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Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*

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SUMMARY

Two cultivars of sorghum (CSH-1 and Ochuti) were grown in the presence and absence of the root hemiparasite *Striga hermonthica* in uniform conditions in the field in Kenya, Africa. *S. hermonthica* had a marked influence on growth and photosynthesis of 'CSH-1'; however, 'Ochuti' showed a less severe response to infection and tolerance of the parasite. The variation in genotype response might be partly explained by later attachment of the parasite and a lower level of infection. Laboratory studies were used to determine the importance of both variables in determining host response to infection. Early infection by *S. hermonthica* had a more negative effect on the host than late infection. The level of parasite biomass supported by the host also influenced host productivity but the relationship was nonlinear. Low degrees of parasite infection had a proportionately much greater effect on host grain weight than at greater parasite loading. Early infection of 'Ochuti' in laboratory conditions resulted in lower stem dry weight than in uninfected plants but not in smaller total plant biomass or lower rates of photosynthesis. In conclusion, the time of parasite attachment affected host performance and might explain much of the variation in host sensitivity both within and between studies. The level of parasite infection affected host performance to a lesser extent. In addition, late attachment and low levels of infection might have implications for control management strategies.

Keywords: parasitic angiosperm, photosynthesis, growth, tropical weeds.

INTRODUCTION

Parasitic angiosperms are at least partly dependent on their host species for the supply of carbon, nutrients and water. Where the host is of agricultural importance, the parasites can become serious weeds and constrain food production (Parker, 1991; Parker & Riches, 1993). In Sub-Saharan Africa, 73 Mha of land is under cereal production and *c.* two-thirds of this area is infected with the obligate root hemiparasite, *Striga* (Sauerborn, 1991). *Striga hermonthica* is the most important of these weeds and exerts its greatest impact in low-input subsistence farming areas (Parker & Riches, 1993; Riches & Parker, 1995), mainly infecting C_4 cereals (maize, sorghum and millet are the most important agricultural species), and has a marked influence on the growth and allometry of its host. Grain losses are difficult to estimate but, on a regional scale, average 5–15 %. Locally, *S. hermonthica* can exert a much greater impact, sometimes resulting in total crop failure (Doggett, 1988; Sauerborn, 1991; Riches & Parker, 1995).

Field and laboratory studies show large differences in the response of cereal species and cultivars to *S. hermonthica* infection which may be attributed to one or more sources of variation: (i) genetic differences between host species and cultivars; (ii) genetic differences between populations of *S. hermonthica*; (iii) interaction between the environment and both genotypes. A preliminary study by Cechin & Press (1993a) demonstrated that early attachment of *S. hermonthica* (3-d-old hosts) had a greater effect on the growth of its sorghum host than later attachment (19-d-old hosts). Thus, timing of infection might be a mechanism that explains at least some of the variation associated with genotypes and environment. In further support of this assertion, studies using transplanted sorghum showed that *S. hermonthica* had a greater effect on directly planted sorghum than on 3–4 wk old plants transplanted from *Striga*-free soil (Dawould *et al.*, 1996). However, in these studies the improved performance of late-infected plants compared with early-infected plants was also accompanied by smaller biomass of the parasite.

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Despite the lack of laboratory evidence for a relationship between the sink size of *S. hermonthica* and the difference in biomass accumulation between infected and uninfected plants (Frost *et al.*, 1997), field studies have often demonstrated an increase in host performance with an associated decrease in the amount of parasite infection (e.g. Ransom & Odhiambo, 1994; Hess *et al.*, 1996; Odhiambo & Ransom, 1996; Kim & Adetimirin, 1997).

In light of the differing sensitivity of cereals to infection (e.g. Gurney *et al.*, 1995), there is an urgent need to identify sorghum genotypes that are more tolerant of or resistant to *S. hermonthica*. Confounding effects of the environment and genotype among *Striga* populations can confuse the interpretation of screening experiments and the synthesis of information from different studies. In this study we examined the response of two sorghum cultivars (CSH-1 and Ochuti) to *S. hermonthica* in the field in western Kenya, in uniform conditions of infestation and environment. The cultivars were selected on the basis of reported differences in response to infection in laboratory conditions (Frost *et al.*, 1997). Subsequently, further laboratory studies were conducted to test the hypothesis that differences in performance in the field could be attributed to different attachment times. Furthermore, the studies were conducted using different densities of *S. hermonthica* seed, in order to address a second hypothesis, that host response is independent of the parasite biomass. Specifically, we report biomass accumulation, rates of gas exchange and grain yield of infected and uninfected sorghum cultivars in order to address our hypotheses.

MATERIALS AND METHODS

Field study

Experimental design and plant material. The study was conducted in the field at the Kenya Agricultural Research Institute at Kibos, near Kisumu in western Kenya, in March 1996 during the long rain season.

Two cultivars of the cereal *Sorghum bicolor* (L.) Moench were studied, selected for their difference in susceptibility to infection by *Striga hermonthica* (Del.) Benth. The susceptible cultivar, 'CSH-1', originated in India (Press *et al.*, 1987; Press & Stewart, 1987; Cechin & Press, 1993a,b) and a landrace cultivar, 'Ochuti', reported to show some tolerance to *S. hermonthica* (Gurney *et al.*, 1995; Frost *et al.*, 1997) came from Kenya. Plants were grown in the absence or presence of *S. hermonthica*.

Twelve experimental plots, each 15 m^2 (3 × 5 m), were established and each treatment was replicated three times. In order that the plants could be grown in the absence of *Striga*, the entire area was fumigated with methyl bromide gas (at a rate of 500 kg ha^{-1}), in late February 1996 (see Gurney *et al.*, 1995). Within each plot the plants were grown 0.5 m apart in rows 0.6 m apart. Only the centre four rows were used for measurement, the outer two comprising the guard rows, with safety margins of 0.5 m between each row. At the time of planting (late March), half the plots were sown with *S. hermonthica* seed collected in Kibos in 1994. The seed was mixed with finely sieved sand and placed 10–15 cm deep around the planting hole to give an infection density of 2000 seeds per host plant.

At planting, all plants received a dressing of tri-superphosphate and ammonium nitrate applied at a rate of 40 kg N and P ha^{-1} and an application of an insecticide (Carbofuran (Furadan), FMC Corp., IL, USA) at a rate of 2 g per plant to protect against early attacks of stem borers; the plants were treated again at 22 dap (days after planting). Plots were hand-weeded of all weeds except *S. hermonthica* at 46 dap.

Growth measurements. At 108 dap stem and grain dry weight were determined for eight individual plants in each treatment. Plant material was oven-dried for 76 h at 70°C before being weighed. *S. hermonthica* plants were harvested at soil level, below-ground biomass discarded, and dried as already described.

Gas exchange measurements. Instantaneous (60–120 s) rates of gas exchange were measured on 12 individual sorghum plants for each treatment at 91 dap. Measurements were made halfway along the length of the youngest fully expanded leaf using a portable infrared gas analyser (LCA-4 ADC, Hoddesdon, UK) at ambient CO_2concentrations (380 ppm) and relative humidity (50%). All measurements were recorded between 10.30 and 14.00 hours, when the photon flux density (PFD) was >2000 μmol quanta m^{-2} s^{-1}. The leaf cuvette had an area of 625 mm^2 (ADC PCL-B, broad leaf plant chamber Analytical Development Company, Hoddesdon, UK), and a flow rate of 300 ml min^{-1}. Differences between the concentration of CO_2 and H_2O vapour in inlet and outlet gas streams were used to calculate rates of photosynthesis and transpiration, using the equations described by von Caemmerer & Farquhar (1981).

Laboratory study

Plant material and growth conditions. Two experiments were conducted June–October 1997 in a glasshouse using ambient light (midday PFD was typically in the range of 1000–1500 μmol quanta m^{-2} s^{-1}) with supplementary heating. Day and night temperatures were maintained close to 30 and 20°C, respectively. Sorghum plants were grown in 2 dm^3 pots filled with sand and connected to a nutrient drip-feed system. The plants were fed with a 40% full-strength Long Ashton solution (Hewitt, 1966) containing 1 mol m^{-3} ammonium nitrate supplied four times during each photoperiod to give a total

volume of 200 cm^3 d^{-1}, sufficient to sustain non-water-limited growth. Pots were place in a randomized design in the glasshouse. Three sorghum cultivars were used in this study, 'CSH-1' and 'Ochuti' (as used in the field study, see above) and 'SRN-39', which showed low production of germination stimulant (Babiker & Reda, 1991; Parker, 1991; Hess *et al*., 1992).

Preconditioning and infection of S. hermonthica. Infestation was carried out using the same source of seed as for the field study. Preconditioning of seed was conducted in a controlled-environment cabinet (Fisons, Fi-totron PG1700, Fijans, Gallen Kamp, Leicester, UK) where day and night temperatures were maintained at 30 and 20°C, respectively. The seeds were surface-sterilized for 5 min in a 5% sodium hypochlorite solution containing a few drops of the surfactant Tween (Sigma Chemical Co., St. Louis, MO, USA), rinsed with distilled water, placed on 9 cm diameter discs of glassfibre filter paper in a sterile Petri dish and moistened with distilled water. The Petri dishes were placed in the controlled-environment cabinet for 14 d.

The preconditioned *S. hermonthica* seeds were used to infect the sorghum plants. After the sand was washed from the base of the stem to expose the root system, seeds were placed on the surface of the roots which were then re-covered with sand. In Experiment 1, infection was carried out on all cultivars at 18, 28 and 38 dap at an infection density of 2000 seeds per host plant. In Experiment 2, infection was carried out on cultivar CSH-1 at 18 dap, with seed densities of 5, 500, 2000 and 5000 seeds per host plant. Eight replicate plants of each cultivar were established in the absence of *S. hermonthica* and at each *S. hermonthica* treatment (time and density of infection).

Growth analysis. Throughout the period of study nondestructive growth measurements were made until the final harvest at 100 dap for Experiment 1. At five intervals between 18 and 85 dap, plant height of each of the eight replicate plants was measured (from the base of the stem to the youngest visible ligule), since this is known to be a sensitive indicator of infection (Press & Stewart, 1987). Nondestructive measurements also included the number of emerged *S. hermonthica* plants per host plant. Final biomass was determined in Experiments 1 and 2 by separating the sorghum plants into roots, stems, leaves and grain (where present). Roots were separated from the sand by careful washing over a 2-mm meshed sieve after which *S. hermonthica* plants were detached from the roots at the point of tubercle attachment. The plant material was oven-dried at 70°C for 72 h before weighing.

Gas exchange measurements. For Experiment 1, rates of photosynthesis are reported for infected and uninfected sorghum plants at 85 dap. Measurements were made using the gas analyser described in the field study. At each time of measurement, 4–5 individual plants in each treatment were sampled, and one record made per plant. Measurements of gas exchange were made halfway along the length of the youngest fully expanded leaf and were recorded after a minimum of 15 min, when steady-state photosynthesis had been reached. Measurements were recorded at a light-saturating PFD of 2000 μmol m^{-2} s^{-1} supplied by a Schott KL1500T lamp (Schott, Mainz, Germany) and ambient CO_2 and relative humidity (*c*. 350 ppm and 50% RH, respectively). Rates of photosynthesis and transpiration were calculated as already described.

Statistical analysis. The responses of each cultivar to *S. hermonthica* infection (time, density or presence of the parasite in the field) were subjected to ANOVA procedures for a randomzed block design (Minitab statistical package, version 10.2 Minitab Inc., PA, USA) and the means were separated using Tukey's multiple comparison tests (Zar, 1984). Because final *S. hermonthica* biomass data for the late-infestation trial could not be normalized, they were analysed by Kruskal-Wallis nonparametric procedures and the means separated using nonparametric multiple comparison tests (Zar, 1984). Statistical analysis for proportion data were performed after arcsin $\sqrt{x}$ transformation of the actual data. The response of grain dry weight to changes in parasite biomass were fitted with an exponential decay curve (Sigma plot, ver. 2.01 SPSS Inc., Chicago, IL, USA).

RESULTS

Influence of S. hermonthica *on field-grown sorghum plants*

Throughout the entire experimental period there no *S. hermonthica* emerged on any of the control plots and examination of root systems of plants grown on these plots confirmed that they were free from *S. hermonthica*. Emergence of *S. hermonthica* was observed at 41 dap on 'CSH-1' and at 48 dap on 'Ochuti'. By the final harvest (108 dap) the parasite biomass supported by infected 'CSH-1' plants was almost four times greater than that supported by 'Ochuti' plants ($P \leqslant 0.001$) (Table 1).

Striga hermonthica had a marked effect on the final biomass of the different plant organs and on photosynthesis of the sorghum host 'CSH-1' compared with uninfected plants. By contrast, 'Ochuti' showed a less severe response to infection (data summarized in Table 1). At harvest, the stem and grain dry weights of infected 'CSH-1' plants were 46 and 47%, respectively, lower than those of uninfected plants. Infected 'Ochuti' plants showed no significant difference in biomass allocation to the

Table 1. *Stem and grain dry weight of* Sorghum bicolor *cultivars measured at 108 days after planting*

Sorghum cultivar	Infection	Stem d. wt (g)	Grain d. wt (g)	A (μmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})	*Striga* d. wt (g)	Time emergence of *Striga* (dap)
'CSH-1'	−S	78.25±2.27	83.96±2.98	31.95±0.46	5.81±0.28	–	–
	+S	42.30±10.6*	42.02±5.41***	14.48±1.35***	3.23±0.24***	7.82±3.15	41
'Ochuti'	−S	127.0±10.1	97.71±4.56	31.61±0.71	4.86±0.24	–	–
	+S	112.4±21.1	75.82±6.51*	27.74±0.86*	4.39±0.21	2.00±0.72	48

Askerisks denote significant differences between uninfected and infected plants within cultivars (*P, $\leqslant 0.05$; ***P, $\leqslant 0.001$).
Plants were grown in the field in western Kenya in the absence (−S) or presence (+S) of *Striga hermonthica*. Final dry weights of emerged *S. hermonthica* and the time of the first sighting of parasites above ground are also reported. Photosynthesis (A) and transpiration (E) in *Sorghum* plants measured at 91 dap are shown. Means±SE, $n = 12$–15.

stem compared with uninfected plants and grain dry weight was only 22% lower than in uninfected plants. *S. hermonthica* had a large effect on the gas exchange of 'CSH-1' plants, and by 91 dap rates of photosynthesis and transpiration were 45 and 67% lower than in uninfected plants. Infected 'Ochuti' plants, however, exhibited rates of photosynthesis only 12% lower than those of uninfected plants and the parasite had no effect on transpiration.

The influence of timing of S. hermonthica *infestation on its cereal host in laboratory conditions*

Infection by S. hermonthica. After each infection, emergence of *S. hermonthica* occurred within 21–24 d (data not shown) and 'CSH-1' plants supported greater biomass of *S. hermonthica* at harvest than 'Ochuti' and 'SRN-39' (Table 2), 'SRN-39' supporting the smallest biomass of *S. hermonthica*. The greatest biomass accumulation of *S. hermonthica* was observed with early infection at 18 dap and the lowest with late infection at 38 dap.

Cereal growth and biomass accumulation. Large differences were observed in the height of the youngest ligules of infected and uninfected 'CSH-1' and 'SRN-39' plants (Fig. 1). The extent to which infected plants showed less internode extension was dependent on time of infection. In 'CSH-1' plants, early *S. hermonthica* infection (18 dap) resulted in less internode extension than later infection (28 and 38 dap). By 49 dap, plants infected at 18 and 28 dap were significantly ($P \leqslant 0.05$) shorter than uninfected plants. By 85 dap, ligule heights of plants infected at 18 and 28 dap were 46 and 19%, respectively, less than those of uninfected plants. Throughout the

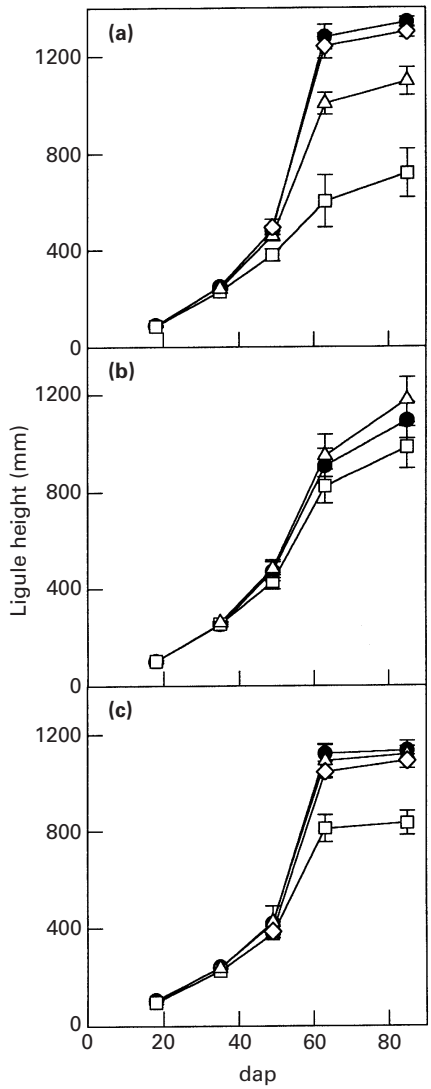

Fig. 1. Distance from the base of the stem to the youngest ligule of *Sorghum bicolor* cultivars. (a) 'CSH-1'. (b) 'Ochuti'. (c) 'SRN-39'. Plants were grown in the absence (closed symbols) or presence (open symbols) of *Striga hermonthica* and infected at 18 (squares), 28 (triangles) and 38 (diamonds) days after planting (dap). Means±SE, n = 4–8.

Table 2. *Total* Striga hermonthica *d. wt per host plant at* 100 *days after planting* (*dap*) *in the glasshouse*

Sorghum cultivar	*Striga hermonthica* d. wt (g)		
	S1	S2	S3
'CSH-1'	3.474 ± 0.583^{c}	1.773 ± 0.242^{b}	0.057 ± 0.017^{a}
'Ochuti'	1.475 ± 0.845^{a}	0.203 ± 0.066^{a}	0
'SRN-39'	0.309 ± 0.108^{c}	0.019 ± 0.011^{b}	0.003 ± 0.001^{a}

Host plants were infected with the parasite at 18 (S1), 28 (S2) and 38 (S3) dap. Means±SE, n = 4–8. Means not sharing a common superscript letter in the same row are significantly different ($P \leqslant 0.05$).

Table 3. *Total plant biomass of* Sorghum bicolor *cultivars grown in the absence* (−*S*) *or presence* (+*S*) *of* Striga hermonthica

Sorghum cultivar	*Striga* treatment	Total plant biomass (g)	Biomass allocation %			
			Root	Stem	Leaf	Grain
'CSH-1'	−S	60.98 ± 3.81^{b}	29.9^{a}	28.5^{b}	13.0^{a}	28.6^{b}
	+S1	40.30 ± 6.59^{a}	53.7^{b}	17.7^{a}	18.9^{b}	9.7^{a}
	+S2	53.97 ± 5.16^{ab}	39.6^{a}	24.4^{b}	15.0^{a}	21.0^{b}
	+S3	58.53 ± 1.77^{b}	30.7^{a}	28.3^{b}	13.7^{a}	27.3^{b}
'Ochuti'	−S	86.55 ± 1.26^{a}	48.7^{a}	29.8^{a}	21.5^{a}	–
	+S1	71.29 ± 6.40^{a}	54.2^{a}	24.0^{a}	21.8^{a}	–
	+S2	71.53 ± 8.36^{a}	51.3^{a}	27.1^{a}	21.6^{a}	–
'SRN-39'	−S	44.63 ± 2.90^{b}	20.7^{a}	33.2^{a}	18.8^{a}	27.3^{a}
	+S1	28.45 ± 1.95^{a}	30.0^{b}	28.4^{a}	27.2^{b}	14.4^{b}
	+S2	38.11 ± 2.70^{ab}	22.7^{ab}	25.9^{a}	21.2^{a}	30.2^{a}
	+S3	45.07 ± 3.04^{b}	19.0^{a}	31.8^{a}	19.8^{a}	29.4^{a}

Host plants were infected with the parasite at 18 (+S1), 28 (+S2) and 38 (+S3) days after planting. Means ± SE, $n = 4$–8; percentage of the biomass allocated to each of the component parts is shown. The data were analysed using ANOVA procedures and those not sharing a common superscript letter in the same column within each cultivar are significantly different ($P \leqslant 0.05$).

study, 'CSH-1' plants infected at 38 dap were not significantly shorter than uninfected plants. The response of 'SRN-39' plants to early infection followed a similar pattern to that of 'CSH-1' and by 85 dap ligule height of infected plants was 27 % less than that of uninfected plants. By contrast with 'CSH-1', ligule heights of 'SRN-39' plants infected at 28 and 38 dap were not significantly different from those of controls. 'SRN-39' supported the lowest parasite biomass; however, 'Ochuti' showed the smallest response to infection. Throughout the study *S. hermonthica* had no significant effect on the ligule height of 'Ochuti' plants.

S. hermonthica had a significant effect on total plant dry weight accumulation in 'CSH-1' and 'SRN-39' (Table 3). Early infection at 18 dap had the greatest effect on biomass accumulation; infected 'CSH-1' and 'SRN-39' plants accumulated 34 and 37 % less biomass, respectively, than uninfected plants. Later infection, at 28 and 38 dap, had no significant effect on total plant biomass. Infection of 'Ochuti' had no significant effect on plant biomass.

S. hermonthica infection had a significant effect on biomass allocation in all the cultivars examined (Table 3). Grain and stem dry weight accumulation were most severely affected by *S. hermonthica* (with the exception of 'Ochuti' which did not produce any grain) while root and leaf components were less affected by the presence of the parasite. Early infection resulted in smallest grain and stem biomass accumulation, with infection at 28 dap having a less marked effect; late infection, at 38 dap, had no significant effect on biomass accumulation. Early infection altered the proportion of biomass allocated to each of the component parts compared with uninfected plants, with a greater proportion of biomass allocated to the root. For example, 'CSH-1' plants infected at 18 dap allocated 53.7 % of biomass to the root and only 9.7 % to the grain, whereas control plants allocated 29.9 % of biomass to the root and 28.6 % to the grain. Early infection of 'CSH-1' and 'SRN-39' resulted in greater biomass allocation

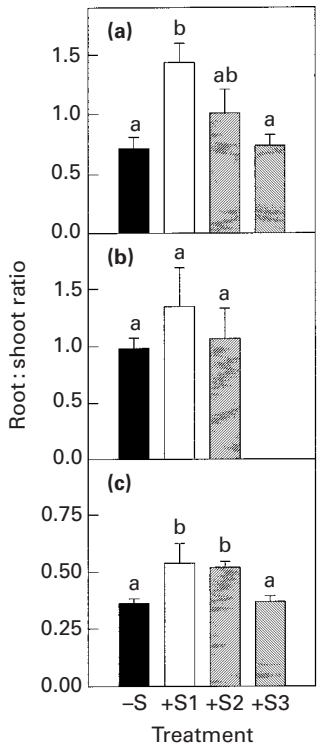

Fig. 2. Root dry weight : shoot dry weight of *Sorghum bicolor* cultivars. (a) 'CSH-1'. (b) 'Ochuti'. (c) 'SRN-39'. Plants were grown in the absence (−S) or presence (+S) of *Striga hermonthica* and infected at 18 (+S1), 28 (+S2) and 38 (+S3) days after planting (dap). Means ± SE, $n = 4$–8. Bars not sharing a common superscript letter are significantly different ($P \leqslant 0.05$). Note that the scales on the *y*-axis differ.

Table 4. *Light-saturated rate of photosynthesis* (*A*) *and transpiration* (*E*) *in* Sorghum bicolor *cultivars measured at 85 days after planting, grown in the absence* (−*S*) *or presence* (+*S*) *of* Striga hermonthica

Sorghum cultivar	Infection	A (μmol CO_2 m^{-2} s^{-1})	E (mmol H_2O m^{-2} s^{-1})
'CSH-1'	−S	20.23 ± 0.57^{c}	1.96 ± 0.14^{b}
	+S1	15.57 ± 0.94^{a}	1.50 ± 0.17^{a}
	+S2	18.30 ± 0.71^{ab}	1.42 ± 0.04^{a}
	+S3	19.55 ± 0.71^{bc}	1.60 ± 0.09^{ab}
'Ochuti'	−S	16.40 ± 0.78^{a}	1.35 ± 0.15^{a}
	+S1	16.45 ± 0.88^{a}	1.35 ± 0.09^{a}
	+S2	16.10 ± 0.65^{a}	1.35 ± 0.08^{a}
'SRN-39'	−S	17.57 ± 0.86^{c}	1.77 ± 0.11^{b}
	+S1	12.40 ± 1.17^{a}	1.35 ± 0.21^{a}
	+S2	13.60 ± 1.25^{ab}	1.50 ± 0.19^{ab}
	+S3	16.17 ± 0.99^{bc}	1.62 ± 0.17^{ab}

Host plants were infected with the parasite at 18 (+S1), 28 (+S2) and 38 (+S3) dap. Means ± SE, $n = 4$–6. Means not sharing a common superscript letter in the same column within each cultivar are significantly different ($P \leqslant 0.05$).

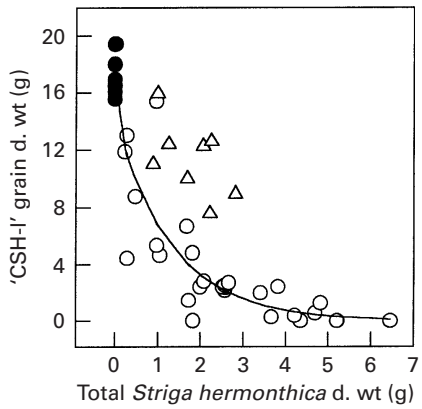

Fig. 3. The relationship between grain dry weight of *Sorghum bicolor* cv. CSH-1 plants and total *Striga hermonthica* dry weight per host plant at the final harvest (100 days after planting (dap)). Plants were grown in the absence (closed circles) or presence (open circles) of *S. hermonthica* and infected at 18 dap at densities of either 5, 500, 2000 or 5000 seeds per host plant. Plants infected with the parasite at 28 dap are represented by triangles. An exponential decay curve was fitted to the data (excluding data from 28 dap).

to the leaves than in the controls. The negative effect of the parasite on stem growth and the increase in biomass allocation to the roots resulted in root : shoot ratios being greater in early-infected than in uninfected plants (Fig. 2) of 'CSH-1' and 'SRN-39' ($P \leqslant 0.05$). The effect on root: shoot ratios of later infection, at 28 and 38 dap, was less severe. Infection of 'Ochuti' plants had no significant effect on root : shoot ratios at any time of infection.

Gas exchange. In 'CSH-1' and 'SRN-39', infection by *S. hermonthica* reduced rates of photosynthesis compared with uninfected plants; by 85 dap, rates of photosynthesis of early-infected plants (18 dap) were 23 and 29% less than those of control plants, respectively (Table 4); infection at 28 dap reduced rates of photosynthesis to 10 and 23% below those of controls, respectively, whereas infection at 38 dap had no significant effect on photosynthesis. Lower rates of photosynthesis were accompanied by lower rates of transpiration; again early infection had a more marked effect on transpiration than later infection. Throughout the study *S. hermonthica* had no effect on the gas exchange characteristics of 'Ochuti' plants irrespective of time of infection.

The influence of S. hermonthica *biomass on its sorghum host*. The relationship between total dry weight of *S. hermonthica* and the grain dry weight of the supporting host, for 'CSH-1' infected at 18 dap, was fitted to an exponential decay curve (Fig. 3). At very small parasite biomass there was an almost linear inverse relationship between grain dry weight and dry weight of *S. hermonthica*; increase in parasite dry weight resulted in lower grain dry weight of the host until the host supported *c*. 2 g parasite dry weight. Parasite biomass above this threshold did not result in further loss of grain dry weight.

Late infection of 'CSH-1' (28 and 38 dap) resulted in greater grain dry weight than early infection (18 dap), which was associated with lower *S. hermonthica* biomass (Table 2). However, the relationship between grain dry weight and *S. hermonthica* dry weight in 'CSH-1' plants infected at 28 dap did not correspond to the curve fitted to Fig. 3, with later infection resulting in greater grain dry weight at a similar parasite dry weight than early infection (18 dap).

DISCUSSION

The response of sorghum cultivars to *S. hermonthica* infection is a function of host genotype and environmental conditions. Their sensitivity to parasite infection may be explained by the time of infection and by the biomass of *S. hermonthica* supported by the host. Of the sorghum cultivars examined, the growth and photosynthesis of 'CSH-1' showed the most severe response to *S. hermonthica* infection in comparison with those of uninfected plants. Few field studies have examined the performance of cereals grown in the presence and absence of *Striga*. This field study showed that the response to *S. hermonthica* of sorghum cultivars 'CSH-1' and 'Ochuti' differed from that of uninfected plants. In addition, the field observations showed earlier emergence of *S. hermonthica* (indicating earlier attachment) on 'CSH-1' than on 'Ochuti' and 'CSH-1' supported a greater parasite biomass. The question arises whether this variation in time of attachment and parasite loading in the field can explain different responses to infection.

To understand the importance of the time of parasite infection, three sorghum genotypes were grown in controlled laboratory conditions and infected with *S. hermonthica* at different times. Early infection (18 dap) of 'CSH-1' had a more severe effect on photosynthesis and biomass accumulation than delayed infection (28 and 38 dap). Few studies have examined the effects of delayed infection of cereals but these results support preliminary laboratory observations by Cechin & Press (1993a) where biomass accumulation in sorghum plants infected with *S. hermonthica* when 3 d old was lower than in those infected when 19 d old. Field studies manipulating the time of *Striga* attachment have also been undertaken using acetolactate synthase inhibiting herbicides. Application of these herbicides provided early-season *Striga* control, delaying parasite emergence by 4 wk. Grain yields were significantly greater where parasite emergence was delayed (Abayo *et al.*, 1996). Cechin & Press (1993a) suggested that the age at which a plant becomes infected by *S. hermonthica* might be an important determinant of the extent to which the parasite can affect host productivity. Laboratory results for *Striga*-susceptible 'CSH-1' and 'SRN-39' but not apparently for 'Ochuti', support this hypothesis. Delayed infection resulted in greater biomass partitioning to the stem than early infection, indicating that the delayed emergence of *Striga* in the field might have contributed to the improved performance of 'Ochuti'. However, early infection in laboratory conditions did not affect photosynthesis or total plant biomass, suggesting the inherent tolerance of 'Ochuti' to *Striga* infection regardless of time of attachment.

Greater productivity of cultivars in which infection is delayed might also result from less parasite loading than in early-infected plants. Alteration of the density of seed inoculum revealed an influence of parasite biomass on grain yield. At low levels of parasite infection grain production was severely affected: comparatively small increases in parasite biomass resulted in a dramatically lower grain yield. However, the response of grain production to increased levels of infection was nonlinear; thus a point was reached where host grain production was independent of parasite biomass. Low parasite biomass with late infestation might have at least two causes. First, lower biomass of the parasite was also associated with fewer attached parasites (data not shown), possibly a result of the ability of the germinated *Striga* seeds to penetrate older sorghum roots being diminished by changes in morphological and biochemical characteristics (Olivier *et al.*, 1991). Second, *S. hermonthica* attached to late-infested plants were younger than those attached to early-infected plants. By manipulating the density of parasite infection it was possible to achieve similar parasite loading in plants infected at 18 and 28 dap. The negative effects of the parasite were reduced by later infection, again demonstrating that both the time and level of *S. hermonthica* infection have important implications for the performance of the host.

A more linear relationship between biomass of infected plants and the biomass of the parasite supported by the host has been observed for the *Orobanche aegyptiaca*–tomato association (Hibberd *et al.*, 1998). Studies of *Orobanche* suggest that the parasite acts as an additional sink for host assimilates and alters the source–sink relations of the host–parasite association (Kharrat *et al.*, 1994; Barker *et al.*, 1995; Barker, 1997). The difference in amount of biomass between infected and uninfected plants can be accounted for by the biomass of the attached parasite (Hibberd *et al.*, 1998). Although *S. hermonthica* acts as a sink, the difference in biomass between infected and uninfected plants cannot be accounted for by parasite biomass (Graves *et al.*, 1989). This raises the possibility that *S. hermonthica* alters host metabolism by other mechanisms, for example, introduction of novel compounds active at low concentrations (Parker & Riches, 1993) or influence on growth regulators in the host (Drennan & El Hiweris, 1979; Taylor *et al.*, 1996; Frost *et al.*, 1997). If the effects of infection are mediated through changes in host metabolism, these might be of less consequence in a larger host.

The reasons for late emergence of *S. hermonthica* in the field are not known but it might be attributable to root architecture patterns that avoid *Striga* in the upper soil profile (Van Delft *et al.*, 1996; Van Delft, 1997) or processes within the plant that inhibit the development of the parasite. The sensitivity of cultivars to low levels of infection demonstrates the importance of *Striga* control in the field. This study clearly demonstrates the necessity for reducing the seed bank concentration in the soil and for improved management techniques to reduce the amount of parasite biomass supported by the host and to avoid early attachment.

In conclusion, the sorghum cultivars studied differ in their sensitivity to *S. hermonthica* infection when grown in uniform conditions in the field. From laboratory studies it appears that the timing of infection might be an important mechanism explaining genotype variation, supporting our original hypothesis. Level of parasite infection might have additional implications for loss of host productivity but even low levels of infection can have dramatic consequences for host performance. The similarity between the responses of 'CSH-1' and 'SRN-39' to widely different degrees of parasite loading, and the tolerance of 'Ochuti' to infection, demonstrate that whereas late attachment and low levels of infection might favour the productivity of the host, genetic tolerance of infection is a key factor in stable performance in *Striga*-infected areas.

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