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Phytotoxicity of Extracts from Sorghum Plant Components on Wheat Seedlings

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ABSTRACT

Wheat (*Triticum aestivum* L.) yield is depressed when the crop is grown after grain sorghum [*Sorghum bicolor* (L.) Moench], a known allelopathic species. Since little is known about the variability of allelopathic potential among sorghum hybrids on wheat, six sorghum hybrids were selected from a 1989–1990 sorghum–wheat sequence for further study. The range in yield depression observed was 16%. The six hybrids were grown in 1991 and separated into plant parts at maturity. A bioassay using wheat seedlings to detect allelopathic potential was developed. Bioassays of water extracts from mature seeds, glumes, leaves, stems, and roots of sorghum were conducted to (i) quantify the allelopathic potential of sorghum on wheat; (ii) compare allelopathic potential of individual sorghum hybrids; and (iii) identify the plant parts that are the most important sources of allelopathic substances. Wheat radicle growth response to water extracts revealed a highly allelopathic hybrid and two hybrids with low allelopathic potential. These were retained for study in 1992. All plant parts, regardless of hybrid, contained water-soluble materials inhibitory to wheat seedling growth. Stems, leaves, and roots were the most inhibitory components of a sorghum plant, reducing wheat radicle elongation by 74.7, 68.5, 64.0%, respectively. Within a sorghum hybrid, an individual plant part was not consistently allelopathic at tbe same level across years. Bioassays can rapidly detect the differences in allelopathic potential that may occur within and among hybrids. These results have implications for using sorghum–wheat rotations where residues of certain sorghum hybrids might negatively influence growth and development of wheat, possibly resulting in decreased wheat yields.

WHEN YIELDS of a second crop in a two crop sequence are reduced, short-term allelopathy is often hypothesized (Hedge and Miller, 1990). Water extracts from residues of the suspected allelopathic crop are usually bioassayed on the receptor crop to support field observations or field experimental results (Putnam and DeFrank, 1983; Rose et al., 1984). A reduction in seedling growth of the indicator crop suggests that the donor crop has allelopathic potential (Guenzi and McCalla, 1967; Guenzi et al., 1964; Hedge and Miller, 1990; Liebl and Worsham, 1983; Shilling et al., 1986; Weston et al., 1989). Allelopathic potential, defined as the degree of growth inhibiting activity of one plant on another, differs among plant species (Bowmick and Doll, 1982; Kimber, 1973), among cultivars within the same species (Guenzi et al., 1967; Hicks et al., 1989; Rose et al., 1984), and among plant parts of the same cultivar (Guenzi et al., 1967). Allelopathic potential of a crop varies depending on stage of growth (Guenzi et al., 1964; Kimber, 1973) and the year (Guenzi et al., 1964).

The allelopathic potential of a plant species, whether a crop (Guenzi et al., 1967; Hedge and Miller, 1990; Liebl and Worsham, 1983; Panasiuk et al., 1986; Rose et al., 1984; Shilling et al., 1986; Weston et al., 1989), a weed (Bowmick and Doll, 1982), or a woody herb (Kil and Yun, 1992) is often measured by germination and radicle and shoot growth of an indicator species (Guenzi and McCalla, 1967; Hedge and Miller, 1990; Panasiuk et al., 1986). The effect of water-soluble inhibitory compounds associated with allelopathic plants is often more pronounced on radicle growth than on germination (Hedge and Miller, 1990) or shoot growth (Bowmick and Doll, 1982; Kimber, 1973) of an indicator plant species. Seed germination of several indicator species were found to be slightly stimulated when bioassayed with germinating sorghum yet both radicle and coleoptile elongation were significantly inhibited (Panasiuk et al., 1986). Radicle growth can be used as the sole parameter to characterize the allelopathic potential of a plant species (Weston et al., 1989).

Bioassays of water extracts from crop residues can be used either to screen cultivars of a species for their ability to tolerate inhibitory effects (Hicks et al., 1989) or for their ability to inhibit surrounding plant growth (Rose et al., 1984). Generally, a petri dish (PD) containing germination paper moistened with plant extracts as a medium for germination and seedling growth is used to assess potential allelopathy (Li et al., 1992; Mason-Sedun et al., 1986; Netzly and Butler, 1986). However, this technique often gives inconsistent results due to nonuniform wetting or localized swelling of the filter paper. Pederson (1986) developed a plant extract agar technique in a PD that showed less variability in studies involving white clover (*Trifolium repens* L.) and recommended its use for allelopathy research. Preliminary bioassays in our laboratory showed high variability in wheat seedling growth response on 1.2% agar as a growth medium in PD.

Sorghum is known to be allelopathic to wheat (Guenzi and McCalla, 1967; Guenzi et al., 1967), but little is known about the variability of the allelopathic potential among hybrids or among sorghum plant parts. Also, a standard bioassay using wheat seedlings to consistently detect allelopathic potential has not been developed. The objectives of this study were to (i) develop a uniform bioassay for measuring wheat seedling response to sorghum plant extracts; (ii) quantify the allelopathic potential of sorghum on wheat; (iii) compare allelopathic potential of individual sorghum hybrids; and (iv) identify the plant parts that are the most important sources of allelopathic substances.

METHODS AND MATERIALS

Collection of Sorghum Plant Materials

Two sorghum–wheat sequences were grown at the University of Missouri Agronomy Research Center near Columbia

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Abbreviations: CV, coefficient of variation; LSD, least significant difference; PD, petri dish; RCBD, randomized complete-block design; RCV, rank of coefficient of variation; TT, test tube; TT+PG, test tube plus pregerminated seed.

in 1991–1992 and 1992–1993 on a Mexico silt loam (fine, montmorillonitic, Mesic Mollic Endoaqualf). Six sorghum hybrids ('Asgrow Topaz', 'Cargill-70', 'Funk's G-522A', 'MFA GS-10', 'Taylor Evans Y-101G', and 'Warner W-744DR') were grown in the first sorghum–wheat sequence, from which three were selected for the second sequence. Sorghum plants were collected at harvest in both years and stored frozen until analysis.

Preparation of Water Extracts

Sorghum plants were washed gently with distilled water. Heads, leaves, stems, and roots were separated. All plant components except heads were chopped into small 1-cm long pieces and dried at 50°C for 24 h. Heads were hand threshed and separated into seeds and glumes. The rachis was added to the stem portion of the plant. An unground 2.5-g portion of each plant component was extracted in 50 mL distilled water. Each sample was placed in a 500-mL flask on a rotary shaker for 24 h at 200 rpm. Extracts were passed through filter paper (Whatman No. 2) under vacuum and centrifuged at 2000 × *g* (12 500 rpm) for 20 min at 8°C. Extracts were filter-sterilized (0.2-μm membrane) using a peristaltic pump (Millipore Corp.[1], Bedford, MA) prior to bioassay.

Bioassay Development

Three bioassay techniques compared were (i) unimbibed wheat seeds placed in 10 × 150-mm PD containing 12 g L^{-1} agar (autoclaved 20 min at 121°C, 124 × 10^3 Pa); (ii) unimbibed wheat seeds placed in 10 × 150-mm test tubes (TT) containing 12 g L^{-1} agar; and (iii) pregerminated wheat seeds placed in test tubes (TT+PG) containing 12 g L^{-1} agar. To efficiently produce uniform pregerminated seeds, a preliminary experiment was conducted. Treatments were one germination paper (Anchor Paper, Minneapolis, MN) in a 20 × 140-mm PD moistened with 15, 14, 13, or 12 mL distilled water and two germination papers each moistened with 12 mL distilled water. In the treatments with one germination paper, seeds were placed on top of the paper, and in the other treatment, seeds were placed between the two sheets of paper. Seeds of 'Cardinal' wheat were surface sterilized with an aqueous solution of sodium hypochlorite (10 g L^{-1}) for 4 min, rinsed five times with sterile distilled water, and blotted between two sterile paper towels. For each treatment, 50 surface-sterilized seeds were placed equidistantly in a PD and incubated at 25°C for 30 h. The number of seedlings with 3-mm-long radicles was counted. The experiment was conducted in a randomized complete-block design (RCBD) with four replications. The treatment that produced the highest number of seeds with uniform 3-mm radicles ($P = 0.05$) was selected for the comparison of techniques experiment.

For the PD bioassay, each PD received five surface-sterilized wheat seeds after solidification of the agar. In bioassays using test tubes, tubes were covered with plastic caps, slanted at a 45° angle and agar contents were allowed to solidify. One surface-sterilized wheat seed was placed with the crease facing the growth medium (embryo up) in each tube. For tubes receiving unimbibed seeds (TT), the embryo was positioned at the middle of the slope. In the TT+PG technique, pregerminated seeds with 3-mm radicles were transplanted into tubes. Within a replication, each treatment was represented by 10 seeds.

[1] Mention of this or other proprietary names does not imply approval by the USDA-ARS or the University of Missouri to the exclusion of others that may be suitable.

The total period for incubation was 60 h at 25°C for each technique. The experiment was conducted in a RCBD with four replications. Variability was measured as a coefficient of variation (CV) for radicle growth among seedlings within the same experimental unit for each technique. For each replication of each treatment, CV was calculated and these values ranked from 1 to 12. Analysis of variance on the ranks of CV (RCV) was computed using SAS (SAS Institute, 1989) and treatment and/or technique means were separated using the least significant difference (LSD) at the 0.05 level of probability.

Growth Medium for Bioassays of Sorghum Extracts

Water extracts of seeds, glumes, leaves, stems, and roots of sorghum hybrids grown during both years were tested for phytotoxicity to wheat seed germination, wheat coleoptile growth, and wheat radicle growth. For bioassays of sorghum extracts, molten agar (≈40°C was amended with 20 mL of each sterile plant part extract to make a water-extract-agar (12 g L^{-1}) as a medium for wheat germination and wheat seedling growth. For seed germination bioassays, surface-sterilized wheat seeds were placed in sterile PD (100 by 15 mm) containing 15 mL of water-extract-agar and incubated 35 h at 25°C. Seeds were considered germinated when the radicle protruded through the seed coat at least 2 mm. Wheat coleoptile and radicle growth were determined using the TT+PG technique. After 35 h incubation at 25°C, lengths of both the coleoptile and central radicle of each wheat seedling were measured. The inhibitory effects [inhibition=((control − treatment)/control) × 100 of sorghum extracts on wheat seedling growth was expressed as percentage of control.

Wheat germination and seedling growth bioassays were conducted in a split-plot design with four replications. The main factor was sorghum hybrid and the subfactor was plant part. A nonamended control was included as a subtreatment. For seed germination bioassays, 25 wheat seeds were plated in three PD for each subtreatment within a replication. For wheat radicle or wheat coleoptile bioassays, an average across a cluster of 10 TT with one pregerminated seed each was used as a single observation for each subtreatment within a replication. Analysis of variance was conducted using SAS (SAS Institute, 1989) and Fisher's protected LSD at the 0.05 level of probability (Steel and Torrie, 1980).

RESULTS AND DISCUSSION

Bioassay Development

Wheat radicles developed abnormally (curled) on a 12 g L^{-1} agar surface in PD resulting in poor contact of the seedlings with the bioassay medium and highly variable radicle lengths (data not shown). Coleoptiles also developed abnormally (concave curling). Thus, precise measurements of radicle and coleoptile lengths were difficult due to growth distortions, and the accuracy of results obtained in PD was questionable, as concluded previously by Leather and Einhellig (1988).

Development of seedlings from unimbibed wheat seeds on agar in TT was also highly variable. In many cases, germination appeared to be inhibited or delayed due to free moisture associated with the agar slants, which may have provided anoxic conditions.

Before evaluating the use of pregerminated wheat seeds in bioassays, a method to efficiently produce large numbers of seedlings with radicles of uniform length was developed. Placing seeds between two sheets of germina-

Table 1. Effects of paper number and volume of water on uniformity of wheat seedling radicles.

Germination papers	SDW†	Uniform seedlings‡
no.	mL	no.
2§	24	23.3
1	15	14.3
1	14	15.0
1	13	17.3
1	12	8.8
LSD (0.05)		2.4

† SDW = sterile distilled water.
‡ Wheat seedlings with a 3-mm radicle out of 50 seeds after incubation at 25°C for 30 h.
§ Wheat seeds between two germination papers each moistened with 12 mL SDW.

tion paper each moistened with 12 mL of water produced a larger number of seedlings with radicles of uniform length than did the other methods tested (Table 1).

Amount and variability (Petersen, 1985) of radicle growth were used as criteria to compare bioassay techniques. Radicle growth was faster in TT than in PD (Table 2). Growth was most rapid when pregerminated seeds were used since all initial phases of germination were completed before the seedlings were placed on agar slants. With unimbibed seeds, the use of agar in TT resulted in 79% more radicle elongation than in PD, suggesting an advantage due to a deeper rooting medium provided by agar slants.

Standard deviations associated with radicle growth were similar for PD and TT+PG (Table 2). However, the CV associated with use of pregerminated seeds in TT was much lower than in PD as a consequence of greater mean radicle growth. Also, the uniformity associated with the use of pregerminated seeds may be attributed to selection of uniform seedlings for transplanting. During the experiment, seedling growth from unimbibed seeds in TT resulted in highest SD and CV values, probably due to nonuniformity in time to germination.

Analysis of variance on the RCV indicated that the seedling growth bioassay using TT with pregerminated seeds more consistently resulted in a lower CV than the other techniques evaluated. The low CV associated with the use of pregerminated seeds was the result of both more rapid and less variable radicle growth. On this basis, the TT+PG bioassay method was selected for testing phytotoxicity of sorghum extracts on wheat.

Table 2. Effects of seedling growth bioassay techniques on mean growth of wheat radicles ($\bar{x}$) and variability [standard deviation (SD), coefficient of variation (CV), and rank of coefficient of variation (RCV)].

	Wheat radicle growth			
Technique†	$\bar{x}$	SD	CV‡	RCV
PD	26.3	6.4	24.0	6.5
TT	47.2	26.5	55.0	10.5
TT + PG	61.5	5.1	8.2	2.5
LSD (0.05)	13.8	NA§	NA	2.5

† PD = petri dish; TT = test tube; TT + PG = pregerminated seed in test tube; LSD = least significant difference.
‡ CV averaged across four replications for each technique and no analysis of variance conducted.
§ NA = not applicable.

Phytotoxicity of Sorghum Hybrids from 1991

Mean phytotoxicity of water extracts across the six sorghum hybrids grown in 1991 differed significantly when measured by wheat radicle growth (Table 3) but not when measured by wheat germination or coleoptile growth. These results are in agreement with earlier studies reporting that water extracts of allelopathic plants have more pronounced effects on radicle growth than on germination (Hedge and Miller, 1990) or shoot growth (Bowmick and Doll, 1982; Kimber, 1973). The mean inhibition of wheat radicle growth by the least allelopathic sorghum hybrid (Asgrow Topaz) was 47% of the inhibition caused by the most allelopathic sorghum hybrid (Funk's G-522A; Table 4). In a similar comparison between extracts of two cultivars of mustard (*Brassica juncea*) the differential in mean inhibition of wheat radicle growth was 75% (Mason-Sedun et al., 1986).

Phytotoxicity of Sorghum Plant Parts from 1991

Extracts from sorghum plant parts showed significant differences in phytotoxicity to wheat seedlings (Table 3). The level of phytotoxicity of extracts from each plant part varied with hybrid and measurement used. Radicle length bioassays provided the greatest differentiation among plant parts. Averaged across all hybrids, plant parts were significantly different from one another except stems and roots, which appeared to have an equal allelopathic potential (Table 4). All extracts reduced wheat radicle growth, compared with the control, with roots, stems, and leaves exhibiting the greatest phytotoxicity (Table 4).

In general, the lowest level of inhibition of wheat radicle growth caused by individual plant parts was found in Asgrow Topaz. Warner W-744DR exhibited a similar inhibition profile except for leaves and seeds. Comparisons within leaf and stem extracts revealed the greatest range in inhibitory activity among hybrids (Table 4).

Wheat coleoptile growth was less severely affected by plant parts relative to the control treatment. Only 15 of 30 plant part × hybrid combinations significantly inhibited coleoptile growth. However, extracts from stems and roots of all hybrids decreased wheat coleoptile growth relative to the control (data not shown).

The sensitivity of the wheat radicle bioassay and significant inhibition of wheat radicle growth by leaf, stem, and root extracts (Table 4) were used as bases for selecting sorghum hybrids for the 1992 study. Assuming a stems/leaves ratio of 1.8:1 based on field measurements (Ben-Hammouda, 1994) and shoot/root biomass dry matter ratio of 7:1 (Heatherly, 1975), greater importance was accorded to allelopathic activity of stems and leaves than of roots. Taylor Evans Y-101G was selected from among the most allelopathic hybrids. Asgrow Topaz and Warner W-744DR were selected as least allelopathic but differing in allelopathic potential of leaf water extracts (Table 4).

Table 3. Mean squares for inhibitory effects of sorghum hybrids and sorghum plant parts on wheat germination, wheat radicle growth, and wheat coleoptile growth in 1991, 1992, and across 1991 and 1992.

Source	1991 mean squares df†	Germination	Radicle growth	Coleoptile growth	1992 mean squares df	Germination	Radicle growth	Coleoptile growth
Replication	3	397.2	652.2*	374.1	3	15.8	139.7	1046.2*
Hybrid (H)	5	205.9	1 361.8**	395.2	2	35.9	87.8	38.9
Error a	15	379.2	195.3	371.7	6	47.2	107.7	206.2
Plant part (PP)	5	207.3**	16 132.5**	655.1**	5	80.0**	11 069.7**	544.7*
H × PP	25	57.1	465.7**	151.9**	10	37.1*	161.9*	41.6
Error b	90	58.4	60.7	76.7	45	15.3	25.2	44.1
		1991 and 1992 mean squares						
Year (Y)	1	338.9*	3 160.2**	84.2				
Replication	6	37.0	217.2	780.5				
H	2	104.3	491.3	166.7				
Y × H	2	102.6	946.3*	58.1				
Error a	12	44.5	194.2	326.8				
PP	5	47.7	15 325.2**	722.7**				
Y × PP	5	119.8**	1 953.1**	82.4				
H × PP	10	50.2	471.4**	90.0				
Y × H × PP	10	40.9	560.9**	210.0**				
Error b	90	28.8	55.6	68.4				

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
† df = degrees of freedom.

Phytotoxicity of Sorghum Hybrids from 1992

In contrast to 1991, the three sorghum hybrids grown in 1992 did not differ significantly with respect to mean phytotoxicity (averaged across all plant parts) on wheat radicle growth (Table 3). The mean wheat response to water extracts was significantly different between years for both wheat germination and wheat radicle growth (Table 3). Studying phytotoxicity of alfalfa (*Medicago sativa* L.) water extracts on corn (*Zea mays* L.) seedlings, Guenzi et al. (1964) also found a significant year effect on shoot growth. Inhibition of wheat germination (data not shown) and wheat radide growth (averaged across all plant parts of Asgrow Topaz, Warner W-744DR, and Taylor Evans Y-101G) were 4.9 and 1.3 times higher, respectively, in 1992 than in 1991.

Phytotoxicity of Sorghum Plant Parts from 1992

Plant parts exhibited significantly different inhibitory activity on wheat radicle growth (Table 5) and wheat germination (Table 3) from one hybrid to another. In the wheat germination bioassay, differences among hybrids were significant only for seeds, yet compared with the control, roots of Warner W-744DR, glumes and roots of Asgrow Topaz, and seeds and glumes of Taylor Evans Y-101G significantly inhibited wheat germination (data not shown). The radicle bioassay again showed greater separation between treatments than did germination and coleoptile growth.

Extracts from plant parts of the three sorghum hybrids significantly reduced wheat radicle growth (Table 5). Guenzi et al. (1967) previously found inhibition of wheat radicle growth by seed extracts of sorghum to be as low as 3%. As in 1991, water extracts of roots, leaves, and stems (across all hybrids) caused the greatest degree of inhibition. Similar growth inhibition resulted from either leaf or stem extracts from each hybrid, with intermediate levels of inhibition caused by glume and root extracts (Table 5). The allelopathic effect of a plant part within a sorghum hybrid on wheat radicle growth was not stable across years. Stem extracts from Warner W-744DR were more phytotoxic in 1992 than in 1991 and were as toxic as leaf extract. Both leaf and stem extracts of Asgrow Topaz were markedly more phytotoxic in 1992 than 1991. In 1992, leaf extract of Taylor Evans Y-101G was as toxic as stem extract. In the wheat radicle bioassay and within the same plant part, only inhibitory activity of glume extracts differed significantly among the three

Table 4. Effects of plant part extracts from six sorghum hybrids grown in 1991 on wheat radicle growth.

Sorghum hybrid	Inhibition of wheat radicle growth Seeds†	Glumes	Leaves	Stems	Roots	Mean‡
	% of control					
Warner W-744DR§	13.4	10.0	66.6	32.6	45.5	28.0
Asgrow Topaz	−0.5	12.1	18.9	25.2	50.8	17.8
MFA GS-10	5.0	11.8	36.4	74.7	64.0	32.0
Taylor Evans Y-101G	6.7	20.6	56.5	74.4	63.2	36.9
Cargill-70	6.4	24.5	53.5	67.4	57.3	34.9
Funk's G-522A	15.1	20.1	63.0	62.9	63.7	37.5
Mean¶	7.7	16.5	49.2	56.2	57.4	

† LSD (0.05) = 13.2 for comparing two hybrids within same source of extracts.
‡ LSD (0.05) = 8.6 for comparing two hybrid means.
§ LSD (0.05) = 10.9 for comparing two sources of extracts within the same hybrid.
¶ LSD (0.05) = 4.5 for comparing two plant part means.

Table 5. Effects of plant part extracts from three sorghum hybrids grown in 1992 on wheat radicle growth.

Sorghum hybrid	Inhibition of wheat radicle growth Seeds†	Glumes	Leaves	Stems	Roots	Mean
	% of control					
Warner W-744DR‡	4.4	16.7	68.5	73.3	37.0	33.3
Taylor Evans Y-101G	2.7	36.9	65.6	65.2	41.6	35.3
Asgrow Topaz	5.7	40.2	70.0	74.7	31.4	37.0
Mean§	4.3	31.3	68.0	71.7	35.7	

† LSD (0.05) = 9.8 for comparing two hybrids with same source of extract.
‡ LSD (0.05) = 7.2 for comparing two sources of extracts within the same hybrid.
§ LSD (0.05) = 4.1 for comparing two plant part means.

sorghum hybrids (Table 5). Throughout this study, glumes significantly inhibited wheat radicle growth compared with very low inhibition (2%) previously reported (Guenzi et al., 1967). Taylor Evans Y-101G stems were more phytotoxic than those of either Warner W-744DR or Asgrow Topaz in 1991 (Table 4) yet no differences were detected between hybrids in 1992 (Table 5). The variability in inhibition of wheat radicle growth by plant parts across years and across hybrids (Table 3) contributed to a reversal of allelopathic potential ranking of Taylor Evans Y-101G and Asgrow Topaz among years. Since there was no significant difference in any plant part ratio to total dry weight among hybrids nor significant difference in total residue production among hybrids (Ben-Hammouda, 1994), the instability of allelopathic potential of a sorghum hybrid may have resulted from the variability with time of two factors: (i) the quantity of total inhibitory substances in the plant tissues and (ii) the composition of these inhibitory substances and their relative concentrations. A recent report (Ben-Hammouda et al., 1995) revealed the inhibitory substances involved to be phenolic compounds.

CONCLUSIONS

A bioassay consisting of pregerminated wheat seeds placed on agar containing sorghum plant extract in TT promoted uniform seedling growth when used for assessing potential allelopathy of different sorghum hybrids.

Bioassays of water extracts from plants of different sorghum hybrids showed that seeds, glumes, leaves, stems, and roots contain water-soluble materials that have the ability to inhibit wheat seedling growth. Leaves, stems, and roots had the highest allelopathic activity, but this activity varied with hybrid and year. In general, stems were the most allelopathic plant part. Overall, sorghum hybrids differed significantly with respect to inhibition of wheat seedling growth in only one year of the study. Factors responsible for the marked contrast in mean inhibitory effect of sorghum hybrids from one year to the next were not identified.

Based on a shoot/root ratio of 7:1 and knowledge that stems comprise the greatest proportion of aboveground biomass, allelopathic potential of sorghum residues can be largely attributed to the stem component. Reduction of wheat seedling growth in bioassays by sterile extracts suggests that the inhibitory activity was a direct effect of water-soluble toxins contained in sorghum tissues.

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