Influence of Conditions and Genotype on the Amount of *Striga* Germination Stimulants Exuded by Roots of Several Host Crops

Yohan Weerasuriya,† Bupe A. Siame,‡ Dale Hess,§ Gebisa Ejeta,† and Larry G. Butler*,‡

Departments of Agronomy and Biochemistry, Purdue University, West Lafayette, Indiana 47907, and Millet Pathology, ICRISAT Sahelian Centre, B.P. 12404, Niamey, Niger

Witchweeds (*Striga* spp.) are important root parasites of many cereals and legumes. *Striga* seeds do not germinate unless exposed to specific chemical signals produced by host and nonhost roots. We report a simple method for obtaining large quantities of relatively clean root exudate from several crop plants. A *Striga* seed germination assay was used to quantify stimulant activity produced and identify potential low stimulant producing resistant host plants. Stimulant activity produced by sorghum cultivars susceptible to *Striga* was several orders of magnitude greater than that of some resistant cultivars. Nonhost plants with capacity to stimulate germination of *Striga* were also identified. Stimulant activity produced was much greater for plants grown using a short day length. In addition to germination stimulants, root exudates also contained inhibitor(s) of germination.

INTRODUCTION

Witchweeds (*Striga* spp.) are angiospermous root parasites that constrain production of cereals and legumes in Africa and the Indian subcontinent. *Striga* is highly adapted to its hosts (Vasudeva Rao and Musselman, 1987) and its environment (Patterson, 1987). *Striga* germination and haustorial initiation occur when in close proximity to the host roots and when stimulated by specific chemical signals exuded by host (and some nonhost) roots. The first *Striga* germination stimulant identified, strigol (Cook et al., 1966), was isolated from the roots of cotton (*Gossypium hirsutum* L.), which is not a host for *Striga*. The first *Striga* germination stimulant identified from a host plant was sorgoleone, from sorghum [*Sorghum bicolor* (L.) Moench] root hair droplets (Chang et al., 1986). We subsequently reported that the levels of germination stimulant activity of sorghum root exudate compounds more stable and more water soluble than sorgoleone correlated highly with sorghum resistance/susceptibility to *Striga asiatica* (L.) Kuntze and *Striga hermonthica* (Del.) Benth, whereas sorgoleone production did not (Hess et al., 1992). Hauck et al. (1992) recently reported the isolation and identification of a strigol analog, sorgolactone, as the major *Striga* water-soluble germination stimulant exuded by sorghum roots. The same group have shown that another strigol analog, alectrol, accounts for most of the *Striga gesnerioides* (Willd.) Vatke germination stimulant activity in cowpea root exudates (Muller et al., 1992). In an accompanying paper we report that strigol accounts for most of the water-soluble germination stimulant activity in root exudate of maize (*Zea mays* L.) and proso millet (*Panicum miliaceum* L.) and a small amount of the activity in sorghum root exudate (Siame et al., 1993).

In the course of this work we developed a simple method for obtaining large quantities of uncontaminated root exudate compounds. We wanted a method that permits comparison of the *Striga* germination stimulants and inhibitor activities in a wide variety of plants, both hosts and nonhosts of *Striga*. This method and the profound effects of environmental conditions on the amount of germination stimulant activity produced are summarized in this paper.

MATERIALS AND METHODS

Sources of Seeds. *S. asiatica* seeds were obtained from Dr. Robert Eplee, USDA/APHIS, Whiteville Methods Development Center, Whiteville, NC. Seeds were stored and handled under quarantine restrictions approved by USDA/APHIS and the Indiana Department of Natural Resources. Sorghum, maize, and pearl millet [*Pennisetum glaucum* (L.) R. Br.] seeds were obtained from the Purdue University Agronomy Research Center. Proso millet seeds was purchased from a commercial source (Gutwein Milling Co. Inc., Francesville, IN). Cowpea [*Vigna unguiculata* (L.) Walp.] seeds were obtained from Dr. L. Murdock, Purdue University. The sorghum cultivars were chosen to represent both *Striga* susceptible (IS-4225, Shanqui Red, P-954063, P-721N, IS-8768, Babadia Fara) and resistant (SRN-39, P-967083, Dobbs, IS-9830, Framida, N-13) varieties. Proso millet, pearl millet, maize, soybean [*Glycine max* (L.) Merr.], lablab beans (*Dolichos lablab*), rice (*Oryza sativa* L.), and barley (*Hordeum vulgare* L.) cultivars were not chosen on the basis of *Striga* resistance/susceptibility because resistant cultivars have not been reported.

Surface Sterilization of Crop Seeds. Sterile (autoclaved) double-deionized water was used in all experiments. Seeds were soaked in 75% ethanol for 2 min. and then in a 1% NaOCl solution (commercial bleach diluted 5-fold) for 10–20 min. The seeds were rinsed three times with water and soaked in a 5% aqueous solution of Captan 50-W [*N*-[(trichloromethyl)thio]-4-cyclohexene-1,2-dicarboximide] (Platte Chemical Co., Fremont, NE) for 1–24 h. The seeds were again washed three times with water, transferred to Petri dishes lined with moist filter paper, and incubated in the dark at 24 °C for 1 or 2 days.

Surface Sterilization and Preconditioning of *Striga* Seeds. About 10 mg of *Striga* seeds was washed twice with 10 mL of water containing 2 drops of 10% Tween 20 (Sigma Chemical Co., St. Louis, MO) to remove sand and debris. The seeds were sonicated for 3 min with occasional swirling in a 10-mL sterilizing and disinfecting solution of 50% sporicidin (the stock sporicidin solution was made by mixing 10.9 mL of buffer and 0.95 mL of activator, both from the Sporicidin Co., Washington, DC, and by diluting 10-fold in water) and rinsed three times with water. The seeds were sonicated again in sporicidin for 3 min and washed three times with water. *Striga* seeds require warm, moist conditions for a period of 10–21 days prior to exposure to a germination stimulant for germination to occur. Cleaned seeds were preconditioned in the dark at 28 °C in 14 mL of water and 1 mL of 0.015% benomyl [methyl 1-(butylcarbamoyl)-2-benzimidazolecarbamate] (Carolina Biological Supply Co., Burlington,

† Department of Agronomy.
‡ Department of Biochemistry.
§ Millet Pathology.

0021-8561/93/1441-1492$04.00/0

NC). After 2–3 days and again after about 12 days, the *Striga* seeds were transferred to a fresh flask containing 15 mL of 0.001% benomyl and returned to the incubator. All *Striga* seeds used for the germination assays were preconditioned in this way for 14–21 days.

Collection of Root Exudate. Seedlings of *Striga* hosts were grown in 250-mL Nalgene bottles from which the bottoms had been cut off. The bottles were inverted with their mouths closed with four layers of cheesecloth held with a rubber band. Small pieces of washed sterile glass wool were loosely placed to a depth of approximately 6 cm, and sterilized germinating seedlings were placed on top of the glass wool. Generally seedlings were transferred to glass wool pots 1 day after germination. More glass wool was added to cover the seeds and to prevent root desiccation. Sufficient water was added to saturate the free-draining pots. The pots were placed in an incubator under a photoperiod of 16 h, relative humidity of 80%, and day/night temperatures of 25/18 °C, respectively, and kept saturated with water at all times. The pots were left uncovered, so the germinating sorghum seeds were fully exposed to light as compared to the normal condition of burial in the soil.

Root exudate containing both stimulants and inhibitors of *Striga* germination was collected daily or on alternate days from the bottles by suction filtration on a Büchner funnel. Sufficient water was added to rinse the bottles and collect about 25 mL of aqueous exudate solution from each bottle at each collection. Root exudates, collected from about the 2nd to 12th days after germination, were diluted and assayed for germination stimulant activity the same day they were collected. Checks without stimulant and with strigol as stimulant were included.

Germination Assays. Root exudates were serially diluted 3- or 10-fold with water, and 500 μL of the diluted exudate was added to individual wells of Falcon 3047 24-well multiwell tissue culture plates (Becton Dickinson and Co., Lincoln Park, NJ). Five microliters (~100–150 seeds) of a water suspension of preconditioned *S. asiatica* seeds was placed in each well, and the seeds were incubated at 28 °C for 20 h. Germinated and nongerminated seeds were counted under a microscope, and germination percentages were calculated for each well. Two or three replicates were performed for each dilution.

Inhibition of Germination. Stimulant and "inhibitor" fractions of the crude root exudate were separated using C_{18} Sep-Pak (Waters) preparatory columns. Sep-Paks were conditioned by first running 5 mL of methanol and then 5 mL of water through the columns. About 40 mL of crude undiluted root exudate was loaded onto the columns, and the columns were washed with 5 mL of water. The water wash had no germination stimulants but contained germination inhibitor. The concentrated stimulant was eluted using 4 mL of methanol and then diluted in water to the original stimulant volume. Inhibitor fractions from crude root exudates collected over several days from many sorghum cultivars (both resistant and susceptible) were isolated. Inhibition assays were performed by measuring the activity of the stimulant fractions in the presence or absence of the inhibitor fraction.

RESULTS AND DISCUSSION

Production of Germination Stimulant throughout Seedling Development. Several cereal seedlings produced considerable amounts of stimulant activity within 2 days after transfer to glass wool (Figure 1). Detailed work with sorghum (cv. IS-4225) showed that stimulant activity increased progressively with time, reached a maximum within about 7 or 8 days, and then declined (Figure 2).

Effect of Photoperiod on Germination Stimulant Production. Under our conditions, stimulant activity produced by IS-4225 seedlings was many-fold higher when grown under short light periods (2 h/day) than under long day conditions (16 h/day) (Figure 3). As much as 10^6-fold differences in stimulant activity were observed in seedlings grown under 2 and 16 h of light. Only genotypes that produced high levels of germination stimulant activity such as sorghum IS-4225 and proso millet showed such large

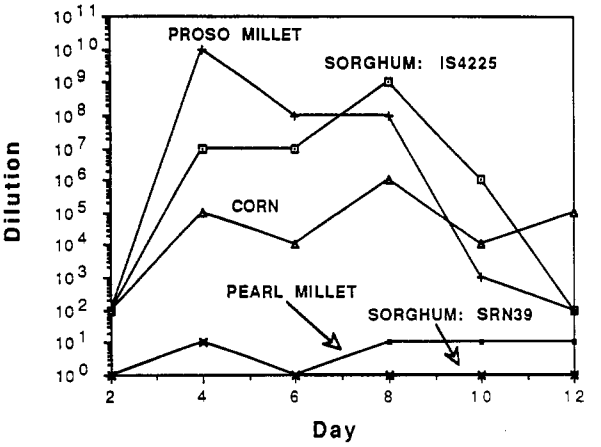

Figure 1. Germination stimulant activity produced by different cereals. The greatest dilution to give at least 25% germination is indicated. Days refer to the time after seedlings were transferred to glass wool pots. Note log scale on *Y* axis (dilutions).

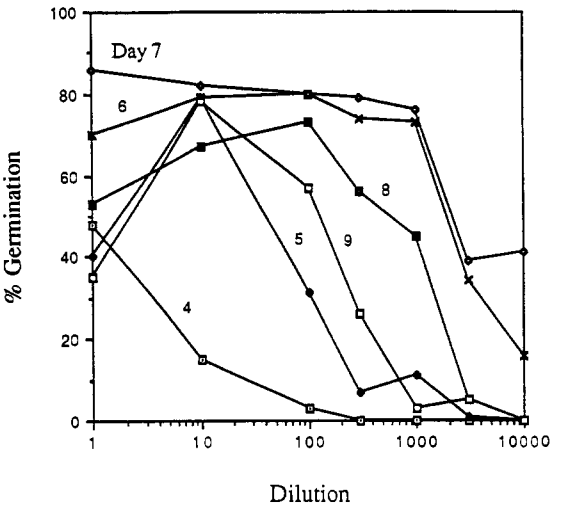

Figure 2. Germination stimulant activity produced by sorghum IS-4225 through days 4–9. Days refer to the time after seedlings were transferred to glass wool pots. Plants were grown using a photoperiod of 16 h.

differential response to photoperiod. Low stimulant producing sorghum genotypes (SRN-39 and IS-9830) did not show a similar response to changes in day length. Determination of the possible significance of day length as a factor influencing *Striga* germination under field conditions and the effect of protection of the seeds from light would require further studies. Manipulation of the photoperiod for optimum stimulant production significantly facilitated isolation and identification of the stimulant components as reported in the companion paper (Siame et al., 1993).

Identification of Low Stimulant Producing Host Cultivars. The amount of germination stimulant activity produced varied widely with respect to cultivar and, as previously shown, with time after germination (Figure 2 and Table I). The duration of stimulant activity production was dependent on seed size (Figure 1). This suggests that stimulant is produced at the expense of energy reserves of the seeds. The seedlings were provided with only water; no fertilizer or mineral solutions were supplied.

Of all the species and cultivars tested, sorghum line IS-4225 and proso millet produced the most stimulant activity (Figure 1). All sorghum cultivars known to be susceptible to *Striga* produced large amounts of stimulant activity (Table I). The rice and barley cultivars tested

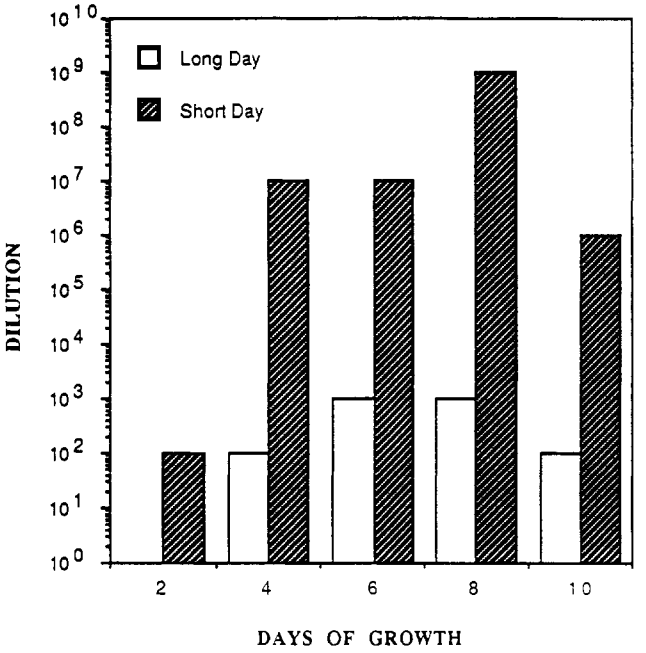

Figure 3. Germination stimulant activity produced by IS-4225 using 2 h of light/day (dark) as compared to 16 h of light/day (light) (note log scale). Days refer to the time after seedlings were transferred to glass wool pots. The greatest dilution to yield at least 25% germination is indicated.

Table I. Germination Stimulant Activity Produced by Different Sorghum Cultivars[a]

sorghum cultivar	field reaction to *Striga*[b]	dilution				
		day 4	day 6	day 8	day 10	day 12
IS-4225	S	10^3	10^4	10^3	10^4	10^3
P-954063	S	10	10^4	10^3	10^4	10^4
P-721N	S	1	10^2	10^2	10^2	10
Shanqui Red	S	10	10^2	10^3	10^2	10^2
SRN-39	R	1	10	10	1	10
IS-9830	R	0[c]	1	10	0[c]	10
Framida	R	0[c]	1	10	0[c]	10
P-967083	R[d]	10	10^2	10^2	10^3	10^3
N-13	R[d]	10^2	10^3	10^3	10^2	10^3
Dobbs	R[d]	10	10^2	10^2	10^2	10^3

[a] The dilution needed to give a germination percentage of at least 25% is indicated. Days indicate the time after seedlings (1-day-old) were transferred to glass wool. Seedlings were grown using a photoperiod of 2 h. [b] Refers to susceptibility (S) or resistance (R) under field conditions. [c] Germination percentage was below 25% at all dilutions. [d] Resistance is due to mechanisms other than low stimulant production.

produced low amounts of stimulant activity like sorghum SRN-39 (results not shown). Although pearl millet is a host of *Striga*, *S. asiatica* seeds showed a very low response to pearl millet root exudates. The pearl millet cultivar tested could be a low stimulant producer, but it is also possible that the seeds of the strain of *S. asiatica* which occurs in the United States do not respond to pearl millet. Strains that are specific for sorghum or millet have been reported for *S. asiatica* (Bharathalakshmi and Jayachandra, 1979) as well as for *S. hermonthica* (Wilson-Jones, 1955; King and Zummo, 1977; Bebawi, 1981).

As expected, some resistant sorghum cultivars (SRN-39, IS-9830, and Framida) produced very little germination stimulant activity (Table I). Sorghums reported to be resistant, but which produced high levels of stimulant activity (P-967083, N-13, and Dobbs), have some other mechanism of resistance rather than low stimulant production. Cultivars N-13 and Dobbs have been reported

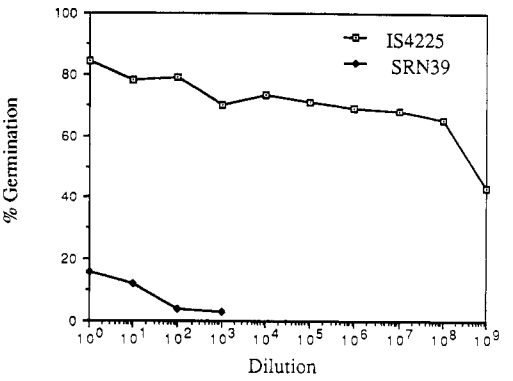

Figure 4. Comparison of germination stimulant activity produced by *Striga* resistant (SRN-39) and susceptible (IS-4225) sorghum cultivars. Stimulant production was measured 8 days after seedlings were transferred to glass wool pots.

to be resistant due to mechanical barriers on the host root that prevent penetration of *Striga* (Maiti et al., 1984; El Hiweris, 1987; Doggett, 1988). Resistance of cultivars P-967083 and N-13 has been attributed to avoidance of interactions between parasitic seeds and host roots due to limited host root growth in the upper soil profile (Dixon and Parker, 1984; Cherif-Ari et al., 1990). Our assay identifies resistance only on the basis of low stimulant production.

Differences in stimulant activity have been shown to correlate well with differences in stimulant production as measured by germination distances for the same cultivars observed in the agar gel assay described by Hess et al. (1992). The results of agar gel assays correlated with field performance, showing that low stimulant production in the first few days of growth indicates *Striga* resistance under field conditions (Ejeta et al., 1993). Using the agar gel assay, *Striga* germination distances from the host root for sorghum lines SRN-39 and IS-4225 were 0.1 and 3.3 cm, a 33-fold difference. By assaying dilutions of crude root exudate, we have shown a more than 10^9-fold difference in stimulant activity produced between these two cultivars (Figure 4). Therefore, the dilution assay is more sensitive than the agar gel assay and better suited for quantifying stimulant activity production in various plants. The agar gel assay is more rapid and simple and is better suited to screening a large number of entries, whereas our dilution assay is applicable to a wider variety of crop plants. Stimulant production in legumes is difficult to measure using the agar gel assay because the larger legume roots break through the agar and disrupt the agar layer. In the dilution assay, stimulant activity produced by many species can be measured easily under different environmental conditions.

Identification of Potential Trap Crops. The germination assay was also used to identify crops that produce large amounts of germination stimulant activity yet are not parasitized by *Striga*. These "trap crops" are grown to induce suicidal germination of *Striga* and thereby decrease the seed population in the soil. A simple laboratory assay for screening nonhost plants as potential trap crops for *Striga* based on stimulant production would be much easier than performing extensive field trials to identify false hosts with potential to be used as trap crops.

Root exudate of all plants tested contained at least a small amount of *S. asiatica* germination stimulant activity (Figure 1; Tables I and II). Identification of germination stimulant(s) produced by soybean, lablab bean, and pearl millet has not been reported. Some of the legumes tested produced sizable levels of stimulant activity (Table II). However, legumes did not grow well under the conditions

Table II. Germination Stimulant Activity Produced by Legumes[a]

cultivar	dilution			
	day 4	day 6	day 8	day 10
soybean	10	10	10	10
lablab bean	0	1	1	10
cowpea: Br 1	10	10	10	10^3
cowpea: VVA	10^3	10	10^2	10^2
cowpea: Cal Blackeye	10	10^2	10^2	10^3

[a] The greatest dilution which produced at least 25% germination is indicated. Plants were grown using a photoperiod of 2 h.

used for the cereals (2 h of light). The cowpea cultivar, California blackeye, produced about 10^3-fold more stimulant activity under 8 h of light than under 2 h of light (results not shown), possibly because of poor growth of the plants exposed to less light. The assay must be modified and optimized for legumes to compare legumes for stimulant production.

In the field, cowpeas are parasitized by *S. gesnerioides* but not by *S. asiatica*. The host spectrum of *S. gesnerioides* (legumes, sweet potato, and tobacco) is different from that of *S. asiatica* (cereals). Our finding that cowpea root exudates contain a stimulant that germinates *S. asiatica* seeds was not unexpected, however, because legumes have been utilized as trap crops. Assuming *S. gesnerioides* responds to the same stimulant from cowpea, it may be possible to screen cowpea cultivars (and possibly other hosts of *S. gesnerioides*) for resistance based on their capacity to germinate *S. asiatica* seeds. Quarantine regulations prohibit the growth of *S. gesnerioides* or *S. hermonthica* in the United States. Because cowpea exudate stimulates *S. asiatica*, germination stimulant specificity cannot be the mechanism that confers its host specificity toward *S. gesnerioides*.

Evidence for a Germination Inhibitor. On days 5 and 9 (Figure 2), germination percentages more than doubled when the root exudate was diluted 10-fold. This decreased germination at high concentrations of root exudate suggests the presence of germination inhibitor(s). Inhibition was seen only when stimulant activity was low and at high concentrations of root exudate, indicating that the effect of inhibitor is diluted out much more readily than that of stimulant. High amounts of stimulant activity seemed to overcome this inhibition.

To look at the activities of inhibitor(s) and stimulant(s) independently, inhibitor and stimulant were separated using a C_{18} Sep-Pak to which stimulant bound but inhibitor washed out with water. Inhibitor activity was tested by diluting both crude exudate and stimulant fraction with inhibitor or with water (control). Dilution of the stimulant with the inhibitor fraction greatly reduced germination (Figure 5) as compared to dilution with water, as expected for the presence of an inhibitor.

All sorghum cultivars tested (both resistant and susceptible) showed similar levels of inhibitor(s) activity (Table III). Inhibition is incomplete and dilutes out more readily than does stimulation (Figure 2). Therefore, it is unlikely that an inhibitor is produced specifically to prevent germination of *Striga* seeds.

Summary. A technique was developed for collecting water-soluble root exudate compounds. A *Striga* seed germination assay was used to quantitate stimulant activity produced by roots of several crop plants, both hosts and nonhosts. Germination stimulant activity exuded by sorghum roots was much higher under conditions of shorter light periods. All susceptible and some resistant (by other mechanisms) sorghum cultivars produced relatively large amounts of germination stimulant activity. This germination assay is useful to screen and identify germ plasm whose resistance is based on low germination stimulant production. Another potential use for the germination assay could be to identify high stimulant producing trap crops of *Striga*. At least one inhibitor of *Striga* seed germination was found to be present, in addition to stimulant, in sorghum root exudates. However, since all plants tested produce comparable levels of inhibitor activity and because high stimulant activity overcame the inhibition, it is unlikely that the inhibitor plays an important role in the germination process.

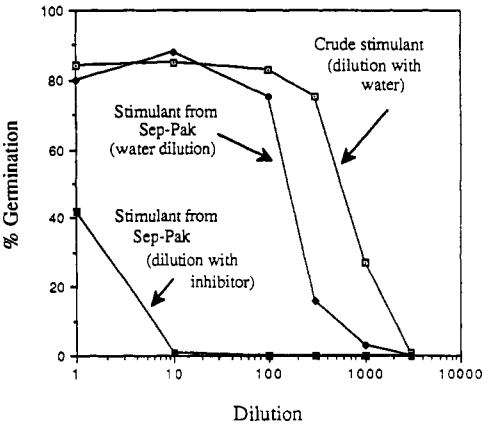

Figure 5. Effect of inhibitor(s) on germination. Stimulant was first diluted in water and then diluted 3-fold with the inhibitor fraction (from the Sep-Paks) or with distilled water to obtain the final stimulant dilution.

Table III. Inhibition of *Striga* Germination by the Inhibitor Fraction from the Root Exudate of Different Sorghum Cultivars[a]

sorghum cultivar (source of inhibitor)	reaction to *Striga*[b]	% inhibition[c]			
		day 1	day 5	day 9	day 11
SRN-39	R	41	81	73	81
IS-9830	R	36	73	84	77
Dobbs	R	37	64	87	80
N-13	R	40	69	84	86
IS-8768	S	46	67	88	93
Babadia Fara	S	33	48	78	69

[a] Germination stimulant collected from Babadia Fara was diluted with either distilled water (control) or inhibitor (collected 1–11 days after the seedlings were transferred to glass wool). Inhibition percentages are compared to that of a control in which the stimulant was diluted with water instead of with inhibitor. [b] Refers to susceptibility (S) or resistance (R) in the field. [c] Control germination stimulant gave a germination percentage of 83% at the dilution used here (30-fold).

ACKNOWLEDGMENT

This is Journal Paper 13754 of the Agricultural Experiment Station of Purdue University. This work was supported by the SADCC/ICRISAT/INTSORMIL Student Training Program, The International Sorghum and Millet CRSP, and Grant GA AS 8905 from the Rockefeller Foundation.

LITERATURE CITED

Bebawi, F. F. Intraspecific physiological variants of *Striga hermonthica*. *Exp. Agric.* **1981**, *17*, 419–423.

Bharathalakshmi; Jayachandra, R. Physiological variants in *Striga asiatica*. In *Proceedings of the 2nd International Symposium on Parasitic Weeds*; Musselman, L. J., Worsham, A. D., Eplee, R. E., Eds.; North Carolina State University: Raleigh, NC, 1979; pp 132–134.

Chang, M.; Netzly, N. H.; Butler, L. G.; Lynn, D. G. Chemical regulation of distance: characterization of the first natural host germination stimulant for *Striga asiatica*. *J. Am. Chem. Soc.* **1986**, *108*, 7858–7860.

Cherif-Ari, O.; Housley, T. L.; Ejeta, G. Sorghum root length density and the potential for avoiding *Striga* parasitism. *Plant Soil* **1990**, *121*, 67–72.

Cook, C. E.; Whichard, L. P.; Turner, B.; Wall, M. E.; Egley, G. H. Germination of witchweed (*Striga lutea* Lour.): isolation and properties of a potent stimulant. *Science* **1966**, *154*, 1189–1190.

Dixon, N. H.; Parker, C. Aspects of the resistance of sorghum varieties to *Striga* species. In *Proceedings of the Third International Symposium on Parasitic Weeds*; International Center for Agricultural Research in the Dry Areas (ICARDA): Aleppo, Syria, 1984; pp 123–134.

Doggett, H. *Sorghum*, 2nd ed.; Wiley: New York, 1988; pp 392–394.

Ejeta, G.; Butler, L.; Babiker, A. G. T. "New approaches to the control of *Striga*. *Striga* research at Purdue University"; Research Bulletin 991; Agricultural Experiment Station, Purdue University, West Lafayette, IN, 1993.

El Hiweris, S. O. Nature of resistance to *Striga hermonthica* (Del.) Benth parasitism in some *Sorghum vulgare* (Pers.) cultivars. *Weed Res.* **1987**, *27*, 305–311.

Hauck, C.; Muller, S.; Schildknecht, H. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a genuine host plant. *J. Plant Physiol.* **1992**, *139*, 474–478.

Hess, D.; Ejeta, G.; Butler, L. G. Selecting sorghum genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga*. *Phytochemistry* **1992**, *31*, 493–497.

King, S. B.; Zummo, N. Physiologic specialization in *Striga hermonthica* in West Africa. *Plant Dis. Rep.* **1977**, *61*, 770–773.

Maiti, R. K.; Ramaiah, K. V.; Bisen, S. S.; Chidley, V. L. A comparative study on the development of *Striga asiatica* (L.) Kuntze on sorghum cultivars. *Ann. Bot.* **1984**, *54*, 447–457.

Muller, S.; Hauck, C.; Schildknecht, H. Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. *J. Plant Growth Regul.* **1992**, *11*, 77–84.

Patterson, D. T. Environmental factors affecting witchweed growth and development. In *Parasitic Weeds in Agriculture*; Musselman, L. J., Ed.; CRC Press: Boca Raton, FL, 1987; Vol. 1, pp 27–44.

Siame, B. A.; Weerasuriya, Y.; Wood, K.; Ejeta, G.; Butler, L. G. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. *J. Agric. Food Chem.* **1993**, preceding paper in this issue.

Vasudeva Rao, M. J.; Musselman, L. J. Host specificity in *Striga* species and physiological strains. In *Parasitic Weeds in Agriculture*; Musselman, L. J., Ed.; CRC Press, Boca Raton, FL, 1987; Vol. 1, pp 13–26.

Wilson-Jones, K. Further experiments on witchweed control. II. The existence of physiological strains of *Striga hermonthica*. *Emp. J. Exp. Agric.* **1955**, *23*, 206–213.

Received for review March 29, 1993. Revised manuscript received June 24, 1993. Accepted July 16, 1993.[⊗]

[⊗] Abstract published in *Advance ACS Abstracts*, August 15, 1993.