Session 6E

Biology and Control of Parasitic Weeds

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STRIGA HERMONTHICA ON SORGHUM: CHEMICAL AND CULTURAL CONTROL

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ABSTRACT

The *Striga* resistant variety SRN 39 supported less *Striga* emergence than the susceptible one Gadam El Hamam. Urea, dicamba, chlorsfuron and its tank mix with dicamba effected good control of the parasite on SRN 39. On Gadam El Hamam, however, only chlorsulfuron and its tank mix with dicamba were effective. Combinations of herbicides and urea displayed increased potency. Intercropping with *Lablab purpureus* suppressed *Striga* emergence and growth. Urea, chlorsulfuron, applied at planting, and dicamba effected insignificant increase in grain yield. Chlorsulfuron and its tank mix with dicamba, each applied 30 days after planting, significantly increased yield of both varieties under irrigation irrespective of urea. However, under rain-fed conditions significant yield increments were only obtained when the herbicides were applied subsequent to a urea treatment. Intercropping with *L. purpureus* decreased time to flowering and increased number of heads and straw yield of Gadam El Hamam. However, its effects on SRN 39 were negligible.

INTRODUCTION

Striga hermonthica is an important parasite on several poaceous crops including sorghum (*Sorghum bicolor*) maize (*Zea mays*) and millet (*Pennisetum americanum*). Annual cereal grain losses associated with the parasite, across Africa, may average about 40% (Lagoke *et al.*, 1993). Available control measures include resistant varieties and complementary agronomic practices viz crop rotation, catch and trap croppings, herbicides and fertilizers. However, high costs, lack of immediate returns, inconsistent performance, sophistications and/or social considerations reduce the technical and economic feasibility of the available control measures (Parker 1983).

The investigations described in this paper were part of a study aimed to develop technically and economically feasible *Striga* control packages, in irrigated and rain grown sorghum.

MATERIALS AND METHODS

Irrigated Sorghum

General

The effects of urea, herbicides and intercropping with *Lablab purpureus* on *Striga* were studied. Sorghum (cv. SRN 39 *Striga* resistant and/or Gadam El Ham, *Striga* susceptible) was planted in an artificially *Striga*-infested plot on ridges 80cm apart at a within row spacing of 15cm. Sub-plots (4 x 7m) were arranged in randomized complete blocks with 4 replicates. The individual treatments are shown with the results in Tables 1-5. Sorghum seedlings were thinned 15 days after emergence. *Striga* was periodically counted and sorghum grain yield was determined at harvest.

Herbicides and urea

Two experiments were undertaken. In both experiments urea (0 or 95kg/ha) was applied at planting. Herbicides were applied as soil directed sprays. In experiment 1 chlorsulfuron (2.4g a.i./ha), dicamba (300g a.i./ha) and their tank mix were applied 30 days after planting (Table 1). In experiment 2 chlorsulfuron (2.4g a.i./ha) was applied at planting and/or 30 days later as a single or a split dose (Table 2).

Intercropping with *L. purpureus*

L. purpureus was planted in holes (2 seeds/hole) 15 cm apart, each midway between sorghum planting holes, on the same ridge as sorghum. It was then thinned to 2 seedlings per hole 15 days after emergence.

Rain grown sorghum

Sorghum was seeded in rows 90cm apart with a press drill in a naturally *Striga*-infested field. Urea (0 or 95kg/ha) was applied in plots (8 x 50m) at planting. Chlorsulfuron (24 g/ha), dicamba (300g/ha) and their tank mix were applied, as sprays direct to the soil 30 days after sowing. *Striga* population and sorghum grain yield were determined in three pre-selected areas in each plot.

RESULTS

Effect on *Striga*

Striga emergence was earlier and more intense on Gadam El Hamam than on SRN 39 (Tables 1-4). In irrigated sorghum all treatments effected and maintained excellent suppression of the parasite on SRN 39. In Gadam El Hamam, however, urea had a negligible effect, dicamba effected moderate control while chlorsulfuron, post-emergence, and its tank mix with dicamba displayed moderate to excellent activity (62 to 97% control). Chlorsulfuron applied at planting or as a split dose had a reduced activity (Table 2).

In the rain grown sorghum urea stimulated *Striga* emergence particularly on Gadam El Hamam. Chlorsulfuron and its tank mix with dicamba effected adequate suppression of *Striga* early in the season; however, late season control was moderate (Table 3). In both irrigated and rain grown sorghum application of herbicides subsequent to urea treatments resulted in increased potency (Tables 1-3).

TABLE 1. Effects of urea and herbicides (post-emergence) on *Striga* control and sorghum yield in irrigated sorghum (Expt. 1).

Sorghum variety	*Striga* (plant/m²)		Grain yield (t/ha)	
Treatment	G/H 60 DAS	SRN 39 60 DAS	G/H	SRN 39
Untreated control	50	34	0.21	0.40
Urea (U)	52	6	1.15	1.38
Dicamba (D)	21	6	0.92	0.86
D + U	35	3	2.02	1.31
Chlor	5	0	2.05	1.73
Chlor + U	2	0	3.96	2.11
Chlor + D	2	0	1.99	1.45
Chlor + D + U	2	0	3.86	1.94
S.E. ±			0.325	

G/H = Gadam El Hamam, DAS = days after sowing, Chlor = chlorsulfuron.

Intercropping of irrigated sorghum with *L. purpureus* delayed *Striga* emergence and suppressed its growth. The suppressive effects of *L. purpureus* increased with time and were more prominent with Gadam El Hamam (Table 4).

Intercropping reduced *Striga* shoots by 42 to 96%, *Striga* dry weight by 89 to 92% and number of fertile capsules by 100% (Table 4).

TABLE 2. Influence of time and methods of application on efficacy of chlorsulfuron in irrigated sorghum cv. Gadam El Hamam (Expt. 2).

Treatment	Application time (DAS)	*Striga* (plant/m²) 60 DAS	*Striga* (plant/m²) 70 DAS	Grain yield (t/ha)
Untreated Control		16	13	0.29
Urea		30	26	0.46
Chlorsulfuron	0	25	21	0.21
Chlorsulfuron + urea	0	16	14	1.57
Chlorsulfuron**	15+30	11	12	0.75
Chlorsulfuron** + urea	15+30	8	10	1.98
Chlorsulfuron	30	4	5	1.36
Chlorsulfuron + urea	30	3	3	2.25
S.E. ±				0.259

** = Applied as a split dose (1.2 g a.i./ha on each date),
DAS = days after sowing

Effects on sorghum

Grain yield of sorghum was considerably reduced by unrestricted *Striga* parasitism. Untreated SRN 39 outyielded the corresponding Gadam El Hamam treatment (Tables 1 and 3). Urea and/or chlorsulfuron applied at planting, and dicamba, were not effective in suppressing *Striga* and grain yield of sorghum was often not significantly increased (Tables 1-3). Chlorsulfuron and its tank mix with dicamba, each applied 30 days after planting increased yield of both varieties (Tables 1 and 3). Under irrigation the attained yield increments were highly significant irrespective of urea (Table 2). However, under rain-fed conditions significant yield increments were only obtained when the herbicides were applied subsequent to a urea treatment (Table 3). Under irrigation Gadam El Hamam gave almost twice the yield of SRN 39. However, under rain-fed conditions similar yields were obtained (Tables 1 and 3).

Intercropping considerably decreased time to flowering and increased the number of heads and straw yield of Gadam El Hamam. However, with SRN 39 only negligible effects were displayed (Table 5).

TABLE 3. Effects of urea and herbicides (post-emergence) on *Striga* control and sorghum yield in rain grown sorghum.

Sorghum variety / Treatment	*Striga* (plant/m²) G/H 60 DAS	*Striga* (plant/m²) SRN39 60 DAS	Grain yield (t/ha) G/H	Grain yield (t/ha) SRN 39
Control	3	3	0.19	0.46
Urea (U)	234	15	0.30	1.00
Chlor	1	2	0.82	0.72
Chlor + U	159	4	1.43	1.85
Chlor + D	1	1	0.93	0.74
Chlor + D + U	96	3	2.17	2.15
S.E. ±			0.245	

Chlor = chlorsulfuron, D = dicamba

TABLE 4. Influence of intercropping with *L. purpureus* on *Striga* population, dry weight and seed production in irrigated sorghum

Treatment	*Striga* (plant/m²)		*Striga* dry weight (g/m²)	Fertile capsules/plant
	50 DAS	120 DAS		
SRN 39	12	9	24.6	7
SRN 39 + L	4	1	1.8	0
G/H	50	46	97.2	15
G/H + L	21	3	3.6	0

G/H = Gadam El Hamam, + L = + *Lablab purpureus* intercropping,
DAS = days after sowing

TABLE 5. Influence of intercropping with *L. purpureus* on number of sorghum heads of *Striga*-infested irrigated sorghum (000/ha).

Treatment	Time after planting (in days)		
	40	70	100
SRN39	89	102	105
SRN 39 + L	90	96	102
G/H	2	13	27
G/H + L	43	71	71
S.E. ±	6.3	8	6.3

G/H = Gadam El Hamam, + L = + *Lablab purpureus*

DISCUSSION

It is evident that the relatively *Striga*-resistant sorghum variety (SRN 39) required less inputs than the *Striga*-susceptible one (Gadam El Hamam) and may best suit subsistence farmers with limited resources. However, SRN 39, being a low stimulant producer (Ejeta *et al.*, 1993) may not enhance rapid demise of *Striga* seeds in soils as seeds persist for 20 years or more (Andrews 1945), while planting a susceptible sorghum variety in conjunction with controlling *Striga* by intercropping, chlorsulfuron or chlorsulfuron in a tank mix with dicamba offer additional options to farmers. Such treatments not only ensure high yield, but also rapid depletion of *Striga* seed reserves in soils. Chlorsulfuron does not inhibit *Striga* germination (Babiker, A.G.T. unpublished). Furthermore, preliminary evidence indicates that chlorsulfuron when applied 30 days after planting is tolerated by most, if not all, the popular sorghum varieties in Sudan. Use of these varieties provides more flexibility than the introduction of new varieties as it does not entail interference with farmers and/or consumer preference.

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NOTES

BIOASSAY STUDIES ON GERMINATION OF OROBANCHE RAMOSA WITH ROOT EXUDATES AND EXTRACTS

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ABSTRACT

The presence of germination stimulant was examined in root exudates from 24 crops using seeds of *Orobanche ramosa*. Stimulant activity varied between crops, but was usually most active after 4 weeks. Extracts of fresh roots usually gave greater activity than exudates. Faba bean root extract maintained activity after freezing and thawing or boiling for 30 minutes; activity was lost after acidification or shaking with activated charcoal. Ether, ethyl acetate and chloroform all removed part of the stimulant activity of root exudates. Ether extracts separated by TLC indicated only one main region of germination stimulant.

INTRODUCTION

Preconditioned *Orobanche* seeds germinate in response to a stimulant from roots of hosts (Brown *et al.* 1952; Hiron 1973; Whitney, 1979) and some non-host plants. Whitney (1979) concluded that both a stimulant and an inhibitor are present.

Two factors are involved in the recovery of active root exudates (Hameed *et al.*, 1973), the stage of growth at the time of collection and the dilution and/or stability of stimulant in the exudate.

The chemical structure of the *Orobanche* stimulant in root exudate has not yet been determined but it may be either an unsaturated lactone such as "strigol" or a benzopyran (Mallet, 1973; Davis *et al.*, 1978).

MATERIAL AND METHODS

Crops used in the investigation included the following hosts: lentil, pea, bean, tomato, eggplant, cucumber, carrot, sunflower, tobacco, chickpea, rapeseed, cabbage, watermelon, mustard and lettuce. Non-host crops were maize, flax, onion, cotton, pepper, sesame, kidneybean, cowpea and dolichos beans. The exudates were collected using the double-pot technique of Parker *et al.*, (1977). Crop seeds were sterilized in sodium hypochlorite and grown in perforated 500 ml plastic cups filled with medium size sand (1-2 mm) in a glasshouse (min. T = 20°C) during April-May 1991. Exudate was collected weekly from the 2nd to 7th week from sowing by placing the perforated cup inside an unperforated one and adding 50 ml water. The percolate and the remaining water obtained by suction on a Buchner funnel were added together and tested on *Orobanche* seeds. Plants were watered daily and given nutrient solution ("Sangral" soluble fertilizer) diluted as recommended and given at

50 ml per pot every week.

Root extract was taken from the same plants at 7 weeks. Roots were separated, washed free of sand, blotted dry and weighed. After freezing at -10°C for 24 hours they were ground with some fine sand and a little water with a mortar and pestle, and then transferred to a beaker with 250 ml water and the suspension stirred for ten minutes. The extract was filtered through cheese cloth, centrifuged at 8000 rpm for 5 minutes, and the supernatant filtered through two Whatman No. 9 filter papers for use as root extract. Root extracts of faba bean were treated as follows. One sample was frozen at -10°C for 4 weeks and then thawed and tested. A further sample was placed in a tube in a 100°C water bath for 30 minutes and tested after cooling. Another sample was diluted to 50%, 10% and 2% of the original concentration. A sample was acidified with 2 ml of N sulphuric acid in 16 ml root extract, shaken to mix and left for 30 minutes, 2 ml of N KOH was then added to neutralize it before it was tested. A 50 ml sample of extract was shaken with 10 g of activated charcoal powder, shaken for 10 minutes, stood for 30 minutes, then filtered and tested.

Root exudates or extracts were bioassayed as follows. Seeds of *O. ramosa* (from an unknown host) obtained from ICARDA, Syria, were sterilized with sodium hypochlorite (1% available chlorine) for 10 minutes and washed thoroughly with sterilised distilled water on a Buchner funnel. When air-dried, batches of 50-100 seeds were placed on 8 mm discs of sterilised glass fibre paper. The discs were then placed on two 9 cm cellulose filter papers in a petri dish and 5 ml of 100 ppm GA3 added to each petri dish and left for 14 days at 22°C to condition in an incubator. The disks were then dried and used within 2 days. For a test they were placed on 2 wet filter papers in a petri dish and the discs were wetted with 15 μl of the solution under investigation and incubated at 25°C for 8-12 days to germinate.

Root exudates of faba bean in water were extracted with ether, ethyl acetate and chloroform by adding 100 ml of each solvent to 200 ml of exudate, shaking thoroughly and removing the solvent layer. Each fraction was dried, redissolved in a few drops of methanol and applied to conditioned seeds at the rate of 15 μl per disk. 200 ml of water was treated in the same way for controls.

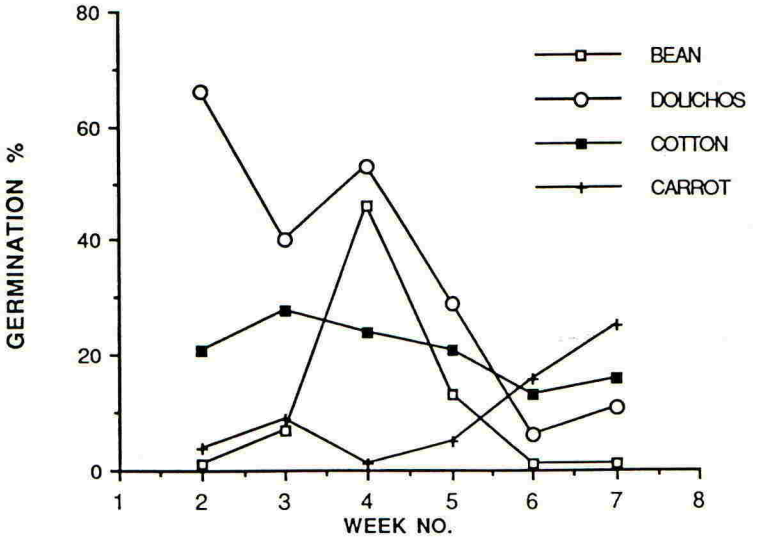
Water exudate from 40 faba bean plants was extracted 3 times with ether and the extracts dried in a fume cupboard. The residue was then dissolved in a few drops of methanol and run on thinlayer plates (TLC) of Silco Gel with Luminescer with hexane:chloroform, (1:1). Eight separate bands were scraped from the plate, taken up in methanol and filtered. The filter was then washed with ether and the combined ether and methanol filtrates combined and dried in a rotary evaporator, redissolved in 4 ml methanol and 15 μl applied to conditioned seeds on the discs as described above.

RESULTS AND DISCUSSION

Comparison of the effects of root exudates showed that the pattern of production of stimulant differed between plants. The general trend was for activity to increase and be most active at 4 weeks and then decrease. There were, however, 4 types of patterns shown in Figure 1. In dolichos bean

activity was high initially but decreased steadily as the plants aged. In faba bean activity rose to a peak at week 4 and then decreased. In carrot activity started low and increased with age, while in cotton activity remained steady over the period.

Figure 1. Germination % of O.ramosa seed treated with root exudation collected at weekly interval



Some known host plants (e.g. tomato, eggplant and tobacco) showed little or no exudate activity while some known non-host or trap plants (e.g. flax, sesame, cowpea and dolichos) showed high exudate activity. Ballard *et al.* (1978) and Hameed *et al.* (1973) both reported that flax root exudate gave better broomrape seed germination than tomato or tobacco. In some plants with low exudate activity germination may only occur when host roots are in very close contact with *Orobanche* seeds. Ballard *et al.*, (1978) also noted different patterns of exudation. Exudates were detected within 3 days growth from flax but only after 15 days with tomato, tobacco or sorghum. Other reports also confirm that root exudates or extracts from tomato have little effect on the germination of *Orobanche* (Zaki and Tewfic, 1974; El-Safwani, 1978; Whitney, 1979;).

Most crops showed extract activity. The exceptions were sunflower and chickpea, both host plants. In most plants root extract activity at 7 weeks was higher than exudate activity at 4 weeks (Fig. 2.). There was no correlation between root fresh weight and stimulant activity of root extracts (Fig. 3.). When the root exudate of faba bean was diluted germination activity was not diminished until diluted to less than 10% dilution. There was no sign of inhibition at high concentrations as reported by Whitney (1979). Adding charcoal to exudates removed all germination activity,

Figure 2.Germination of O.ramosa seed treated with root exudate collected at 4 weeks and root extract made at 7 weeks

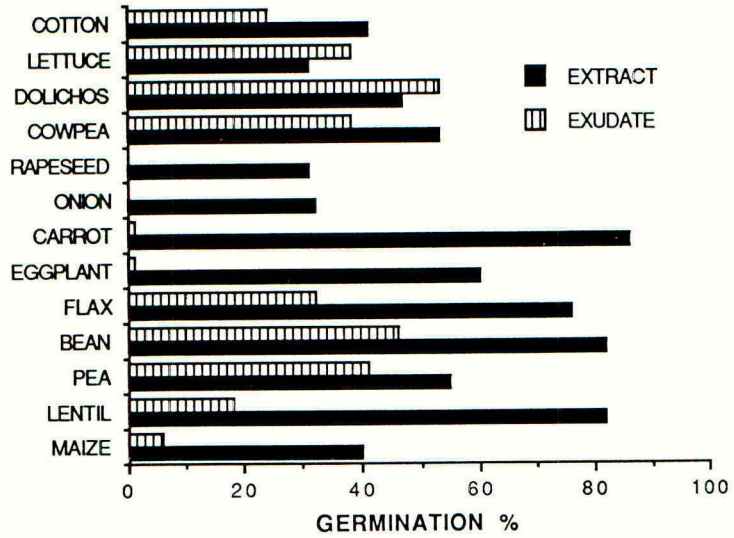
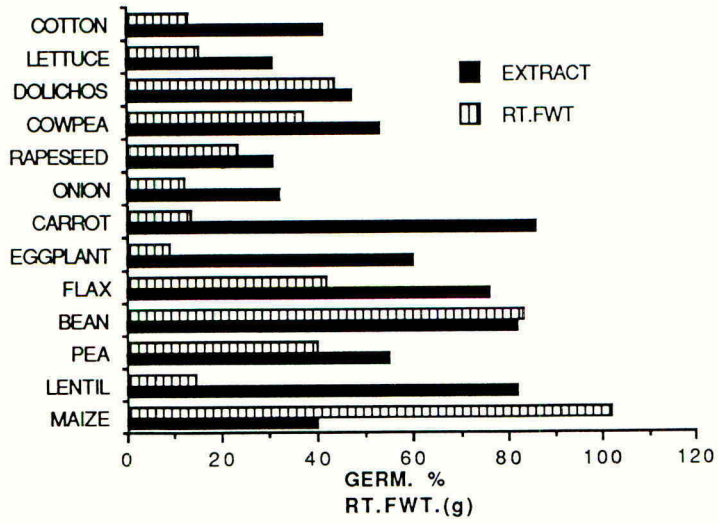


Figure 3. Comparison of germination of O.ramosa seed treated with root extracts made at 7 weeks and fresh weight of roots at that time .



presumably by adsorption. Loss of activity also occurred when the exudate was acidified. Root exudates of flax have been reported by others to be stable in both alkaline and acid treatments (Brown *et al.*, 1951; Khalaf *et al.*, 1991). Germination activity was maintained when the exudate was frozen and thawed or boiled for 30 minutes.

The sequential extraction of faba bean root exudate indicated that each solvent removed some stimulant activity and the residual water was also still active. This may indicate that more than one compound or group of compounds is present but may also indicate that several extractions with the same solvent may be needed to partition the full activity in each one. Accordingly, sequential extraction with ether was then carried out.

TLC plates seen by UV light indicated 8 different fluorescent regions but only one region was active in stimulating seed germination to 6% compared to 22% for a GR7 standard.

This study confirms the very wide range of hosts and non-hosts which are capable of stimulating germination of *O. ramosa*. The low stimulant activity found in tomato and eggplant was surprising since these two species grown at the same time were rapidly parasitised and supported many plants of *O. ramosa*. This may mean that there needs to be close contact between host root and seed for stimulation to occur either because of very small stimulant amounts or stimulants which do not migrate from the root surface. Resistance to *Orobanche* in tomato may therefore require a different strategy from that applicable to hosts with a readily diffusable stimulant. The relatively high stimulant activity released when roots are damaged before extraction begs the question whether this is similar to the diffusable stimulants exuded by living roots and may indicate some relationship between root damage and stimulant release leading to infections. It also remains to be established whether the diffusable stimulants from different plants are similar. Improved separation and identification techniques are still needed to answer these intriguing questions.

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ISOENZYME ANALYSIS DEMONSTRATES HOST SELECTION OF PARASITE PATHOTYPES IN THE ASSOCIATION BETWEEN COWPEA AND *STRIGA GESNERIOIDES*

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ABSTRACT

A single seed population of the angiosperm parasite, *Striga gesnerioides*, was sown against two host cowpea cultivars. 23 enzyme systems were surveyed in the parasite revealing 48 different isoenzyme bands. Eight polymorphic bands in four enzyme systems allowed comparison of *S. gesnerioides* plants emerging on each of the cowpea lines. We report here the selection of specific virulent pathotypes of *Striga* by different cowpea lines. This observation has profound implications for the development of cowpea-*Striga* resistance breeding programmes. By definition the most virulent genotypes have been selected by each cowpea cultivar, suggesting that resistance will be rapidly overcome in the new genetically homogeneous cowpea lines with single gene resistance such as Suvita-2. Host-directed evolution may initiate a gene-for-gene response in *S. gesnerioides* mimicking the gene-for-gene systems described in fungi.

INTRODUCTION

S. gesnerioides, is an autogamous, obligate root hemi/holoparasite which parasitises at least 25 species in 14 different plant families including cowpea (*Vigna unguiculata*) in West Africa. *Striga* infection causes extensive loss of carbohydrates, chlorosis and severe wilting in the host resulting in reduced seed size and yield losses of 50-100% (Obilana, 1987). A single plant of *S. gesnerioides* can produce up to 500,000 seeds (Aggarwal, 1985), which can remain viable in the soil for up to 20 years (Worsham, 1987) under stable conditions, so maintaining a large soil seed bank. In recent years, the problem has been exacerbated by the adoption of continuous cultivation as pressure on land use increases.

The most promising control strategy is the development of *Striga* resistant cultivars. A number of "resistant" lines have been identified (Singh & Emechebe, 1991), and resistance to *Striga* controlled by a single dominant gene has been reported for Suvita-2 (Aggarwal et al., 1986), and for B301 (Singh & Emechebe, 1990). The criteria used to define this resistance, however, are imprecise (Obilana, 1987) being based most often on the number of emerged *Striga* plants, and sometimes taking into account the number of attached *Striga* below the soil surface, but not considering the effect of these on the host. Even the most resistant lines can usually be found to have a small number of attachments below ground.

Furthermore, the resistance detected so far is not complete. The most promising cowpea line identified to date, B301 from Botswana, is reported to be resistant to *Striga* samples from Burkina Faso, Niger, Mali and Cameroon (Parker & Polniaszek, 1990). Virulence on this line, however, has recently been confirmed in Benin (Lane et al., 1993).

MATERIALS AND METHODS

Seed collection and cultural procedures

A single bulk seed population of *S. gesnerioides* growing on cowpea (collected from the CNRA-Projet Lutte Integreé Research Station at Tarna near Maradi in Niger), was sown against a susceptible cowpea line, Botswana Blackeye (85-11), and against Suvita-2 which shows differential resistance in West Africa, being resistant to *Striga* in Burkina Faso, moderately resistant in Niger and Mali, and susceptible in Nigeria (Aggarwal et al., 1986). The seed was mixed with soil (1:1 ratio of John Innes No.2 : Sand) and then sown in 5 inch pots at a rate of 1,500 seeds per pot. The pots were bottom watered and incubated at 32°C for one week to precondition the seed, before being sown with the appropriate cowpea cultivar. The position of the pots was randomised, and they were left to grow at 32°C with 16 hours daylight : 8 hours darkness.

Extraction and electrophoresis

Striga plants emerged in all of the pots sown for each cultivar, and were sampled at the onset of flowering so as to standardise the physiological age of the plants being sampled. *S. gesnerioides* in common with other highly adapted parasitic plants, has a reduced morphology with small scale like leaves. For this reason, it was decided not to follow normal practice and use leaf material, but to sample the floral spike instead.

35 mg of floral tissue was extracted with 1-2 μl/mg (fresh weight) of ice cooled extraction medium (0.1M Tris, 10 mM KCl, 1.0 mM $MgCl_2$, 1.0 mM EDTA, 0.1 M absorbic acid, 1% (v:v) 2-mercaptoethanol, 10% PVPP and 10% PVP-40; modified from Roose & Gottlieb, 1978). The samples were then run on 11% aq. starch gels (Brewer, 1970) for 2000 Volt Hours at 280 Volts constant voltage. 23 enzyme systems were surveyed using standard staining methods (Shaw & Prasad 1970) and appropriate gel and electrode buffers for each enzyme system [EST(col), EST(fluor), PPC, IDH, ALD, LAP, GDH, PGM, F-1,6DP, DIA, SKDH, α-D-GAL, ME, MDH, AAP, PY-K, G-6PDH, 6-PGDH, ADH, ACP, GOT, MNR, ß-D-GAL].

Scoring

A genetic analysis was not possible because of a number of technical difficulties associated with growing *Striga* in the U.K. In particular *S. gesnerioides* has a very short flowering period of approximately three weeks, and the tiny flowers are often cleistogamous. Conservative estimates of the level of variation were therefore obtained by adopting a rigorous scoring procedure. Bands were only scored as polymorphic where direct comparison on the same gel was possible. Only when a missing band was present in another extract on the same gel, was it scored as absent. If no cross comparison was possible, the band was coded as missing and treated differently from absent bands. A total of 93 *Striga* plants were scored - 32 on Suvita-2 and 61 on Botswana Blackeye.

RESULTS

A total of 48 different isoenzyme bands were detected of which 16 were polymorphic in eight enzyme systems. The remaining 15 enzyme systems were invariant. Of the eight variable enzyme systems, four containing eight polymorphic bands (Table 1.), were chosen for statistical analysis because they allowed direct comparison of all plants. A Chi-square analysis shows that there were significant differences in the frequency of isoenzyme banding phenotypes for MDH and ß-D-GAL of parasites growing on each host cultivar.

TABLE 1. Distribution of *S. gesnerioides* plants between isoenzyme variants when grown up on two cowpea cultivars - Botswana Blackeye and Suvita-2.

		Suvita-2		Botswana Blackeye	
Enzyme System	Band Number	Band Present	Band Absent	Band Present	Band Absent
GOT	1	2	29	6	55
	2	2	29	6	55
ACP	1	23	8	45	16
	2	18	13	47	14
MDH	3*	21	10	61	0
	4*	30	1	61	0
ß-D-GAL	2*	31	0	43	18
	3*	22	9	61	0

* Significant departure from random, probability of a greater Chi-Square is <0.01

TABLE 2. Discriminant Analysis: comparison of the discriminant scores for the isoenzyme banding phenotypes detected in plants of *Striga gesnerioides* from a single population grown up on two cowpea lines - Botswana Blackeye and Suvita-2.

Cowpea	n	Sum of Squares	S^2	F-Ratio
Botswana	61	23.457	0.3845	
Suvita-2	32	67.543	2.1107	5.489

A discriminant analysis on the combined isoenzyme patterns of individual plants indicates that there are significant differences between the mean discriminant scores of the different sub-populations of *Striga* growing on each host cultivar (Table 2). The separation of the two

sub-populations is illustrated in Fig. 1. Both these analyses indicate that Botswana Blackeye has selected a narrower range of isoenzyme phenotypes than Suvita-2. The cluster analysis, however, shows that there is no significant difference in the amount of variation present in each sub-population (Table 3).

Fig. 1. Separation of the *Striga gesnerioides* subpopulations selected by each cowpea cultivar based on a discriminant analysis of their isoenzyme scores.

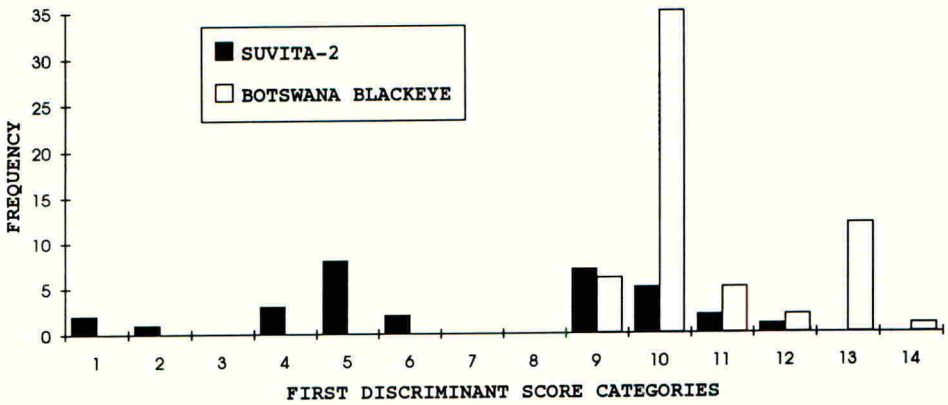

TABLE 3. Cluster Analysis: comparison of variances for the isoenzyme phenotypes obtained from plants in a single *Striga gesnerioides* population grown up on two cowpea lines - Botswana Blackeye and Suvita-2.

Cowpea	n	Total Euclidean Sum of Squares	S^2	F-Ratio
Botswana	61	4.367	0.0728	
Suvita-2	32	2.889	0.0932	1.28

DISCUSSION

Our results show that there a selection of specific *S. gesnerioides* isoenzyme phenotypes by each cowpea host cultivar. The scoring method employed had the effect of reducing the data set on which analyses could be calculated, but even with only eight polymorphic bands, clear differences between sub-populations of *S. gesnerioides* could be detected. The selected isoenzyme phenotypes probably relate very directly to genotypes since the experimental conditions were rigorously standardised so as to reduce the possibility of artifacts. Thus virulence is selected for and the cowpea host directly influences the genetic constitution of a *Striga* population.

Host selection of particular genotypes out of the parasite seed population presents problems when analysing the isoenzyme banding patterns of a parasitic plant using traditional population genetic techniques. Frequencies of particular morphs do not necessarily represent frequencies in the seed population. A susceptible host can be used but this does not ensure that it is not itself selecting a range of successful parasite genotypes because "resistance" and "susceptibility" are variable and relative only to a particular source of *Striga*. Genetic models have been applied to isoenzyme polymorphism in the absence of genetic evidence even in *Striga* (Bharathalakshmi & al. 1990, Wunderlin & al. 1979), but in our opinion this is a dubious practice for parasitic plants.

Both host and parasite are annuals maintained by strong inbreeding. West Africa is a secondary centre of diversity for cowpea (Baudoin & Maréchal, 1985), which is cultivated as many distinct and more or less homogeneous local cultivars or land races, each maintained by strong inbreeding. Each of these cowpea land races exerts a strong selection pressure on *S. gesnerioides* so that the net effect is to maintain a pattern of diversity in the parasite which matches that of the host. It is possible that inbreeding in *S. gesnerioides* may have arisen in response to this pattern of variation in the host.

The success of the parasite depends not only upon its ability to rapidly penetrate the host's root, flower and set seed while conditions are favourable, but also on its ability to maintain genetic diversity under strong selection pressure by the host. We have shown in other work (unpublished), that in spite of being predominantly an inbreeder, there is sufficient outbreeding occurring in *S. gesnerioides* to maintain a significant level of genetic variation within populations. In addition, the production of up to 500,000 seeds per plant combined with long term seed viability of up to 20 years, must be seen as an adaption to maximise the evolutionary potential of *Striga*.

CONCLUSIONS

The effect of host selection on *S. gesnerioides* populations has important consequences for cowpea breeding programmes. The combination of the presence of genetic variation, upon which selection can act, and a breeding system which can very effectively multiply any successful genotype, has the potential to rapidly overcome the resistance of new cowpea lines unless they have broad generalised, horizontal resistance with low specificity. The selection of cowpea lines with single gene resistance such as Suvita-2 and B301, may afford only short term benefits as any virulent genotypes that are selected out will quickly build up a large seed bank resulting in the rapid breakdown of resistance. In the process, many natural partly resistant land races of cowpea will have been eliminated. Given the differential resistance shown by lines such as B301 and Suvita-2, it is very important therefore, that farmers monitor sites where new cowpea lines have been introduced.

Lastly, it is interesting to speculate from these results that the single gene resistance seen in lines such as Suvita-2 and B301, could be mirrored by single gene avirulence in some *Striga* genotypes. This would extend the gene-for-gene hypothesis described for fungal (Flor, 1942) and other host parasite (Sidhu, 1975) interactions to higher plant parasites.

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EFFECT OF INTERCROPPING PEARL MILLET WITH COWPEA ON THE DENSITY OF EMERGED *STRIGA HERMONTHICA* IN MALI

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ABSTRACT

Three trials were conducted in pearl millet to determine the effects of cultivar, sowing date and spatial arrangement of a cowpea intercrop on *Striga hermonthica* populations. The presence of cowpea was found to reduce the density of emerged *S. hermonthica*. This may be due to reduced emergence or an increased mortality of emerged shoots. Establishment of a cowpea ground cover was associated with a marked reduction in soil temperature. Less *S. hermonthica* shoots were present with early than with late sowing of the cowpea, but density was not influenced by cowpea cultivar or spatial arrangement.

INTRODUCTION

Striga hermonthica is a serious pest of pearl millet (*Pennisetum americanum*) in several West African countries. The conditions in N.W. Mali are typical of those where *Striga* is most problematic; millet is grown, often continuously, in farming systems where inputs are low, rainfall erratic and soils poor.

Numerous methods are suggested for the control of *Striga* but, in practice, the options open to farmers are often very limited. Millet is grown mainly by subsistence farmers and cash investment in crop production is low. The use of high cost inputs is rare and harsh conditions mean that few alternative crops are available. Resistant varieties of some crops provide a practical alternative for the resource poor farmer, but there has been little progress to date in the search for resistance in millet (Parker, 1991).

Carson (1989) showed that intra-row intercropping of sorghum (*Sorghum bicolor)* and groundnut (*Arachis hypogaea*) significantly reduced *S. hermonthica* emergence. This was associated with a decrease in soil temperature in the intercropped plots. Cereals are rarely intercropped with groundnut in N.W. Mali, though intercropping millet with cowpea (*Vigna unguiculata*) is common. The sowing density of cowpea is currently low and increasing the density could be a means of suppressing *S. hermonthica*. Trials were conducted to determine the effect of cultivar, sowing date and spatial arrangement of a cowpea intercrop on *S. hermonthica* emergence. The trials were conducted during 1991 (Field 1) and 1992 (Fields 2 and 3) in the Cercle of Nara (14°35'N, 7°25'W).

METHODS

Trials were established in 3 fields known to have a history of *S.hermonthica* attack. The trials comprised 2x2x2 factorials, set in 3 randomised blocks. Plot size ranged from 14x6m (Field 1) to 12x8m (Fields 2 and 3). The factors were as follows:

1. cowpea cultivar: (a) Amary-sho (70-90 day, semi-erect, determinate cowpea, developed in Mali); (b) Suvita-2 (70 day, determinate cowpea from Burkina Faso, selected for its resistance to *Striga gesnerioides*).

2. cowpea sowing date: (a) sowing with the millet (farmer practice); (b) sowing 15 days later (at the first weeding).

3. cowpea spatial arrangement: (a) sown into the millet hill (farmer practice) (in-hill); (b) sown 15cm away from hill (apart).

Millet was sown in a pure stand as an additional treatment.

Fields 1 and 2 were sown after the start of the monsoon rains (9th July and 28th June respectively) and Field 3 before the rains (14th June). The millet was a short cycle (70-90 day) type. Sowing density was 80cm between and within rows. The fields were weeded twice (15 and 30 days after sowing) and insecticides applied every 10 days (cypermethrin 36g a.i./ha) for the control of grasshoppers. Millet was thinned to leave 3-4 plants per hill and the cowpea to one plant per hill.

In Field 1, counts were made at harvest of emerged *S. hermonthica* plants in the 20 central hills per plot. In Fields 2 and 3, counts were made in 20 random hills per plot at weekly intervals beginning at early *S. hermonthica* emergence (8 August -12 September). An additional count was taken at harvest (22 September) in 50 random hills per plot. In field 2, measures of soil temperature (at a depth of 15cm) were taken at weekly intervals over a period of four weeks (1-22 August). On each occasion, temperatures were read from 08.30h to 16.30h at hourly intervals, and the mean taken from five readings per plot.

RESULTS

The presence of a cowpea intercrop had no significant effect on millet yield in any of the trials (Table 1).

In Field 1, with a late sowing, there was no difference between cowpea cultivars in grain or fodder yield (data not shown). At the beginning of the growing season the rains are unreliable and, with an earlier sowing in Fields 2 and 3, Amary-sho proved susceptible to drought. Grain yield of Amary-sho at both sowing dates (322.9 and 93.8kg/ha) was significantly lower than the yield of Suvita-2 (1072.9 and 708.3kg/ha) (p>0.001, S.E.M.: 439.6 and 52.08 respectively). *S. gesnerioides* was present on Amary-sho and not on Suvita-2, but was not sufficiently dense to seriously affect yield.

In all fields, cowpea yield was significantly higher with early sowing than with late sowing and, in Fields 2 and 3, a significant interaction was recorded (p>0.01) between variety and sowing date (Table 2): the degree of difference between dates being greater in Suvita-2. In Field 2, there was also a significant interaction between sowing date and spatial arrangement (p=0.006). With an early sowing, cowpea grain yield was higher when sown in the millet hill (1089.6kg/ha) than when sown apart (817.7kg/ha), but with a late sowing, yield was lower when sown in the hill (383.3kg/ha) than apart (512.5kg/ha) (S.E.M.: 62.29).

As with grain yield, fodder yield (kg dry weight) of Suvita-2 was higher than Amary-sho in Fields 2 and 3. In Field 3, where Amary-sho was most severely affected by early season drought, the difference was significant (p>0.001, S.E of the means: 103.09), with yields of 1372.9 and 643.8kg/ha respectively. In Field 2, the trend was consistent, though not statistically significant (1390.6 and 1094.8kg/ha respectively). In both fields, fodder yield was significantly greater with early (1701 and 1196.9kg/ha) than with late sowing (784.4 and 818.8kg/ha) (p>0.001 and p=0.02; S.E.M.: 105.27 and 103.09 respectively).

TABLE 1. Millet yield (kg/ha): yield of sole cropped millet and intercropped treatments (mean of cowpea varieties).

	Field 1	Field 2	Field 3
Early sown cowpea	305.1	908.0	1499.0
Late sown cowpea	330.0	880.2	1285.8
Sole cropped millet	377.0	730.0	1531.3

TABLE 2. Cowpea grain yield (kg/ha) in Fields 2 and 3: interaction between cultivar and sowing date.

	Field 2 Early sown	Field 2 Late sown	Field 3 Early sown	Field 3 Late sown
Amary-sho	429.2	226.0	102.1	75.0
Suvita-2	1479.2	669.8	919.8	503.1
S.E.M.	62.29		73.75	

In measurements of *S. hermonthica* emergence, the results from Field 1 were not conclusive and were affected by great variability in the distribution of *Striga* across the field. However, there was a consistent trend of reduced emergence with early compared to late sown cowpea (Table 3).

In Fields 2 and 3, there were significantly fewer emerged *S. hermonthica* by harvest in all plots where millet was intercropped with cowpea. Table 4 shows the number of emerged *S. hermonthica* plants in Field 2 at weekly intervals (from early emergence to harvest) according to cowpea cultivar and sowing date. Table 5 shows density of emerged *S. hermonthica* at harvest in Field 3.

In Field 2 there were significantly less emerged *S. hermonthica* plants at harvest with early (1.13) rather than late sown cowpea (5.59) (p>0.001, S.E.M: 0.546). The same trend was consistent in Field 3 (Table 5), though differences were not statistically significant. Spatial arrangement of cowpea had no observed effect on *S. hermonthica* emergence in any trial. In Fields 1 and 2, cowpea cultivar also had no observed effect while in Field 3, there were consistently fewer *S. hermonthica* plants under Suvita-2 than under Amary-sho, though these differences were not statistically significant.

TABLE 3. Field 1: mean number of emerged *S. hermonthica* plants per hill at harvest.

		Early sown	Late sown
Amary-sho	Sown in hill	5.32	16.93
	Sown apart	5.15	13.17
Suvita-2	Sown in hill	8.77	14.50
	Sown apart	16.80	24.37
Millet in pure stand		11.78	

TABLE 4. Field 2: mean number of emerged *S. hermonthica* plants per hill at weekly intervals (8 Aug.-22 Sept.).

	8/8	15/8	22/8	28/8	5/9	12/9	22/9
AMARY-SHO							
Early sown	0.09	0.51	0.84	1.24	1.24	1.31	1.38
Late sown	0.05	0.41	1.52	1.52	4.08	4.28	5.58
SUVITA-2							
Early sown	0.16	0.38	0.90	0.92	1.08	0.94	0.88
Late sown	0.13	0.39	1.37	2.11	4.60	4.97	5.60
Millet alone	0.20	0.27	0.82	2.43	3.15	6.43	11.23
Probability	NS	NS	NS	0.02	0.02	0.001	0.001
S.E.D.(df=16)	0.078	0.217	0.195	0.561	1.145	0.769	1.252

TABLE 5. Field 3: mean number of emerged *S.hermonthica* plants per hill at harvest.

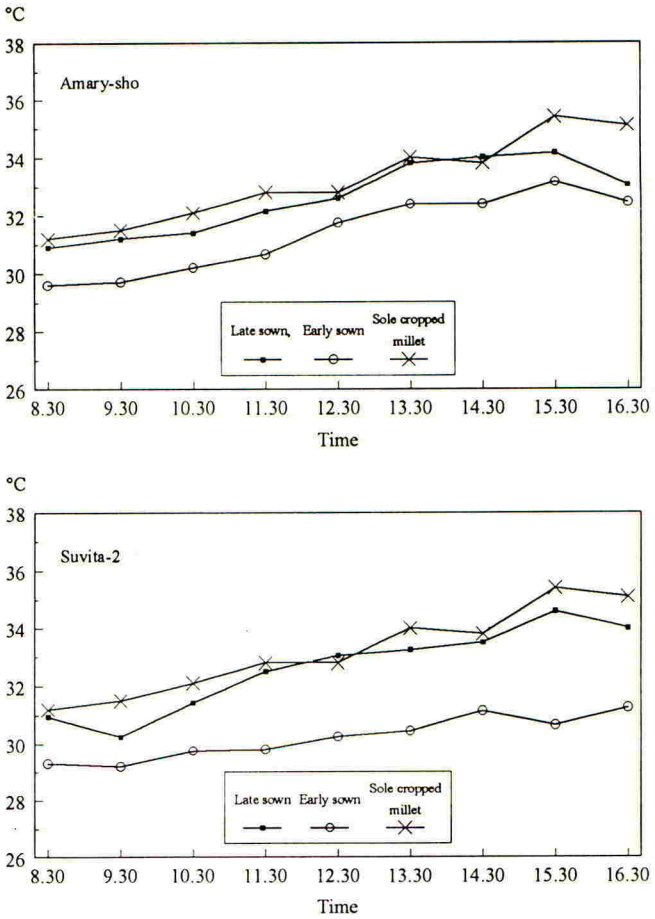
	Early sown		Late sown
Amary-sho	9.49		12.02
Suvita-2	5.66		8.61
No cowpea		17.70	
S.E.D. (df=16)		2.297	

On 1st August, little difference in soil temperature was evident between treatments. Maximum daily soil temperature (15.30h) was 35°-36°C in all plots except under early sown Suvita-2, where temperature was 33°C. Here the cowpea had established a more extensive cover than other cowpea treatments. As the season progressed, the temperature differential between treatments progressively increased. Figure 1 shows the daily temperature profile for each treatment on 22 August. By this time, all early sown Suvita-2 had established a dense cover and soil temperature at 15.30h was 4°C lower than under sole cropped millet. Peak daily temperature in these plots did not exceed 31°C, the temperature recorded under sole cropped millet at 08.30h. Early sown Amary-sho had a maximum soil temperature of 33°C at 15.30h, 2°C lower than sole cropped millet. Late sown cowpea of both varieties was little different from the pure millet; spatial arrangement also had little effect.

DISCUSSION

S. hermonthica began to emerge 4-6 weeks after crop germination (from 1st August in Fields 2 and 3), a pattern which is similar to that recorded by Andrews (1945) for *S. hermonthica* on sorghum. By this time, early sown cowpea was well established, and a reduction in soil temperature was already apparent under Suvita-2 planted apart. During the following three weeks, no difference was recorded in emerged parasite density between sole cropped and intercropped plots. Differences only became apparent one month after emergence, and subsequent to this the degree of difference between treatments progressively increased until harvest.

Figure 1: Soil temperature profile on 22nd August (at a depth of 15 cm) for sole cropped millet and cowpea intercrop treatments (mean of planting arrangements).



Andrews (1945) found that the total number of attached *S. hermonthica* seedlings per sorghum plant increased up to the fourth week after crop sowing (i.e. until parasite emergence) and then decreased from the fifth week. In the current trials, the lack of treatment effect in the three weeks following emergence suggests that the influence of cowpea on emerged *S. hermonthica* density is not through an effect on germination, attachment or early parasite development. This is contrary to the conclusion of Carson (1989), who suggested that intercropping affects parasite density through reducing soil temperature to below the optimum required for *S. hermonthica* germination. The present results suggest that the effect is more likely to be through reduced emergence or increased mortality of emerged shoots later in the season.

Once a dense cover of cowpea was established, differences between treatments in the number of emerged *S. hermonthica* plants became evident . The degree of difference recorded at harvest appeared related to the quality of the cowpea cover: lowest parasite density being recorded on plots with the highest cowpea dry weight (fodder yield). For example, in all three fields, *S. hermonthica* density was lower with early sown rather than late sown cowpea. In Field 3, where establishment of Amary-sho was poor and fodder yield significantly lower than Suvita-2, *S. hermonthica* density was lower with Suvita-2.

In plots where a cowpea cover was established more rapidly, differences in *S. hermonthica* density became evident at an earlier stage. By 28 August, early sown cowpea had a dense cover which was reflected in a reduction in soil temperature. In these plots, differences in emerged *S. hermonthica* density were already apparent. In late sown cowpea, a complete cover had not yet developed and soil temperature and *S. hermonthica* density were not different from those in sole cropped millet. Weekly counts of emerged *S. hermonthica* showed that once a dense cover of cowpea was established, there was no further change in parasite numbers. From 28 August, the number of emerged parasite plants under early sown cowpea remained constant. Under late sown cowpea, it took longer to establish a dense cover and the 'levelling-off' in parasite numbers was reached at a later date and at a higher overall density.

The results of the trial confirm that cowpea intercropped with pearl millet can reduce the density of emerged *S. hermonthica*. The reduction in *S. hermonthica* numbers in intercropped plots was associated with a decrease in soil temperature, but Parker (1991) suggested that this alone is unlikely to be sufficient to cause the reduction; the effect of shade and relative humidity may also be important. In addition to an influence on emergence, cowpea root exudates are known to stimulate the germination of *S. hermonthica* (Parker and Reid, 1979). Reduced emergence may therefore be accompanied by a depletion of the *Striga* seed bank. This intercropping system will not provide complete control of *S. hermonthica*, but could be a valuable tool as part of an integrated control package.

Yield advantages of this intercropping system over the same crops grown in pure stands have been well documented. However, Ntare and Williams (1992) found that early planting of cowpea with long cycle (120 day) millet in Niger significantly reduced millet yield. The aim of the farmers is generally to have full production of millet, the staple crop; any grain or fodder from the cowpea is an added benefit, but the fear of a millet yield loss causes farmers in N.W. Mali to sow the cowpea at a very low density. The results of these trials suggest that cowpea can be intercropped at a high sowing density with the local short cycle millet, with little or no loss in millet yield. In such an intercrop, overall yield benefits would be accompanied by suppression of one of the most difficult weed problems.

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INFLUENCES OF NITROGEN ON THE INTERACTION BETWEEN *STRIGA HERMONTHICA* AND ITS SORGHUM HOST: IMPLICATIONS FOR CONTROL

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ABSTRACT

Nitrogen (supplied as NH_4NO_3) has an adverse effect on the development of *S. hermonthica*. N reduces the biosynthesis and/or leakage of germination stimulant(s) from host roots. Following germination, N also has a negative influence on the attachment and development of juvenile *S. hermonthica* plants. Losses in host productivity result from diversion of C to the parasite, and from impairment of host photosynthesis. The latter is more marked at low N supply.

INTRODUCTION

Striga species are angiosperm root hemiparasites which infect major cereal crops (maize, sorghum and millets) in the semi-arid tropics. Potential grain yield losses probably average 5-15%, but can be much greater under heavy infestations, and can result in total crop failure. In addition it is not uncommon for farmers to abandon severely infested land or to adopt a different cropping pattern in an attempt to avoid the weed. *Striga* is therefore a serious economic problem.

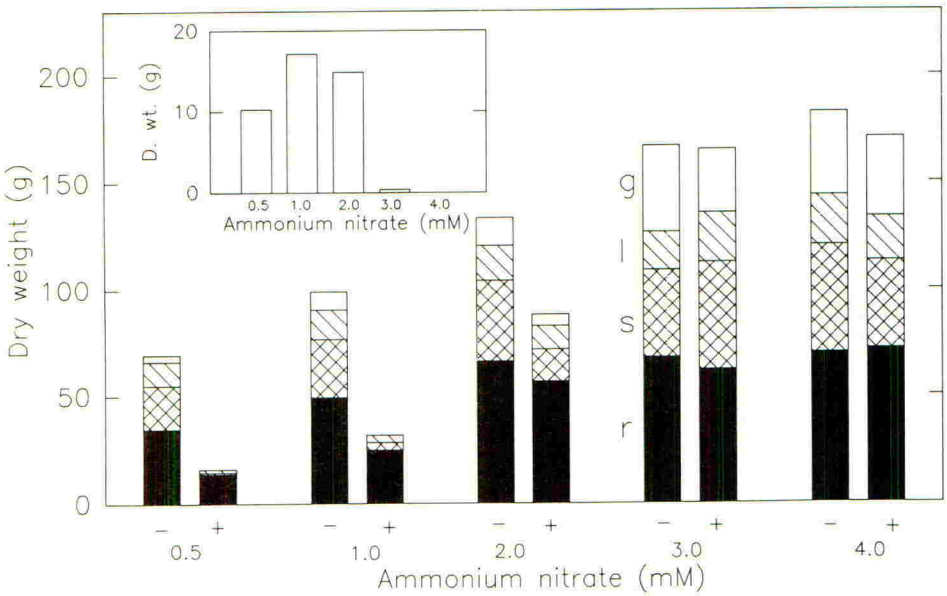
Striga species are associated with low soil fertility. In particular, soil nitrogen status has a major effect on the productivity of both host and parasite (see e.g. Farina *et al.*, 1985), stimulating the former and inhibiting the latter. Despite the large number of nitrogen fertilizer experiments which have been performed (see reviews in Pieterse & Verkleij, 1991; Sauerborn, 1992) there is no consistency in the rates or forms required for a significant effect, and no clear dose-response has been identified (Parker, 1991). In order to achieve this, it is necessary to understand how nitrogen influences the interaction between *Striga* and its host. In this paper we report the influence of ammonium nitrate on the interaction between one provenance of *S. hermonthica*, collected from a sorghum host in Sudan in 1985, and one cultivar of sorghum (*Sorghum bicolor* cv. CSH-1).

INFLUENCE OF NITROGEN ON SORGHUM GROWTH

Growth responses to N supply were investigated over 140 d by growing sorghum plants in the presence and absence of *S. hermonthica* in sand and supplying them with a N-free nutrient solution amended with different concentrations of NH_4NO_3, from 0.5 to 4 mM (Cechin & Press, 1993a). By the end of the experiment large differences in the growth and architecture of uninfected and infected sorghum plants were seen in the 0.5, 1 and 2 mM treatments (Fig. 1). There was a positive relation between N concentration and growth, with the difference between infected and uninfected sorghum

decreasing with increasing N concentration. The final biomass of infected plants was 22, 30 and 66% of uninfected controls, when supplied with 0.5, 1 and 2 mM NH_4NO_3, respectively. Of particular interest was the large difference in total biomass, and particularly grain yield, of 1 and 2 mM NH_4NO_3-grown plants, despite relatively small difference in the biomass of *S. hermonthica* which they supported (Fig. 1).

FIG. 1. Partitioning of dry weight in sorghum plants grown in the presence (+) and absence (-) of *S. hermonthica*, and dry weight of *S. hermonthica* (inset) 140 days from sowing. For sorghum, the key to the shadings is marked on one of the bars: r=root, s=stem, l=leaf and g=grain.



Three and 4 mM NH_4NO_3 continued to stimulate sorghum growth, but the total biomass of infected plants did not differ significantly from uninfected plants. However, in the 3 mM treatment, grain yield was still significantly lower (by 27%), and there were significant differences in dry matter partitioning between root and shoot (Cechin & Press, 1993a). Having quantified the effect of N on host and parasite productivity, we next considered the influence of N on specific stages of the association.

GERMINATION OF *S. HERMONTHICA*

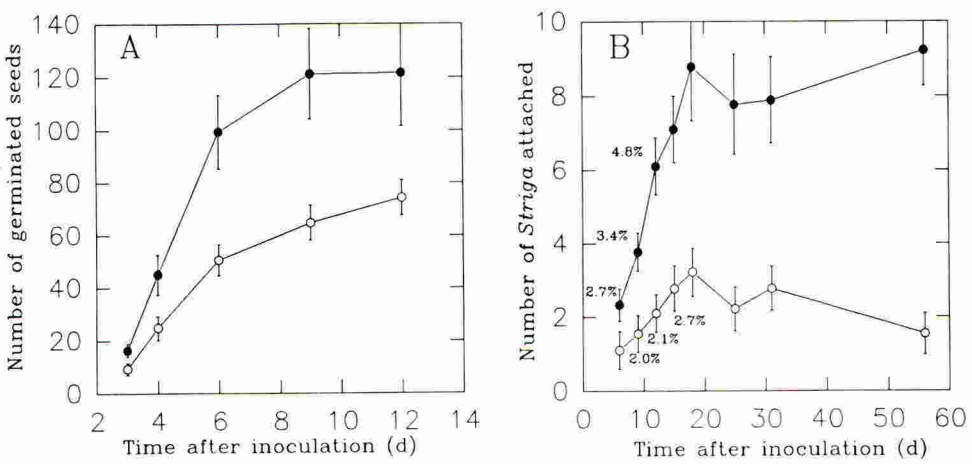
Striga seeds germinate in response to a chemical trigger present in the exudate of host (and some non-host) roots. The influence of a low (1 mM NH_4NO_3) and a high (3 mM NH_4NO_3) N culture solution on parasite seed germination was investigated on plants grown in liquid culture. Germination of *S. hermonthica* seeds occurred 3 d after inoculation of sorghum roots at both concentrations of N. However fewer seeds germinated at high N, and this

difference increased progressively with time (Fig. 2A).

In order to separate the influence of N on stimulant production or exudation from sorghum roots from processes which occur post-exudation, *S. hermonthica* seeds were preconditioned and then exposed to a solution containing sorghum root exudate (Cechin & Press, 1993b). The solution containing the exudate was amended such that it contained either 1 or 3 mM NH_4NO_3. The proportion of *S. hermonthica* seeds which germinated was not affected by addition of N. Storage of the exudate for 24 h (at 5 °C in the dark) with low and high N also had no influence on its ability to stimulate *S. hermonthica* seed germination. Thus nitrogen affects neither the germination recognition system nor the stability of active substances once exuded from sorghum roots, and may therefore affect either exudate biosynthesis or release from host roots.

In order to confirm the influence of N on stimulant production or exudation, Cechin & Press (1993b) added N to solutions used for the culture of sorghum seedlings. Subsequent germination bioassays using these solutions showed that germination rates at low N were approximately three times greater than at high N. Concurrent measurements of potassium efflux from sorghum roots grown at low and high N revealed no difference in leakage rates over a period of 24 hours. Thus it is tempting to suggest that N influences *S. hermonthica* seed germination through its effects on exudate biosynthesis, although patterns of exudation can differ between groups of compounds. Thus we conclude that N has a major effect on the germination of *S. hermonthica*, but exerts it effects via processes which occur in sorghum roots, involving either the biosynthesis of stimulants and/or their specific leakage from roots.

FIG. 2. Time course (days) for germination (A) and attachment (B) of *S. hermonthica* in response to N concentration (closed symbols = 1 mM NH_4NO_3, open symbols = 3 mM NH_4NO_3). On Fig. 2B, the percentage of germinated seeds attached the host root over the first 12 days is indicated. Points are means±SE of 9 replicates.



ATTACHMENT OF *S. HERMONTHICA*

Following germination N also influences the number of *S. hermonthica* plants which attach to the host root (Cechin & Press, 1993b). Of those seeds which germinated, 4.8% had attached to the roots of sorghum supplied with low N after 12 d, compared to 2.7% supplied with high N (Fig. 2B). Maximum numbers of attachments were observed after 18 d at both N concentrations, but at high N only 48% went on to form juvenile plants, compared to almost 100% at low N. Thus N not only influences attachment, but also the subsequent development of a successful union with the host.

As with germination, the time at which attachment started did not differ between low and high N treatments, commencing approximately six days after inoculation (Fig. 2B). However the subsequent rate of attachment did differ between the treatments. Rates of attachments were linear between 6 and 18 d from inoculation, but were greater at low N than at high N, with rates of 0.54 and 0.18 parasite/host/d, respectively.

ABOVE-GROUND GROWTH AND PHOTOSYNTHESIS OF *S. HERMONTHICA*

Once *S. hermonthica* has emerged above ground, growth of individual shoots is positively correlated with host N status. A positive linear relationship was also observed between light-saturated rates of photosynthesis and leaf N concentration in *S. hermonthica*, with rates ranging from *ca.* 4 to *ca.* 8 μmol CO_2 m^{-2} s^{-1}, in plants supplied with 0.5 and 3 mM NH_4NO_3, respectively (Cechin & Press, 1993a). Concomitant with this increase in autotrophic C fixation, is a decrease in the proportion of host-derived C in parasite leaf tissue. Gas exchange and stable carbon isotope measurements suggested that *S. hermonthica* leaves derived 27% and 6% of their C from the host when supplied with 0.5 and 3 mM NH_4NO_3, respectively. However the relationship was not linear, and values of 22% were calculated for plants supplied with both 1 and 2 mM NH_4NO_3 (Cechin & Press, 1993a).

INFLUENCE OF *S. HERMONTHICA* ON HOST PHOTOSYNTHESIS

Differences in productivity between uninfected and infected sorghum plants not only result from the transfer of carbon from host to parasite (Press *et al.*, 1987a), but also from a parasite-induced reduction of host photosynthesis (Press *et al.*, 1987b). The underlying mechanisms have yet to be elucidated, but may result from an influence of *S. hermonthica* on host electron transport capacity (Cechin & Press, unpublished). The carbon budget model of Graves *et al.* (1989) suggests that photosynthetic disfunction may account for up to 80% of the difference in productivity between uninfected and infected sorghum plants.

N clearly reduces the likelihood of a *S. hermonthica* seed making a successful union with the host plant, and thus the potential strength of additional sinks for host C. However, for any given loading of *S. hermonthica* (which will also depend on seed density in the soil), the magnitude of this flux will depend on N supply, since N will influence the balance between autotrophic and heterotrophic C acquisition. Simultaneous measurements of growth and photosynthesis are required in order to construct models which describe the proportion of carbon diverted from host to parasite with different N supplies.

Host N has been shown to have an important influence on the extent of photosynthetic disfunction, the phenomenon being greatest at lowest N supplies (Cechin & Press, 1993a). In plants supplied with 0.5 mM NH_4NO_3, photosynthetic activities of 16 and 11 μmol CO_2 m^{-2} s^{-1} were measured on uninfected and infected sorghum plants, respectively, at high photon flux densities. At higher N concentrations this difference was smaller, with both sets of plants reaching 26 μmol CO_2 m^{-2} s^{-1} at 4 mM NH_4NO_3. Varying the level of *S. hermonthica* infection showed that the effect of N on host photosynthesis can not be explained simply by differences in the mass or number of parasites supported by the host (Cechin & Press, 1993a).

DISCUSSION

Nitrogen can influence the *S. hermonthica*-sorghum association at several stages of the life-cycle. Deriving an empirical relationship between N supply and host response is difficult for a number of reasons. There are surprisingly few data relating the level of *Striga* infection and host response, and the relation between these two variables seems not always to be strong. Although diversion of host C to parasite will be largely, but not exclusively (see above), determined by parasite biomass, the influence of infection level on host photosynthetic activity is weaker, and photosynthetic disfunction may be insensitive to infection levels above a certain threshold. Thus although N may reduce levels of infection through processes which occur pre-emergence, lower levels of infection may not necessarily have proportionally beneficial effects on yield. Yield losses may be determined more by the influence of the parasite on host photosynthesis. Nitrogen is an important component of photosynthetic machinery, and the relationship between photosynthesis and nitrogen supply may differ markedly between cereal cultivars. It is thus important to understand the photosynthesis/N relationship of different cultivars, and how they are influenced by the parasite. Scaling up from leaf to plant, C gain by the host is not only determined by the rate of CO_2 fixation but also by the allometry and architecture of the plant, both of which may be radically altered by *S. hermonthica* infection (Graves *et al.*, 1989). Thus a better understanding of these processes in different cultivars is also desirable.

Nitrogen influences the rate at which below-ground processes occur, and the age at which sorghum roots are inoculated with *S. hermonthica* seed is also an important determinant of host growth and photosynthesis (Table 1). The extent to which cultivars differ in their age-related sensitivity to *S. hermonthica* infection also requires further investigation.

TABLE 1. Influence of inoculation time on photosynthesis and growth of sorghum in liquid culture. Means within a column followed by the same letter are not significantly different.

Inoculation time	Photosynthesis (μmol m^{-2} s^{-1})	Height (cm)
Uninfected	18.5a	81a
3 d old sorghum	12.2b	60b
19 d old sorghum	15.8c	76a

There is little information on the effect of supplying infected plants with N at different stages of their life-cycle, and judicious application of N fertilizer might allow effective control at lower levels of fertilization.

The extent to which N influences the host-parasite association can also be influenced by the provenance of *S. hermonthica* seed. For example, important differences were found between provenances in a preliminary study of the effects of N on parasite biomass, host biomass and photosynthetic impairment (Cechin & Press, unpublished).

The concentrations of N used in the laboratory studies reported here are at the upper end of the range employed under field conditions. Concentrations of 0.5 and 4 mM NH_4NO_3 are equivalent to application rates of 56 and 448 kg ha^{-1}, respectively (calculated from pot size and N supply rate). However, direct comparison is difficult because most field investigations have not quantified the availability of soil N, and therefore the absolute supply of N is unknown. In addition, there is little information regarding the interaction of N with other soil nutrients, water availability, and other environmental variables.

The data presented here demonstrate clearly that N is capable of controlling *S. hermonthica*, exerting its influence at a number of stages in the host-parasite life cycle. There is now a need to examine responses to N form and concentration, under both laboratory and field conditions, using different cultivars of sorghum and provenances of *S. hermonthica*, as well as extending this approach to maize.

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HOST-SPECIFICITY OF *STRIGA* SPECIES AND EVALUATION OF COWPEA AND *SORGHUM* GERMPLASM FOR RESISTANCE

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ABSTRACT

New sources of resistance to *Striga gesnerioides* were identified in cowpea (*Vigna unguiculata*) landrace germplasm (varieties APL-1 and 87-2). Resistance was expressed after penetration of cowpea roots by *S. gesnerioides* and resulted in parasite death with an associated necrosis of surrounding host tissue. Plants of variety 87-2 were propagated by cuttings and grown for seed production. Variety APL-1 and progeny of 87-2 were also resistant to *S. gesnerioides* in pot experiments. *S. gesnerioides* was not virulent on other *Vigna* and legume species. The resistance response of six *Vigna*, *Phaseolus* and *Glycine* species to *S. gesnerioides* was the same as that expressed in cowpeas APL-1 and 87-2. Lentil (*Lens culinaris*) and common vetch (*Vicia sativa*) were partially susceptible to *S. gesnerioides*. Small parasite tubercles formed on lentil and common vetch roots, but they developed more slowly than those on susceptible cowpea plants. Fourteen wild sorghums (*Sorghum arundinaceum*) were susceptible to *S. hermonthica*. The need for cereal germplasm with resistance to *Striga* is discussed.

INTRODUCTION

Striga species are parasitic angiosperms which infest cereal and legume crops in sub-Saharan Africa. Yield losses in crops parasitised by *Striga* can be up to 100% (Parker, 1991). *Striga* is an obligate root pathogen and each plant produces up to 90,000 seeds which can remain viable for about 20 years. Control of *Striga* is difficult for resource-poor farmers and crop resistance offers the most potentially effective method. Resistance has been identified in cowpea, including one variety (B301) which is resistant to *S. gesnerioides* across West Africa (Parker & Polniaszek, 1990). This germplasm is being used in breeding programmes in West Africa and cowpeas with resistance to *S. gesnerioides* will be available to farmers within 1-2 years (Singh & Emechebe, 1991; Lane & Bailey, 1992). Recently, however, a new race of *S. gesnerioides* with virulence on variety B301 was characterised (Lane *et al.*, 1993b). In other crops infested by *S. asiatica* and *S. hermonthica*, i.e. maize (*Zea mays*), sorghum (*Sorghum bicolor*), pearl and finger millets (*Pennisetum glaucum* and *Eleusine coracana*), there are no examples of the absolute resistance as found in cowpea, although some sorghum varieties have partial resistance to *Striga* (Parker, 1991).

An *in vitro* system was developed in order to study the expression of resistance of cowpea to *S. gesnerioides* and two different mechanisms of resistance were characterised (Lane *et al.*, 1991; Lane *et al.*, 1993a). Both mechanisms were expressed after penetration of cowpea roots by *S. gesnerioides*; one resulted in the death of the parasite, while in the other, parasite infections failed to develop normally. Cowpea is the principal host of *S. gesnerioides*, but tobacco (*Nicotiana tabacum*) and hairy indigo (*Indigofera hirsuta*) are also parasitised, possibly by host-specific forms (Wild, 1948;

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Musselman & Parker, 1981). This aim of the present study was to screen cowpea and wild *S. arundinaceum* germplasm for resistance to *Striga* using *in vitro* methods, and to investigate the extent and basis of the host specificity of *S. gesnerioides*.

MATERIALS AND METHODS

Legume seeds were grown in moist vermiculite for 6 to 12 d in a Fisons F600H growth cabinet at 30/25°C (light/dark temperature), 67% RH with a 16 h daylength. *Sorghum* seeds were grown in compost (Fisons F2) for 6 d in the growth cabinet. Seed of *S. gesnerioides* was collected from parasitised cowpea plants at Cinzana, Mali in 1985 (LARS no. SG85-15) whereas *S. hermonthica* seed was collected from parasitised sorghum plants at Rahad, Sudan in 1985 (SH85-12). Parasite seeds were surface sterilized, washed and imbibed for 12 (*S. hermonthica*) or 17 d (*S. gesnerioides*) in the growth cabinet. Imbibed *Striga* seeds were pipetted on to 8 mm discs of glass fibre filter paper, which were then placed in contact with host roots growing on glass fibre filter paper and tissue paper in plastic trays (Lane *et al.*, 1991). The trays were enclosed in a polyethylene bag and surrounded with aluminium foil to exclude light from the roots. Nutrient solution as described by Lane *et al.* (1991) was added to the filter paper at daily intervals.

After 24 or 72 h (*S. hermonthica* and *S. gesnerioides*, respectively), 10 to 60% of parasite seeds had germinated. *Striga* seedlings were viewed with a stereo-microscope and transferred from the filter paper on to the surface of adjacent host roots using a fine paint brush. Up to 50 parasite seedlings were placed on each host root system and two to nine plants were used of each variety. Trays were enclosed as described previously and returned to the growth cabinet. Infections were viewed with a stereo-microscope and the development of *Striga* and the responses of the infected roots were assessed at 6, 14 and 18, 19 or 21 d after inoculation. The number of parasite tubercles with stems and their diameters were measured at the third assessment date.

Cowpea variety 87-2 plants, shown to be resistant to *S. gesnerioides* using the *in vitro* system, were cloned by taking nodal cuttings which were grown in compost for 14-21 d in a propagator in a glasshouse (min. temperature 25 °C, 12 h daylength). Rooted cuttings were transferred to soil in pots and grown to produce seed. Seed of these plants and variety APL-1 were also assessed by growing plants in pots containing soil mixed with *S. gesnerioides* seed (about 1000 seeds per pot). The number of parasites that emerged above the soil surface was counted after ten weeks.

RESULTS

Resistance of cowpea to *S. gesnerioides*

There was good germination of parasite seed with all eleven cowpea varieties. Penetration of cowpea roots occurred 3-4 d after placing *S. gesnerioides* seedlings on the roots. Parasite tubercles of between 2-4 mm in diameter formed within 14 d on the susceptible cowpea, cv. Blackeye. *S. gesnerioides* seedlings penetrated the roots of varieties APL-1 and 87-2 but died with an associated necrosis of host tissue around sites of parasite penetration. There was no successful parasite development on the roots of cowpea varieties 87-2 and APL-1, except for two tubercles on one 87-2 plant (Table 1). Numerous parasite tubercles formed on the roots of the other eight cowpea varieties, although on KVX-65-114, KVX-183-1 and TVU 7614 plants, the tubercles were about half the size of those on the cv. Blackeye. Plants of variety APL-1 and progeny of cuttings of 87-2 plants which had resisted *S. gesnerioides* were grown in pots in soil mixed with *S. gesnerioides* seeds. All four plants of variety APL-1 tested and four of the six 87-2 plants tested were resistant to *S. gesnerioides*; there were no emerged parasite stems. Seven *S. gesnerioides* stems emerged on two 87-2 plants, but

TABLE 1. Assessment of cowpea germplasm with *S. gesnerioides* from Mali using the *in vitro* system.

Cowpea variety	Cowpea plants	*Striga* inoculated	Striga penetrated	*Striga* tubercles	Mean diameter of tubercles (mm)
87-2	6	300	42	0/2[a]	-[b]
APL-1	3	150	24	0	0
KVX-183-1	2	74	46	7	1.1
KVX-65-114	2	83	24	7	1.1
TVU 7614	2	77	16	3	1.2
KVX-30-1663G	3	63	22	6	1.6
KVX-30-305G	4	166	30	4	1.9
Cipea	2	70	13	5	2.7
90-168	3	67	8	3	3.3
90-164	3	70	8	5	3.4
Blackeye (min.)	2	100	9	1	2.3
Blackeye (max.)	2	91	44	43	3.6

Cowpea germplasm originated from Mali (KVX-183-1, TVU 7614, KVX-65-114, KVX-1663G, KVX-30-305G, Cipea), Niger (87-2), Nigeria (APL-1, 90-164, 90-168) and USA (Blackeye). Two plants of cowpea cv. Blackeye and two or three other cowpea varieties were used in each experiment. The minimum and maximum values for cv. Blackeye are presented. [a]Five 87-2 plants had no parasite tubercles but there were two tubercles on one 87-2 plant, [b]value not measured.

far fewer than on the susceptible cv. Blackeye (111 *S. gesnerioides* stems on six cowpea plants).

Host specificity of *S. gesnerioides*

All 12 legume species stimulated germination of *S. gesnerioides*. *S. gesnerioides* seedlings did not penetrate the roots of groundnut (*Arachis hypogaea*), winged bean (*Psophocarpus tetragonolobus*) or bambara groundnut (*Vigna subterranea*) and died with no further development (Table 2). Parasite seedlings penetrated the roots of nine legumes within 3-4 d and in similar numbers to those on the cowpea cv. Blackeye. On the roots of six of these legumes there was no further parasite development, i.e. french bean (*Phaseolus vulgaris*), lima bean (*Phaseolus lunatus*), aduki bean (*Vigna angularis*), black gram (*Vigna mungo*), mung bean (*Vigna radiata*) and soyabean (*Glycine max*). On all these plants, *S. gesnerioides* seedlings died 2-3 d after penetration of the roots with an associated necrosis of host root tissue around sites of parasite infections.

No legume species, except cowpea, was completely susceptible to *S. gesnerioides*. However, small *S. gesnerioides* tubercles with stems formed on lentil (*Lens culinaris*) and on common vetch (*Vicia sativa*) roots. At 22 d, parasite tubercles were 1 mm in diameter on lentil roots compared with 4-5 mm on cowpea roots. In a second experiment, *S. gesnerioides* tubercles were 2 mm in diameter on common vetch roots at 18 d compared with up to 6 mm in diameter on cowpea roots (cv. Blackeye). Parasite stems emerged after 60 d on lentil plants grown in pots in soil mixed with *S. gesnerioides* seeds, compared with 30 d on cowpea cv. Blackeye (Lane, Child & Birkbeck, unpublished data).

TABLE 2. Response of legumes grown using the *in vitro* system to infection by *S. gesnerioides* from Mali.

Species	Response of *S. gesnerioides*			
	Germination	Penetration of roots	Death and host necrosis	Tubercles
Arachis hypogaea	+	-	-	-
Glycine max	+	+	+	-
Lens culinaris	+	+	-	(+)
Phaseolus lunatus	+	+	+	-
Phaseolus vulgaris	+	+	+	-
P. tetragonolobus	+	-	-	-
Vicia sativa	+	+	-	(+)
Vigna angularis	+	+	+	-
Vigna mungo	+	+	+	-
Vigna radiata	+	+	+	-
Vigna subterranea	+	-	-	-
Vigna unguiculata	+	+	-	+

Legume seed was obtained from UK suppliers and inoculated with *S. gesnerioides* as described. + = positive response, - = negative response and (+) = limited parasite development.

Assessment of wild *Sorghums* for resistance to *S. hermonthica*

Wild *Sorghum* germplasm from Africa and India was inoculated with *S. hermonthica*. *Sorghum* plants were grown for 6 d using the *in vitro* system prior to the addition of *S. hermonthica*. Four sorghum plants (cv. Serena) were compared with each wild *Sorghum* sample. All fourteen samples of *Sorghum* were susceptible as there were parasite tubercles on the roots of all samples. All samples tested stimulated good parasite germination and by 18 d parasite development ranged from 49-87% on all samples. However, on one *Sorghum* from Kenya (LARS no. 92.014), parasite development was slower than that on Serena roots. On plants grown in soil mixed with parasite seed, some 92.014 plants had fewer emerged parasites than on cv. Serena, although some plants were completely susceptible.

DISCUSSION

Two new sources of resistance to *S. gesnerioides* were identified in cowpea landraces. The resistance response of the two landraces to *S. gesnerioides* was the same 'hypersensitive' response as that observed in other resistant cowpea varieties (Lane *et al.*, 1993a). Resistance of the two landraces to *S. gesnerioides* was confirmed in pot trials and in field trials in Mali (G. Hoffmann, personal communication). The *in vitro* techniques described have allowed individual cowpea plants to be assessed for resistance and resistant material to be cloned. This is essential for utilising any landrace material which is heterogenous for resistance to *S. gesnerioides*, as found with variety 87-2. The recent characterisation of a race of *S. gesnerioides* with virulence on variety B301 has highlighted the need for additional resistance genes (Lane *et al.*, 1993b). Varieties 87-2 and APL-1 are resistant to the new parasite race from Benin and also have good grain characteristics, so could immediately be used in those areas where variety B301 is susceptible (Lane *et al.*, 1993b).

S. gesnerioides collected from cowpea was only virulent on cowpea and was not virulent on related *Vigna* species or *Phaseolus* and *Glycine* species. These legumes expressed the same hypersensitive resistance mechanism to *S. gesnerioides* as previously described for cowpea variety 58-57 (Lane *et al.*, 1993a). Since cowpea has no tertiary gene pool, and more distant relatives such as *Vigna angularis* are resistant, it would be interesting to assess the virulence of *S. gesnerioides* on *Vigna nervosa*, the only member of the secondary gene pool of cowpea (Ng & Marechal, 1985). However, efforts to produce seed from the few collections of *V. nervosa* have proved unsuccessful (R.F. Mithen, personal communication). *S. gesnerioides* showed limited virulence on lentil and common vetch. Parasite infections were able to develop but much more slowly than those on cowpea. The limited susceptibility of these two species has some similarities to *S. gesnerioides* infections on cowpea variety B301, in that small tubercles formed, but parasite tubercles failed to develop normally on B301 plants (Lane *et al.*, 1993a). *S. gesnerioides* occurs sporadically in the near East and northern Africa (Parker & Wilson, 1987) where lentil and common vetch are cultivated; *S. gesnerioides* may thus represent a potential threat to these crops.

Previous surveys of *S. gesnerioides* collected from cowpea also revealed strong host specificity. No parasite development was recorded on a range of legumes grown in soil mixed with *S. gesnerioides* seed (Musselman & Parker, 1981; Igbinnosa & Okonkwo, 1991). Lentil and common vetch are not closely related to cowpea, yet were partially susceptible to *S. gesnerioides*, whereas several *Vigna* species were resistant. There is clearly no predictive relationship between the virulence of *S. gesnerioides* and the taxonomic proximity of different legume species to cowpea. A similar conclusion was reached for the specificity of the biotrophic cowpea rust fungus (*Uromyces vignae*) on a range of legume species (Elmhirst & Heath, 1989).

The results presented herein indicate that sources of resistance are most likely to be found in landraces and wild cowpeas and that this germplasm can be the basis of resistance breeding programmes for *S. gesnerioides*. In cowpea, 'cellular' resistance, i.e. resistance expressed in root tissues after the penetration by *Striga*, is highly effective and is widely used in breeding programmes in Africa. Cowpeas incorporating 'cellular' resistance genes to *S. gesnerioides* will be released to farmers within 1-2 years (K.F. Cardwell, personal communication). 'Cellular' resistance has so far been found in only one sorghum variety, IS-7777 (Olivier *et al.*, 1991). On the basis of the results with cowpea, a limited survey of 14 wild sorghums was done. It failed to identify any complete resistance to *S. hermonthica*, although the development of *S. hermonthica* was slower on sample 92.014 than on other *S. arundinaceum*. Since no complete resistance has yet been identified in most cereal crops infested by *Striga*, wild relatives of maize, millets and sorghum are currently being evaluated for resistance to *Striga*. Resistant germplasm will then be assessed to determine whether the resistance genes can be transferred into agronomically important cereals and, thus, be used in plant breeding programmes in Africa. *Striga*-resistant crops are probably the most durable and sustainable method for controlling these parasitic species.

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