

Potentials and prospects of sorghum allelopathy in agroecosystems

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ABSTRACT

The promising allelopathic potential of sorghum [*Sorghum bicolor* L. (Moench)] opens a fruitful area of research to exploit this phenomenon in weed control and regulation of nutrients cycle. The data suggests that sorghum allelopathy can be exploited in different cropping practices [cover crop, smother crop, companion crop, mixing crop and smother crop to control weeds and inhibition of nitrification] and application of its water extracts in fields controls the weeds and enhances the crops productivity. The herbicidal and allelopathic properties of sorgoleone, a compound isolated from root exudates of sorghum and other allelochemicals in sorghum deserve further work to identify the enzymes responsible for the biosynthesis of these compounds and the genes encoding them. Besides there is need to use genetic engineering to manipulate the identified genes in sorghum or in other crops to enhance their ability to suppress the weeds. This review addresses the research on the role of allelopathic potential in different cropping systems and the approaches developed in weeds management.

Key words: Allelopathy, crop mixture, crop rotation, cropping systems, intercropping, mulch, nitrification inhibition, sorghum, weed control.

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1. ALLELOPATHY IN AGROECOSYSTEMS

In agroecosystems, all biotic and abiotic factors play an important role (75) and several agricultural practices [crops domestication, monoculture of high yielding crops, use of new technology and high inputs of agrochemicals] have been adopted to increase the food production demand. These practices have led to the dominance of monocropping systems in modern agrosystems, which reduces the plants diversity and have made the crops susceptible to pests (weeds, insects and pathogens). The pests control heavily depends on use of pesticides, which have led to (i) development of resistance in pests, (ii) pollution of the environment and (iii) health hazards. Thus such practices are not sustainable and must be changed. Therefore, use of crop rotation, companion planting, and polycropping may lead to sustainability (3). Allelopathy provides numerous chemical interactions between crop-crop, crop-weed, and tree-crop that may benefit the agroecosystems. Soil microbes, weeds and crop influence each other through chemical signals. A better understanding of these interactions under field conditions can be used to develop new sustainable cropping systems with improved crop productivity, genetic diversity, ecosystem stability, nutrient cycling and conservation, weed control and disease management (9,31,47,48).

2. ALLELOPATHIC EFFECTS OF SORGHUM ON CROPS

The early work on the allelopathic effects of sorghum [*Sorghum bicolor* (L.) Moench] on crops was conducted by Guenzi and McCalla (41). They collected residues of several crops including sorghum from fields in Nebraska. Sorghum stalks were extracted with cold and hot water and one half of each water extract was autoclaved for one hour. The electrical conductivity and osmotic pressure of all extracts were determined and adjusted with KCl and glucose, respectively. The bioactivity of sorghum extract was assayed against growth of wheat seedling. Seed germination of wheat was significantly reduced by cold and hot non-autoclaved extracts by 100 and 72%, respectively. Hot and cold autoclaved water extracts had slight allelopathic effects on germination. Non autoclaved extracts of sorghum inhibited root growth more than autoclaved water extracts. Cold water extracts were more inhibitory to root and shoot of wheat seedlings. Bhowmik and Doll (13) found that sorghum and corn residues stimulated the growth (plant height) of soybean.

Kim *et al.* (49) tested the allelopathic potential of sorghum residues on germination and growth of rice, wheat and corn. They found that germination and lengths of roots and tops were significantly reduced by water extracts of sorghum residues while corn was less sensitive. Chung and Miller (22) studied the allelopathic potential of nine grasses including sorghum on seed germination and growth of alfalfa under laboratory and green house conditions. It was found that seed germination was inhibited by 79.8 % of control by sorghum extracts. Similarly sorghum extracts caused the highest inhibition in total length and dry matter of alfalfa seedlings. Ben-Hammouda *et al.* (12) tested the allelopathic potential of different parts of several sorghum hybrids. All plant parts tested revealed significant differences in their phytotoxicity to wheat seedlings regardless of the

hybrid. Sorghum root and stem appeared to be the most inhibitory components of sorghum plants.

In Pakistan intensive research work has been done in Weed Science Laboratory, University of Agriculture, Faisalabad to investigate the allelopathic potential of *sorghab* (water extract of mature sorghum plant) and sorghum mulches on several crops namely wheat (17,18), maize (1), mung bean (21) cotton (2,19) and mustard (11). These studies indicated that spraying of sorghab on the test crops at different times after sowing and application of sorghum mulch at different rates significantly increased the yield of the test crops over control owing to weeds suppression. The increase of yield was very striking in some crops, for example the yield of cotton and maize sprayed with sorghab increased up to 69 and 44% of control, respectively (1,19). In all cases, the increase in the yield of the test crops was attributed to the weed suppression by sorghab and sorghum mulch and to increase in most of agronomic traits including some of the yield components.

3. ALLELOPATHIC EFFECTS OF SORGHUM ON WEEDS

The occurrence of allelopathic traits in crops has attracted the attention of scientists for their potential use in weed management. During the last four decades, extensive work has been done on this approach and the following methods have been developed for weeds control : (i) use of sorghum extracts to control weeds, (ii) use of sorghum residues as cover crop and mulch, (iii) use of sorghum as smothering crop, (iv) use of allelopathic crops in crop rotation, and (v) use of allelopathic crop in crop mixture and intercropping. In this review, some work related to the role of sorghum allelopathy in these methods has been reviewed.

3.1. SORGHUM EXTRACTS TO CONTROL WEEDS

In our previous work (6) we tested the allelopathic activity of plant water extracts of four sorghum cultivars varied in their allelopathic potential of root exudates against *Amaranthus retroflexus*. The plant extract of all genotypes was inhibitory to *A. retroflexus*. However, root exudates from the genotypes (219 and 260) were more inhibitory than the plant extract from the other genotypes (177 and 264) (Table 1). Similarly decaying residues of genotypes 219 and 260 showed maximum inhibition to germination and seedling growth of *A. retroflexus* (Table 2).

Table 1. Allelopathic potential of aqueous extracts of selected genotypes of *Sorghum bicolor* against *Amaranthus retroflexus* (Source 6)

Sorghum genotypes	Oven dry weight (mg/plant)*			Seed germination (% of Control)
	Root	Shoot	Whole plant	
Control	34.3a	114.0a	148.3a	100
219	4.8c	15.4c	20.2c	71
260	3.8c	13.7c	17.5c	71
177	8.1c	26.3b	34.4b	90
264	6.5b	26.4b	32.9b	86

* Average of at least 20 seedlings, mean within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test.

Table 2. Effects of Allelopathic potential of decaying residues of selected genotypes of *Sorghum bicolor* against *Amaranthus retroflexus* (Source 6)

Sorghum genotypes	Oven dry weight (mg/plant)*			Seed germination (% of Control)
	Root	Shoot	Whole plant	
Control	52.5a	166.1a	218.6a	100
219	12.2c	79.2d	91.4d	40
260	19.5b	103.6c	123.1c	41
177	23.3b	134.6b	157.9b	45
264	20.9b	128.0b	148.9b	47

* Average of at least 20 seedlings, mean within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test.

Cheema *et al.* (20) tested the allelopathic potential of water extract of sorghum and sunflower against weeds in the field of wheat crop and found that spray of 100% water extracts of sorghum and sunflower, 30 days after sowing significantly reduced the total weed density up to 48 and 32% and weed dry weight up to 51%. The inhibition varied between weed species. In another study, Cheema and his colleagues showed that spray of sorghab on cotton crop suppressed weed density by 13-54% and weed dry weight by 87% (19). Additional work indicated that spraying of sorghab on wheat, maize, mung bean, soybean and mustard at different time of sowing drastically reduced total weed density and dry biomass of weeds in these crops (1,11,18,19,46). In all studies the reduction in weed density and biomass led to a significant increase of the yield of test crops. The use of sorghab was more economically feasible than hand weeding and herbicides application. Thus it appeared that using of sorghab is an effective method for weed control. However, it would be fruitful to test the combined effect of different concentrations of sorghab and sub recommended doses of herbicides. It might be possible to obtain a combination more inhibitory to weeds and reduce the amount of herbicides added to agroecosystems.

3. 2. SORGHUM RESIDUES AS COVER CROP AND MULCH

Cover crops and smother crops are old practices used by farmers of different regions of the world to reduce soil erosion, conserve soil moisture, improve nutrient status and manage weeds. However, during the last four decades, it has been noted that allelopathic cover crops may provide an alternative herbicidal method of weed suppression. This method is first explored by Putnam and his colleagues who found that allelopathic crops used as cover crops provided a great weed suppressing capacity (63,64,66).

Sorghum is one of the strongest allelopathic crops which has been extensively used as a cover crop or through incorporation of its residue in soil to control weed. Putnam and DeFrank (63) found that mulches of sorghum or Sudan grass applied to apple orchards in early spring reduced weed biomass by 90 and 85%, respectively. Forney *et al.* (37) indicated that sorghum is often selected as annual cover crop because of its rapid growth and ability to suppress weeds. They added that sorghum incorporated as green manure strongly reduced annual weed population and growth in the succeeding alfalfa crop. Sudex (*Sorghum bicolor* × *Sorghum sudanese*) is widely used in USA trees nurseries as a cover crop. The growth of *Cerecis canadensis* was significantly reduced when fresh and dry leaves of sudex were incorporated into growing medium even with additional amount

of NPK in the nutrient solution (38). The reduction was proportional to the amount of incorporated leaf materials. In personal communication with Smeda, Weston indicated that spring – planted sorghum residues provide up to 90% reduction in weed biomass for 6 to 8 weeks in no-till summer planted soybean (72).

In Pakistan, a multi-years investigation of the effects of sorghum mulching on density and growth of weeds grown in the fields of wheat, cotton, mung bean and maize had been conducted (1,2,17,19,21). The results of these studies clearly indicated that sorghum mulches applied at different rates reduced the density and dry biomass of weeds. In some cases the reduction depended on stage of sorghum incorporation, the quality of sorghum biomass added into the soil, growth condition and the weed species. The reduction in weed density and biomass led to a significant increase in the yield of the test crops.

Recently, several hundreds of sorghum cultivars were introduced and cultivated in Iraq to select the most promising genotypes in terms of production, weeds competition and fitness to local environment. Ten cultivars were selected. Field observations revealed that growth and population of companion weeds were variable among the stands of selected genotypes (5). Also, differential growth and population variation were observed on weeds grown in the field after sorghum harvest. This suggests that allelopathy could be the mechanism responsible for the reduction of weeds growth and population and the differences among stands could be due to differences in the allelopathic potential of the test cultivars. Several experiments were conducted to test this hypothesis. Results indicated that residues of all test cultivars significantly inhibited the growth of *Lolium temulentum* weed over the control (Table 3). The phytotoxicity of residues differed among the test genotypes. Of the 10 genotypes tested, 3 cultivars (Giza 15, Giza 115 and Enkath) reduced mean dry weight of weed by more than 71%. Rabeh was the least allelopathic cultivar, with growth reduction of 56%.

Table 3. Effects of residues of sorghum genotypes incorporated in soil on above ground biomass (g. plant⁻¹) of *Lolium temulentum* (Source 5)

Sorghum cultivars	Residues rate (g. kg ⁻¹ soil)		Mean
	3	6	
Control	2.217	2.617	2.410
Rabeh	1.123	0.982	1.053
F10-R-2002	1.034	0.819	0.927
Arbel	0.916	1.100	1.008
Dewardo	0.886	0.861	0.873
Kafeer	0.856	0.734	0.799
Argence	0.835	0.803	0.819
Rabeh x F4	0.835	0.803	0.819
Enkath	0.806	0.577	0.691
Giza 115	0.708	0.698	0.700
Giza 15	0.685	0.525	0.605
Mean	0.887	0.825	

LSD = 0.05: Genotypes = 0.224, Residues rate = 0.141, Genotypes × Residues rate = 0.365.

Experiment conducted in a field infested with *Lolium rigidum*, *Lolium temulentum*, *Malva pariflora*, *Carthamus oxycantha*, *Silybum marianum*, *Melilotus indica*, *Chenopodium album*, *Beta vulgaris*, *Polypogon monspeliensis*, *Trifolium repense* and *Plantago ovata* revealed that the above ground biomass and number of all weeds were reduced by the residues of the test sorghum cultivars incorporated in to field soil at rates of 3 and 6 g/kg soil. However, the response varied among the weed species (data not included). Residues of cultivars Giza 15, Giza 115 and Enkath provided 67, 59 and 63% reduction in average weed numbers and 58, 66 and 58% reduction in average weed biomass respectively (Table 4). Residues of Rabeh cultivars inhibited average weed numbers and average weed biomass by 41 and 52% respectively. Weeds numbers were significantly decreased with increasing rate of residues of the stronger allelopathic cultivars in soil.

Table 4. Effects of residues of sorghum cultivars incorporated in soil on Weeds density and their above ground biomass (Source: 5)

Rate of residues (g.kg ⁻¹ soil)	Sorghum cultivars					Mean
	Control	Giza 15	Giza 115	Enkath	Rabeh	
	Weeds density/m²					
3	76.3	27.0	36.3	34.6	48.0	44.4
6	72.3	21.3	25.0	20.3	40.0	35.8
Mean	74.3	24.2	30.7	27.5	44.0	
LSD=0.05	Genotypes: 15.3, Residues rate: 10.2, Genotypes x Residues rate: 11.2					
	Weeds biomass (g/m²)					
3	421.1	196.8	178.8	172.2	198.5	233.5
6	432.4	161.2	115.6	182.7	215.4	221.5
Mean	426.8	179.0	147.2	177.5	206.9	
LSD=0.05:	Genotypes: 00.8, Residues rate:159.3, Genotypes × Residues rate: 133.3					

Table 5. Effects of residues of sorghum cultivars decomposed for different periods on seedling length (cm) of *Chenopodium album* (Source: 5)

Sorghum cultivars	Amount of residues mixed (g . kg ⁻¹ soil)	Decomposition periods (weeks)*					
		1	2	4	6	8	10
Giza 15	0	4.72 ^a	5.41 ^a	4.93 ^a	3.75 ^a	4.19 ^a	4.33 ^a
	25	3.03 ^b	3.92 ^b	3.25 ^b	2.91 ^b	3.98 ^a	3.89 ^a
	50	2.85 ^b	2.59 ^c	2.75 ^c	2.33 ^c	2.93 ^b	4.03 ^b
Giza 115	0	4.77 ^a	5.45 ^a	5.28 ^a	4.34 ^a	4.21 ^a	4.22 ^a
	25	3.95 ^b	3.90 ^b	3.70 ^b	3.62 ^b	3.94 ^a	3.96 ^{ab}
	50	3.40 ^c	3.36 ^c	2.73 ^c	2.78 ^c	3.08 ^b	3.70 ^b
Enkath	0	4.83 ^a	5.29 ^a	5.13 ^a	4.33 ^a	4.19 ^a	4.63 ^a
	25	3.70 ^b	3.78 ^b	3.16 ^b	3.14 ^b	4.02 ^a	3.88 ^b
	50	2.96 ^c	2.84 ^c	2.61 ^c	2.46 ^c	3.08 ^b	3.25 ^c
Rabeh	0	4.64 ^a	4.58 ^a	4.42 ^a	4.49 ^a	4.45 ^a	4.43 ^a
	25	4.20 ^{ab}	3.88 ^b	3.93 ^b	3.91 ^b	4.15 ^{ab}	4.33 ^{ab}
	50	3.80 ^b	3.66 ^b	3.28 ^c	3.18 ^c	3.83 ^b	3.85 ^b

* Numbers with each column for each cultivar sharing with same letter are not significantly different according to Duncan's multiple range tests.

The persistence of sorghum phytotoxic residues in soil was monitored using *Chenopodium album* in the bioassay (Table 5). The phytotoxicity started after one week of decomposition and persisted for 8 weeks at the low rate of residues and for 10 weeks at the higher rate of residues. The reduction was proportional to the amount of residues in soil during the first 6 weeks of decomposition. Giza 15, Giza 115 and Enkath varieties were more phytotoxic than Rabeh cultivar at all decomposition periods.

3. 3. SORGHUM AS SMOTHERING CROP

Smother crops are grown in rotation or as catch crop and shade out the weeds due to their quick growth and their thick stand (75). This practice has been used for several years to prevent soil erosion and control weeds. The farmers employed this practice assuming that smother crops have the ability to suppress weed through competition only. However during the past five decades it was found that these crops suppress weeds through competition and allelopathy. None crop plant species could also offer a possibility to smother weeds when associated with crop or planted in rotational sequence with them by producing allelochemicals inhibitory to weeds but not harmful to the growing crop (39).

Sorghum has been reported to have a greater ability to smother weeds. Putnam (65) found that several smother crops including sorghum × Sudan grass hybrid were very effective in reduction of weed population. Wheat residues stimulated seed germination while forage crops smothered weeds (55). The smothering ability of the test crop was varied with test forage crop. Pear millet was most effective as reduced weeds by 90% followed by maize, sorghum, cluster bean and cowpeas. Narwal (57) indicated that inclusion of fodder crops (sorghum, pearl millet and maize) in the field before the rice crop in rice – wheat rotation significantly reduced weed biomass in the succeeding rice crop and may reduce the use of herbicides. In Southern USA, growers are customarily used sorghum × Sudan grass hybrid as a smother and cover crop to prevent soil erosion and reduced weed infestation during the succeeding year (80). The hybrid reported to have strong allelopathic inhibitory effects on weeds. The suppression effects of the residues even persistent in the next crop.

3. 4. SORGHUM IN CROP ROTATION

Crop rotation is defined as a cropping system in which two crops are in a fixed sequence on a piece of land without disturbing the soil fertility (52). Several factors such as soil fertility, soil structure, plant nutrient, choice of suitable crop have been considered in the developing of a crop rotation system. Allelopathy, however, was not included in these factors. Allelochemicals may release in to the soil in rotation system by root exudation and/or decomposition of the allelopathic crop and inhibited or stimulated the growth of the subsequent crop.

Sorghum has an allelopathic effect on the succeeding crops. The first indication of sorghum autotoxicity was observed by Burgos-Leon (15). He observed that growth of sorghum is markedly reduced following sorghum in sandy soil but not in soil high in monotorillonite. Additional work Burgos-Leon and his colleagues (16) investigating the reasons of these observations concluded that sorghum roots and tops incorporated in the sandy soil significantly inhibited growth of sorghum seedlings. No growth inhibition was observed when residues were added in soil high in monotorillonite. However, sorghum residues incorporated in soils high in monotorillonite significantly reduced growth of

sorghum seedlings under sterile soil conditions. Water extracts of sorghum roots and tops significantly inhibited growth of sorghum seedlings. Three major phytotoxins *p*-coumaric, *m*-hydroxy-benzoic and protocatechuic acids were identified from root residues. Acid hydrolysis of root extracts released large quantity of *o*-hydroxybenzoic acid. When the sterile water extracts of sorghum root was inoculated with *Trichoderma viride* or *Aspergillus* sp, the toxicity disappeared in a short time. Additional experiments with non-sterile and non inoculated field soil revealed that several weeks were required to detoxify the soil after addition of root residues of sorghum.

Alsaadawi *et al.* (6) conducted screening experiment to examine the activity of root exudates of 100 cultivars of sorghum to inhibit seed germination and seedling growth of *Amaranthus retroflexus* in sand culture medium. The response of weed was varied among the test cultivars. They found 82% of the control reduction in seed germination in 25 cultivars. Ten cultivars inhibited growth of *A. retroflexus* by more than 79% of control. Collection and identification of root exudates revealed that neutral fraction was more inhibitory than acidic and basic fractions. Netzly *et al.* (59) demonstrated that hydrophobic root exudates of sorghum significantly stimulated witch weed (*Striga asiatica*) parasite and this can furnish a potential method to reduce the seed bank of this weed in soil. Alsaadawi *et al.* (5) screened the allelopathic activity of root exudates of sorghum cultivars varied in their allelopathic potential to the companion weed *Echinochloa colonum*. All cultivars significantly reduced biomass of the test weed. However, cultivars with high allelopathic potential (Giza 15 and Enkath) were found to be more inhibitory than those with low allelopathic potential (Table 6).

Table 6. Effects of root exudates of sorghum cultivars on growth of *Echinochloa colonum* weed (Source: 5)

Sorghum cultivars	<i>Echinochloa colonum</i> *	
	Dry weight (mg)	Inhibition %
Control	177.0 ^a	--
Giza 15	142.5 ^b	19.5
Giza 115	127.3 ^c	28.1
Enkath	122.5 ^c	30.8
Rabeh	151.0 ^b	14.7

*Numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test.

Einhellig and Leather (30) determined weed biomass in strip cropping of sorghum, soybean and maize in the following year. They found that weed biomass was significantly reduced in plot where sorghum had been grown the year before compared to soybean and maize plots. Additional work by Einhellig and Rasmussen (32) revealed that grain sorghum crop reduced weeds in crop of the following year. They attributed the reduction of weed biomass in the sorghum plot to allelopathic effects of sorghum. Others found that incorporation of plant residues of various crops including sorghum reduced weed biomass and density in the order pearl millet–maize–sorghum–cluster bean–cowpea (55). Sene *et al.* (74) found that peanut seedling establishment was better between rows than on rows of previous sorghum crop. They proposed a geometrical sowing pattern for peanuts between the rows of previous sorghum crop to escape the latter "allelopathic

heritage". They also examined the phenolic content of the row and inter row soils but did not find consistent data from year to year suggesting possibly that phenolics are not the principle compounds responsible for sorghum allelopathy.

Ploughing of mature sorghum residues in soil delayed the growth of following wheat crop but did not affect yield probably due to allelochemicals degradation; however no-tillage stovers reduced grain yield of wheat crop possibly because the allelopathic compounds leached slowly (73).

3. 5. SORGHUM IN CROP MIXTURES AND INTERCROPPING

Intercropping is an ancestral practice used by the farmers of the developing world to maximize crop production, reduce risk failure and soil erosion and suppress weeds (8,54). Narwal (56) stated that productivity of crop mixture may be increased or decreased depending on stimulatory and inhibitory effects of component crops on each other provided growth resources such as light, water, nutrients and space are not limiting factors. Root exudates play a major role in increasing growth and yield of crop mixtures by improving ions uptake and reduce weed population. Sorghum is one of the allelopathic crops used in intercropping systems to increase yield of crop components and reduce weed infestation (50,76). Intercropping practice may be enhanced using crops with highly allelopathic root exudates that can suppress weeds without harming the crop. This approach could help in controlling weed infestation and reduce herbicide application. It has been reported that the allelopathic potential of root exudates was variable among the sorghum genotypes. Recently, Weston and Czarnota (78) studied the allelopathic potential of root exudates of 25 genotypes of sorghum against *A. retroflexus* using hydroponic culture system and they found that root and top growth of the weed was variable among the test genotypes.

4. ALLELOPATHIC EFFECTS OF SORGHUM ON WEEDS

Allelopathy proved to affect several biological processes in nitrogen cycle such as nitrogen fixation and nitrification (4,6,46,79,68,81). However, much needs to be done to integrate this allelopathic mechanism in cropping systems to regulate the use of nitrogen added to the soil by plant through nitrification inhibition and avoid the inhibition of biological nitrogen fixation. Huber *et al.* (45) concluded that inhibition of nitrification may markedly increase the efficiency of food production, reduce energy requirements for growing crops, decrease the incidence of plant disease and reduce the pollution potential of nitrogen fertilizers. Some crops appeared to have potential inhibitory effects on nitrogen fixation and nitrification processes (4,69,70,71).

Alsaadawi *et al.* (6) tested the inhibitory effects of four sorghum genotypes (varied in their allelopathic potential) on soil nitrification using soil incubation method. Residues of all test genotypes reduced the nitrification rate with maximum inhibition achieved by the higher allelopathic cultivars. Additional experiment by Alsaadawi *et al.* (7) revealed that sorghum plants from seeds exposed to stimulatory doses of gamma irradiation (0.5, 1, 1.5 K rad) have more inhibitory level in their extract and decaying residues on nitrification. The allelopathic effects of the hybrid (*Sorghum bicolor* × *Sorghum sudanese*) on growth and nitrogen fixation were investigated under green house

conditions by Alsaadawi and Sakeri (unpublished data). It was found that residues of the hybrid incorporated at rates of 4.4 and 8.8 g per kg soil significantly inhibited growth of kidney bean, nodulation and hemoglobin content of nodules. The reduction of hemoglobin was increased with the increased concentration of the hybrid residues in soil.

5. ALLELOCHEMICALS IN SORGHUM

Sorghum is major cereal crop grown in semiarid areas of the world for food and fodder (77) and is also used as green manure or as cover crop to suppress weeds in integrated pest management systems (80). The allelopathic effect of sorghum was first reported as 'soil sickness' in crops grown in rotation with sorghum (14). Many compounds produced by sorghum roots were postulated to play a role in the allelopathic potential of this species. In particular, the action of several classes of water-soluble compounds such as phenolics was studied (6,42,43,51,62). Recently, Alsaadawi *et al.* (5) quantified the level of phenolic acids in the extracts of highly allelopathic cultivars of sorghum (Giza 115, Giza 15 and Enkath) and low allelopathic cultivar (Rabeh) by HPLC. The analyses revealed the presence of vanillic, syringic, ferulic, *p*-hydroxybenzoic, *p*-coumaric and gallic acids in the residues of Giza 15 and Enkath cultivars (Table 7). All these phytotoxins except gallic acid were found in the residues of Giza 115, while, residues of Rabeh cultivar contained all phytotoxins except *p*-coumaric acid. Residues of Giza 115 and Giza 15 contained up to 5 times more *p*-hydroxybenzoic acid than Rabeh cultivar, whereas, Enkath accumulated up to 3 times more than Rabeh cultivar. Total isolated phytotoxins were higher in Giza 115 and Giza 15 than in the other cultivars. However, sorghum roots also release an oily exudate containing the lipid benzoquinone sorgoleone (2-hydroxy-5-methoxy-3-[(8'Z, 11'Z)-8', 11', 14'pentadecatriene]-*p*-benzoquinone) which has been identified as the main source of the allelopathic potential of sorghum (58). The oily exudate is now known to be a mixture of sorgoleone and a closely related dimethylated resorcinol analog (Figure 1) (27,35).

Table 7. Phytotoxins isolated from the residues of different sorghum cultivars (Source: 5)

sorghum cultivars	Phytotoxins (microgram/g residues) ^{*,**}						Total
	vanillic acid	syringic acid	ferulic acid	<i>p</i> -hydroxy-benzoic acid	<i>p</i> -coumaric acid	gallic acid	
Control	--	--	--	--	--	--	--
Giza 15	1.42 ^b	1.50 ^a	5.10 ^a	8.00 ^a	1.24 ^a	1.60 ^a	18.84 ^a
Giza 115	1.10 ^b	0.94 ^b	3.20 ^b	8.14 ^a	0.80 ^b	--	14.80 ^b
Enkath	1.00 ^b	0.41 ^c	2.53 ^c	4.40 ^b	0.90 ^b	1.05 ^b	10.29 ^c
Rabeh	4.30 ^a	1.04 ^b	2.33 ^c	1.66 ^c	--	1.15 ^b	10.48 ^c

^{**}Numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test. ^{*}Each value is an average of 3 replicates.

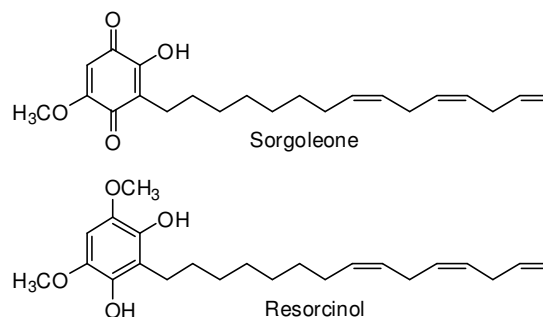


Figure 1. Structure of sorgoleone and its dimethylated resorcinol analog.

Sorgoleone has the strongest herbicidal activity on small-seeded weeds (28,29,34,58,60,72). Large seeded weeds tend to be less sensitive to sorgoleone possibly because they may avoid the herbicidal effect by rapidly growing beyond the zone of the sorghum rhizosphere where the lipophilic exudate accumulates. Sorgoleone is active on many molecular target sites, inhibiting photosynthesis by competing for the plastoquinone binding site on PSII (33,40,60,72), affecting mitochondrial functions (67), inhibiting the enzyme p-hydroxyphenylpyruvate dioxygenase (HPPD) (53), and interfering with root H^+ -ATPase and water uptake (44). Whether the allelopathic potential associated with sorgoleone is the result of inhibiting one or more of these molecular target sites is still unknown. While sorgoleone is a potent inhibitor of PSII in isolated chloroplasts, Hejl and Koster have shown that photosynthesis of 7-d to 10-d old plants does not appear to be affected by this lipid benzoquinone (44). Furthermore, they correctly pointed out that it remains to be established whether this highly lipophilic natural herbicide is actually taken up by roots and translocated to the foliage where it must enter the chloroplast and inhibit PSII in the thylakoid membrane (44). Therefore, while sorgoleone is a strong inhibitor of several physiological and biochemical processes *in vitro*, its primary role in mechanism of action remained unclear. Dayan *et al.* (27) investigated the problems posed by the spatial separation between the location of sorgoleone exudation (soil) and its putative site of action (foliage) as a PSII inhibitor by monitoring the absorption and translocation of this lipophilic natural herbicide. Sorgoleone is not translocated acropetally in older plants, but can be absorbed through the hypocotyl and cotyledonary tissues. Therefore, the mode of action of sorgoleone may be the result of inhibition of photosynthesis in young seedlings in concert with inhibition of its other molecular target sites in older plants (27).

The biosynthesis of sorgoleone has been elucidated using retrobiosynthetic NMR analysis (25,36) and mature sorghum root hairs contain the entire genetic material and biochemical machinery required for the production of this bioactive benzoquinone (10,23,26,61). Sorgoleone biosynthesis is the results of the convergence of two metabolic pathways. A fatty acid synthase and fatty acid desaturases produce the obligatory 16:3-CoA that subsequently serves as the starter unit of a specialized type III polyketide synthase. The resulting lipid resorcinol is acted upon by a type I SAM-dependent O-methyltransferase and a P450 monooxygenase to produce the reduced (hydroquinone) form of sorgoleone (Figure 2) (25). This pathway is highly efficient, generating 20-30 μ g

of exudate/mg root dry weight (24,27). The pathway appears to be feedback inhibited when too much exudate accumulates at the tip of the root hairs. However, washing the exudate releases the pathway and more lipophilic exudate is produced.

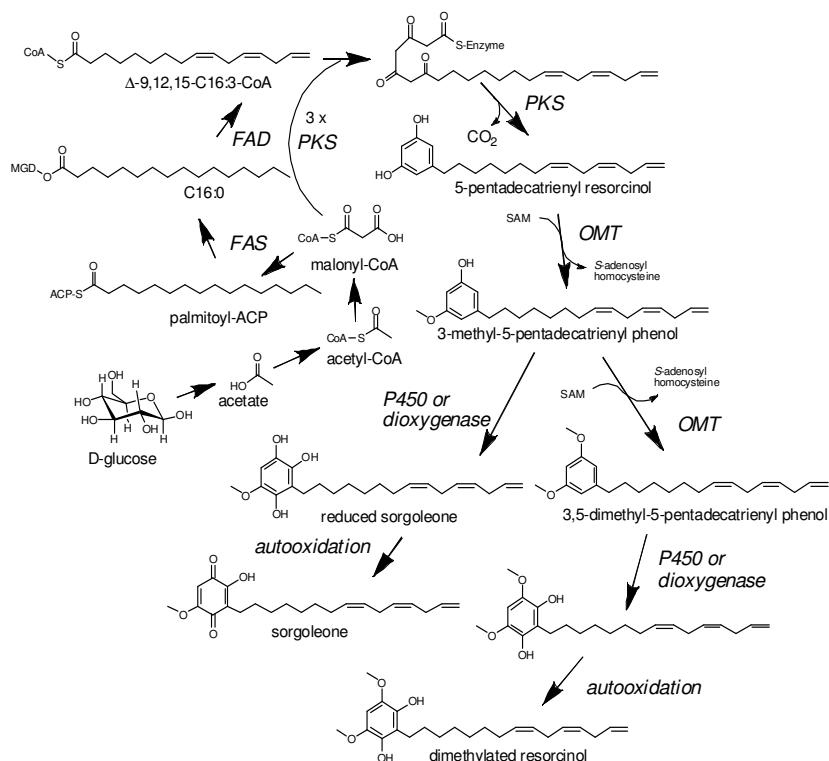


Figure 2. Biosynthesis of sorgoleone and the dimethylated resorcinol analogue.

Manipulation of the genes involved in sorgoleone biosynthesis may lead a better understanding of the role of sorgoleone in plant-plant interactions. Genetically enhanced sorghum cultivars may be generated with greater natural weed control ability. Additionally, the possibility of introducing some of these genes in other species such as rice could provide new environmentally friendly weed management tools.

6. FUTURE RESEARCH AREAS

This review addresses the allelopathic potential of grain sorghum and its related species for their ability to control weeds and improve yield of crops in different cropping systems. To achieve these goals the following researches need to be done:

- (i). The traditional cropping pattern in which sorghum is used needs to be revived with the new developed approaches such as: cover crop, smother crop, intercropping and crop rotation.
- (ii). The allelopathic potential of sorghum in crop rotation could be used to enhance the production of crop simply by exploiting favorable interactions such as weed control and avoiding inhibitory effects of sorghum by selecting crops resistant to sorghum phytotoxins. Thus sorghum to crop relationships need to be investigated thoroughly to determine which crop can follow sorghum with least inhibitory or having stimulatory effect.
- (iii). Screening of sorghum genotypes needs to be continued to select genotypes with greater weed suppression ability to exploit them in the newly developed approaches of cropping systems.
- (iv). The promising herbicidal and allelopathic properties of sorgoleone and other allelochemicals in sorghum deserve further work to identify the enzymes responsible for the biosynthesis of these compounds and the genes encoding them. The other necessary step is to use the genetic engineering to manipulate the identified genes in sorghum or in other crops to enhance their ability to suppress weeds.
- (v). Application of water extract of sorghum plants is a promising method to control weeds and enhance crop production. However more work is recommended to test the water extracts of highly allelopathic accessions of sorghum and species of the related genus *Sorghum* such as *Sorghum halepense*. Also, it would be fruitful to test the combined effect of different concentrations of sorghab and low doses of herbicides in order to obtain a more effective control of weeds while reducing input of synthetic herbicides in agroecosystem. Besides, allelochemicals in water extract must be identified.

7. CONCLUSIONS

The future looks bright for using allelopathic properties of sorghum in developing the cropping systems to control weeds and develop sorghum cultivar(s) with superior ability to inhibit weeds using biotechnology techniques.

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