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Vegetative growth of sorghum and *Striga hermonthica* in response to nitrogen and the degree of host root infection

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Abstract

The effects of nitrogen and the extent of sorghum root infection by *Striga hermonthica* on host-parasite association during vegetative growth were studied using a split root system in a 3 × 3 factorial combination of N (37 mg on one, 18.5 or 37 mg on both root-halves) and *Striga* (no, one or both root-half infection). High N increased sorghum shoot weight by 22% more than low N, but did not significantly affect *Striga* growth 64 days after transplanting sorghum (DAP). *Striga* reduced sorghum stem height and weight by 22% and 25% at 38 DAP, and by 34% and 36% at 64 DAP, respectively. Leaf weight was not affected. *Striga* stimulated root growth 38 DAP, but not 64 DAP. In partially infected sorghum, 64 DAP, the parasite shoot number, shoot height and shoot dry weight were 36%, 46% and 35%, respectively and host shoot dry matter was 142% of those in fully infected plants, indicating an inverse relationship between the degree of host root infection and the level of resistance. The results suggest that sorghum released resistance-confering substances to the infection points after sensing infection. When infection points are widely distributed as in fully infected sorghum, less of such substances appear to render the host more vulnerable.

Abbreviations: DAP – days after transplanting sorghum; vs. – versus; df – degrees of freedom.

Introduction

Sorghum (*Sorghum bicolor* (L.) Moench), in sub-Saharan Africa, is grown by subsistence farmers on more than 48 million hectares. *Striga hermonthica* (Del.) Benth. is the witchweed that parasitises this crop in low input well-drained infertile soils where drought is also a problem (Nour et al., 1986). The estimated grain-area in Africa infested by *Striga* is 21 million hectares, and the loss in grain production is 4.1 million tons. The potential loss in grain production in Africa alone might amount to 44 million tons (Sauerborn, 1991).

The parasite affects the host directly through competition and indirectly by inducing pathological effects. The latter starts before the emergence of the parasite and accounts for 80% of the loss in production (Press et al., 1990). *Striga* infection results in stunted shoots. Grain and stem weights are reduced but often the roots remain relatively unaffected (Egly, 1971; Graves et al., 1989; Press and Stewart, 1987; Raju et al., 1990). As a result, plant allometry is altered.

Studies have shown that the parasite tends to do poorly in the presence of high levels of added N with a concomitant improvement on host growth (Last, 1960; Bebawi and Farah, 1981; Bebawi and Abdelaziz, 1983; Gworgwor and Weber, 1991; Cechin and Press, 1993a,b; Mumera and Below, 1993; Raju et al., 1990). Nitrogen delays emergence, and reduces infestation and growth (height and weight) of the parasite.

The mechanism by which N delays or reduces the effect of *Striga* in sorghum is not clearly understood. Nitrogen may inhibit seed germination and radicle extension (Pesch and Pieterse, 1982) by weakening stimulant strength, reducing its quantity or delaying stimulant exudation by the sorghum roots (Raju et al., 1990). Cechin and Press (1993a) found that nitrogen did not affect the stability of the active components of root exudate, or the perception of the chemical signal by the parasite seed. They suggested that high N affected either the production of stimulatory compounds, or their specific leakage from host roots, thus reducing attachment of the parasite radicle and early growth of the plant.

Reports on the effect of the degree of infection on host-parasite association are scarce. Press and Stewart (1987) using a split-root system found similar responses by the host to partial or complete infection, and concluded that the effects of *Striga* on the growth of sorghum are independent of the degree of parasitism to which the host is subjected to. They, nevertheless, did not give information on parasite growth in their system.

The objectives of this study were to examine: (1) changes in growth and allometry of uninfected and *S. hermonthica*-infected sorghum in relation to nitrogen supply; (2) whether there would be a differential response by the host to partial infection using a split-root system, and the extent to which this response is modified by N supply level; (3) the degree of suppression of the parasite by N application; and (4) the reaction of the parasite to partial exposure of the host root system to infection by the same amount of parasite seeds.

Materials and methods

The experiment

About 50 seeds of sorghum *cv. Maldando* from the Sudan were sown in standard Levington Composts, grade F2 (with sand) in a single row, close to one side of a tray 15 cm × 20 cm on 14 May 1994. There were three trays. The trays were kept on a bench in glass house. The seeds emerged after four days, and the trays were put in an inclined position to allow the roots to grow down the base of the trays. Two-week-old seedlings were transplanted individually into a pair of 12 cm × 12 cm pots, clipped together by paper clips. The pots were half-filled with a 1 : 1 sand to loam soil for transplanting. The seedlings were placed in a notch in the middle of the joint wall where the sides of the two pots were held together, with the roots split approximately equally between the two-halves, and each root half oriented to grow downward into the pots before being lightly covered in soil and watered. The shoots were supported against a short cane.

S. hermonthica seeds obtained from the Sudan from a sorghum host were pre-conditioned at 30 °C for two weeks and spread on to the soil surface as evenly as possible at the rate of 50 mg per host plant on either one or both halves, as per the requirement of the treatments, six days after transplanting. After this, the remaining half of the pots was filled with the same soil to give about a kg of soil in each pot of the double set.

A tap water–urea solution, as the N source, was made to a concentration of 4.6 g N l^{-1} solution, and applied two weeks after transplanting sorghum using a plastic syringe to one or both root-halves, as required for each treatment. The treatments are basically a 3 × 3 factorial combination of N (37 mg on one side, 18.5 or 37 mg on both sides) and *Striga* (no, one side or both sides infection) (Table 1) arranged in a completely randomised design. A satellite treatment, +N0,−N2, which is a variation of +N2,−N0, was added to see whether N and *Striga* placement on the same side is significantly different from N and *Striga* placement on the opposite sides of the split-root system. To study effects on the parasite growth, the treatment structure is a 2 × 3 factorial combination of *Striga* (one side or both side infection) and N (as above) with the additional satellite treatment of +N0,−N2.

The plants were grown under natural light from May to August, but with supplementary heating. Mean

Table 1. The list and description of treatments (Note: + or − for *Striga*; N0 = 0, N1 = 18.5, and N2 = 37 mg N pot^{-1}; ‘,’ to identify N and *Striga* combinations occurring in each half of the double pot set)

Number	Treatment code	Treatment description
0	−N1, −N1	No *Striga*, 18.5 mg N on each side
1	−N2, −N0	No *Striga*, 37 mg N on one side
2	−N2, −N2	No *Striga*, 37 mg N on each side
3	+N1, +N1	*Striga* plus 18.5 mg N on each side
4	+N2, +N0	*Striga* on both sides, 37 mg N on one side
5	+N2, +N2	*Striga* plus 37 mg N on each side
6	+N1, −N1	*Striga* on one side, 18.5 mg N on each side
7[†]	+N0, −N2	*Striga* on one side, 37 mg N on the other side
8	+N2, −N0	*Striga* plus 37 mg N on one and the same side
9	+N2, −N2	*Striga* on one side, 37 mg N on each side

[†]Satellite treatment.

day/night temperatures were 40 °C/20 °C. The plants were watered daily. Two harvests were taken of six replications each. The first harvest was made 38 DAP when the first *Striga* shoots became evident. The plants were harvested at the ground level, and plant height was measured from the base of the stem to the point of unfolding of the upper most leaf. The above ground host biomass was separated into leaf and stem, and fresh weights were recorded. Leaves were oven-dried at 80 °C for 48 h, and stems for 96 h, for dry weight measurements. Roots were washed, blotted dry and weighed fresh. Each of leaf, stem and total shoot mass was reported on dry matter basis, and root and shoot to root ratio was expressed on fresh weight basis. Dates of the first *Striga* emergence and *Striga* density at harvest were taken.

The last harvest was made 64 DAP. In addition to the data collected for the first harvest, the height of the three tallest *Striga* plants in each pot, and fresh and dry weight of the emerged parasite were recorded. Data on *Striga* and host root were taken for each root-half separately. Damage to the crop was scored for *Striga*-infected treatments visually on a 0 to 9 scale (Table 2) based on the degree of leaf discoloration and stunting (Kim, 1991). The average performance of *Striga*-free plants was used as a benchmark.

Table 2. Description of the degree of damage by *S. hermonthica* on vegetative growth of sorghum on a 0–9 scale

Rating	Description
0	No symptom (no chlorosis, no blotching, no leaf scorching) and normal growth.
1	Symptom just visible, normal plant growth.
2	Mild leaf blotching and scorching on about 10% of leaves with purplish-brown necrotic spots, almost normal plant growth. No stunting.
3	Slightly moderate leaf blotching and scorching on about 20% of leaves with some purplish-brown necrotic spots. Mild stunting.
4	Moderate leaf scorching on about 30% of leaves with some purplish-brown necrotic spots; some stunting.
5	Complete leaf scorching on about 40% of leaves with grey brown necrotic spots. Some stunting.
6	Complete leaf scorching on about 50% of leaves with mostly grey necrotic spots. Some stunting.
7	Complete leaf scorching on about 60% of leaves with severe grey necrotic spots and leaf wilting and rolling. Definite stunting.
8	Complete leaf scorching on about 70% of leaves with definite grey necrotic spots. Conspicuous stunting, leaf wilting.
9	Complete scorching of all leaves, death of host plant.

Data analysis

A preliminary analysis of variance was made using all the treatments, i.e. including the satellite treatment (+N0, −N2). Since, however, this treatment was not significantly different from its variant (+N2, −N0), it was dropped from the analysis. Consequently, all the analysis of variance results reported in the paper refer to the 3 × 3 factorial for host growth and the 2 × 3 factorial for parasite growth. To study the effects of groups of treatments (Table 1) on host growth, the eight single degree of freedom (df) orthogonal contrasts obtained from the 3 × 3 treatment structure were partitioned into:

1. *Striga* main effect (2 df) split into infection, i.e. uninfected (0, 1, 2) vs. infected (3, 4, 5, 6, 8, 9), and, within the infection group, extent, i.e. complete (3, 4, 5) vs. partial (6, 8, 9).
2. Nitrogen main effect (2 df) split into N rate, i.e. high N (2, 5, 9) vs. low N (0, 1, 3, 4, 6, 8), and, within low N, placement, i.e. one side (1, 4, 8) vs. both sides (0, 3, 6).
3. *Striga* × N interaction (4 df) split into the interaction of the above *Striga* and N contrasts, i.e. infection × N rate, infection × N placement, extent × N rate and extent × N placement.

To assess the effects of groups of treatments on *Striga* growth per host plant, from the 2 × 3 factorial structure, there were five single df orthogonal contrasts that were partitioned into extent, i.e. complete (3, 4, 5) vs. partial (6, 8, 9), N rate, i.e. low (3, 4, 6, 8) vs. high (5, 9), and, within low N, placement, i.e. one-half (4, 8) vs. both (3, 6). The remaining two df were used to assess the extent × N rate and extent × N placement interactions. Means and standard deviations were correlated for *Striga* number and dry weight per host plant. As a result, these two variables were log-transformed before variance analysis.

Parasite growth data recorded separately from each root-half across hosts receiving different treatments were analysed to see the effects of N at three levels [0 (N0), 18.5 mg (N1), and 37 mg N kg^{-1} soil (N2)] on *Striga* growth in each root-half. Results of this analysis should, however, be treated cautiously as a valid comparison of N effect on parasite growth in individual root-halves could be made for the +N2, +N0 treatment only. Data for both halves were pulled together to study the effects of treatments on the parasite growth on per host plant basis. Furthermore, a chi-square test was used to see whether the number of parasite shoots in partial infection was significantly different from 50% of that in full infection. A paired *t*-test was carried to see whether the root mass in infected and uninfected halves of the partially infected plants were similar. Variance analysis was performed using the SAS statistical package (SAS Institute Inc., 1988).

Results

Growth of Striga *38 DAP*

By 38 DAP, *Striga* had emerged on only 45% of the *Striga* receiving hosts. On a per host basis, differences for the number of emerged *Striga* plants among the six *Striga* receiving treatments (Table 1) were not significant. On average, there were 10.6 *Striga* plants per host with complete infection and 5.8 *Striga* plants per host with partial infection. Also the number of emerged *Striga* was less when N was placed on both root-halves than when N was applied in one-half of the host root system. Nevertheless, these differences were not significant owing to the large within treatment variation. The number of *Striga* plants under high and low N (74 mg vs. 37 mg $host^{-1}$) were similar averaging 8.2. The extent × N rate and extent × N placement interactions were not significant.

On an individual root-half basis, the mean effect of N application reduced the number of emerged *Striga* plants per pot from 9.4 under N0 to 6.0 (mean of N1 and N2). There were 7.3 and 4.8 emerged *Striga* plants per pot in N1 and N2 treatments, respectively. However, differences between the treatments were not significant ($P > 0.05$).

Growth of Striga 64 DAP

By this time, *Striga* had appeared on 92% of the sorghum plants that received *Striga*, and therefore these data, rather than the early harvest data, were analysed to determine the effect of the treatments on days to first *Striga* emergence. Averaged over all the treatments, the mean number of days to first *Striga* emergence was 43.3. Partial infection significantly delayed *Striga* emergence by 8.4 more days than complete infection (Tables 3 and 4).

The average effect of the degree of *S. hermonthica* infestation on the total number of parasite shoots on each host plant was highly significant. Partially infected plants supported only about 36% of the parasite shoots in fully infected plants (Tables 3 and 4). Based on a chi-square test, this was also significantly less than half the number of *Striga* plants in the complete infection. The partial infection treatments +N1, −N1

Table 3. Variance ratios, probabilities of variance ratios, and residual mean squares of single degree of freedom orthogonal contrasts for the effects of the extent of infection, N rate, N placement and their interactions on *Striga* growth 64 days after transplanting sorghum

Contrast	Days to emergence	Shoot number	Plant height	Shoot weight	Damage score
Extent of infection (complete vs. partial)					
Variance ratio	11.44	13.63	11.35	7.09	5.52
F-probability[†]	0.0021	0.0009	0.0021	0.0125	0.0259
N rate (high N vs. low N)					
Variance ratio	0.62	0.11	1.21	0.83	0.51
F-probability	0.4390	0.7432	0.2801	0.3696	0.4814
N placement (one-half vs. both halves)					
Variance ratio	2.33	2.67	0.30	0.09	0.01
F-probability	0.1379	0.1134	0.5900	0.7718	0.9161
Extent × N rate					
Variance ratio	0.88	0.05	0.57	0.67	0.06
F-probability	0.3551	0.8202	0.4563	0.4204	0.8137
Extent × N placement					
Variance ratio	1.05	4.15	1.48	0.39	0.01
F-probability	0.3132	0.0507	0.2330	0.5379	0. 9161
Residual mean square (30 df)	54.15	0.39	118.8	0.07	3.69

[†]Probability of variance ratio under the null hypothesis of no effect.

Table 4. The influence of the degree of *S. hermonthica* infestation and nitrogen on the growth of the parasite 64 days after transplanting sorghum

Treatments	Days to emergence	Shoot number† [log (no. + 1)]	Plant height (cm)	Shoot weight (g) [log (gm + 1)]	Host damage score (0–9)
3. +N1, +N1	40.2	1.76	24.8	0.42	5.2
4. +N2, +N0	38.7	1.86	22.0	0.39	5.0
5. +N2, +N2	39.0	1.78	22.0	0.39	4.8
6. +N1, −N1	50.0	0.69	9.1	0.17	3.7
8. +N2, −N0	42.3	1.43	16.8	0.26	3.7
9. +N2, −N2	50.8	0.93	5.6	0.05	3.0
SED (30 df)‡	4.2	0.36	6.3	0.15	1.1
F-probability¶	0.0214	0.0122	0.0328	0.1628	0.3413
Complete mean	39.3	1.80	22.9	0.40	5.0
Partial mean	47.7	1.02	10.5	0.16	3.4
F-probability	0.0021	0.0009	0.0021	0.0125	0.0259

†Data for shoot number and shoot weight are averages of log of (original values +1).
‡Standard error of a difference between means and its degrees of freedom.
¶Probability of variance ratio under the null hypothesis of no effect.

and +N2, −N2 supported the lowest number of emerged *Striga* with a mean of about 26 shoots per host plant. Each of the fully infected plants had greater parasite densities than any of the partially infected ones averaging about 90 *Striga* plants per host plant. On a per host basis, the effects of N rate, N placement, extent of infection (extent) × N rate and extent × N placement interactions were not statistically significant. Nevertheless, as can be seen from a relatively larger variance ratio, N placement on both sides at either N1 or N2 levels gave less *Striga* shoots than N2 application to one side only (Tables 3 and 4).

The overall effect of treatments on parasite shoot height on a per host plant basis was significant. Partitioning of the treatment effects into logical contrasts gave a highly significant effect of the degree of infection on parasite plant height. The *Striga* plants in the partial infection treatments were on average shorter by about 50% than those in the complete infection treatments (Table 4). The main effect of N rate, N placement and the interaction effects of extent × N rate and extent × N placement on parasite plant height were not significant (Table 3). When individual treatments were considered, the smallest parasite height was obtained from +N2, −N2 treatment followed by +N1, −N1 treatment, which also had the fewest *Striga* shoots.

Mean parasite shoot weight per host was not significantly altered by the N rate or placement (Table 3). Averaged over all treatments, partially infected sorghum supported only about a third of the weight of *Striga* with complete infection. The effect of individual treatments on the parasite dry shoot weight was not statistically significant ($P = 0.1628$). However, examination of the data indicates a marked effect of some of the treatments on the parasite shoot weight. As for height, the +N2, −N2 treatment supported the least parasite weight (Table 4).

Generally, the N treatments in individual root-halves did not significantly affect *Striga* growth. Nonetheless, consistent with the finding at 38 DAP, the mean effect of N reduced the number of *Striga* plants per pot from 52.7 in N0 to 36.6 when N was applied.

Growth of sorghum 38 DAP

While the mean effect of the presence of *Striga* on height of sorghum was highly significant, the difference between the degrees of infection was not (Table 5). The rate or method of N application or any of the interactions was not significant either (Table 6). On average, sorghum plants were tallest (averaging 108 cm) where there was no *Striga*, and shortest where *Striga* was applied to both sides of the host plant. Overall, *Striga* resulted in 22% reduction in height. The mean heights for partial and complete infection were 88.6 and 80.6 cm respectively, averaging 9% less (Table 5).

The average effect of *Striga* infection significantly reduced shoot dry matter yields by 17% below the uninfected control (Table 5). The difference due to the

Table 5. Effects of *S. hermonthica* infestation and the degree of host root infection on the growth of sorghum 38 and 64 DAP sorghum

DAP	*Striga*†	Plant height (cm)	Leaf weight (g)	Stem weight (g)	Shoot weight (g)	Root fresh weight (g)	Shoot to root ratio
38	No	107.8	5.3	8.9	17.2	32.8	5.89
	Yes	84.6	5.6	6.7	14.2	58.3	2.52
	F-probability‡	0.0007	0.5945	0.0086	0.0544	0.0002	0.0001
	Complete	80.6	5.5	6.5	13.7	65.3	2.01
	Partial	88.6	5.6	6.9	14.7	51.4	3.02
	F-probability	0.2791	0.8437	0.7128	0.5416	0.0646	0.0445
64	No	201.2	16.5	38.6	55.1	83.9	3.78
	Yes	132.3	14.8	24.7	39.5	77.8	3.04
	F-probability	0.0001	0.2252	0.0001	0.0003	0.4712	0.0043
	Complete	128.6	12.3	20.4	32.6	73.1	2.73
	Partial	136.1	17.4	29	46.4	82.5	3.35
	F-probability	0.2687	0.0026	0.0101	0.0048	0.3428	0.0318

†No, yes = absence or presence of *Striga*, and complete, partial = presence of *Striga* in both or one of the root-halves, respectively.
‡Probability of variance ratio under the null hypothesis of no effect.

Table 6. Variance ratios, probabilities of variance ratios, and residual mean squares of single degree of freedom orthogonal contrasts for the effects of infection, extent of infection, nitrogen rate, nitrogen placement and their interactions on sorghum growth 38 days after transplanting sorghum

Contrast	Plant height (cm)	Stem weight (g)	Leaf weight (g)	Shoot weight (g)	Root fresh weight (g)	Shoot to root ratio
Infection (infected vs. uninfected)						
Variance ratio	13.27	7.54	0.29	3.90	16.09	66.07
F-probability†	0.0007	0.0086	0.5945	0.0544	0.0002	0.0001
Extent (complete vs. partial)						
Variance ratio	1.20	0.14	0.04	0.38	3.59	4.27
F-probability	0.2791	0.7128	0.8437	0.5416	0.0646	0.0445
N rate (high N vs. low N)						
Variance ratio	2.19	0.03	1.80	3.37	2.65	0.80
F-probability	0.1456	0.8607	0.1859	0.0729	0.1107	0.3763
N placement (one-half vs. both halves)						
Variance ratio	1.31	1.36	1.93	0.22	0.92	1.61
F-probability	0.2584	0.2505	0.1720	0.6400	0.3434	0.2104
Infection × N rate						
Variance ratio	0.29	0.15	0.38	1.22	0.21	0.99
F-probability	0.5951	0.6957	0.5399	0.2744	0.6499	0.3251
Infection × N placement						
Variance ratio	0.40	0.14	0.13	0.00	3.00	6.29
F-probability	0.5298	0.7101	0.7194	0.9461	0.0903	0.0158
Extent × N rate						
Variance ratio	0.02	0.42	0.93	0.12	1.25	1.73
F-probability	0.8755	0.5200	0.3389	0.7255	0.2699	0.1952
Extent × N placement						
Variance ratio	0.08	0.09	0.07	0.04	0.42	0.09
F-probability	0.7790	0.7637	0.7896	0.8515	0.5183	0.7678
Residual mean square (45 df)	486.52	8.04	2.55	27.07	487.08	2.08

†Probability of variance ratio under the null hypothesis of no effect.

Table 7. Effects of *S. hermonthica* infestation and nitrogen on growth of sorghum 38 days after transplanting sorghum

Treatment	Plant height (cm)	Leaf weight (g)	Stem weight (g)	Shoot weight (g)	Root fresh weight (g)	Shoot to root ratio
0. −N1, −N1	120.0	5.5	9.4	15.8	22.5	7.36
1. −N2, −N0	105.0	5.0	8.8	15.1	33.4	5.06
2. −N2, −N2	98.3	5.5	8.5	20.6	42.4	5.26
3. +N1, +N1	83.8	5.9	7.2	14.0	76.4	1.62
4. +N2, +N0	81.2	4.9	6.2	12.7	54.5	2.01
5. +N2, +N2	76.7	5.7	6.1	14.3	65.0	2.42
6. +N1, −N1	95.2	5.5	7.5	14.2	50.8	3.24
8. +N2, −N0	87.5	4.8	5.8	13.7	40.6	3.28
9. +N2, −N2	83.1	6.5	7.4	16.2	62.7	2.54
SED (45 df)†	12.7	0.9	1.64	3.0	12.7	0.83
F-probability‡	0.0336	0.6922	0.3020	0.3451	0.0031	0.0001

†Standard error of a difference between means and its degrees of freedom.
‡Probability of variance ratio under the null hypothesis of no effect.

extent of infection was not significant ($P = 0.5416$). In addition, neither the main effects of N rate and N placement nor the interaction effects were significant (Table 6). The trends were similar for stem weight; stems of infected plants were only about 75% as heavy as those of non-infected. There was no obvious effect of any treatment on leaf weight (Tables 5, 6 and 7).

On average, *Striga*-infected plants had greater root weight than uninfected plants. The root weights of *Striga*-free plants were only 56% of the root weights of *Striga*-infected plants. Fully infected plants tended to have greater root weights than partially infected plants (Table 5). In partially infected plants, the root weights in the infected and *Striga*-free halves were statistically similar. At this stage, the effects of N rate, N placement or the interactions were not significant (Table 6). There were highly significant root fresh weight differences among individual treatments (Table 7). Because of the above changes in crop architecture, allometric ratio was significantly altered due to infection. *Striga*-free plants had greater shoot to root weight than *Striga*-infected plants. Likewise, the ratio was greater for partially infected plants than for fully infected plants (Table 5). Nitrogen application rate or method did not significantly alter the ratio. Also, all the interaction effects except infection × N placement were not significant for the ratio (Table 6). In the absence of infection, N placement on both root halves increased the allometric ratio, but when infection was present the allometric ratios were somewhat similar for both methods of N placement.

Growth of sorghum 64 DAP

By 64 DAP, the difference in height of sorghum plants among the treatments had usually increased (Table 8) relative to the magnitude of the corresponding treatment differences 38 DAP (Table 7). All the plants with *Striga* infection were distinctly and significantly shorter than those plants without *Striga*. On average, *Striga*-free plants were 201.2 cm tall; the presence of *Striga* reduced plant height by 34%. In the period between 38 and 64 DAP, *Striga*-free plants gained 93 cm in height, while infected plants gained only 48 cm (Table 5). Nitrogen application method had no effect on height (Table 9) but plants that received 74 mg N (160.3 cm) were taller than those that received 37 mg N plant^{-1} (152.8 cm) (Table 8). Nevertheless, the contrast still was not significant. Like the measurement at 38 DAP, the main effect of the extent of infection, and the interaction effects of infection × N rate, extent × N rate and extent × N placement were not significant. The infection × N placement interaction was, however, significant for plant height as well as the weight traits (Table 9). This interaction was significant because of the better growth of infected sorghum plants when N was applied on both root-halves than on one root-half, but poorer growth of both side placement than one side placement when the host was free of *Striga*. The reason for such a lower performance of −N1, −N1 than −N2, −N0 was not clear. Among the *Striga*-infected treatments, only plants receiving partial infection plus the high dose of N (+N2, −N2) treatment were significantly

Table 8. Effects of *S. hermonthica* infestation and nitrogen fertilisation on growth of sorghum 64 days after transplanting sorghum

Treatment	Plant height (cm)	Leaf weight (g)	Stem weight (g)	Shoot weight (g)	Root fresh weight (g)	Shoot to root ratio
0. −N1, −N1	183.7	12.6	28.1	40.7	62.6	3.59
1. −N2, −N0	216.3	18.4	45.6	64.0	97.8	3.92
2. −N2, −N2	203.7	18.6	42.0	60.6	91.4	3.84
3. +N1, +N1	135.3	12.5	22.4	34.9	72.6	3.04
4. +N2, +N0	119.6	10.2	15.8	26.0	68.3	2.40
5. +N2, +N2	130.5	14.1	22.9	36.9	78.5	2.77
6. +N1, −N1	133.3	16.8	27.8	44.6	79.1	3.37
8. +N2, −N0	128.3	15.7	24.0	39.7	79.4	3.20
9. +N2, −N2	146.8	19.8	35.2	55.0	89.1	3.48
SED (45 df)[†]	11.6	2.7	5.5	7.9	16.7	0.48
F-probability[‡]	0.0001	0.0152	0.0001	0.0002	0.5175	0.0562

[†]Standard error of a difference between means and its degrees of freedom.
[‡] Probability of variance ratio under the null hypothesis of no effect.

Table 9. Variance ratios, probabilities of variance ratios, and residual mean squares of single degree of freedom orthogonal contrasts for the effects of infection, extent of infection, nitrogen rate, nitrogen placement and their interactions on sorghum growth 64 days after transplanting sorghum

Contrast	Plant height (cm)	Stem weight (g)	Leaf weight (g)	Shoot weight (g)	Root fresh weight (g)	Shoot to root ratio
Infection (infected vs. uninfected)						
Variance ratio	138.61	25.44	1.51	15.42	0.53	9.07
F-probability[†]	0.0001	0.0001	0.2252	0.0003	0.4712	0.0043
Extent (complete vs. partial)						
Variance ratio	1.26	7.23	10.24	8.83	0.92	4.91
F-probability	0.2687	0.0101	0.0026	0.0048	0.3428	0.0318
N rate (high N vs. low N)						
Variance ratio	1.64	4.72	5.05	5.22	1.30	0.18
F-probability	0.2074	0.0352	0.0297	0.0272	0.2608	0.6706
N placement (one-half vs. both halves)						
Variance ratio	0.35	0.54	0.27	0.47	1.17	0.37
F-probability	0.5576	0.4660	0.6049	0.4947	0.2847	0.5485
Infection × N rate						
Variance ratio	0.22	0.05	0.00	0.03	0.02	0.01
F-probability	0.6413	0.8170	0.9986	0.8727	0.9028	0.9316
Infection × N placement						
Variance ratio	9.06	11.41	4.98	9.73	3.31	1.54
F-probability	0.0043	0.0015	0.0308	0.0032	0.0758	0.2215
Extent × N rate						
Variance ratio	0.78	0.64	0.06	0.41	0.01	0.05
F-probability	0.3834	0.4275	0.8084	0.5241	0.9313	0.8199
Extent × N placement						
Variance ratio	0.42	0.14	0.09	0.13	0.04	0.44
F-probability	0.52	0.7133	0.7707	0.7197	0.8493	0.5085
Residual mean square (45 df)	406.72	90.17	22.40	187.03	837.07	0.6836

[†]Probability of variance ratio under the null hypothesis of no effect.

taller than +N2, +N0 treatment. Nonetheless, based on Duncans multiple range test, these treatments were not statistically different from the rest (Table 8).

Stem and shoot weight responses were similar (Tables 5, 8 and 9). The mean effect of *Striga* infestation significantly reduced shoot dry matter yield by 28% below the uninfected control. The mean effects of the extent of infection and N rate were significant as well. Both total shoot and stem dry matter of fully infected plants weighed 70% of those of partially infected plants. Each of stem and total shoot weights were increased by about 22% when N was increased from 37 to 74 mg $plant^{-1}$. The mean effect of N application method was not significant. Stem weight of *Striga*-infected plants was only 64% of that of non-infected plants. Individual treatment effects were also significant (Table 8). Consistent with the early harvest, 38 DAP, the +N2, +N0 treatment yielded the least. Among the infected treatments, +N2, −N2 plants had the highest and statistically similar stem and shoot dry matter to the two high yielding *Striga*-free treatments. In each of fully and partially infected plants, though not significant, high N split on both sides was best, low N split on both sides was intermediate, and low N applied only on one side was the least at both early and late harvests. Among uninfected treatments, −N1, −N1 yielded less stem and total shoot weight than either −N2, −N0 or −N2, −N2. This, however, was the highest yielding treatment 38 DAP and, therefore, its low yield at 64 DAP cannot be attributed to treatment effects.

Overall, *Striga* infection did not result in a significant change in leaf weight. However, partial infection resulted in a significantly greater leaf weight than complete infection (Table 5). On average, high N was significantly different from low N increasing leaf weight by 21.5%. Like at 38 DAP, the effect of N placement on leaf weight was not statistically significant. Individual treatment effects on leaf weight were significant (Table 8) and followed the pattern of stem or total shoot weight. There was no obvious effect of any treatment on root weight on per host plant basis (Tables 5, 8 and 9). However, based upon *t*-test, root mass in the infected half of partially infected hosts was significantly less by 18% than the *Striga*-free half. While the mean effect of *Striga* infestation and the extent of infection significantly altered shoot to root ratio (Table 5), N application rate, N application method or any of the interactions did not (Table 9).

Damage to the crop

There was no significant difference among individual treatments for visual score of crop damage. However, group comparisons indicate a statistically significant difference between the means of partially and fully infected plants. Fully infected plants suffered more damage than partially infected plants (Tables 3 and 4).

Discussion

Striga growth – nitrogen effect

Studies have shown that nitrogen hampers the growth of *Striga* through delayed emergence, reduced infestation and growth in height and weight of the parasite (Cechin and Press, 1993a; Raju et al., 1990; Bebawi and Abdelaziz, 1983; Farina et al., 1985). In the present study, it is apparent that the mean effect of N (N1 and N2), in delaying days to first *Striga* emergence over N0 in individual root-halves, was not substantial. Neither did high N (74 mg $host^{-1}$) delay *Striga* emergence better than low N (37 mg $host^{-1}$) on a per host basis. This may be because the N levels used could be too low to give a better delay in emergence. Gworgwor and Weber (1991) recorded a difference of 7.5 days to *S. hermonthica* emergence between the control and the lowest level of 0.5 g N kg^{-1} soil, and 16.3 days between the control and 2 g N kg^{-1} soil. The lowest level of N which was used to bring about a delay of 7.5 days over the zero nitrogen was about 13 times higher than that used in this study. On the other hand, examination of the zero N and the 37 mg N halves of the same host plant in the +N2, +N0 treatment indicated a better contrast in days to first *Striga* emergence: N2 delayed emergence by more than three days when compared to no N. This difference was, however, not evident when the data were averaged for the N treatments in individual root-halves over all the *Striga* infestation levels.

In the root-halves, N application reduced *Striga* shoot number over the zero N control by 36.2% at 38 DAP and by 30.5% at 64 DAP. Many workers (Farina et al., 1985; Raju et al., 1990; Bebawi and Farah, 1981; Bebawi and Abdelaziz, 1983; Mumera and Below, 1993; Cechin and Press, 1993b) reported similar reductions in *Striga* density and shoot growth due to N application.

In this study, N had a predictable pattern of suppressing parasite shoot number at 38 DAP, with 37 mg N kg^{-1} soil reducing *Striga* counts more than 18.5 mg N kg^{-1} soil. This difference however did not persist until 64 DAP. In a pot experiment, Gworgwor and Weber (1991) found significant differences in *Striga* shoot number and dry matter between the control and N treatments, but despite very high and a great range of N levels used, differences between the levels were not significant. They applied whole doses of N treatments at sowing, and reported that they had watered the plants as much as necessary every day. Likewise, the lack of a substantial difference between N levels for the parasite growth in our study may be attributed to the frequent watering, coupled with only a single whole dose application of N, that might have leached the nutrient through the perforated bottom of the pots to such a level that significant effects could not be detected between the N treatments. Because of this, it is likely that the influence which the parasite had on the growth of the host was not modified as much as expected by the N application. In many other controlled environment studies, the N treatments were split over a number of applications spaced at some intervals. Egly (1971) and Cechin and Press (1993b) applied their respective nutrient solution treatments three times a week throughout the period of their experiments.

So far, the mechanism by which N delays or reduces *Striga* infestation is not clear. Pesch and Pieterse (1982) indicated that N inhibits seed germination and radicle extension. In contrast, Mumera and Below (1993) argue that the physiological mechanism responsible for N-mediated reduction in *S. hermonthica* infestation occur after *Striga* germination and early vegetative growth. Both this and the direct post-exudation effect of N on *S. asiatica* proposed by Raju et al. (1990), however, were disproved by Cechin and Press (1993a) who reported adverse effect of N on germination, haustoria formation and the early growth of *S. hermonthica*. In this study, there were no significant differences for days to first emergence, shoot count, height or weight between the treatment that received N and *Striga* on only one and the same side, and the other treatment with the same N and *Striga* on opposite sides. At least *in vivo* and in the soil medium, had N influenced *Striga* germination, attachment and subsequent growth directly, it is reasonable to assume that some notable differences between these two treatments for the above parameters should probably have shown up. This was not the case and, therefore, it may be assumed that the direct effect is not the major cause for suppression of the parasite by N. Instead, it is likely, as suggested by Cechin and Press (1993a), that N acted indirectly through the host. Nevertheless, examination of observations on days to first *Striga* emergence, parasite shoot number, height and fresh weight of N0 and N2 sides of the fully infected treatment (+N2, +N0) indicate, on average, greater suppression of the parasite on the N2 side. However, because of an inadequate number of replications and large variability, the differences were not statistically significant. As a result, this deserves further testing.

Striga growth – extent of root infection

Though the same amount of 50 mg *Striga* seed per host plant was applied, fully infected plants supported taller and more numerous *Striga* shoots with greater parasite weight per host than partially infected sorghum plants. The mean parasite shoot number in partial infection 64 DAP was only about 36% of that under complete infection. This may be because having *Striga* seed placement on both sides increased the chance of more host roots getting nearer to more *Striga* seeds, ensuring a better supply of germination stimulants for the parasite seeds, and more contact of the parasite seedlings with the host root. If it were, however, assumed that there was an equal distribution and growth of the roots of each plant into the two pots, the partially infected plants would be expected to yield at least half the shoot number of the parasite of the complete root infection treatments. A chi-square test, however, indicated that the observed emergence was significantly lower than would normally be expected and hence the above reasoning cannot explain the difference in infestation levels.

In this study, comparison of root masses in infected vs. uninfected hosts, partial vs. complete infection, and infected root-half vs. uninfected half indicated the stimulation of host root growth due to infection early in the association; but as the sources for photosynthates suffered more with progressive pressure from the parasite, root weight declined with an increase in the intensity of infection. The lower root mass in infected half of partially infected hosts suggests that the presence of some infection sensing mechanism might have enabled the host to respond by restricting root growth in the infected half, at the same time allowing more growth in the *Striga*-free half. Such a lower root mass in the infected half might also have decreased the chance of the parasite seed getting germination stimulant and access to a host root resulting in a lower parasite density in partially infected plants than in fully infected ones.

Another possibly more convincing reason is that the host had somewhat greater resistance towards the parasite when it was only partially infected than when most of its root system was infected. Three mechanisms of resistance in sorghum to *Striga* attack have been mentioned (Oliver et al., 1991), but those which pertain to developing mechanical strength and/or metabolic inhibition of full development of the parasite after attachment were suspected. It is not possible here to explain the type of partial resistance involved but it is possible to suggest that there may be an interaction between the degree of infection and the level of host resistance. A host may well resist the infection of a certain proportion of its root mass if the rest is uninfected, but if it all has some degree of infection, it is not able to resist. Protective materials (for example, cellulose or silica) and/or inhibitory substances are unlikely to be in the root in sufficient quantities before the host senses infection, but are possibly released in response to infection. Each infection point on the root could then be a sink for such substances; the more widely distributed such sinks are, as in complete infection, the less of such substance will partition to them, and the less effective would be the resistance.

Sorghum growth

A *Striga*-infested crop has stunted above ground parts of sorghum with marked reductions in stem weights (Egly, 1971; Graves et al., 1989; Press and Stewart, 1987; Gworgwor and Weber, 1991), but roots often remain relatively unaffected (Egly, 1971; Graves et al., 1989; Press and Stewart, 1987). As a result, plant allometry is altered (Egly, 1971; Cechin and Press, 1993b; Graves et al., 1989). In this study, the presence of *Striga* reduced stem weight 38 DAP but increased root weight, yielding a reduction in the shoot to root ratio of 57%. Later (64 DAP), the decline in stem weight was more marked but root weight was not affected, producing a 20% reduction in the shoot to root ratio due to infection. Leaf weight was not affected at either stage. Graves et al. (1989) also reported little effect of the parasite on leaf and root weights of the host. They reasoned that roots and leaves, being organs for the capture of resources from the environment, were little affected by *S. hermonthica* infection because of a favourable photosynthate allocation to them under such stress conditions.

Parker (1984) suggested that the weight of infected sorghum plants can be reduced by more than 50 times the weight of *Striga* plants they support. In our study, the loss in sorghum shoot weight at 64 DAP exceeded the mass of *Striga* it supported by a factor of five on a fresh weight basis and by a factor of 12 on a dry weight basis. In a study by Graves et al. (1989) the corresponding figure on a dry weight basis was greater than three.

Infected sorghum plants are prone to water stress (Press et al., 1987), but in our trial frequent watering ensured an adequate root supply. Therefore, the observed difference in growth between infected and uninfected plants can only be attributed to carbon partitioning to the parasite (Graves et al., 1989) and reduced CO_2 flux (Press et al., 1987; Cechin and Press, 1993b) in host leaves with the resultant impairment of photosynthesis.

Press and Stewart (1987) observed that neither reducing the number of parasite seeds by 50% nor freeing half the root system from *Striga* alleviated the effects on host growth. In our study, we used the same seed rate in partial and complete infection, but freed half of the root system from parasite infection in the partial infection treatment, and found strong evidence that sorghum growth was dependent on the extent of infection. As a result, we conclude that, besides N, there is evidence that the extent of host root infection mediates the damage inflicted by *S. hermonthica* on sorghum.

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