TOTAL PHENOLIC CONTENT OF SOILS PLANTED TO SORGHUM

Sorghum hybrid	Total phenolics (μg ferulic acid equiv/g)[a]	Seedling inhibition (% of control)[b]
No plants	0.07	3.7
Asgrow Topaz	0.09	6.9*
Warner W-744DR	0.08	5.9*
Taylor Evans Y-101G	0.20	27.8*

[a] Total phenolics expressed in ferulic acid equivalents per gram of soil.
[b] Inhibition of wheat seedling radicle growth from bioassay (Ben-Hammouda, 1994). Values followed by (*) differ significantly from the water control (LSD test, $P < 0.05$).

6). The highest phenolic acid content, which was predominantly SYR, was found for Taylor Evans Y-101G soil extract. Taylor Evans Y-101G soil extract also exhibited the highest inhibition toward wheat seedling growth (Table 5), suggesting that SYR may be a major source of allelopathic activity in this sorghum hybrid. SYR was detected in the other soil extracts at about 47% lower concentrations and only slightly inhibited wheat seedling growth. Antagonism of activity of SYR by other phenolic compounds in these extracts may partially account for the lower inhibitory activity (Patterson, 1989).

Phenolic acids detected in control soil extracts may have originated from microbial synthesis (Waniska et al., 1988) or humic acid degradation (Kobsa and Einhellig, 1987). Phenolic acids released from above-ground plant parts were prevented from reaching soil, thus phenolic acids detected were of root or soil origin. Higher amounts of POH and SYR in Asgrow Topaz and Taylor Evans Y-101G soil extracts, respectively, compared to control soil indicated root exudation. High concentrations of POH and SYR in vegetative tissues of

TABLE 6. PHENOLIC ACID CONTENT OF SOILS PLANTED TO SORGHUM

Sorghum hybrid	Phenolic acid[a]	Concentration (mg/kg soil)
No plants	POH	0.007
	VAN	0.000
	SYR	0.020
Asgrow Topaz	POH	0.032
	VAN	0.015
	SYR	0.020
Warner W-744DR	POH	0.000
	VAN	0.000
	SYR	0.020
Taylor Evans Y-101G	POH	0.000
	VAN	0.000
	SYR	0.038

[a]FER and PCO were not detected in any soil extract.

Asgrow Topaz and Taylor Evans Y-101G suggest that excess production of these phenolic acids may be released by roots into soil. VAN was not detected in control extracts, consequently VAN detected in Asgrow Topaz soil extracts suggests that root exudates are also a primary source of VAN in soil.

In conclusions, the allelopathic potential of sorghum plant parts was positively correlated with total phenolic content. Within plant parts, the relationship was more qualitative than quantitative. Three phenolic acids (POH, VAN, SYR) were found in all sorghum plant parts, while PCO and FER were detected inconsistently. Individual phenolic acids were significantly associated with inhibition of wheat radicle growth. The variability of allelopathic potential of plant parts within a sorghum hybrid was difficult to attribute to individual phenolic acids or a combination of phenolic acids. Allelopathic potential may be a result of either antagonism or synergy, depending on the presence of a specific phenolic acid, its proportion relative to other phenolic acids, or a combined action of several other allelochemicals present in plant tissues and exudates.

Sorghum roots exuded phenolics including POH, VAN, and SYR. Under favorable field conditions, exudates may contribute to the overall allelopathic potential of sorghum during growth and after harvest when vegetative and root residues remain in the field prior to planting a subsequent crop.

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