

CONTROL OF WITCHWEED *Striga hermonthica* BY INTERCROPPING WITH *Desmodium* spp., AND THE MECHANISM DEFINED AS ALLELOPATHIC

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Abstract—During investigations into the control of insect damage to maize crops in subsistence farming in Kenya, which involved intercropping with repellent plants, the fodder legumes silverleaf (*Desmodium uncinatum*) and greenleaf (*D. intortum*) were also found to reduce dramatically the infestation of maize by parasitic witchweeds such as *Striga hermonthica*. This effect was confirmed by further field testing and shown to be significantly greater than that observed with other legumes, e.g., cowpea, as were the concomitant yield increases. The mechanism was investigated, and although soil shading and addition of nitrogen fertilizer showed some benefits against *S. hermonthica* infestation, a putative allelopathic mechanism for *D. uncinatum* was observed. In screenhouse studies, a highly significant reduction in *S. hermonthica* infestation was obtained when an aqueous solution, eluting from pots in which *D. uncinatum* plants were growing, was used to irrigate pots of maize planted in soil seeded with high levels of *S. hermonthica*. Growth of the parasitic weed was almost completely suppressed, whereas extensive infestation occurred with the control eluate. Laboratory investigations into the allelopathic effect of *D. uncinatum*, using samples of water-soluble chemical components exuded from cleaned roots, demonstrated that this

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involved a germination stimulant for *S. hermonthica* and also an inhibitor for haustorial development.

Key Words—Allelopathy, maize, *Striga*, *Desmodium*, nitrogen, shading, silver-leaf, germination stimulant, suicidal germination.

INTRODUCTION

The witchweeds are parasitic plants that, after germination, attach to the roots and cause considerable interference with normal development of their host plants (Parker and Riches, 1993). Witchweeds threaten the staple food of over 100 million people in Africa (M'boob, 1989; Musselman et al., 1991; Lagoke et al., 1991). Of the 23 species prevalent in Africa, *Striga hermonthica* (Scrophulariaceae) is the most significant, parasitizing a wide range of crops including maize, sorghum, millet, fonio, rice, and sugar cane (Musselman, 1994; Berner et al., 1996). Other witchweed species of importance in Africa are *S. aspera*, *S. asiatica*, and *S. passargei* on cereals, *S. gesnerioides* on cowpea, and *Alectra vogelli* (Scrophulariaceae) on cowpea, groundnut, and soybean. Although *S. aspera* originally parasitised wild grasses, it now has an extended host range that includes maize (Carson, 1989). Seeds can remain viable in the soil for up to 20 years and can be spread by both mechanical and cultural processes. This study focuses on *S. hermonthica*, for which there are currently no viable control methods suitable for the socioeconomic conditions of the most afflicted regions in Africa (Lagoke et al., 1991; Berner et al., 1995).

Control of *S. hermonthica* was observed during the development of a control strategy against stem borers in maize in eastern Africa. The strategy involved creating a push-pull effect using highly attractive trap crops to aggregate oviposition of adult stem borers, for example, *Busseola fusca* (Noctuidae) and *Chilo partellus* (Pyralidae), away from the central maize stand, and intercropping between the maize rows with repellent plants (Khan et al., 2000). The most effective of the repellent intercrops was molasses grass, *Melinis minutiflora*, and this plant additionally caused an increase in parasitization of those stem borers that were not aggregated away from, or directly repelled from, the maize (Khan et al., 1997). However, the legumes silverleaf, *Desmodium uncinatum*, and greenleaf, *D. intortum*, were also investigated as intercrops because of their high value as cattle forage and for their role in fixing atmospheric nitrogen. In trials in the Suba district of Kenya, where *S. hermonthica* is highly prevalent, these legumes were found to give an unexpected and dramatic reduction in infestation by this witchweed.

The objective of the current study was to compare directly the effect of *Desmodium* species with that of other plants reported to reduce colonization by witchweeds (Carson, 1986) and to investigate the mechanism by which control of the parasitic plant is effected. This could be by increasing available nitrogen, by

offering shade, or by an allelopathic effect involving chemicals associated with the roots, all of which are mechanisms known to give some control of these parasitic weeds (Press and Gurney, 2000).

METHODS AND MATERIALS

Seeds. Seeds of the following plants were employed in these studies: silverleaf, *Desmodium uncinatum* (Jacq.) DC. (Fabaceae), greenleaf, *Desmodium intortum* (Mill.) Urb. (Fabaceae), maize, *Zea mays* L. (Poaceae) (var. Hybrid 513), African witchweed, *Striga hermonthica* (Del.) Benth. (Scrophulariaceae), soybean, *Glycine max* (L.) (Fabaceae) (var. EAI 3600), sun hemp, *Crotalaria juncea* L. (Fabaceae), and cowpea, *Vigna unguiculata* (L.) (Fabaceae) (var. ICV 2).

Field Trials. Field trials were conducted at ICIPE's Mbita Point Field Station in the Suba District of Kenya, on the shores of Lake Victoria, where *S. hermonthica* poses a serious constraint to the cultivation of cereals. Field plots with at least 100 *S. hermonthica* seeds/250 g soil were used for all experimental trials.

To evaluate the effects of different legumes on the reduction of witchweed infestation, maize was intercropped in alternate rows with one of five species of legumes: cowpea, soybean, sun hemp, greenleaf, or silverleaf. Maize was planted with a row-to-row distance of 75 cm and a plant-to-plant distance of 25 cm within a row. A control plot of a maize monocrop was also included. The six treatments were randomized and planted in six replications in a 6 × 6 quasicomplete Latin square design (Baily, 1984; Smart et al., 1994). Each treatment plot was 6 m × 6 m. The maize used was a witchweed-susceptible, medium maturity commercial variety, Hybrid 513, recommended for mid-altitude regions with moderate rainfall. The trials were planted during the 1998 long rainy season (March to July). Infestation levels were assessed nondestructively by selecting, at random, 63 maize plants in each treatment plot and counting the number of emerged *S. hermonthica* plants present. Crop yields were evaluated by harvesting a 5-m × 5-m block in the center of each plot, leaving a 1-m unharvested border to avoid edge effects.

To investigate the role of shading, nitrogen, and allelopathy in witchweed suppression by *D. uncinatum*, field trials were established during the long rainy season of 1999 and the short rainy season of 1999–2000. Field plots, 6 m × 6 m, were arranged in a six-block quasicomplete design (Baily, 1984; Smart et al., 1994). Each treatment appeared next to every other treatment twice in both rows and columns, thus balancing out treatment interactions. The treatments were: (1) maize intercropped with *D. uncinatum* with or without 120 kg nitrogen/ha, (2) a maize monocrop with or without 120 kg nitrogen/ha, and (3) a maize monocrop with artificial ground shading made of maize straw (Hybrid 513) with or without 120 kg nitrogen/ha. The *S. hermonthica* seed level in each plot, before and after each cropping season, was measured at the National Sugar Research Centre, Kenya

Agricultural Research Institute, Kibos, Kenya, using the method described by Eplee and Norris (1990). Nitrogen content in each plot, before and after each cropping season, was measured at the National Agricultural Research Laboratory, Kenya Agricultural Research Institute, Nairobi, Kenya, using the Kjeldahl method (Shugar et al., 1981). During the experiment, light intensity, soil temperature, and humidity were monitored four times in all treatments, when the maize was 30, 60, 90, and 120 days old, and the results were averaged. Emergence and attachment of *S. hermonthica* to maize were measured, and maize plant height and cob yield were recorded.

Pot Culture Experiments. An experiment to investigate the effect of nitrogen availability in soil on witchweed infestation was conducted in a screenhouse by planting maize (Hybrid 513) and *D. uncinatum* together in pots (20 cm diam.) with autoclaved soil to which nitrogen (at the rate of 0, 30, 60, and 120 kg/ha) had been added. The tests were conducted with or without the presence of a nitrogen-fixing bacterium, *Rhizobium* sp., inoculum CB 627 (the taxonomy of this group is ambiguous and has not yet been assigned a species by molecular sequencing). The soil in each pot was infested with approximately 3000 *S. hermonthica* seeds, and emergence of witchweed in each pot and height of maize plants were measured at intervals.

To investigate the possibility of an allelochemical mechanism for *S. hermonthica* suppression, an aqueous solution of chemical components, eluting from 20 cm pots in which *D. uncinatum* plants were growing, was used to irrigate maize planted in soil infested with approximately 3000 *S. hermonthica* seeds/pot. To compare the effect of fixed nitrogen with that of the allelochemicals alone, *D. uncinatum* was planted with or without the nitrogen-fixing bacterium, *Rhizobium* sp. (CB 627). Autoclaved soil was used in all experiments, and no additional nitrogen was applied. The pots containing *D. uncinatum*, which received distilled water at a rate of 1.25 ml/min, were placed on shelves, thus allowing the flow of water by gravity through the pots into the maize pots situated below (Figure 1). Comparisons were made between maize plants irrigated by root eluates from *D. uncinatum* (with or without *Rhizobium* sp.) and those irrigated by water passing through pots containing only autoclaved soil (with or without *Rhizobium* sp.). Emergence and attachment of *S. hermonthica* to maize, and maize plant heights, were monitored in all treatments.

Laboratory Experiments. For surface sterilization and preconditioning of *S. hermonthica*, seeds were soaked in a 1% NaOCl solution (commercial bleach diluted fivefold) for 6–8 min with continuous shaking, rinsed with distilled water five times, and 30–40 seeds transferred to glass fiber disks (1.1 cm diam., GF/A). Each disk was wetted with distilled water (50 μ l), and 10 such discs were placed in a plastic Petri dish (9 cm diam.), wrapped with Parafilm to prevent the disks from drying, placed in a polythene bag, and incubated at 25°C for 14 days.

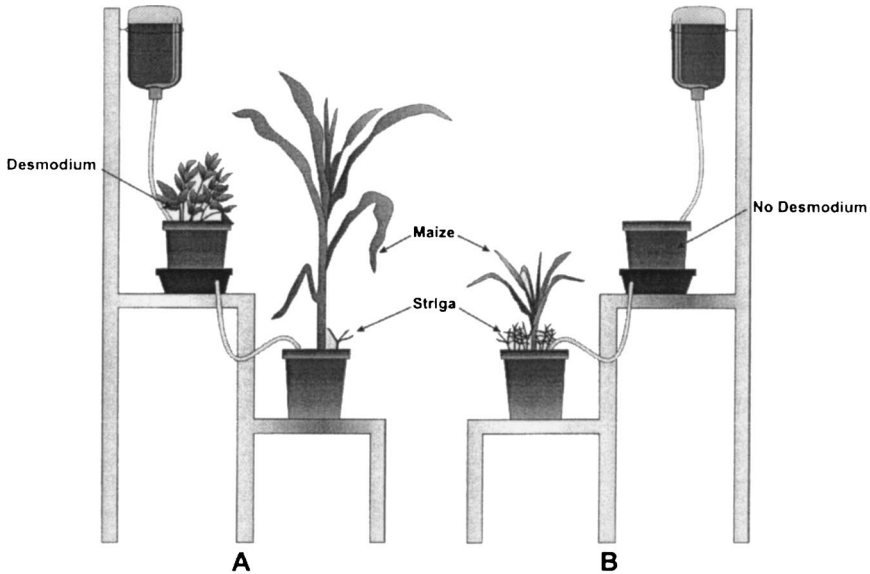


FIG. 1. Diagram of experiment to investigate the allelochemical mechanism of *Desmodium uncinatum* in suppressing *Striga hermonthica* infestation of maize. Comparison was made between maize plants irrigated by root eluates of *D. uncinatum* (A) with those irrigated by water passing through pots containing only autoclaved soil (B).

For the germination assay, glass fiber disks containing preconditioned *S. hermonthica* seeds (30–40/disk) were placed on filter paper (Whatman No. 1) to remove most of the moisture. The disks were returned to the Petri dish, and the test solution (50 μ l) was applied to each disk. The Petri dish was wrapped with Parafilm and placed in an incubator at 35°C. Germinated seeds were counted under a dissecting microscope after 24–48 hr.

For the haustorium growth assay, haustorium lengths from the germinated *S. hermonthica* seeds were measured with an ocular meter (calibrated at $\times 20$ magnification) mounted on a dissecting microscope 24 hr after the germination assay. The Petri dish containing germinated seeds was then placed in an incubator at 25°C and the haustorium length measured again after a further 24 hr.

For the collection of chemicals exuded from roots, *D. uncinatum* plants were grown in autoclaved soil (3 kg) containing different numbers of *S. hermonthica* seeds (0, 350, 700, and 1400/kg soil) in plastic pots (20 cm diam.) for varying periods (10, 15, 19, 20, 35, 45, 55, 69 days). At the end of each period, the soil was carefully washed off and the *D. uncinatum* plants (eight per treatment) transferred to glass columns (3.5 cm diam.) containing distilled water (20 ml) to collect the chemicals exuded by the cleaned roots. The aqueous exudate was assayed after

24 hr. Maize plants (four per treatment) were similarly grown in soil (3 kg) for two weeks, washed, and transferred to glass columns (3.5 cm diam.). These samples were used as the control.

For both field and pot experiments, differences in means were analyzed using one-way analysis of variance (ANOVA), and means were compared using Tukey's studentized range test (SAS Institute, 1996). Data in Table 3 (below) were analyzed using Student's *t*-test. In all studies, a $P \leq 0.05$ indicated significance.

RESULTS

In the field, intercropping of maize with the fodder legumes *D. uncinatum* and *D. intortum* significantly reduced *S. hermonthica* infestation, when compared to the maize monocrop, and significantly increased maize yields (Table 1). Of the other legumes tested, only cowpea gave a significant reduction in *S. hermonthica* infestation, but significantly less than the *Desmodium* spp. and with no increase in the maize yield.

The nitrogen and shading treatments, and the combined nitrogen and shading treatment, gave some suppression of *S. hermonthica* as compared to the maize monocrop plots (Table 2). However, a significantly greater reduction in *S. hermonthica* infestation was achieved by the *D. uncinatum* intercrop and the combined *D. uncinatum* and nitrogen treatments. As expected, there was a strong correlation between the numbers of witchweed plants per maize plant and the maize plant height and crop yields, and for both seasons, *D. uncinatum* had a greater effect on these than all the other treatments. Although shading had a significant effect on the *S. hermonthica* infestation, particularly in the 1999–2000 short rains, there was no commensurate increase in maize yield. A significant reduction in the numbers of *S. hermonthica* seeds in the soil was recorded in plots where *D. uncinatum* had been intercropped with maize (Table 3), with other treatments showing no change or a significant increase in the seed count. The only treatment showing a consistent

TABLE 1. EFFECTS OF VARIOUS LEGUME INTERCROPS ON *Striga hermonthica* INFESTATION AND MAIZE YIELDS IN FIELD PLOTS^a

Treatment	<i>S. hermonthica</i> /63 maize plants	Maize yield (t/ha)
Maize monocrop	153.8 a	3.4 a
Maize and soybean	141.3 a	4.1 a
Maize and sun hemp	98.7 a	3.8 a
Maize and cowpea	67.6 b	3.6 a
Maize and <i>Desmodium uncinatum</i>	4.2 c	5.8 b
Maize and <i>D. intortum</i>	3.9 c	6.0 b

^aNumbers in a column followed by a different letter are significantly different ($P < 0.5$) by Tukey's studentized range test. Data are means of six replications.

TABLE 2. EFFECTS OF NITROGEN, SHADING, AND *Desmodium uncinatum* INTERCROP ON *Striga hermonthica* INFESTATION, MAIZE PLANT HEIGHT, AND YIELDS IN FIELD PLOTS^a

Treatment	<i>S. hermonthica</i> / 63 maize plants	Maize plant height (m)	Maize yield (t/ha)
1999 Long rains			
Maize monocrop	459 a	1.61 a	3.62 a
Maize + shading	181 b	1.93 b	3.65 a
Maize + nitrogen (N)	245 ab	1.97 b	4.30 ab
Maize + shading + N	85 c	1.94 b	4.48 b
Maize + <i>D. uncinatum</i>	27 d	1.98 b	4.70 bc
Maize + <i>D. uncinatum</i> + N	8 d	2.19 c	5.04 c
1999–2000 Short rains			
Maize monocrop	769 a	1.67 a	2.53 a
Maize + shading	286 b	1.72 a	3.31 a
Maize + nitrogen (N)	486 ab	1.91 b	4.84 b
Maize + shading + N	113 c	1.94 b	5.00 b
Maize + <i>D. uncinatum</i>	13 d	2.09 c	5.20 bc
Maize + <i>D. uncinatum</i> + N	3 d	2.11 c	5.52 c

^aNumbers in a column followed by a different letter are significantly different ($P < 0.5$) by Tukey's studentized range test. Data are means of six replications.

rise in the level of available nitrogen over both seasons was the maize/*Desmodium* intercrop (1999 short rains: +108.5%, $P < 0.01$; 1999–2000 long rains: +19.9%, $P < 0.05$). Data for soil temperature, light intensity and relative humidity in the plots are shown in Table 4.

TABLE 3. EFFECTS OF NITROGEN, SHADING, AND *Desmodium uncinatum* INTERCROP ON NUMBERS OF *Striga hermonthica* SEEDS IN SOIL (FIELD TRIALS, SUCCESSIVE SEASONS ON SAME PLOTS)^a

Treatment	<i>S. hermonthica</i> seeds/250 g soil (N)					
	1999 short rains			1999–2000 long rains		
	Before	After	%change	Before	After	% change
Maize monocrop	253	421	+66.4**	421	607	+44.2**
Maize + shading	114	157	+37.7*	157	203	+29.3*
Maize + nitrogen (N)	239	256	+7.1 NS	256	298	+16.4*
Maize + shading + N	184	179	-2.7 NS	184	159	-11.2 NS
Maize + <i>D. uncinatum</i>	107	75	-29.9*	75	49	-34.7 NS
Maize + <i>D. uncinatum</i> +N	105	81	-22.8*	81	44	-45.7*

^aNumbers before and after each season are significantly different at: * $P < 0.05$, ** $P < 0.01$ by Student's *t*-test; NS = not significant. Data are means of six replications (each replication comprises 10 soil samples).

TABLE 4. EFFECTS OF SHADING AND *Desmodium uncinatum* INTERCROP ON SOIL TEMPERATURE (ST), RELATIVE HUMIDITY (RH), AND LIGHT INTENSITY (LI) IN MAIZE PLOTS DURING 1999 LONG RAINS^a

Treatment	ST (°C)	RH (%)	LI (lux)
Maize monocrop	27.2 a	58.7 a	0.2 a
Maize + shading	26.8 ab	58.4 a	0.004 b
Maize + <i>D. uncinatum</i>	26.6 b	65.4 b	0.0 c

^aNumbers in a column followed by a different letter are significantly different ($P < 0.5$) by Tukey's studentized range test. Data are means of six replications; each replication is a mean of four observations at different growth stages of maize.

The pot experiment to investigate the effects of nitrogen and *D. uncinatum* on suppression of *S. hermonthica* infestation in maize demonstrated that, in control pots, high levels of nitrogen application reduced and delayed emergence (Table 5). However, the effect of *D. uncinatum*, with or without nitrogen-fixing bacteria, was significantly greater in this regard compared to the nitrogen application alone. At all stages of maize development, the height of maize plants intercropped with *D. uncinatum* was greater than that of control plants with or without nitrogen (Table 6).

The dramatic effect of the aqueous solution of chemicals eluting from pots in which *D. uncinatum* plants were growing (Figure 1) on suppression of *S. hermonthica* infestation, and the concomitant increase in maize plant height, are shown in Figures 2 and 3. The aqueous samples of chemicals exuded by cleaned *D. uncinatum* roots were tested in laboratory experiments to investigate the mode of

TABLE 5. SUPPRESSION OF *Striga hermonthica* INFESTATION OF MAIZE PLANTS GROWN IN POTS, AT VARIOUS LEVELS OF NITROGEN, WITH OR WITHOUT *Desmodium uncinatum* AND NITROGEN-FIXING BACTERIA

	No. <i>S. hermonthica</i> plants/25 pots ^a											
	Maize + <i>D. uncinatum</i> + <i>Rhizobium</i> sp.				Maize + <i>D. uncinatum</i>				Maize (control)			
	0	30	60	120	0	30	60	120	0	30	60	120
Nitrogen level (kg/ha)												
Maize plant age (days)												
20	0	0	0	0	0	0	0	0	55	5	5	8
30	0	0	0	0	0	0	0	0	163	42	24	14
40	0	0	1	0	0	0	0	0	287	78	10	7
50	3	3	0	0	0	0	1	4	362	133	63	12
60	1	1	0	1	0	0	2	3	452	258	190	39
75	0	2	4	5	0	0	1	3	441	427	447	172

^a3000 seeds per pot. Data are means of 50 replications.

TABLE 6. HEIGHT OF MAIZE PLANTS GROWN IN POTS IN *Striga hermonthica* INFESTED SOIL, AT VARIOUS LEVELS OF NITROGEN, WITH OR WITHOUT *Desmodium uncinatum* AND NITROGEN-FIXING BACTERIA^a

Treatment	Maize plant height (cm)							
	35 days				60 days			
	0	30	60	120	0	30	60	120
Nitrogen level (kg/ha)	0	30	60	120	0	30	60	120
Maize (control)	30 a	39 a	40 a	53 a	40 a	54 a	81 a	109 a
Maize + <i>D. uncinatum</i>	58 b	69 b	71 b	84 a	119 b	144 b	158 b	179 b
Maize + <i>D. uncinatum</i> + <i>Rhizobium</i> sp.	63 b	76 b	78 b	88 a	135 c	183 c	186 c	197 c

^aNumbers in a vertical column followed by a different letter are significantly different ($P < 0.5$) by Tukey's studentized range test. Data are means of 50 replications.

action. There was no evidence for the production of a germination inhibitor by *D. uncinatum*, since the root exudate induced germination of *S. hermonthica* as effectively as the maize root exudate (Table 7). Indeed, it would appear that, in the initial stages (days 15–19), the *D. uncinatum* root exudates were more effective in this aspect than the maize root exudate. Furthermore, exudates from roots of *D. uncinatum* grown in soil at increasing densities of *S. hermonthica* infestation did not subsequently inhibit germination of *S. hermonthica* seeds (Table 8). However, when the seeds were exposed to root exudates from *D. uncinatum* and examined

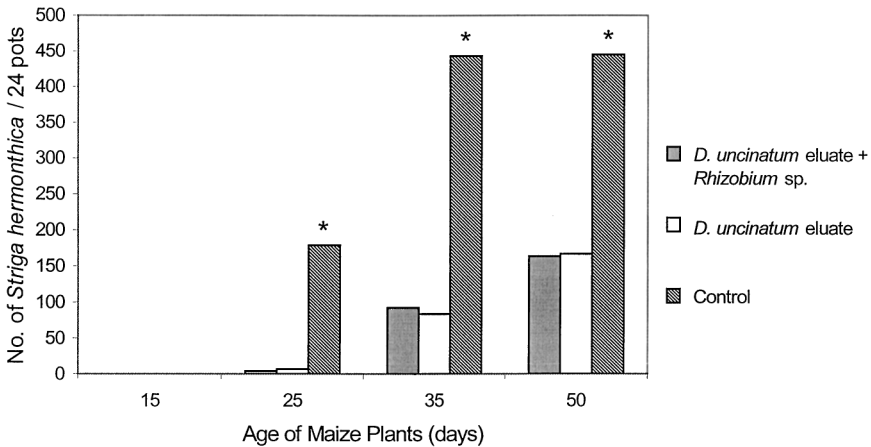


FIG. 2. Effect of *Desmodium uncinatum* root eluate (with and without nitrogen-fixing *Rhizobium* sp. bacteria) on numbers of *Striga hermonthica* parasitizing maize. Within each age group of maize, the treatment marked with an asterisk is significantly different ($P < 0.05$) by Tukey's studentized range test.

TABLE 7. GERMINATION OF *Striga hermonthica* SEEDS TREATED WITH AQUEOUS ROOT EXUDATES FROM *Desmodium uncinatum* OF DIFFERENT AGES

Treatment	Germination (%)				
	15	19	35	55	69
Age of <i>D. uncinatum</i> (days)					
Maize exudate + water (1:1)	21.7 ± 2.7 a	21.7 ± 2.7 a	47.9 ± 2.7 a	44.1 ± 2.6 a	44.1 ± 2.6 a
<i>D. uncinatum</i> exudate	50.5 ± 2.8 b	35.7 ± 3.4 b	50.8 ± 3.2 a	42.8 ± 3.6 a	54.7 ± 2.6 a
Maize exudate + <i>D. uncinatum</i> exudate (1:1)	51.7 ± 2.7 b	44.3 ± 3.9 b	50.3 ± 2.6 a	43.6 ± 3.0 a	44.4 ± 4.0 a
Distilled water	0.0 ± 0.0 c	0.0 ± 0.0 c	0.9 ± 0.5 b	0.0 ± 0.0 b	0.0 ± 0.0 b

^aNumbers in a column followed by a different letter are significantly different ($P < 0.05$) by Tukey's studentized range test. Data are means of 10 replications, 30–40 seeds.

after 24 and 48 hr, the primary haustoria were significantly shorter relative to those exposed to maize exudates (Table 9). Inhibition of the primary haustoria was observed irrespective of whether the *D. uncinatum* had been grown in *S. hermonthica* infested or clean soil.

DISCUSSION

The initial field trial clearly demonstrated that intercropping with *D. uncinatum* and *D. intortum* produced significant and dramatic reductions in the infestation of maize plants by *S. hermonthica*. The overall yield increases result from a

TABLE 8. GERMINATION OF *Striga hermonthica* SEEDS TREATED WITH AQUEOUS ROOT EXUDATES FROM *Desmodium uncinatum* GROWN IN SOIL WITH VARYING *S. hermonthica* SEED DENSITIES^a

<i>S. hermonthica</i> density (seeds/kg soil)	<i>D. uncinatum</i> germination (%)	
	10 days old	20 days old
1400	19.7 ± 3.2 a	40.5 ± 3.0 ab
700	26.0 ± 3.3 a	43.5 ± 2.0 ab
350	21.4 ± 3.1 a	32.1 ± 4.4 b
0	20.4 ± 2.5 a	47.0 ± 4.3 a
Maize exudate	27.8 ± 3.2 a	38.2 ± 3.4 ab
Distilled water	0.0 ± 0.0 b	1.0 ± 0.0 c

^aNumbers in a column followed by a different letter are significantly different ($P < 0.05$) by Tukey's studentized range test. Data are means of 10 replications, 30–40 seeds.

TABLE 9. GERMINATION AND HAUSTORIAL DEVELOPMENT OF *Striga hermonthica* SEEDS TREATED WITH AQUEOUS ROOT EXUDATES FROM *Desmodium uncinatum* GROWN IN *S. hermonthica*-INFESTED OR CLEAN SOIL^a

Treatment	Germination (%) ^b	Haustorial development			
		24 hr		48 hr	
		Haustorium length (mm)	Inhibition ^c (%)	Haustorium length (mm)	Inhibition ^c (%)
<i>D. uncinatum</i> exudate (+ <i>S. hermonthica</i>)	39.3 ± 3.2 a	0.65 ± 0.04 a	18.8	0.85 ± 0.05 a	24.1
<i>D. uncinatum</i> exudate (- <i>S. hermonthica</i>)	43.0 ± 2.5 a	0.69 ± 0.03 a	13.8	0.75 ± 0.05 a	33.0
Maize exudate (control)	43.0 ± 2.5 a	0.80 ± 0.04 a	0.0	1.12 ± 0.06 b	0.0
Distilled water	0.0 ± 0.0 b				

^aNumbers within a column followed by a different letter are significantly different ($P < 0.05$) by Tukey's studentized range test. Inhibition of haustorial development by *D. uncinatum* exudate is expressed relative to the mean length of haustoria treated with maize exudate.

^bData are means of 10 replications, 30–40 seeds.

^cData are means of 30 replications.

combination of witchweed and stem borer control, the latter arising from the use of the *D. uncinatum* intercrop to repel gravid stem borers from the maize. However, these data are presented as an indication of the ability of the overall strategy to address both aspects of the maize pest complex, with subsequent studies directed solely at control of *S. hermonthica*. Many claims have been made for the value of intercropping with other plants, for example, *Celosia argentina* L. (Amaranthaceae) and *Dolichos lablab* L. (Fabaceae), in witchweed control, but the effects reported are weak (e.g., Carson, 1986). Indeed, some suggested intercrops such as sweet potato, *Ipomoea batatas* L. (Convolvulaceae) (Oswald et al., 1999), would present considerable competition to the maize itself.

The use of *Desmodium* species to control parasitic witchweeds is showing promise. This has stimulated further investigations into the mode of action, for which a number of possible mechanisms have been considered, i.e., by increasing the available nitrogen in the soil, by offering shade, or through an allelopathic effect caused by chemicals released from *Desmodium* spp. roots. Such mechanisms are known to give some control of witchweeds (Press and Gurney, 2000). In the context of allelopathy for root-derived chemicals, three possible mechanisms were investigated: (1) inhibition of *S. hermonthica* seed germination by an exudate from *D. uncinatum*; (2) production by *D. uncinatum* of a germination inhibitor following attempts by *S. hermonthica* seedlings to attach to the plant; (3) inhibition of growth of the primary and/or upper haustoria.

Although, in the field, the nitrogen and shading treatments and the combination of nitrogen and shading suppressed *S. hermonthica* emergence, maximum suppression was provided by *D. uncinatum* and the combined *D. uncinatum* and nitrogen treatment. There is documented evidence of suppression of witchweed by added nitrogen sources (Mumera and Below, 1993; Press and Gurney, 2000). *D. uncinatum* is capable of fixing 100–180 kg nitrogen/ha under Kenyan conditions, and there is evidence that some of the nitrogen is passed to the companion plant (Muyekho *et al.*, unpublished report). It has also been proposed that the suppression of witchweed by a leafy intercrop may be due to shading effects (Parker and Riches, 1993; Press and Gurney, 2000). This may reduce temperature and raise humidity over the emerging witchweed plants, thus reducing transpiration and the supply of nutrition from the host plant. Although, in this study, there were benefits from nitrogen and shading on suppression of *S. hermonthica* and growth of maize in the field, the laboratory pot experiments clearly demonstrated an additional allelopathic effect associated with *D. uncinatum*. The greater effect of *D. uncinatum* compared to physical and nutritional factors indicated an additional activity strongly suggestive of allelopathy, which is also reflected in the depletion of viable *S. hermonthica* seeds in the soil after both cropping seasons.

An allelopathic mechanism was demonstrated by the pot experiments described in Figures 1–3, i.e., water-soluble chemical components associated with *D. uncinatum* roots are responsible for suppression of *S. hermonthica* infestation. The role of chemicals specifically released by cleaned *D. uncinatum* roots was further investigated, but there was no evidence of germination inhibition, which had

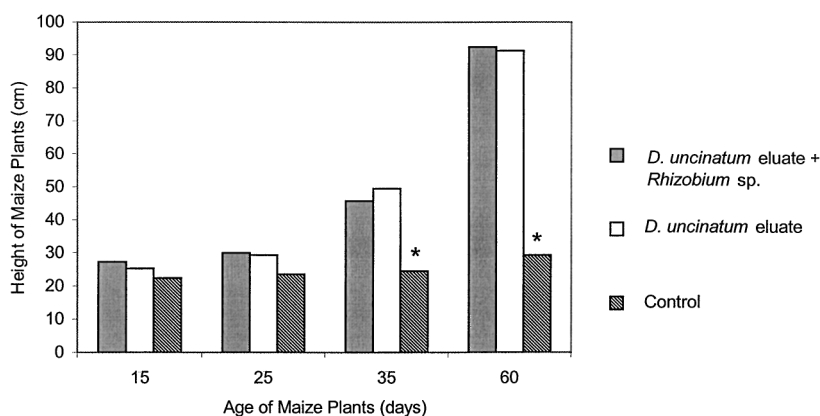


FIG. 3. Effect of *Desmodium uncinatum* root eluate (with and without nitrogen-fixing *Rhizobium* sp. bacteria) on height of maize plants growing in *Striga hermonthica* infested soil. Within each age group of maize, the treatment marked with an asterisk is significantly different ($P < 0.05$) by Tukey's studentized range test.

originally been expected. The first possible mechanism (1, above) is, thus, discounted. Indeed, there is evidence for the production of a potent germination stimulant by root exudates of *D. uncinatum*. The second possibility (2, above) is discounted because of the demonstration that root exudates from *D. uncinatum* growing in soil infested with *S. hermonthica* at increasing densities did not subsequently inhibit germination of *S. hermonthica* seeds. The fact that chemical components of *D. uncinatum* root exudates gave a significant inhibition of haustorial growth after 48 hr demonstrated a mechanism (3, above), in which haustorial development in the parasitic process is implicated.

The discovery of the potential of *Desmodium* spp. in the suppression of *S. hermonthica* infestation has opened the possibility for new practical witchweed control methods commensurate with East African subsistence farming (Khan et al., 2000). The allelopathic effect of chemicals exuded from the roots that interfere with haustorial development, combined with the potent chemical stimulants causing suicidal germination, provide not only direct witchweed control, but also a significant depletion of viable seeds in the soil. Full chemical elucidation of the allelopathic agents is ongoing, but fractionation by HPLC has already demonstrated that the germination stimulants in *D. uncinatum* root exudates can be isolated from the haustorial inhibitors. Certain novel polyphenolic compounds have been tentatively identified from active fractions and await confirmation of activity and structures in synthesis studies.

Research into the factors stimulating germination of flowering parasitic weeds has been under way for a number of years (e.g., Netzly et al., 1988), and work on eliciting suicidal germination is ongoing (e.g., Wigchert et al., 1999). In addition, a great deal is known about the chemistry involved (Sugimoto et al., 1998; Welzel et al., 1999). However, no practical exploitation in weed control has yet ensued. The sophisticated mode of action demonstrated here, comprising both germination stimulation and haustorial inhibition, when fully elucidated, may give exploitable leads that are urgently needed, not only in subsistence agriculture, but also to address future world demands in agricultural production and in developing new approaches for molecular biology in weed control (Gressel, 2000).

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