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New sources of resistance of cowpea *(Vigna unguiculata)* to *Striga gesnerioides*, a parasitic angiosperm

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Summary

Thirty-seven accessions of cowpea and yard-long bean were assessed for resistance to *Striga gesnerioides*. Cowpea plants were grown using an *in vitro* method, then inoculated with young seedlings of *S. gesnerioides* produced from seed from three West African countries. Resistance was assessed by comparing the number and size of *S. gesnerioides* tubercles on these accessions with those on a known susceptible cowpea, cv. Blackeye. Two cowpea landraces, APL-1 and 87–2, were completely resistant to *S. gesnerioides* from Burkina Faso, Mali and Cameroon and partially resistant to *S. gesnerioides* from Niger. Complete resistance was expressed either as a hypersensitive response of infected root tissues or as a severely retarded development of successful infections. All other accessions, including three samples of yard-long bean were susceptible to *S. gesnerioides*. The original 87–2 plants segregated for resistance and susceptibility. However, uniformly resistant progeny were obtained by producing seed from vegetatively propagated clones of single resistant 87–2 plants. Resistance of APL-1 and 87–2 to *S. gesnerioides* was confirmed in pot and field trials. Neither of these cowpeas were resistant to *Alectra vogelii*. Varieties APL-1 and 87–2 provide additional sources of resistance to most races of *S. gesnerioides*, including a newly discovered virulent race from Benin.

Abbreviations: ICRISAT - International Crops Research Institute for the Semi-Arid Tropics, IITA - International Institute of Tropical Agriculture, SAFGRAD - Semi-Arid Food Grain Research and Development

Introduction

The widespread occurrence of *Striga gesnerioides* (Willd.) Vatke on cowpea (*Vigna unguiculata* ssp. *unguiculata* (L.) Walp.), the principal food legume grown in West Africa, presents severe difficulties for subsistence farmers, with recorded yield losses of up to 50% (Aggarwal & Ouedraogo, 1989). Control strategies based on the use of herbicides are too expensive for low-input farming systems, whilst cultural practices offer mainly long term benefits (Parker, 1991). Resistant varieties are potentially an easy, effective and economical method to control *S. gesnerioides* (Aggarwal, 1991). Breeding for resistance to *S. gesnerioides* started in 1980 and several resistant cowpea varieties, i.e. 58–57, Suvita-2 and B301, were identified using pot and field screening techniques (Parker & Polniaszek, 1990; Aggarwal, 1991). Subsequently, three parasite races with differential virulence on a series of cowpea varieties were identified from West Africa (Parker & Polniaszek, 1990). Most varieties were only resistant to the races from Burkina Faso or Mali and were susceptible to the race from Niger. In contrast, variety B301 was resistant to all three races. As a consequence, B301 is being widely used as a source of resistance in breeding programmes in West Africa (Singh & Emechebe,

Table 1. Country of origin of plant species

Plant species/accession	Origin (location)
V. unguiculata ssp. *unguiculata*	
NA14	Antilles
B301	Botswana
KVX18-31, KVX30-305-3G,, KVX30-166-3G, KVX61-2, KVX61-74, KVX65-114	Burkina Faso
F98	Ecuador
Ghana natural hybrid 1 and 2	Ghana
EC6216, GIC2, GIC872, VAR 57	India
90-171, Cipea 82671, Gao 87, Sebougou 85, Amary Sho, Niban	Mali
185 Sosta, 256 Katike Bodi	Nepal
90-164, 90-165, 90-168, Perou Gao, 87-2	Niger
APL-1, TVU7614, TVU7616, TVU10731, TVU7627	Nigeria
ACC6533, Blackeye, HB8, VU46, VU47	USA
V. unguiculata ssp. *sesquipedalis*	
VS51	Niger
VS50	Senegal
VS51HR6	Unknown
S. gesnerioides	
Sg 90-74	Benin (Zakpota)
Sg 85-26	Burkina Faso (Fada N'Gourma)
Sg 87-02, Sg 87-05	Cameroon (Lare Kaela)
Sg 85-15	Mali (Cinzana)
Sg 85-20, Sg 87-29	Niger (Magaria, Maradi)
A. vogelii	
Av 89-01	Botswana (SE)

1991). In 1991, however, a new race capable of attacking B301 was found in southern Benin (Lane et al., 1994a).

Cowpea is also susceptible to another parasitic angiosperm, *Alectra vogelii* (L.) Benth. The incidence of *A. vogelii* in West Africa has recently increased, so there is a need for cowpeas with resistance to both *Striga* and *Alectra* (Singh & Emechebe, 1991). *Alectra*-resistant cowpeas already exist, mostly from landraces tested in Botswana and a number of these are also resistant to *A. vogelii* from West Africa (Polniaszek et al., 1991).

In the present study, an *in vitro* system was used to screen a wide range of cowpea germplasm for new sources of resistance to *S. gesnerioides*. Cowpeas identified with resistance to *S. gesnerioides* were subsequently tested in pot trials in the UK and in field trials in Mali for resistance to both *S. gesnerioides* and *A. vogelii*.

Methods

Source and growth of plants in the in vitro *system*

The origins of seeds of cowpea and yard-long bean (*Vigna unguiculata* ssp. *sesquipedalis* (L). Verdc.), *S. gesnerioides* and *A. vogelii* are listed in Table 1. Cowpea seeds were sown in Vermiculite and maintained in a glasshouse at a minimum temperature of 25°C and a 16 h photoperiod. After 5 d, Vermiculite was washed from the cowpea roots and the cowpea plants were placed in shallow plastic trays (110 × 170 × 12 mm) lined with two layers of tissue paper and glass fibre filter paper (Lane et al., 1991). Nutrient solution, with a double concentration of Fe, was added daily (Drew & Saker, 1986). A fungicide, benlate (methyl 1-butyl carbonyl-2-benzimidazole carbamate), at 0.01 mg l^{-1} active ingredient, was included in the nutrient solution to suppress growth of contaminating fungi. The trays were wrapped in polyethylene and surrounded with aluminium foil. Plants were maintained in a Fisons F600H growth cabinet at a temperature of 30°C light/25°C dark, 67% RH and a 16 h daylength. Photosynthetic photon flux density was 180 μmol m^{-2} s^{-1}.

Seeds of *S. gesnerioides* and *A. vogelii* were sterilized in a sodium hypochlorite solution (1% available chlorine) for 5 min, rinsed in distilled water and placed on moist glass fibre filter paper (GF/A, Whatman) in a Petri dish. *Striga* and *Alectra* seeds were imbibed in the growth cabinet for 19 and 7 d, respectively. Imbibed seeds were transferred to 6 mm discs of glass fibre filter paper, which were placed over the tips of lateral roots of cowpea plants growing in trays. Seeds of *S. gesnerioides* germinated after 72 h, those of *A. vogelii* after 48 h. Approximately 50 germinated seedlings were transferred to the roots of each cowpea plant using a fine brush.

One to four cowpea accessions were tested in each experiment. There were between one and five plants of each accession in each experiment. The number of parasites that penetrated the roots was counted after 6 d, and the number that developed shoots and the diameter of tubercles were measured after 17–21 d. All experiments included three or four cv. Blackeye plants, a variety known to be susceptible to both parasites (Lane et al., 1993; Polniaszek et al., 1991).

The experiments were carried out over a period of 18 months. It was assumed that the factors which caused variability of *S. gesnerioides* development on cv. Blackeye during this time were similar to those on the other cowpea varieties. On this basis, data from each cowpea variety was compared with cv. Blackeye for each experiment. The numbers of *S. gesnerioides* seedlings which formed tubercles were analyzed using a generalized linear model (GLM) with a binomial distribution and a logit link function (McCullagh & Nelder, 1989). The results of these analyses are presented as the relative odds of tubercle infection for each cowpea compared with cv. Blackeye. Where the percentage tubercle formation was 0% or 100% for an individual cowpea or for cv. Blackeye, the logit is undefined, so a χ^2 test of independance has been used as an approximate test of the difference between two proportions. All statistical analyses were carried out using the Genstat statistical package (Payne et al., 1987).

In all experiments, the mean diameter of *S. gesnerioides* tubercles on the test cowpeas was compared with that of cv. Blackeye using an analysis of variance. The results are presented as mean diameter and also as a percentage of the diameter of tubercles on cv. Blackeye, along with an indication of significant differences. The number of *A. vogelii* seedlings that penetrated the roots and the number of these which survived were analysed using a GLM with binomial distribution and logit link. The results are presented as the mean percentage of *A. vogelii* infections which developed from the total number of seedlings inoculated on the roots, along with 95% confidence intervals.

Propagation of cowpea variety 87–2

Nodal cuttings containing a leaf and axillary bud from plants of variety 87–2, which had been grown using the *in vitro* system, were placed in Fisons F2 compost. The plants were maintained in a propagator in a glasshouse at a minimum temperature of 25°C with a 12 h photoperiod for 14–21 d. Rooted cuttings were transplanted to soil in 1 l pots (Mendip loam:grit and sand:peat: 6:2:4) with 5 g l^{-1} Osmocote) and grown for a further 10 weeks to produce seed.

Studies using plants grown in soil

Cowpeas were grown in soil (Mendip loam:grit and sand:peat: 3:3:2) containing 3.75 g l^{-1} Osmocote in 1 l pots in a 16 h photoperiod glasshouse at 25°C. The uppermost 0.5 l of soil contained about 500 seeds of *S. gesnerioides* or *A. vogelii*. Two cowpea seeds were sown in each pot and thinned to one per pot after emergence. Four or six cowpea plants of each variety were used for each parasite sample. At 10 weeks, the total number of parasite stems was counted. Means for each cowpea variety were compared with means on cv. Blackeye using an analysis of variance. Numbers of *Striga* or *Alectra* stems that emerged on each host plant were analysed using a GLM with Poisson distribution and logarithmic link. The mean number of parasites per plant are presented, along with respective 95% confidence intervals.

Field trials in Mali

Seeds of *S. gesnerioides* and *A. vogelii* were collected in Mafeya village, 80 km NE of Bamako in Mali. Cowpeas were evaluated in 1992 and 1993 at the ICRISAT field station at Samanko, near Bamako. Three treatments were used: uninfested soil (4 plots), soil artificially infested with *A. vogelii* seed (4 plots in 1992, 3 in 1993) and soil artificially infested with *S. gesnerioides* seed (1 plot in 1992 and 1993). The paucity of *S. gesnerioides* seeds collected from Mafeya prevented replication of this treatment. Plots (4.2 × 7 m) had 18.5 g of parasite seed incorporated into the soil of each 7 m row. Cowpeas were sown 0.4 m apart with a spacing of 0.6 m between rows. The plots were weeded at 15 and 30 d after sowing. The number of emerged parasite stems was counted each week until harvest, which occurred 13 to 14 weeks after sowing. The number of *Alectra* stems were analysed using a GLM with a Poisson distribution and logarithmic link and presented as the mean number of parasite stems per field plot, along with 95% confidence intervals.

87-2 original seed

Assessment of resistance using *in vitro* methods		Assessment of resistance using *in vitro* methods		
Plants susceptible to *Striga* from Mali (Table 3)	Plants resistant to *Striga* from Burkina Faso or Mali (Table 2 and 3)	Plants resistant to *Striga* from Burkina Faso (Table 2)	Plants resistant to *Striga* from Mali (Table 3)	Plants partially resistant to *Striga* from Niger (Table 5)
	Clonal propagation	Clonal propagation	Clonal propagation	Clonal propagation
	Seed A	Seed C1	Seed C2	Seed C3
	Assessment of resistance using soil-filled pots (Table 6)	Assessment of resistance to *Striga* from Benin (Table 4)	Assessment of resistance to *Striga* from Mali (Table 3)	Assessment of resistance of *Striga* from Mali (Table 3) and Niger (Table 5)
	Plants resistant to *Striga* from Mali		Assessment of resistance to *A. vogelii* using soil-filled pots (Table 7)	
	Clonal propagation			
	Seed B			
	Field trials in Mali (Table 7)			

Fig. 1. Selection, propagation, and multiplication of variety 87-2.

Results

Selection and propagation of cowpea variety 87–2

In preliminary assessments of resistance, some plants of 87–2 were totally resistant to *S. gesnerioides*, but others were susceptible. It was, therefore, necessary to select true breeding material. Plants from the original collection of 87–2 seed were assessed for resistance *in vitro*. Plants that were resistant to *S. gesnerioides* from Burkina Faso or Mali were clonally propagated by nodal leaf cuttings to produce about 1000 seeds (sample A) (Fig. 1). Sample A was assessed with *S. gesnerioides* from Mali in a pot experiment; again, some plants were resistant and some were susceptible. Cuttings were taken from resistant 87–2 plants to produce seed sample B which was later used for field trials in Mali. In a second experiment, using plants grown from the original 87–2 seed, cuttings were taken from those plants which were resistant to *S. gesnerioides* from Burkina Faso or Mali or partially resistant to *S. gesnerioides* from Niger. Approximately 1000 seeds were collected from these groups of plants when raised from cuttings (C1, C2 and C3).

Development of S. gesnerioides *in vitro*

All cowpeas and yard-long bean accessions stimulated germination (20–80%) of every *S. gesnerioides* sample. At 6 d after inoculation, *S. gesnerioides* seedlings successfully penetrated the roots of all cowpeas and yard-long beans tested. As a result, only data on parasite development that took place subsequent to root penetration is presented. Parasite tubercles developed on the roots of cv. Blackeye within 14–21 days and soon afterwards the shoots began to elongate.

Resistance of Vigna *accessions to* S. gesnerioides *from Burkina Faso*

Cowpea varieties tested against *S. gesnerioides* from Burkina Faso were the KVX varieties from the SAFGRAD/IITA programme, which had shown indications of resistance to the parasite, and cowpeas from sites in West Africa where no *S. gesnerioides* was present. No *S. gesnerioides* tubercles were observed on the roots of varieties APL-1 or 87–2 (Table 2). Parasite tubercles formed on all other cowpeas. However, on cowpea varieties KVX18–31, KVX30–305–3G and Cipea

Table 2. Response of cowpea accessions, grown *in vitro*, to *S. gesnerioides* from Burkina Faso (Sg 85–26)

Cowpea variety	Number of cowpea plants	Total number of *Striga* seedlings placed on roots	Number of *Striga* seedlings which penetrated roots	*Striga* tubercles Number	Relative odds[1]	Diameter (mm) [% of Blackeye][2]
APL-1	3	143	54	0	a***	-
87–2 (original)	3	150	32	0	a***	-
87–2 (original)	3	207	18	0	a***	-
KVX30–305–3G	3	140	43	8	0.044***	1.6 [42]***
TVU7614	1	38	11	6	0.10**	2.5 [73]*
Cipea 82671	1	40	22	13	0.12**	2.7 [77]**
KVX18–31	5	161	47	23	0.19***	1.4 [36]***
90–165	3	129	33	26	0.48	-[3]
KVX30–166–3G	3	62	49	24	0.66	2.6 [64]**
90–164	3	98	55	24	b***	2.5 [66]***
90–168	3	86	43	23	b***	2.4 [63]***
TVU10731	1	18	16	10	b**	3.7 [81]*
KVX65–114	1	27	10	6	b**	1.0 [22]***
TVU7627	1	12	9	8	b	2.7 [59]***
TVU7616	1	23	9	8	b	1.9 [41]***
90–171	3	93	37	37	c*	-[3]
Blackeye (min.)	2	44	32	19	-	4.0
Blackeye (max.)	2	48	26	26	-	3.9

The data presented are from several experiments comprising of between 1 and 4 cowpea varieties and a susceptible cowpea, cv. Blackeye in each experiment. The maximum and minimum relative odds of tubercle formation for cv. Blackeye, are presented for comparison.

[1] calculation of relative odds is described in the Methods; *** $p<0.001$, ** $p<0.01$, * $p<0.05$.

[2] mean tubercle diameter of *S. gesnerioides* is shown, and also expressed as a percentage of the mean diameter of *Striga* tubercles on Blackeye plants in the same experiment.

[3] data not recorded.

a) relative odds were zero because no tubercles formed on the test cowpeas.

b) relative odds were zero because all penetrating *Striga* seedlings on cv. Blackeye produced tubercles.

c) relative odds were ∞ because all penetrating *Striga* seedlings on the test cowpea produced tubercles.

For a, b, and c, a χ^2 test was used as an approximate test of differences.

82671, the odds of parasite seedlings developing tubercles was less than on cv. Blackeye ($p<0.01$). The diameter of tubercles on cowpea varieties KVX30–305–3G, KVX18–31, KVX65–114 and TVU7616 was less than half those on cv. Blackeye.

Resistance of Vigna *accessions to* S. gesnerioides *from Mali, Benin and Cameroon*

The same cowpea varieties, as described previously, and five other varieties (Gao 87, Niban, Sebougou 85, TVU 7614 and KVX 61–74) from the Mali national programme were assessed against *S. gesnerioides* from Mali. Tubercles did not form on the roots of varieties APL-1, progeny of 87–2 (C2 and C3) or plants grown from original seed of 87–2, except for two tubercles on one 87–2 plant grown from original seed (Table 3). Tubercles developed on all other cowpeas. On four cowpeas, KVX65–114, KVX30–305–3G, KVX18–31 and TVU7614, the odds of parasite seedlings forming tubercles was significantly less than on cv. Blackeye ($p<0.001$) and the mean tubercle diameter on these four cowpeas was less than half that of tubercles on cv. Blackeye. Cowpea varieties Niban, KVX61–74 and TVU7616 also had smaller odds of tubercle formation cv. Blackeye ($p<0.01$).

Cowpea varieties APL-1 and 87–2 were also assessed for resistance to *S. gesnerioides* from Benin and Cameroon. No parasite tubercles developed on the roots of these varieties with either of the *S. gesnerioides* samples. In contrast, there were numerous tubercles on the roots of cv. Blackeye (Table 4).

Table 3. Response of cowpea accessions, grown *in vitro*, to *S. gesnerioides* from Mali (Sg 85–15)

Cowpea variety	Number of cowpea plants	Total number of *Striga* seedlings placed on roots	Number of *Striga* seedlings which penetrated roots	*Striga* tubercles		
				Number	Relative odds[1]	Diameter (mm) [% of Blackeye][2]
APL-1	3	135	21	0	a***	-
87–2 (C3)	4	200	20	0	a***	-
87–2 (C2)	3	150	18	0	a***	-
87–2 (original)	3	189	14	0	a***	-
87–2 (original)	3	150	24	2	b***	-
KVX65–114	2	83	24	7	0.010***	1.1 [30]***
KVX30–305-3G	4	166	30	4	0.011***	1.9 [43]***
KVX18–31	2	74	46	7	0.013***	1.1 [25]***
TVU7616	1	31	4	2	0.023**	1.8 [49]*
Niban	2	46	13	2	0.033**	-[3]
Gao 87	2	48	6	1	0.037**	-[3]
KVX61–74	2	66	15	3	0.046**	-[3]
TVU7627	1	78	15	10	0.046***	2.0 [57]***
TVU7614	2	77	16	3	0.070***	1.2 [30]***
90–168	3	67	8	3	0.085	3.3 [54]*
TVU10731	1	39	14	12	0.14	3.0 [83]
Cipea 82671	2	70	13	5	0.19*	2.7 [69]*
90–164	3	70	8	5	0.24	3.4 [55]*
90–165	3	134	27	16	1.5	-[3]
KVX30–166-3G	3	63	22	6	3.4	1.6 [63]
90–171	3	100	16	13	4.3	-[3]
Sebougou 85	2	41	7	7	c	-[3]
Blackeye (min.)	2	100	9	1	-	2.3
Blackeye (max.)	2	80	19	19	-	3.6

Assessments carried out as described in Table 2.

Table 4. Response of cowpea accessions 87–2 and APL-1, grown *in vitro*, to *S. gesnerioides* from Cameroon and Benin

Striga origin/sample no/Cowpea variety	Number of cowpea plants	Total number of *Striga* seedlings placed on roots	Number of *Striga* seedlings which penetrated roots	Number of *Striga* tubercles
Cameroon (Sg 87–05)				
Blackeye	3	150	19	19
87–2 (orig.)	3	200	20	0
Cameroon (Sg 87–02)				
Blackeye	3	110	35	33
APL-1	2	78	23	0
Benin (Sg 90–74)				
Blackeye	4	105	59	46
87–2 (C1)	2	80	37	0
APL-1	5	92	53	0

Table 5. Response of cowpea and yard-long bean accessions grown *in vitro*, to *S. gesnerioides* from Niger (Sg 87–29)

V. unguiculata/species/ accession	Number of cowpea plants	Total number of *Striga* seedlings placed on roots	Number of *Striga* seedlings which penetrated roots	*Striga* tubercles		
				Number	Relative odds [1]	Diameter (mm) [% of Blackeye][2]
ssp. *unguiculata*						
87–2 (original)	3	190	12	4	0.028**	0.8 [55]
KVX61–74	3	144	21	6	0.065***	1.8 [93]
KVX61–2	3	152	58	18	0.073***	-[3]
APL-1	3	144	56	28	0.080***	4.1 [98]
KVX30–305–3G	2	53	8	3	0.085	4.7 [117]
90–168	2	76	14	9	0.11	3.9 [104]
Sebougou 85	2	94	14	7	0.13*	3.8 [56]**
Cipea 82671	2	88	4	2	0.14	3.0 [75]
90–164	3	108	30	21	0.15	3.7 [98]
VU46	4	200	32	8	0.17***	2.7 [147]***
KVX65–114	3	138	50	26	0.18***	1.9 [98]
90–165	3	128	21	10	0.19*	-[3]
Perou Gao	3	164	14	11	0.22	1.7 [85]
KVX18–31	2	87	32	20	0.24	5.0 [125]
HB8	3	132	22	18	0.27	1.6 [82]*
Ghana 1	3	125	28	23	0.27	1.8 [88]
VU47	3	140	35	14	0.34*	2.5 [149]**
GIC2	3	126	34	25	0.46	-[3]
TVU7614	2	100	7	4	0.52	2.8 [65]*
87–2(C3)	4	200	16	5	0.58**	2.4 [61]
TVU7627	3	133	9	6	0.78	2.8 [65]**
TVU10731	3	152	35	24	0.85	2.9 [66]***
Niban	3	145	32	28	0.91	4.9 [72]**
EC6216	3	157	38	33	1.1	-[3]
VAR 57	1	50	19	4	1.2	3.5 [98]
ACC6533	1	50	4	3	1.2	3.5 [89]
256 Katike Bodi	1	30	21	16	1.3	3.2 [80]*
90–171	3	109	15	13	1.4	-[3]
Ghana 2	3	155	31	23	1.5	-[3]
Gao 87	2	101	18	11	1.6	6.1 [89]
GIC872	3	100	39	19	4.2**	3.1 [85]
F98	2	108	9	7	b	5.0 [69]*
NA14	2	65	18	15	b	6.9 [95]
TVU7616	4	51	4	4	c	1.8 [41]***
185 SOSTA	1	52	2	2	c	4.5 [114]
Blackeye (min.)	2	100	38	7	-	4.0
Blackeye (max.)	2	102	68	65	-	-[3]
ssp. *sesquipedalis*						
VS51HR6	2	100	23	15	1.3	-[3]
VS50	2	96	14	7	0.67	-[3]
VS51	2	101	19	9	0.60	-[3]
Blackeye	2	100	35	21	-	-[3]

Assessments carried out as described in Table 2.

Resistance of Vigna *accessions to* S. gesnerioides *from Niger*

Thirty-seven accessions were tested against the *S. gesnerioides* sample from Niger. Tubercles developed on all cowpeas, including APL-1 and 87–2, and the three accessions of yard-long bean (Table 5). On six cowpeas, APL-1, 87–2 original, KVX61–74, KVX61–2, VU46, and KVX65–114, the odds of *S. gesnerioides* seedlings developing tubercles was significantly less than on cv. Blackeye ($p \leq 0.001$) (Table 5). On all cowpeas tested, except 87–2 (original), Sebougou 85 and TVU7616, tubercles were of a similar size or larger than those on cv. Blackeye. On these three cowpeas, the diameters of parasite tubercles were about half of those on cv. Blackeye.

Expression of resistance of cowpeas 87–2 and APL-1 to S. gesnerioides

The initial development of *S. gesnerioides* on the roots of cowpeas APL-1 and 87–2 grown using the *in vitro* system was similar to that on cv. Blackeye. Some *S. gesnerioides* seedlings died after 3 days with an associated necrosis of host root tissue surrounding the penetration site on both APL-1 and 87–2 roots. A second resistance response was observed on 87–2 plants infected with all *S. gesnerioides* samples, except that from Niger, and on APL-1 plants infected with *S. gesnerioides* from Burkina Faso. Tubercles formed but they subsequently failed to enlarge, and stems were not produced.

Development of S. gesnerioides *on cowpeas 87–2 and APL-1 grown in pots and in field trials in Mali*

No parasite stems emerged on variety APL-1 grown in soil mixed with *S. gesnerioides* from Mali (Table 6). Progeny of these resistant plants were also resistant to the race from Mali (Child *et al.*, unpublished data). Three of the four APL-1 plants tested with *S. gesnerioides* from Niger were susceptible but on the fourth plant, no parasite stems emerged (Table 6). Progeny of this apparently resistant plant were tested using the *in vitro* system against the Niger parasite sample. All were totally susceptible (Child *et al.*, unpublished data). Four 87–2 plants (A) were resistant to *S. gesnerioides* from Mali and two were susceptible, whilst five of six 87–2 plants tested were susceptible to the parasite sample from Niger (Table 6), though analysis showed that fewer parasites emerged on 87–2 plants than on cv. Blackeye.

Table 6. Response of cowpea accessions APL-1 and 87–2, grown in pots, to *S. gesnerioides* from Mali and Niger

Striga origin/sample no/Cowpea variety	No. of cowpea plants with emerged *S. gesnerioides* stems	Mean no. of *S. gesnerioides* stems per cowpea plant (95 % confidence interval)
Mali (Sg 85–15)		
APL-1	0[1]	0.0
Blackeye	3[1]	30.7 (5.0 – 54.3)
87–2(A)	2[2]	1.2 (0.1 – 12.2)
Blackeye	6[2]	21.5 (12.4 – 37.3)
Niger (Sg 87–29)		
APL–1	3[1]	17.5 (5.5 – 55.6)
Blackeye	4[1]	23.7 (8.8 – 64.1)
Niger (Sg 85–20)		
87–2 (A)	5[2]	5.7 (1.9 – 16.6)
Blackeye	6[2]	14.5 (7.4 – 28.4)

[1] 4 plants each of APL-1 and Blackeye tested.
[2] 6 plants each of 87–2 and Blackeye tested.

In a field trial in Mali in 1992, no *S. gesnerioides* developed on cowpea varieties APL-1, 87–2 (B) or the known resistant variety, B301. In 1993, similar results were obtained, although the variety B301 was not used due to insufficient harvest of seed in 1992, and was replaced with Amary Sho, a local susceptible variety. On cv. Blackeye, there was a maximum of 56 *S. gesnerioides* plants m^{-2} in 1992 and 121 plants m^{-2} in 1993. The grain yield of the cowpeas in the infested plots in 1993 was 607 kg ha^{-1} for APL-1, 180 kg ha^{-1} for 87–2, 119 kg ha^{-1} for Blackeye. These yields were much greater than those (4 kg ha^{-1}) from the variety Amary Sho. In the same trial in plots with no *Striga* present, the yields were 910 kg ha^{-1} for APL-1, 430 kg ha^{-1} for 87–2, 377 kg ha^{-1} for Blackeye, and 254 kg ha^{-1} for Amary Sho.

Responses of cowpeas APL-1 and 87–2 to A. vogelii in vitro, *in pots and in field trials in Mali*

APL-1 and 87–2 were susceptible to *A. vogelii* in the *in vitro* system (Table 7). *A. vogelii* emerged on two of the four APL-1 plants tested in pots, whilst the parasite developed on all ten 87–2 (C2) plants tested. However, there were significantly fewer parasite stems on both APL-1 and 87–2 plants than on cv. Blackeye.

Table 7. Response of cowpea accessions 87–2 and APL-1, grown *in vitro*, in pots and in the field, to *A. vogelii*

Cowpea variety	Number of cowpea plants (A,B) or field plots (C)	*A. vogelii* stems (95% confidence interval)
A: *In vitro* assessments:		
Blackeye	3	38.3 (25.7 – 52.6)[1]
APL–1	3	35.0 (26.5 – 44.6)[1]
Blackeye	3	10.0 (1.2 – 49.8)[1]
87–2 (C2)	3	9.3 (1.7 – 37.7)[1]
B: Pot experiments:		
Blackeye	4	19.8 (11.9 – 32.9)[2]
APL-1	4	1.5 (0.2 – 9.5)[2]
Blackeye	4	24.8 (20.6 – 29.7)[2]
87–2 (C2)	10	2.3 (1.6 – 3.4)[2]
C: Field trials:		
1992		
Blackeye	3	11.3 (1.4 – 90.3)[3]
APL-1	3	28.0 (7.5 – 104.7)[3]
87–2 (B)	3	55.3 (21.6 – 141.5)[3]
B301	3	0
1993		
Blackeye	3	0
APL-1	3	5.2 (0.4 – 69.1)[3]
87–2 (B)	3	18.1 (4.0 – 81.4)[3]
Amary Sho	3	19.3 (4.5 – 83.9)[3]

[1] Percentage of total *A. vogelii* seedlings placed on roots which had produced successful infection. Number of seedlings placed on roots varied from 81 to 177.
[2] Mean number of *A. vogelii* stems per cowpea plant.
[3] Mean number of *A. vogelii* stems per field plot.

In field trials in Mali in 1992, cowpeas APL-1, 87–2 (B) and Blackeye were all susceptible to *A. vogelii*. Variety B301 was resistant (Table 7). In 1993, APL-1, 87–2 (B) and Amaricho were all susceptible to *A. vogelii*.

Discussion

The *in vitro* screen has identified two cowpeas, APL-1 and 87–2, with resistance to four races of *S. gesnerioides*. The expression of resistance was similar to that found on other resistant cowpea varieties, i.e. B301 and 58–57 (Lane et al., 1993). Varieties APL-1 and 87–2 were resistant to a new race of *S. gesnerioides* recently discovered at Zakpota in Benin. This new race is pathogenic on B301 (Lane et al., 1994a), a variety which is being used across West Africa as a source of resistance in breeding programmes. These additional sources of resistance should prove extremely valuable for breeding cowpeas resistant to the strain from Benin. In addition, cowpeas APL-1 and 87–2 yielded well in a field trial in Mali in 1993, and this trait would be useful to incorporate into released varieties for this region. Varieties APL-1 and 87–2 were susceptible to *A. vogelii* in all tests. There is no general cross-resistance for *Alectra* and *Striga*. Other varieties, e.g. Suvita-2 and IT82D-849, which are resistant to *S. gesnerioides*, are also highly susceptible to *A. vogelii* (Polniaszek et al., 1991). Cowpeas APL-1 and 87–2 were only partially resistant to *S. gesnerioides* from Niger. Partial resistance was evident as lower numbers of tubercles and slower growth of parasite infections. In previous studies, and in the present assessments, most other varieties were totally susceptible to the Niger race. Although not as effective as the resistance shown by APL-1 and 87–2 to the other races of *S. gesnerioides*, their partial resistance may have value to breeding programmes, until such time as new sources of complete resistance to the Niger strain are identified. Several other cowpeas, notably KVX30–305–3G and KVX18–31, showed partial resistance to *S. gesnerioides* from Burkina Faso and Mali. These two varieties had been developed by SAFGRAD/IITA from another *Striga*-resistant variety, Suvita-2 and they have good grain characteristics, bruchid-resistance and drought-tolerance (Aggarwal, 1991).

The *in vitro* screen has been found to be a highly reliable method for identifying resistance to *S. gesnerioides* in cowpea. Cowpea varieties APL-1 and 87–2 gave similar responses to the different *S. gesnerioides* races when assessed using the *in vitro* screen, pot experiments or field experiments. In addition, it was possible to remove individual resistant plants from the *in vitro* screen, transfer them to pots, where they were grown and propagated to produce seed. Since cowpea is an autogamous species (Rachie, 1985), the progeny was uniformly resistant. This form of plant selection proved essential for utilising the resistance identified in the original heterogeneous seed sample of 87–2.

In this study, the two new resistances to *S. gesnerioides* were identified in landraces, whilst most improved cowpeas were susceptible. Previously, partial resistance was found in a wild relative of cowpea, *V. unguiculata* ssp. *dekindtiana* var. *mensensis* (Lane et al., 1994b). There is much less genetic diversity in *V. unguiculata* and cultivated relatives than in wild cowpeas (Vaillancourt et al., 1993). This indicates that future searches for resistance should focus on germplasm containing maximum genetic diversity, i.e. on both wild cowpea relatives and landrace material, rather than cultivated cowpea germplasm. The *in vitro* screen allows resistance to be reliably identified, the response to different races established, and where necessary, progeny can be produced. In this way, the discovery and deployment of resistance should be much more effective.

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