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Germination Stimulants of Witchweed (*Striga asiatica*) from Hydrophobic Root Exudate of Sorghum (*Sorghum bicolor*)[1]

DAVID H. NETZLY, JAMES L. RIOPEL, GEBISA EJETA, and LARRY G. BUTLER[2]

Abstract. Hydrophobic exudate from roots of sorghum [*Sorghum bicolor* (L.) Moench. #[3] SORVU 'IS 8768'] contain four *p*-benzoquinones which in the dihydroquinone form are active as germination stimulants of witchweed [*Striga asiatica* (L.) Kuntz. # STRLU]. The three minor *p*-benzoquinones were partially characterized and found to be structurally similar to sorgoleone, the major *p*-benzoquinone of this exudate. Herbicidal activity of the hydrophobic exudate was due to concentration- and pH-dependent inhibition of root elongation in some but not all weeds tested. Witchweed has apparently adapted these "defense" compounds of sorghum as host-specific germination stimulants.

Additional index words. Sorgoleones, *p*-benzoquinones, allelochemicals, contact allergens, *Lactuca sativa*, STRLU, SORVU, AMARE.

INTRODUCTION

Witchweed is an angiospermous, obligate parasite of many agronomically important cereals and legumes. No economical method of control of witchweed is available. Witchweed seeds will only germinate in the presence of a chemical stimulant(s), usually exuded from roots of a host plant (8). Use of a stimulant to promote germination in the absence of a host has been proposed as a possible method of control (6, 7). Efforts have been made to identify the natural stimulant(s) from host plants (1, 2, 20).

Recently, a novel compound was isolated from hydrophobic exudates of root hairs of sorghum (9) and identified as 2-hydroxy-5-methoxy-3-[(8′Z,11′Z)-8′,11′,14′-pentadecatriene]-*p*-benzoquinone (4). The highly unstable dihydroquinone form of this quinone, which we have named sorgoleone, is active as a potent germination stimulant for witchweed (4). The oxidized, stable quinone form is inactive.

Along with sorgoleone and its dihydroquinone, other components separable by HPLC (9) have been detected in the hydrophobic exudate. In this paper, we report that three of the components are *p*-benzoquinones similar to sorgoleone. These quinones, in their dihydroquinone form, are also active as germination stimulants of witchweed.

MATERIALS AND METHODS

Plant growth conditions and collection of root exudates. IS 8768 sorghum seeds were surface sterilized and grown on filter paper in petri dishes containing distilled water as previously described (9). Seven days after planting, about 400 seedlings with roots still attached to the caryopsis were dipped in 20 ml of CH_2Cl_2 (methylene chloride) containing 50 μl of concentrated acetic acid. The CH_2Cl_2 solution was taken to dryness in vacuo (35 C).

For studies of soil-grown plants, 'BR 64' sorghum and corn (*Zea mays* L. 'A_{632}') were grown to maturity in a greenhouse in 5-gal pots containing unsterilized Terra-lite 360[4], perlite[5], and Indiana topsoil mixed in a volume ratio of 10:3:2, respectively. Plants were watered every other day. Once every other week Hoagland's solution was added. Intact soil and root systems were placed on a 25-cm-diam büchner funnel containing a 24-cm Whatman #4 filter paper disk. Water (14 L) was percolated through the soil to remove all water-soluble materials. Methylene chloride (4 L) was then percolated through the soil, collected, and taken to dryness in vacuo.

Separation of components. Methylene chloride-soluble exudate from petri dish-grown seedlings or from soil-grown plants was separately fractionated by high-performance liquid chromatography (HPLC) using a 10- by 0.4-cm LiChrosorb (5 μm) C_{18} reversed-phase column. The solvent system was that of Netzly and Butler (9). Components detected at 280 and 420 nm were collected and taken to dryness in vacuo. Individual benzoquinone fractions may contain both the quinone and its corresponding dihydroquinone. Both are nearly inseparable by the HPLC method used here.

Spectrometry. ^{1}H NMR spectra of the separated components from petri dish-grown IS 8768 sorghum were obtained at 470 MHz[6] using a 5-mm probe, locked on deuterium of the solvent $CDCl_3$ and referenced by tetramethylsilane (0.00 ppm). Electron impact and chemical ionization (isobutane) mass spectrometry[7] was performed at 70eV (100 C), and high resolution mass spectrometry[8] was performed at 70eV (200 C).

Germination and growth bioassays. Individual components, sorgoleone mixtures, or the hydrophobic exudate were redissolved in methanol, quantitated [A_{molar} = 20,000 at A_{286} (4)], and tested for stimulation of witchweed germination or for herbicidal activity. For witchweed germination bioassays, exudate samples (<1 mg) from petri dish-grown

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[3] Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

[4] Grace Horticultural Products, W. R. Grace & Co., Cambridge, MA 02140.

[5] Silbrico Corp., 6300 River Rd., Hodgkins, IL 60525.

[6] Nicolet NT 470 spectrometer.

[7] Finnigan Model 4000.

[8] Kratos MS 50.

or soil-grown plants were dissolved in 200 μl of absolute methanol, and a 10-μl portion was added to a well of a microtiter dish containing about 50 preconditioned seeds of witchweed submerged in 1 ml of sterilized H_2O (11). Three serial dilutions (100-fold each) of the above assay mixture were also tested. The assay was performed in an incubator without light (27 C) and the percentage germination was determined 48 h after stimulant was added. Control solutions were: positive, 1 ml aqueous solution containing 10 μl of methanol and 10^{-6} M strigol; negative, 1 ml of double-distilled H_2O.

For herbicidal bioassays, exudate from petri dish-grown IS 8768 sorghum seedlings was used. Solutions of hydrophobic exudate containing 1 mg or 4 μg of sorgoleones/1.5 ml methanol were separately applied to 9-cm-diam filter papers (1.5 ml/disk) completely saturating the paper. After evaporation of the methanol, 10 or 20 plant seeds that had been imbibed in distilled water for 6 h were surface dried and placed in each petri dish. Distilled water (2 ml) or 5 mM sodium phosphate buffer (2 ml), pH 5.5 or 7.5, was added to the petri dishes. Actual concentrations of sorgoleones could not be determined because sorgoleones are not readily soluble in aqueous solutions. Therefore, only the known amounts applied to the filter papers were reported. After 4 days, the seedlings were individually weighed and the length of each shoot and/or primary root was measured.

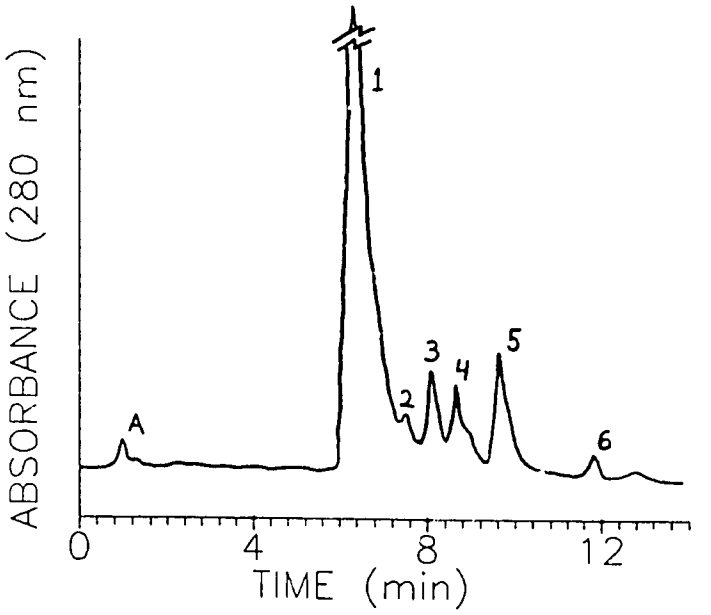

Figure 1. HPLC separation of hydrophobic exudate from root hairs of petri dish-grown IS 8768 sorghum. Chromatograms of soil-grown BR 64 sorghum were similar. Components are sorgoleone-358 (*1*); dihydroquinone of sorgoleone-358 (*2*); sorgoleone-360 (*3*); sorgoleone-386 (*4*); sorgoleone-362 (*5*); benzoquinone *6*; and a labile, component *A*.

RESULTS AND DISCUSSION

Chemical characterization of exudate components. A typical HPLC chromatogram of the hydrophobic exudate from petri dish-grown IS 8768 sorghum contained sorgoleone *1* and its dihydroquinone *2* [previously characterized (4)], as well as five other components, *A*, *3*, *4*, *5*, and *6* (Figure 1). Four of these components (*3*, *4*, *5*, and *6*) had UV-visible spectra identical to that of sorgoleone *1* (Figure 2). Labile component *A*, the only detectable nonquinonoid compound present in the hydrophobic exudate, elutes from the HPLC within the first 1.5 min (Figure 1) and has an absorbance peak around 482 nm. Though HPLC chromatograms of exudate from soil-grown BR 64 sorghum were similar to those of IS 8768, only IS 8768 components were collected for structural characterization.

Electron impact mass spectrometry of components *3*, *4*, and *5* showed very similar fragmentation patterns to that of sorgoleone *1* (Figure 3). The apparent molecular ion (M^+) assignments for sorgoleone *1* (m/z 358) and components *3* (m/z 360), *4* (m/z 386), and *5* (m/z 362) were supported by chemical ionization mass spectrometry data in which $(M+H)^+$ ions were the base peaks. As with sorgoleone *1*, components *3*, *4*, and *5* had ions at m/z 167, 168, and 169 that represent a typical quinone (Q) fragmentation pattern corresponding to Q^+, QH^+, and QH_2^+, respectively (Figure 3).

^{1}H NMR spectra of these three minor components confirmed the presence of a methoxyl (δ 3.9,s,3H), hydroxyl (δ7.2,s,1H), and hydrogen (δ5.9,s,1H), which were nearly identical chemical shift values for those same substituents of sorgoleone *1*, indicating that these substituents on the quinone ring have the same regiochemistry. A series of low

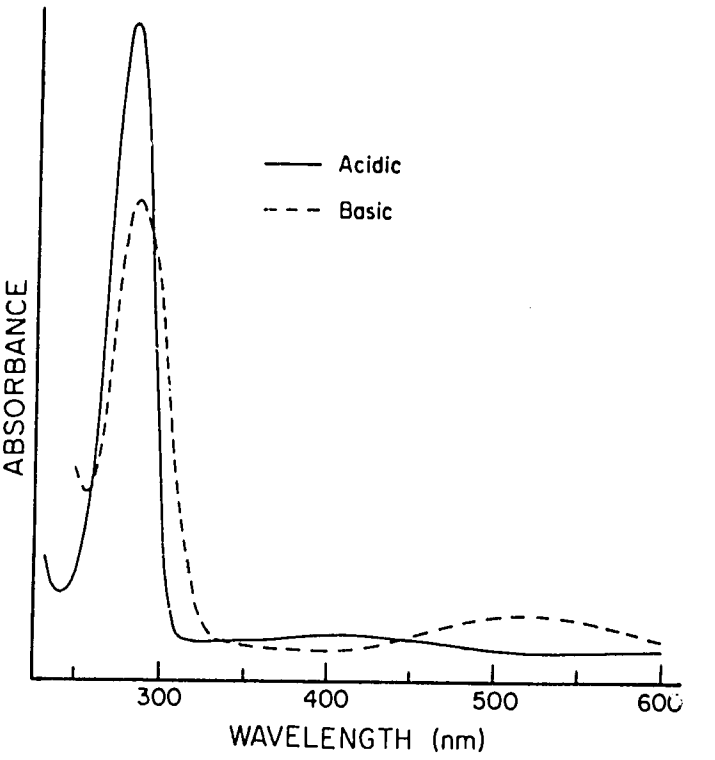

Figure 2. Absorbance spectrum representative of sorgoleone-358, sorgoleone-360, sorgoleone-386, sorgoleone-362, and benzoquinone *6* isolated from petri dish-grown IS 8768 sorghum.

molecular ion fragments 14 m/z units apart and the NMR signals (δ1.2–1.4) containing multiple hydrogens indicated that the fourth substituent on the quinone ring of each of these minor components was a long aliphatic chain. From the above data and high resolution mass spectrometry, it was deduced that the aliphatic substituent on components *3*, *4*, and *5* consisted of two double bonds in a 15-carbon chain, three double bonds in a 17-carbon chain, and one double bond in a 15-carbon chain, respectively (Figure 4). Since these compounds apparently differ only slightly in structure, we suggest that collectively they be called sorgoleones, and individually be identified on the basis of their molecular weights (Figures 1 and 3).

The small amounts obtained of purified components *A* and *6* precluded extensive chemical characterization of these two components. However, from the mass spectrum of component *6*, major ions at m/z 133, 134, 135, and its UV spectra (identical with sorgoleones) suggest it to be a benzoquinone and we have referred to it as "benzoquinone *6*".

Germination activity of exudate fractions. Stimulation of witchweed germination by the hydrophobic exudate, sorgoleones (combined), and individual components from petri dish-grown IS 8768 sorghum seedlings was compared to that of strigol, one of the most effective stimulants of witchweed germination known (5) (Table 1). With respect to strigol, the hydrophobic exudate also consists of highly effective stimulants of witchweed germination. The degree of efficacy for the exudate fractions is a conservative value, since their concentrations shown (Table 1) are not the actual concentrations but represent theoretical 100% solvation of the known amounts applied of the nearly water-insoluble material. Secondly, exudate fraction concentrations are based upon the amount of inactive, stable quinones and not that of active, unstable dihydroquinones that are generally present in amounts of one to two orders of magnitude lower than the indicated concentration of the quinones.

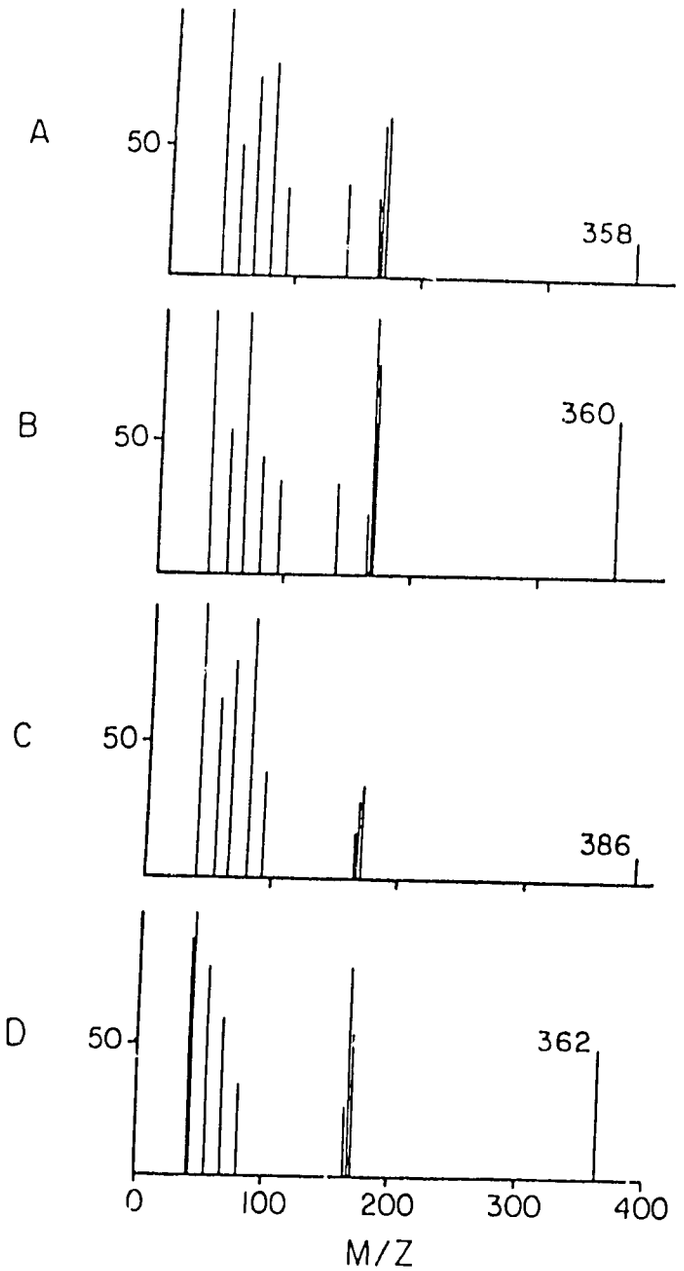

Figure 3. Mass spectra of A) sorgoleone-358, B) sorgoleone-360, C) sorgoleone-386, and D) sorgoleone-362 isolated from petri dish-grown IS 8768 sorghum.

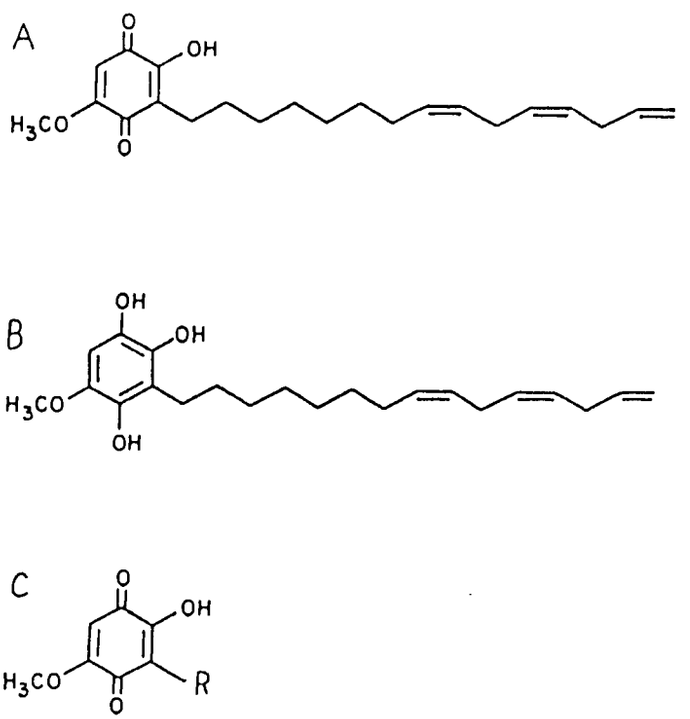

Figure 4. Structures of A) sorgoleone-358, B) dihydroquinone of sorgoleone-358, and C) sorgoleone-360, R = 15-carbon chain with two double bonds; sorgoleone-386, R = 17-carbon chain with three double bonds, sorgoleone-362, R = 15-carbon chain with one double bond.

Table 1. Efficacy of stimulation of witchweed germination by hydrophobic exudate, sorgoleones, and individual components from petri dish-grown IS 8768 sorghum seedlings[a]

Exudate fractions	Amount[b]	Germination[c]			
	(μg/assay)	(%)			
Hydrophobic exudate[d]	3.5	92	90	39	6
Sorgoleones (combined)[e]	3.5	63	0	0	0
Sorgoleone-358	3.5	52	0	0	0
Sorgoleone-360	3.5	25	0	0	0
Sorgoleone-386	3.5	25	0	0	0
Sorgoleone-362	3.5	15	0	0	0
Benzoquinone *6*	3.5	0	0	0	0
Component *A*	3.5	0	...	...	...
Strigol (pos. control)	0.35	100	100	84	5
H_2O (neg. control)	0	0	0	0	0

[a]Values are an average of two experiments.

[b]Values are based on theoretical 100% solvation and the amount of stable quinones. The actual amounts of active principle (unstable dihydroquinone) and the actual amounts solubilized are much less but not known.

[c]Columns to the right of the first column of data represent three 100-fold serial dilutions from the initial exudate fraction concentrations given.

[d]Hydrophobic exudate in all components labeled in Figure 1.

[e]Sorgoleones are quinones 1 through 5 combined (Figure 1).

Table 2. Effect of differing pH pretreatments of hydrophobic exudate from petri dish-grown IS 8768 sorghum seedlings on the ability of the exudate to stimulate the germination of witchweed[a].

Amount of sorgoleones	Germination[b]									
	Apparent pH									
	3.3	3.4	4.4	4.8	5.4	6.6	7.6	8.0	9.6	10.2
(ng/assay)	(%)									
1500	31	90	10	0	10	0	0	0	7	0
15	0	6	2	0	0	0	0	0	0	0

[a]Hydrophobic exudate (0.3 mg sorgoleones) was dissolved in 11 ml methanol. To ten 1-ml aliquots was added 100 μl of differing mixtures of 5 M acetic acid and 5 M triethanolamine. Apparent pH was determined by taking 100 μl of the methanolic solutions and adding them to 3 ml H_2O and the pH determined with a pH meter. Aliquots were taken to dryness and assayed as described in MATERIALS and METHODS.

[b]Values are an average of two experiments.

All of the individual sorgoleone fractions were active as germination stimulants of witchweed; presumably each contained a small amount of its corresponding dihydroquinone form responsible for the stimulant activity. The combined and individual sorgoleone fractions were much less active than the hydrophobic exudate. When these solutions were tested again for activity a week later, the hydrophobic exudate retained its potency while the combined and individual sorgoleone fractions generally lost 60 to 70% of their activity. It is likely that these losses of activity were due to further oxidation of the dihydroquinones to the inactive quinones. It is not known why the dihydroquinones in the hydrophobic exudate remained much more active for a longer period of time than those same individual, purified components. It may be that component *A* and/or benzoquinone *6* contribute in some way to stabilizing the dihydroquinones of the hydrophobic exudate. It is significant that purified benzoquinone *6* or component *A* were not active as germination stimulants.

The application of nitrogen (ammonia, urea) to the soil is reported to diminish witchweed parasitization in infested fields (13). Because this treatment could elevate soil pH, we investigated the effect of pH on the capacity of the hydrophobic exudate from petri dish-grown IS 8768 sorghum to stimulate witchweed germination. When aliquots of root exudate were stored for 6 days at room temperature in solutions ranging from pH 3.3 to 10.2, significant germination activity was found only in the samples between pH 3.3 and 4.4 (Table 2). Therefore, the cultural practice of applying ash to the soil to diminish witchweed parasitism (13) may be partially explainable at the germination level. Increased soil pH might cause a more rapid oxidation of the dihydroquinone forms of sorgoleones to the inactive quinones.

Lack of haustoria initiation activity of sorgoleones. After germination, witchweed and other root parasites require a chemical signal to initiate development of the haustorium (14, 15, 16). This organ attaches and penetrates into the host vascular tissue. Neither the hydrophobic exudate nor the individual sorgoleones from IS 8768 or BR 64 sorghum were consistently active as haustorial inducers of witchweed.

In roots of sorghum, 2,6-dimethoxy-*p*-benzoquinone has been extracted and identified as a haustorical inducer of witchweed (3). This and several other natural compounds known to induce haustoria are not active as germination stimulants (3, 16). These two separate signals, stimulation of germination and initiation of the haustorium, are triggered by two separate groups of compounds in sorghum.

Distribution and quantity of sorgoleones in exudates. For petri dish-grown sorghum cultivars studied (IS 8768, IS 0469, Dabar, P 967083), we found the amount of exudate ranged from 1.5 to 2% of the dry weight of the roots. There is little accumulation of sorgoleones in the roots. Less than 10% of the amount collected as exudate can be recovered from homogenates of the same roots.

Using the procedure for sorghum, no sorgoleones have been detected from roots of foxtail millet (*Pennisetum americanum* L.), corn (*Zea mays* L. 'Pioneer L3369'), white and red winter wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L. 'Canadian bonanza'), or from commercial varieties of mungbean (*Phaseolus aureus* L.) or rye (*Secale cereale* L.).

Soil-grown plant studies. Sorghum grown in petri dishes optimizes visualization of the release of these compounds (9). It is important to establish their presence also in soil-grown sorghum. To be sure that the production of the

quinone-rich exudate was not an artifact of petri dish-grown seedlings, we tested for these compounds from both BR 64 sorghum and A_{632} corn plants grown in a greenhouse in identical potting soils as described in MATERIALS and METHODS. Soil containing sorghum roots yielded 160 to 230 mg (equivalent to 10^{-4} to 10^{-5} mol/L in the soil) of sorgoleones, but soil containing corn roots yielded none. Alternatively, after the sorghum or corn roots had been carefully removed, CH_2Cl_2 extraction of the soil also yielded significant quantities of sorgoleones (again only from soil in which sorghum had grown), which were strongly active as germination stimulants. Though corn is a natural host for witchweed, sorgoleones were not present in the extract, nor was there any activity in the extract. It is probable that the germination stimulant(s) of corn are much more labile under the conditions used here.

Our data indicate that the hydrophobic compounds of sorghum migrate from the root surface into the soil. The extent of the migration, the stability of the compounds in soil, and their interactions with microorganisms is unknown. The rapid conversion from the active germination stimulant to the inactive quinone, along with its hydrophobic character, results in limited soil mobility and provides a restricted rhizosphere promotion zone. These characteristics are ideal as a host signal for witchweed germination. This strategy conserves witchweed seeds and optimizes opportunities for host attachment.

Physiological roles of sorgoleones. Hydrophobic exudate from petri dish-grown IS 8768 sorghum, at applied amounts of 1 mg of sorgoleones/petri dish under unbuffered conditions, severely inhibited root elongation of lettuce (*Lactuca sativa* L. 'Great Lakes') seedlings by 86%, and seedling fresh weight decreased by 43% compared to controls (Table 3). However, at amounts of 4 μg/petri dish there was a slight increase in root elongation of lettuce at pH 7.5 and no significant differences at pH 5.5 (Table 4). At pH 7.5, the same amount of sorgoleones inhibited redroot pigweed (*Amaranthus retroflexus* L. # AMARE) root elongation by 66% (Table 4). Neither IS 8768 sorghum, tall morningglory [*Ipomoea purpurea* (L.) Roth # PHBPU], nor velvetleaf (*Abutilon theophrasti* Medic. # ABUTH) were affected by sorgoleones under our test conditions. Both concentration and pH are important factors in determing the severity of herbicidal activity. In addition, sorgoleones appear to be selective rather than broad range in their effects.

Sorgoleones are also active as contact allergens. Approximately 500 μg of hydrophobic exudate dissolved in methanol was applied to the forearm of two human subjects resulting in an itchy rash which persisted for several days. Sorgoleones are similar in both their effects and their structures to the urushiols, the principle allergens in poison ivy (18). We suggest that sorgoleones normally function as allelochemicals inhibiting the growth of certain plant competitors of sorghum (10). Witchweed has apparently adapted to utilize these "defense" compounds of sorghum as host recognition cues for successful germination.

Dihydroquinone forms of sorgoleones are the first compounds that have been identified as germination stimulants from roots of a witchweed host. Strigol is a potent stimulant previously isolated from cotton, a nonhost for witchweed (5). Its structure is quite different from that of sorgoleones. Both sorghum and corn roots are also known to exude water-soluble germination stimulants (17, 19, 20), but no structures have been identified.

Attemps have been made to promote suicidal germination of witchweed using trap crops and ethylene, but these approaches have not proven to be effective in third world countries where the effects of witchweed are particularly devastating (12). The dihydroquinone forms of sorgoleones provide a new molecular model, simple in structure, that actively promotes germination of this parasitic weed. Only their solubility and stability appear to limit their application as control chemicals. Future research is required to

Table 3. Effects of sorgoleones and other naturally occurring compounds from sorghum on lettuce seedling germination and growth[a].

Compound	Amount	Seed germination	Root length	Seedling fresh wt
	(mg/dish)	(%)	(mm)	(mg)
None (control)	0	97	14	14
Sorgoleones	1	99	2	8
Apforol	1	99	13	13
Luteoforol	1	98	14	13
Apigeninidin	0.1	97	12	16
Luteolinidin	0.1	98	11	15

[a]Twenty lettuce seeds were placed in each petri dish and assayed as described in MATERIALS and METHODS. Values represent an average of two experiments.

Table 4. Effect of sorgoleones on the growth of lettuce, sorghum, tall morningglory, pigweed, and velvetleaf[a].

Plant	Amount of sorgoleones	Length[b] Roots pH 5.5	Roots pH 7.5	Shoots pH 5.5	Shoots pH 7.5
	(μg/dish)	(mm)			
Lettuce	4	13 ± 3	14* ± 3	12 ± 3	6* ± 2
	0	14 ± 3	10 ± 2	14 ± 4	13 ± 3
Sorghum	4	38 ± 7	34 ± 8	7 ± 3	8 ± 2
	0	42 ± 13	37 ± 8	10 ± 2	6 ± 1
Tall morningglory	4	41 ± 12	42 ± 16	28 ± 8	25 ± 9
	0	49 ± 15	50 ± 15	33 ± 8	26 ± 12
Redroot pigweed	4	13 ± 6	6* ± 2	6 ± 4	4 ± 2
	0	18 ± 5	18 ± 5	7 ± 4	7 ± 6
Velvetleaf	4	36 ± 11	36 ± 5	14 ± 6	14 ± 4
	0	...	36 ± 5	...	15 ± 2

[a]Ten seeds were placed in each petri dish and assayed as described in MATERIALS and METHODS. Values are an average of three experiments.

[b]Asterisk (*) denotes significant differences between treatments (4 μg/petri dish) and controls (0 μg/petri dish) at $P<0.01$ based on Student's t-test.

determine if these characteristics can be improved while retaining promotion of germination. The relatively simple structure of these sorgoleones compared to strigol (5) suggests it may be possible to economically synthesize more stable, yet active analogues to be used as "suicidal" germination stimulants for the eventual eradication of the weed (6).

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LITERATURE CITED

1. Brown, R., A. W. Johnson, I. Robinson, and A. R. Todd. 1949. The stimulant involved in the germination of *Striga hermonthica*. Proc. R. Soc. B 136: 1–12.
2. Brown, R., A. W. Johnson, I. Robinson, and G. J. Tyler. 1952. The Striga germination factor. 2. Chromatographic purification of crude concentrates. Biochem. J. 50: 596–600.
3. Chang, M., and D. G. Lynn. 1986. Haustoria and the chemistry of host recognition of parasitic angiosperms. J. Chem. Ecol. 12: 561–579.
4. Chang, M., D. H. Netzly, L. G. Butler, and D. G. Lynn. 1986. Chemical regulation of distance. Characterization of the first natural host germination stimulant for *Striga asiatica*. J. Am. Chem. Soc. 108: 7858–7860.
5. Cook, C. E., L. P. Whichard, M. E. Wall, G. H. Egley, P. Coggon, P. A. Luhan, and A. T. McPhail. 1972. Germination stimulants. II. The structure of Strigol — a potent seed germination stimulant for witchweed (*Striga lutea* Lour.). J. Am. Chem. Soc. 94: 6198–6199.
6. Egley, G. H., and J. E. Dale. 1970. Ethylene, 2-chloroethyl phosphonic acid, and witchweed germination. Weed Sci. 18: 586–589.
7. Johnson, A. W., G. Roseberry, and C. Parker. 1976. A novel approach to Striga and Orobanche control using synthetic germination stimulants. Weed Res. 16: 223–227.
8. Musselman, L. J. 1980. The biology of *Striga*, *Orobanche*, and other root-parasitic weeds. Annu. Rev. Phytopathol. 18: 463–489.
9. Netzly, D. H., and L. G. Butler. 1986. Roots of *Sorghum bicolor* exude hydrophobic droplets that contain biologically active materials. Crop Sci. 26: 775–778.
10. Netzly, D. H., G. Ejeta, T. Housley, D. Hess, and L. Butler. 1986. Mechanisms of resistance to *Striga* in sorghum. Pages 50–51 *in* Proceedings of a Workshop on Biology and Control of Orobanche. LH/VPT, Wageningen, The Netherlands.
11. Nickrent, D. L., L. J. Musselman, J. L. Riopel, and R. E. Eplee. 1979. Haustorial initiation and non-host penetration in witchweed (*Striga asiatica*). Ann. Bot. 43: 233–236.
12. Nour, I., M. Press, G. Stewart, and J. Tuohy. 1986. Africa in the grip of witchweed. New Sci. 109: 44–48.
13. Pesch, C., A. H. Pieterse, and W. A. Stoop. 1983. Inhibition of germination in Striga by means of urea. Pages 37–38 *in* Proceedings of the Second International Workshop on Striga. ICRISAT, Ouagadougou, Upper Volta.
14. Riopel, J. L., and W. V. Baird. 1987. Morphogenesis of the early development of primary haustoria in *Striga asiatica*. Pages 107–125 *in* L. J. Musselman, ed. Parasitic Weeds in Agriculture. Vol. I. *Striga*. CRC Press, Boca Raton, FL.
15. Riopel, J. L., and L. J. Musselman. 1979. Experimental initiation of haustoria in *Agalinis purpurea*. Am. J. Bot. 66: 570–575.
16. Steffens, J. C., D. G. Lynn, V. S. Kamat, and J. L. Riopel. 1982. Molecular specificity of haustorial induction in *Agalinis purpurea* (L.) Raf. (Scrophulariaceae). Ann. Bot. 50: 1–7.
17. Sunderland, N. 1960. The production of the Striga and Orobanche germination stimulants by maize roots. I. The number and variety of stimulants. J. Exp. Bot. 11: 236–245.
18. Symes, W. F., and C. R. Dawson. 1954. Poison ivy "urushiol". J. Am. Chem. Soc. 76: 2959–2963.
19. Van Staden, J. 1976. The release of cytokinins by maize roots. Plant Sci. Lett. 7: 279–283.
20. Worsham, A. D. 1987. Germination of witchweed seeds. Pages 45–61 *in* L. J. Musselman, ed. Parasitic weeds in Agriculture. Vol. I. *Striga*. CRC Press, Boca Raton, FL.