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GROWTH AND BIOMASS PARTITIONING OF MAIZE DURING VEGETATIVE GROWTH IN RESPONSE TO *STRIGA HERMONTHICA* INFECTION AND NITROGEN SUPPLY

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SUMMARY

The effect of the root hemiparasitic angiosperm *Striga hermonthica* on the gowth, photosynthesis and partitioning of biomass in maize was studied in glasshouse experiments in two seasons. In both seasons, nitrogen was applied to the plants at rates equivalent to 20, 60 and 120 kg ha^{-1}. There was no significant *Striga* × nitrogen interaction on the responses measured. Averaged across all nitrogen treatments, maize plants infected with *S. hermonthica* had smaller leaf areas and accumulated less biomass, than did uninfected plants. The leaf area of infected and uninfected plants increased asymptotically from emergence to the final harvest (about the 18-leaf stage) at which time the leaf area of infected plants was 63% that of uninfected plants. The rates of photosynthesis of the youngest, fully expanded leaves of infected plants, averaged across N treatments, were significantly lower than for uninfected plants. However, stomatal conductance and the sub-stomatal CO_2 concentration were unaffected by *Striga* infection. Although infection with Striga significantly reduced shoot biomass (dry weight at final harvest was 37% that of uninfected plants in 1995 and 63% in 1996), there were no significant effects of *Striga* infection on root biomass so that the infected plants partitioned a significantly greater proportion of their total biomass to roots compared with the uninfected plants. The allometric coefficients, though, were similar for both infected and uninfected plants. Averaged across infected and uninfected plants, application of nitrogen increased total leaf area per plant and root and shoot biomass but did not change the proportion of total biomass partitioned to roots. These results did not show a major effect of nitrogen on the relative growth response of maize to infection with *Striga*.

INTRODUCTION

Striga hermonthica (Scrophulariaceae) is a root hemi-parasite of Poaceae in the semi-arid tropics and an important weed of maize, sorghum, millet and rice crops. Symptoms of *Striga* infestation include reduced vigour, stunted growth, wilting and chlorosis, with yield losses of between 30–50% or total crop failure under varying

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degrees of infestation (Parker, 1991). Graves *et al.* (1990) reported an 80% reduction in grain yield and a 53% reduction in stem dry weight in pearl millet (*Pennisetum typhoides*) infected with *S. hermonthica* and increases of 41% in leaf growth and 86% in root growth compared with uninfected plants. This indicated an alteration in the architecture of infected millet plants.

Infestation of *Striga* generally is greater in soils of low fertility especially soils low in nitrogen (N) (Pieterse and Verkleij, 1991). However, the effects of N fertilization on *Striga*-host relations are still unclear. Doggett (1984; 1988) reported that the addition of N fertilizers reduced *Striga* emergence on fertile soils but increased infestation levels on infertile soils. In contrast, Egley (1971) and Parker (1984) observed that high N levels in the soil enhanced the growth of both the host and parasite. Cechin and Press (1993) found that the response of sorghum (*Sorghum bicolor*) to infection changed depending on the concentration of N in the rooting medium. In a solution-culture experiment, biomass at 140 d was 22, 30 and 66% lower in infected plants at 0.5, 1 and 2 mol N m^{-3} respectively, whereas there was little difference in biomass when grown at 3 and 4 mol N m^{-3}. A field study by Gurney *et al.* (1995) indicated that N fertilizer applied at levels between 0 and 150 kg ha^{-1} affected neither growth nor the rate of photosynthesis of individual leaves, nor did it influence the response of maize (*Zea mays*) and sorghum to *Striga*. Similarly, Kim and Adetimirin (1997) reported that the application of N fertilizer (60 and 120 kg ha^{-1}) to maize in the field in Nigeria did not affect the emergence of *S. hermonthica*. In another study, Kim *et al.* (1997), applied N in the range 0–150 kg ha^{-1} and found that the emergence of *S. hermonthica* was significantly reduced only at 120 and 150 kg ha^{-1}. While published work on the *S. hermonthica*-sorghum association abounds, less is available on the *S. asiatica*-maize association and even less on the *S. hermonthica*-maize association.

The objective of this study was to quantify the effect of N fertilizer on the growth, photosynthesis, and accumulation and partitioning of biomass in maize infected with *Striga hermonthica*. The hypothesis tested was that the effect of increasing additions of N on maize biomass would be relatively smaller in plants infected with *S. hermonthica*, and that a greater proportion of dry matter would be partitioned to the roots (to support the requirements of the *Striga*).

MATERIALS AND METHODS

Experimental conditions

Two experiments were conducted in 1995 and 1996 in a glasshouse at The University of Reading (51°27′ N, 00°56′ W), UK between May and September each year. Day and night temperatures in the glasshouse were maintained at 30 and 20°C respectively. The design of the experiments was a completely randomized three (N applications equivalent to 20, 60 and 120 kg ha^{-1}) × two (*Striga* infection) factorial, replicated four times in 1995 and three times in 1996. With five sampling times in Experiment 1 and six in Experiment 2, this gave 120 pots in Experiment 1 and 108 pots in Experiment 2. At each sampling time the pots were

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re-randomized to minimize the effects of environmental gradients in the glasshouse.

Seed of *S. hermonthica* was collected and conditioned before use as described by Aflakpui *et al.* (1998). The same source of seed was used in both seasons. In the first experiment (1995), about 3500 Striga seeds in 200 g sand were added to 1.3 kg washed river sand in 200-mm diameter pots and covered with another 500 g sand to give a total of 2 kg sand per pot. In the second experiment (1996), the growing medium was a 1:1 mix of sterilized loam (8% silt, 18% clay, 74% sand, 3% organic matter) and coarse sand. The mixture had a mean pH of 7.2; 0.78% total C; 0.05% total N; 31.8 mg kg^{-1} extractable P; and 0.31 $cmol_c$ kg^{-1} exchangeable K. Each pot was filled with 4 kg of the growing medium plus 5 g of *Striga* seed/sand mixture containing about 3500 seeds. In both seasons, pots without the *Striga* seed/sand mixture were also filled with the rooting medium.

Seed of maize cv. Okomasa was surface sterilized with 1% sodium hypochlorite for five minutes, washed with water and planted at a depth of about 25 mm. Two seeds were sown in each pot and subsequently thinned to one after expansion of the first leaf. Plants were watered with 200 ml full strength, nitrogen-free Long Ashton nutrient solution three times per week. On other days the plants were watered with tap water. Nitrogen was applied at rates equivalent to 20, 60, 120 kg ha^{-1} at the three-leaf stage (nine days after planting (DAP) in Experiment 1 and 14 DAP in Experiment 2).

Measurements

Plants were sampled at 12, 29, 61, 90 and 104 DAP (at approximately the 4-, 8-, 12-, 16- and 18- leaf stages respectively) in Experiment 1 and at 29, 43, 57, 78, 87 and 99 DAP in Experiment 2 (leaf numbers were not recorded). At each harvest, maize plants were divided into leaf, stem and root and dried at 80°C to constant weight. In Experiment 1, leaf area per plant was measured with a Delta-T leaf area meter prior to drying. The allometric coefficient k, which represents the ratio of the logarithmic growth rate of the shoot to that of the root was determined as:

$$\log_e S_w = \log_e b + k \log_e R_w \qquad (1)$$

where S_w and R_w are shoot and root biomass and k and b are constants (after Hunt, 1990).

In Experiment 1, the number of *S. hermonthica* shoots and their dry weight was recorded on the same days as the sampling of the maize.

In Experiment 1, photosynthesis of maize leaves was measured at 35, 42, 49, 56, 63 and 70 DAP. A portable infra-red gas analyser (LCA-3, Analytical Development Company, Hoddesdon, UK) was used to make instantaneous measurements on the youngest fully expanded leaves of both infected and uninfected maize plants. All measurements were made in the morning between 09.00 and 11.30 h at ambient CO_2 concentrations (approximately 350 μmol mol^{-1}) at a temperature of 25–27°C. The leaf cuvette had an area of 625 mm^2

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(ADC PLC) with a fitted halogen lamp to give a photosynthetically active radiation (PAR) of about 950–1200 μmol m^{-2} s^{-1}. The concentrations of CO_2 entering and leaving the cuvette were recorded with an ADC data logger. The data were later used to compute CO_2 exchange rates per unit leaf area, stomatal conductance and internal CO_2 concentration using the equations described by von Caemmerer and Farquhar (1981).

Statistical analyses

All data were subjected to analysis of variance and the N effect on all measured responses partitioned into linear and quadratic components using orthogonal polynomials with SAS (GLM Procedure). Leaf area per plant (LA) over the five sampling times was further analysed as asymptotic exponential curves (SAS NLIN Procedure).

RESULTS

Statistical analyses showed no significant N × *Striga* interaction for any result so only the main effects of N and *Striga* are presented.

S. hermonthica *infection*

S. hermonthica first emerged at 38 DAP on plants grown with N fertilizer applied at a rate of 20 kg ha^{-1} and 5–7 d later at rates of 60 and 120 kg ha^{-1}. At 61, 90 and 104 DAP the numbers of emerged *Striga* shoots were similar at all rates of N fertilizer applied (means were 4.67, 5.67, and 6 plants respectively). The dry weight of these *Striga* shoots was also not affected by N although at 90 DAP there was a trend of decreasing dry weight with increasing N (0.32, 0.29, 0.21 g pot^{-1} for N applications of 20, 60 and 120 kg ha^{-1} respectively).

Leaf area

The increase in leaf area from the four-leaf stage approached an asymptote by the 18-leaf stage (Figure 1). Leaf area of maize infected with *Striga* was less than that of the uninfected maize at all sampling times. At the four-leaf stage (12 DAP) leaf area of infected maize was 86% that of uninfected maize but the difference increased with growth so that at the 18-leaf stage (104 DAP) infected maize had only 63% of the leaf area of uninfected maize. Application of N increased (P<0.001) the leaf area of maize at all sampling times.

Photosynthesis

The rate of net photosynthesis in both infected and uninfected plants decreased with time during the period of measurement (Figure 2). At the time that each measurement was made, the rate of net photosynthesis in uninfected plants was greater (P<0.001) than that in infected plants. Although leaves of infected plants had smaller rates of net photosynthesis, stomatal conductance and the substomatal CO_2 concentration were not significantly different (data not shown). The appli-

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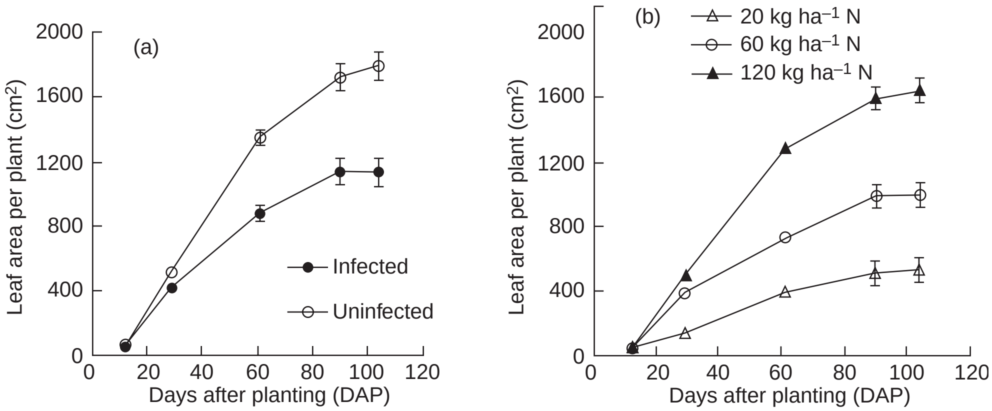

Figure 1. Effect of (a) *Striga hermonthica* infection and (b) the rate of N on total leaf area per plant of maize in Experiment 1. Vertical bars are *s.e.*s of means; some bars are smaller than the symbols.

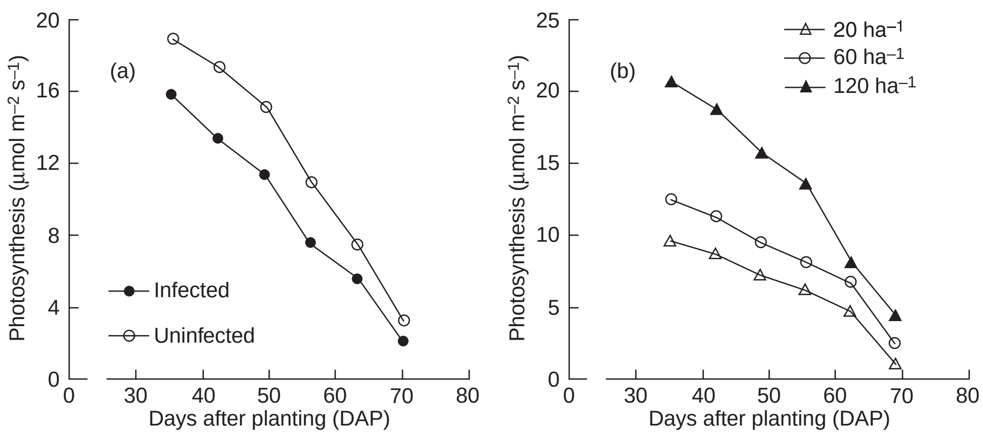

Figure 2. Effect of (a) *Striga hermonthica* infection and (b) the rate of N on the rate of net leaf photosynthesis of maize in Experiment 1. *S.e.* bars are smaller than the symbols.

cation of N increased the rate of photosynthesis at all times, averaged across the infected and uninfected treatments (Figure 2b).

Accumulation and partitioning of biomass

In both experiments, shoot biomass of infected maize, averaged across N rates, was smaller ($P<0.001$) than that of uninfected maize and increased almost linearly with time in all treatments (Figures 3a and Table 1). The relative effect of the *Striga* infection increased with time in both experiments. In Experiment 1, shoot biomass of infected maize at the four-leaf stage (before any *Striga* shoot had emerged above ground) was about 93% that of uninfected maize but by the 18-leaf stage (104 DAP) it was only 37% that of uninfected maize. Similarly, in Experiment 2, shoot biomass of infected maize was 93% that of uninfected maize

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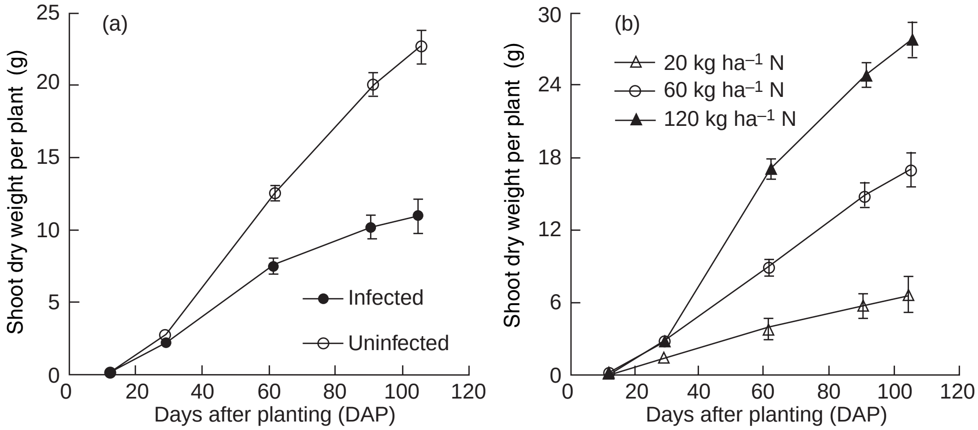

Figure 3. Effects of (a) *Striga hermonthica* infection and (b) the rate of N on shoot biomass per plant in Experiment 1. Vertical bars are *s.e.*s of means; some bars are smaller than the symbols.

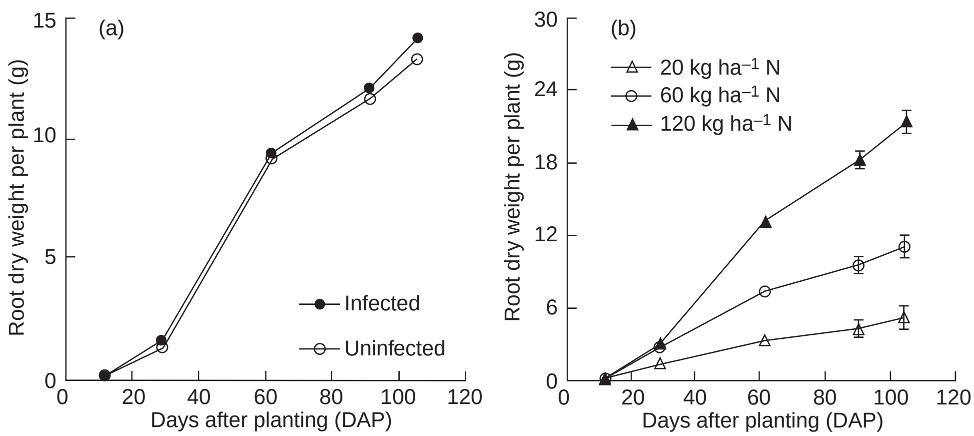

Figure 4. Effects of (a) *Striga hermonthica* infection and (b) the rate of N on root biomass per plant in Experiment 1. Vertical bars are *s.e.*s of means; some bars are smaller than the symbols.

at 29 DAP but only 63% at 99 DAP. Shoot biomass averaged across *Striga* infection levels, also increased (P<0.001) with increased rate of N fertilizer in both experiments (Figure 3b and Table 1). There was no significant difference in root biomass between infected and uninfected plants at all sampling times in both experiments (Figure 4a and Table 2). However, the application of N fertilizer significantly increased root biomass after the first sampling time (Figure 4b and Table 2).

Because *Striga* infection decreased shoot biomass but root biomass was unaffected, the percentage of total biomass per plant partitioned to roots differed (P<0.001) between infected and uninfected maize, except at the four-leaf stage in Experiment 1 (Table 3). In general, maize infected with *Striga* partitioned a higher percentage of its biomass (51–54% in Experiment 1 and 30–44% in

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Table 1. Shoot biomass of maize at different sampling times as affected by *Striga hermonthica* infection and nitrogen supply in Experiment 2.

	Days after planting					
	29	43	57	78	85	99
	Shoot biomass (g plant^{-1})					
Infected	3.53	9.39	15.98	21.36	27.57	33.3
Uninfected	3.79	12.63	27.24	40.70	44.22	52.28
s.e.	0.29	0.49	0.86	0.91	0.98	1.11
Nitrogen (kg ha^{-1})						
20	2.41	7.82	13.33	17.67	27.87	27.61
60	3.43	11.52	22.24	31.66	37.50	43.58
120	4.04	15.66	28.77	42.02	50.78	56.90
s.e.	0.35	0.58	1.04	1.09	1.20	1.37
Contrasts						
Striga	NS	**	***	***	***	***
Nitrogen						
Linear	*	**	***	***	***	***
Quadratic	NS	NS	NS	NS	NS	NS
Striga × N	NS	NS	NS	NS	NS	NS

Data are means of three replicates.
*s.e.*s are for means in each column; *, **, *** contrasts for means in each column differ at $P<0.05$, $P<0.01$ and $P<0.001$, respectively; N.S. – not significant.

Table 2. Root biomass of maize at different sampling times as affected by *Striga hermonthica* infection and nitrogen supply in Experiment 2.

	Days after planting					
	29	43	57	78	85	99
	Root biomass (g plant^{-1})					
Infected	1.57	7.14	12.63	15.97	19.57	22.46
Uninfected	1.33	5.29	10.65	14.82	17.72	20.18
s.e.	0.12	0.90	1.86	1.88	1.70	2.38
Nitrogen (kg ha^{-1})						
20	0.97	2.54	4.37	4.92	5.86	6.78
60	1.78	6.24	10.87	11.88	16.07	18.10
120	2.42	9.19	15.12	22.98	25.36	25.88
s.e.	0.15	1.11	2.37	2.28	2.14	2.97
Contrasts						
Striga	NS	NS	NS	NS	NS	NS
Nitrogen						
Linear	NS	*	**	***	***	***
Quadratic	NS	NS	NS	NS	NS	NS
Striga × N	NS	NS	NS	NS	NS	NS

Data are means of three replicates.
*s.e.*s are for means in each column; *, **, *** contrasts for means in each column differ at $P<0.05$, $P<0.01$ and $P<0.001$, respectively; N.S. – not significant.

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Table 3. Total biomass of maize partitioned to the root at different sampling times as affected by *Striga hermonthica* infection and nitrogen supply.

	Experiment 1					Experiment 2					
DAP	12	29	61	90	104	29	43	57	78	85	99
Striga											
Infected	46.1	51.9	52.3	53.1	54.3	30.9	43.2	44.2	42.8	41.5	40.3
Uninfected	43.1	41.5	39.6	33.5	32.1	25.8	29.5	28.1	26.7	28.6	27.9
s.e.	1.7	4.3	2.2	2.6	2.7	1.23	2.25	2.36	2.41	2.29	2.67
Nitrogen (kg ha^{-1})											
20	48.6	45.7	44.3	40.3	39.2	28.7	24.5	24.7	21.8	21.9	20.2
60	50.8	44.2	46.1	41.2	38.8	34.2	35.1	32.9	27.3	30.0	29.4
120	47.8	44.5	45.9	43.1	38.4	37.5	36.9	34.5	35.5	33.3	31.3
s.e.	2.1	5.3	2.7	3.2	3.3	2.38	3.87	4.67	5.48	4.79	4.94
Contrasts											
Striga	NS	***	***	***	***	*	***	***	***	***	***
Nitrogen											
Linear	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Quadratic	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Striga × N	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Data are the mean of four replicates in Experiment 1 and three replicates in Experiment 2.
*s.e.*s are for means in each column. Contrasts for means in each column differ at P<0.05 (*) and P<0.001(***); N.S. not significant.

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Experiment 2) to the root compared with the uninfected maize (34–43% in Experiment 1 and 25–29% in Experiment 2). In both experiments, however, the percentage of the total biomass partitioned to roots was unaffected by the quantity of N fertilizer applied (Table 3).

Calculation of the allometric coefficients of Equation 1 by linear regression gave values in Experiment 1 for the constants b and k of 0.167 and 1.01 for infected maize ($r^2 = 0.974$) and 0.369 and 1.15 for uninfected maize ($r^2 = 0.979$) with no significant difference between treatments. Similar results were obtained in Experiment 2 (corresponding values of 0.789, 0.92, 1.022, 0.97). The allometric coefficients were also not significantly different between the N treatments. In Experiment 1, values of b and k were 0.027 and 1.13 for 20 kg N ha^{-1} ($r^2 = 0.949$), 0.033 and 1.09 for 60 kg N ha^{-1} ($r^2 = 0.973$) and 0.066 and 1.04 for 120 kg N ha^{-1} ($r^2 = 0.983$). For Experiment 2 the corresponding values were 0.425, 1.02, 0.595, 1.09, 1.27, and 1.08.

DISCUSSION

Leaf area

Infection with *S. hermonthica* reduced the leaf area of the maize host from emergence to final harvest in both experiments. This result confirms those reported for the sorghum-*S. hermonthica* association obtained by Press and Stewart (1987), Cechin and Press (1993), Frost *et al.* (1997), and for the millet-*S. hermonthica* association obtained by Graves *et al.* (1990). The previous studies reported leaf area at only a single stage of development. In this study, leaf area for both infected and uninfected maize plants increased asymptotically from the first to the last sampling date but the differences in leaf area between infected and uninfected maize increased with time, demonstrating the progressively deleterious effect of *Striga* on its host.

Leaf photosynthesis

The reduced rate of net photosynthesis in young leaves of *Striga*-infected maize is consistent with the results of Graves *et al.* (1990) for millet, and Smith *et al.* (1995) and Gurney *et al.* (1995) for maize, but contrast with those of Frost *et al.* (1997) and Clark *et al.* (1994) who did not find any effect on photosynthesis in field-grown sorghum. The application of N fertilizer increased the rate of net photosynthesis, a phenomenon that has also been reported by Cechin and Press (1993; 1994). Cechin and Press (1993), however, found that the effect of *S. hermonthica* infection decreased as the rate of N supplied increased and, at the highest rate of 4 mol N m^{-3} solution, photosynthesis in sorghum was unaffected. In the present study there was no such interaction between the level of N applied and *S. hermonthica* infection. This may be because the highest rate of N applied here was only equivalent to the lower levels of N supplied by Cechin and Press (1993). The increased rate of photosynthesis with increased N supply in this study contrasts with the results of Gurney *et al.* (1995) who did not find any effect of

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increased N supply on photosynthesis in field-grown maize and sorghum infected with *S. hermonthica*.

Neither stomatal conductance nor substomatal CO_2 concentrations were affected by *Striga* infection. The lack of effect of *Striga* infection on stomatal conductance contrasts with the findings of Press and Stewart (1987), Cechin and Press (1994), and Frost *et al.* (1997) who found reduced stomatal conductances in *Striga*-infected sorghum (cv. CSH-1). Graves *et al.* (1992) obtained a similar result with *Striga*-infected cowpea (*Vigna unguiculata*). However, the results of the present study are similar to those of Hibberd *et al.* (1996) who also reported no effect on the stomatal conductance of *Striga*-infected cowpea and of Frost *et al.* (1997) for sorghum (cv. Ochuti). The lack of effect of *Striga* infection on substomatal CO_2 concentration is, however, entirely consonant with the results of Hibberd *et al.* (1996), and Cechin and Press (1994).

Several mechanisms may be responsible for depressing photosynthetic rates in host plants infected with *Striga* spp. Firstly, infection may result in changes in host metabolism and/or production of toxins that perturb the biochemistry of host photosynthesis (Musselman, 1980) or change the balance of plant growth hormones (Drennan and El Hiweris, 1979; Taylor *et al.*, 1996; Frost *et al.*, 1997). Secondly, the removal of host C may feed back to influence host-C metabolism and subsequent CO_2 fixation. Thirdly, the removal of other resources such as N, P and water may disturb C metabolism in the host. These mechanisms may operate individually or in concert.

Accumulation and partitioning of biomass

Infection of maize by *S. hermonthica* did not affect root biomass but led to smaller shoot biomass; the differences in shoot biomass between uninfected and infected plants increased with time. However, the proportion of total biomass per plant partitioned to roots differed between infected and uninfected plants in both experiments. The results from this study contrast with those of Graves *et al.* (1990), Press *et al.* (1996) and Taylor *et al.* (1996) but are similar to those of Graves *et al.* (1989) and Cechin and Press (1994). Graves *et al.* (1990) reported that leaf and root biomasses in *Striga*-infected millet were increased by 41 and 86% respectively while grain yield was reduced by 80% and stem dry weight by 53%. Similarly, Taylor *et al.* (1996) found higher root biomass in infected maize than in uninfected maize, and Press *et al.* (1996) reported a marked shift in allocation of dry matter to roots in two sorghum cultivars, CSH-1 and Ochuti, infected with *S. hermonthica*. Frost *et al.* (1997) showed that although the biomass of *Striga*-infected sorghum (CSH-1 and Ochuti) was lower than that in uninfected plants, shoot biomass was affected more than was root biomass. In sorghum, Graves *et al.* (1989) reported a reduction in grain and stem dry weights while leaf and root dry weights remained similar for infected and uninfected plants.

The physiological basis for these differences in response is unknown. It is possible that variations in genetic composition of different host crops and cultivars of the same species to different strains of the parasite may play a part. In addition,

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changes in the balance of plant growth hormones may be responsible for some of the differences in allometry (Drennan and El Hiweris, 1979; Taylor *et al*., 1996; Frost *et al*., 1997). Another possible reason for the observed differences in allometry may be the time of emergence of parasites above ground. The data from this study showed that differences in leaf area and shoot biomass between infected and uninfected plants increased with time and the development of the *Striga* shoots. These results, however, did not support the hypothesis that higher applications of N would reduce biomass of infected maize relatively more than uninfected maize.

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