Gas Exchange Characteristics of the Sorghum-*Striga* Host-Parasite Association

MALCOLM C. PRESS*, JANET M. TUOHY, AND GEORGE R. STEWART
Department of Botany and Microbiology, University College London, Gower Street, London WC1E 6BT, United Kingdom

ABSTRACT

Gas exchange characteristics are reported for both members of the sorghum-*Striga* host-parasite association. Both *Striga hermonthica* (Del.) Benth and *Striga asiatica* (L.) Kuntze had transpiration rates considerably in excess of those of sorghum (*Sorghum bicolor* (L.) Moench, cv CSH1). Stomatal conductance in both *Striga* spp. showed little response to periods of darkness and moderate water stress. Low rates of net CO_2 fixation and high rates of dark respiration led to no net daily (24 hours) C gain, and *Striga* would appear to be reliant on its host for photosynthate. Infection of sorghum plants with either *S. hermonthica* or *S. asiatica* reduced host photosynthetic capacity. Infected sorghum plants were also more prone to water stress, but reduced rates of CO_2 fixation could not be accounted for in terms of lower stomatal conductance. Lower stomatal conductances were associated with an increase in water use efficiency (WUE) in uninfected sorghum; however, *Striga*-infected sorghum plants had lower WUE than those of uninfected plants. We suggest that *Striga* exerts a specific effect on processes affecting C acquisition in sorghum leaves. The water relations of *S. hermonthica* and *S. asiatica* are not characteristic of plants growing in semiarid environments and are more likely to reflect the nature of the parasitic life-style. Despite transfer of water and solutes from host to parasite, the reduction in C fixation observed in infected sorghum plants appears to be the major determinant of growth reductions observed in sorghum supporting *Striga*.

Parasitic angiosperms rely on one or more neighboring plants (the host) either partially or totally for the acquisition of water, inorganic and organic solutes. Transfer is achieved via the haustorium, which may be located either above ground (*e.g.* green leafy mistletoes) or below ground (*e.g. Striga*) and links the vascular systems of the two plants. Although parasitic angiosperms are present in all habitats, ranging from arctic tundra to hot deserts, the water, carbon and nutritional relations of these plants have, until recently, received relatively little attention.

Following the early work of Hull and Leonard (7, 8), Ehleringer, Schulze and co-workers (5, 18) have shed light on the principles underlying diversion of host resources to xylem-tapping mistletoes. A common feature is that mistletoe leaves have a Tn[1] in excess of that of their host, thus favoring the flux of resources to the parasite. Although mistletoes derive water and inorganic solutes from their host, they are capable of an independent C supply (5).

Striga hermonthica and *Striga asiatica* (Scrophulariaceae) are parasitic on members of the Gramineae. They are the most serious cause of yield reduction in sorghum in the rainfed semiarid tropics (3). Their low photosynthetic activity compared to autotrophic Scrophulariaceae (12, 19) coupled with the reduction in productivity of host plants (1), suggests a dependence on host photosynthate. In addition, *Striga* has only a vestigial root system, making independent uptake of water and inorganic solutes unlikely.

In comparison with autotrophic Scrophulariaceae, *Striga* has a high Tn and poor stomatal control (19) and may have mechanisms in common with the mistletoes for the withdrawal of host transport fluids.

In this paper we compare the C and H_2O relations of sorghum and *Striga*, and consider: (a) the extent to which *Striga* is reliant on host photosynthate, (b) the effects of parasitism on host C acquisition, (c) the extent to which *Striga* employs a high Tn for the diversion of host water and solutes, and (d) the consequences of an additional water sink on the water status of the host.

MATERIALS AND METHODS

Plant Material and Growth Conditions. Sorghum (*Sorghum bicolor* (L.) Moench cv CSH1) seeds were germinated on moist filter paper, and after 24 h each seed was placed into a 15-cm diameter pot containing 1.6 dm^3 of a 50:50 mixture of John Innes No. 2 compost and sand. The soil was either unamended (control sorghum plants) or inoculated with seeds of either *Striga hermonthica* (Del.) Benth (collected from Abu Naama, Sudan) or *Striga asiatica* (L.) Kuntze (collected from Patancheru, India) at a density of 65 mg dm^{-3}. Each treatment was replicated 11 times.

The plants were grown in a glasshouse under natural light, but with supplementary heating, between June and August. Mean day and night temperatures were 38 and 30°C, respectively.

Experimental Design. Transient foliar gas exchange rates (30–60 s) were measured on all plants 67 and 74 d from sowing. Both species of *Striga* had emerged by d 32. Measurements of gas exchange were made throughout the day (24 h) at regular intervals (see Figs. 1 and 2). For the sorghum plants, the first fully emerged leaf was used, and one measurement was taken per plant. For *S. hermonthica* and *S. asiatica* between 10 and 20 measurements were made on the upper leaves at each sampling interval.

On d 75 each of the three sorghum treatments was divided into three groups, and each was subjected to a different watering regime: normal water supply (soil constantly moist from twice-daily watering), one-third water supply, and no water supply. Measurements of gas exchange and determination of leaf RWC

---

[1] Abbreviations: Tn, transpiration rate; A, rate of CO_2 fixation; A_{max}, rate of CO_2 fixation at saturating PPFD; Ci, concentration of CO_2 in substomatal cavity; Gs, stomatal conductance; PPFD, photosynthetic photon flux density; RWC, relative water content; Wd, rate of dark (night time) respiration; WUE, water use efficiency.

were made on uninfected sorghum, *S. hermonthica*-infected sorghum, *S. asiatica*-infected sorghum, and *S. hermonthica* during the subsequent 48 h period.

Foliar Gas Exchange Measurements. Transient exchange rates of CO_2 and H_2O were measured using a portable infra-red gas analysis system (Analytical Development Company (ADC), Hoddesdon, UK; model LCA2). The CO_2 partial pressure of air entering and leaving the cuvette and the percent relative humidity in the cuvette were recorded on a data logger (ADC, LCA2), together with air temperature and PPFD. These were later used to calculate A, Ci, Gs, and Tn using the equations described by von Caemmerer and Farquhar (22). Boundary layer resistances were determined according to Parkinson (11). Exchange rates were expressed on a leaf area basis. For sorghum, the leaf always filled the cuvette (2.5 cm × 2.5 cm); in the case of *Striga*, individual leaves were tagged, and the area of leaf enclosed within the cuvette was determined at the end of the experiment using a Li-Cor portable area meter (LI-3000). RWC was calculated from determinations of leaf fresh weight, leaf turgid weight, and leaf dry weight (2).

Statistical Analysis. The following function was fitted to the A versus PPFD curves (14):

$$A = \frac{A_{max} \cdot \alpha PPFD}{A_{max} + \alpha PPFD} - Wd (\exp M \cdot PPFD)$$

where A = flux of CO_2; A_{max} = flux of CO_2 at saturating PPFD; α = quantum efficiency of chemical process; PPFD = photosynthetic photon flux density; Wd = rate of dark respiration; M = coefficient relating Wd to PPFD. Parameters were fitted using nonlinear least squares regression.

RESULTS

Sorghum plants infected with both *S. hermonthica* and *S. asiatica* showed reduced Gs, and fluxes of CO_2 into the leaf and H_2O to the atmosphere were lower than in uninfected plants (Fig. 1). The daily (24 h) pattern of CO_2 fixation in *S. hermonthica* and *S. asiatica* (Fig. 2) mirrored those of sorghum, except that the amplitude of the cycle was much reduced. These data were used to construct A versus PPFD curves (Figs. 3 and 4). A_{max} of sorghum infected with either *S. hermonthica* or *S. asiatica* was approximately 30% of that of uninfected control plants (Table I). The characteristic shape of the A versus PPFD curve for C4 plants (demonstrated by uninfected sorghum) is damped
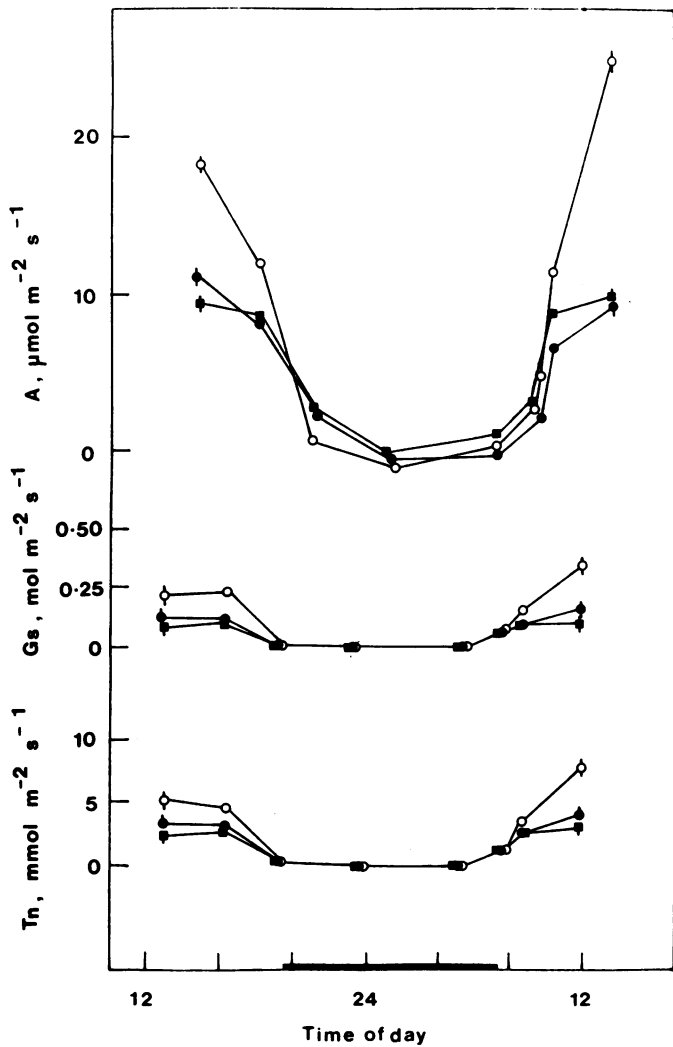

FIG. 1. Daily (24 h) course of A, Gs, and Tn in uninfected sorghum plants (O) and sorghum plants infected with *S. hermonthica* (●) and *S. asiatica* (■), at 74 d from sowing. Similar trends were observed at 67 d. Means and standard errors of 11 measurements are reported (for clarity errors shown on about 12.00 h measurements only). Black bar indicates hours of darkness.
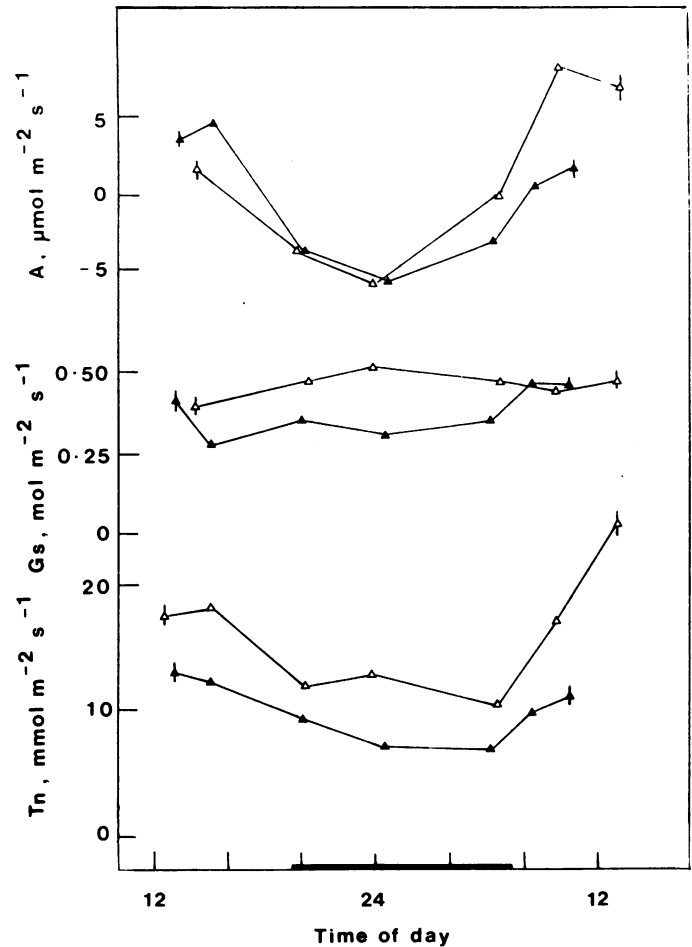
FIG. 2. Daily (24 h) course of A, Gs, and Tn in *S. hermonthica* (▲) and *S. asiatica* (△). Measurements made on 74-d-old sorghum hosts. Similar data were obtained for *S. hermonthica* and *S. asiatica* on 67-d-old host plants. Means and standard errors (10–20 measurements) are reported. Black bar indicates hours of darkness.

Table I. *Values of A_{max}, α, and Wd Characterizing Response of A versus PPFD in Host and Parasite*

Species	Treatment	A_{max}	α	Wd
		$\mu mol\ m^{-2}\ s^{-1}$		$\mu mol\ m^{-2}\ s^{-1}$
Sorghum	Uninfected	29.01	0.07	1.33
	+ *S. hermonthica*	12.13	0.09	1.66
	+ *S. asiatica*	10.90	0.10	1.29
S. hermonthica		6.01	0.76	5.51
S. asiatica		4.56	0.95	6.79

when the plants are supporting *Striga*, and these curves are more typical of plants lacking the C4 mechanism of photosynthesis. A_{max} for both species of *Striga* is about half that of the infected sorghum plants. The *Wd* of *Striga* is of the same order as A_{max}, and this exceeds the *Wd* of sorghum by a factor of four (Table I).

Integration of CO_2 fixation rates measured over 24 h show that *Striga* leaves make little or no net C gain (Table II). Inclusion
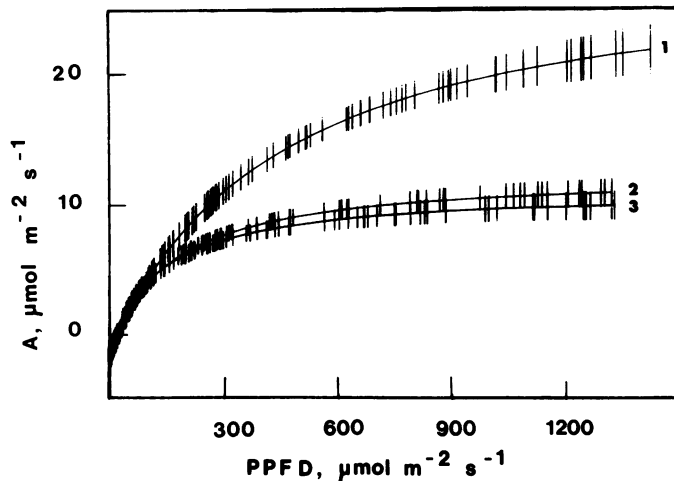

FIG. 3. Response of *A* to PPFD in uninfected sorghum plants (1) and sorghum plants infected with *S. hermonthica* (2) and *S. asiatica* (3). Curves fitted using nonlinear least squares regression (see text). Predicted means and 95% confidence limits for measurements made at both 67 and 74 d are reported.
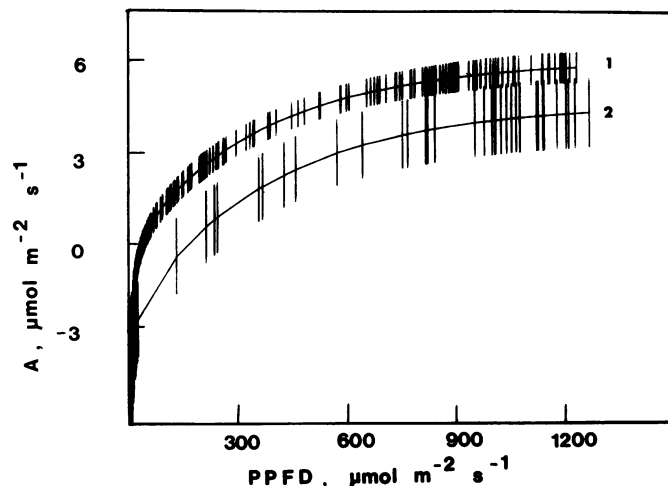

FIG. 4. Response of *A* to PPFD in *S. hermonthica* (1) and *S. asiatica* (2). Details as in legend to Figure 3.

of the stem and below-ground parts in these estimates would result in a more negative C balance, thus suggesting an absolute requirement of host C for growth.

Infected sorghum plants gained approximately 60% of the C per unit leaf area compared to plants grown in the absence of *Striga*. This value is reduced to 30% on a per plant basis (Table II), since infected plants have smaller leaf areas and fewer leaves. This, however, is only a crude estimate, since it does not take into account variation in photosynthetic capacity of the leaves of a sorghum plant. The relationship between Ci and A in sorghum (Fig. 5) suggests that the lower CO_2 fixation rate of *Striga*-infected plants cannot be explained in terms of a lower Gs. The *Striga*-infected and uninfected plants form two distinct subsets in Figure 5.

S. hermonthica and *S. asiatica* have Tn values which greatly exceed those of their host (Table III), and show little response to darkness (Fig. 2), maintaining a large and constant flux of H_2O to the atmosphere. Droughting, by withholding water, also had a relatively small effect on Gs in *S. hermonthica* (Fig. 6). In sorghum, at a RWC of between 85 and 90%, transpiration had virtually ceased. However, at this RWC in *S. hermonthica* Tn was in excess of 0.5 mmol $m^{-2}s^{-1}$, and complete stomatal closure was not achieved until the leaves had reached approximately 70% RWC. A closer examination of these data (Fig. 7) reveals that withholding water from uninfected sorghum did not result in any reduction in Tn, and only those plants supporting *Striga* demonstrated a response to the application of water stress.

The WUE of sorghum exceeds that of *S. hermonthica* and *S. asiatica* by an order of magnitude (Table III). The WUE of *S. hermonthica*-infected sorghum is significantly less than that of the uninfected plants (P < 0.001), although this is not the case for *S. asiatica*-infected plants. Our measurements for uninfected sorghum show that during stomatal closure the rate of H_2O loss is reduced more than that of C gain, leading to an increase in WUE (data not presented). This has been observed elsewhere for sorghum during moderate water stress (15). Our relationship between Tn and WUE was used to predict WUE in *Striga*-infected plants from their Tn (Table III). In both *S. hermonthica*-infected and *S. asiatica*-infected sorghum, predicted values of WUE were significantly greater (P < 0.001) than both the respective measured WUE and the WUE of control plants. Thus, the predicted rise in WUE is offset by a disproportionately large reduction in the rate of CO_2 fixation.

Table II. *Daily (24 h) C Balance in Sorghum and Striga*
The data are calculated over two periods of daily measurements.

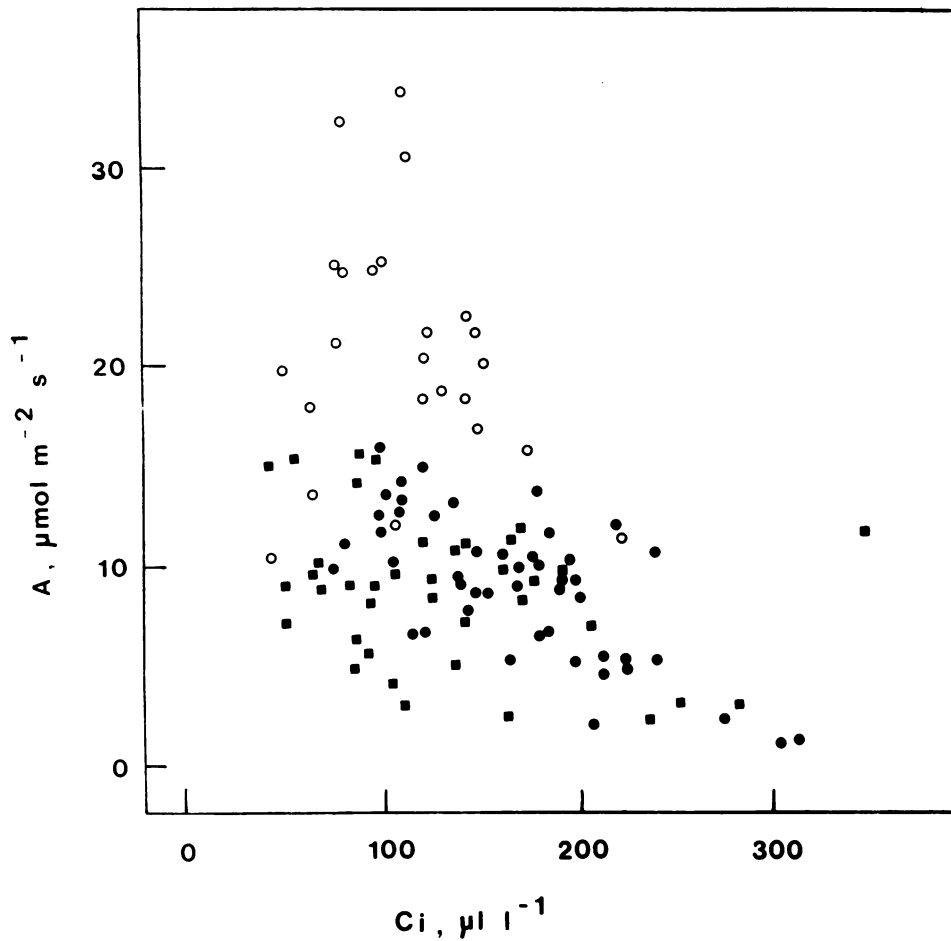| Species	Treatment	C Balance	
		$g\ m^{-2}\ d^{-1}$	$g\ plant^{-1}\ d^{-1}$
Sorghum	Uninfected	5.20	4.45
	+ *S. hermonthica*	3.21	1.27
	+ *S. asiatica*	3.32	1.64
S. hermonthica		0.01	
S. asiatica		−0.31	

FIG. 5. Relationship between A and Ci in uninfected sorghum plants (O) and plants infected with *S. hermonthica* (●) and *S. asiatica* (■). Data are for measurements made where A is relatively unresponsive to PPFD (see Fig. 3): > 900 μmol m^{-2} s^{-1} for (O); > 300 μmol m^{-2} s^{-1} for (●) and (■).
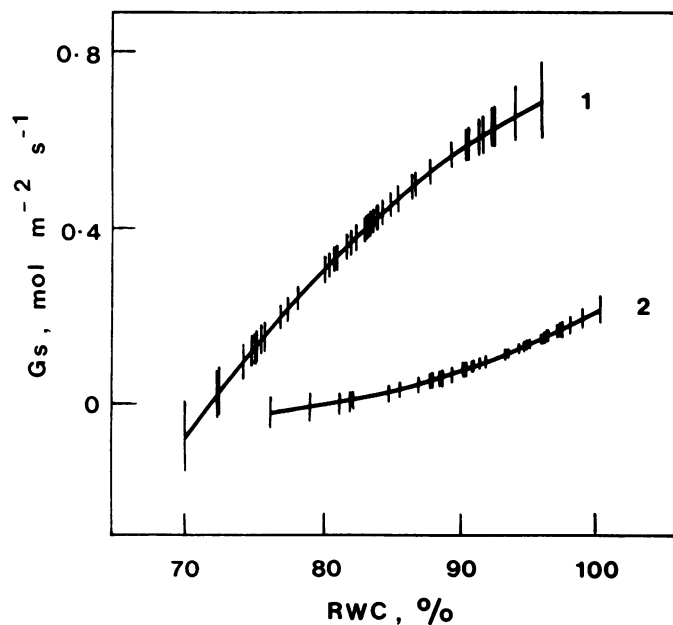

FIG. 6. Relationship between RWC and Gs in *S. hermonthica* (1) and sorghum (all treatments) (2). Points are predicted means, with 95% confidence limits, fitted using second order polynomial functions. Sorghum plants, 75 to 77 d old at time of measurement, had been subjected to different watering regimens in order to induce drought stress.
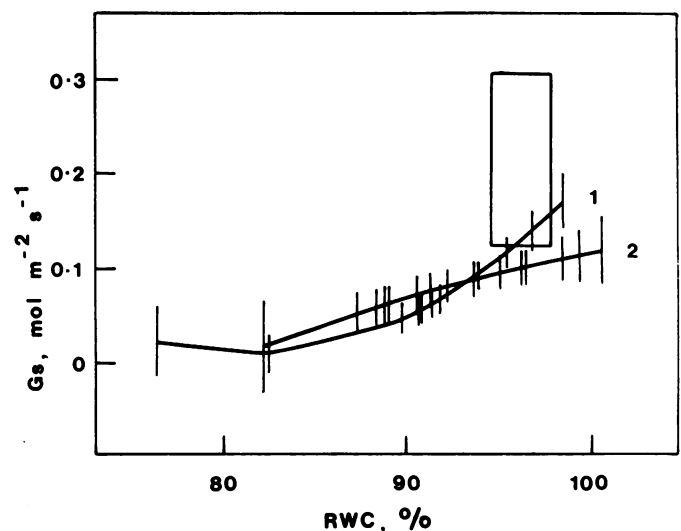

FIG. 7. Relationship between RWC and Gs in sorghum. Curves fitted as in Figure 6. (1) = *S. hermonthica*-infected plants; (2) = *S. asiatica*-infected plants; rectangle = area occupied by predicted means from uninfected plants.

DISCUSSION

Gas exchange between plant leaves and the atmosphere is usually tightly controlled. However, this maxim does not apply to the parasitic angiosperms *S. hermonthica* and *S. asiatica*. The

Table III. *Tn, Measured and Predicted WUE in Host and Parasite, for PPFD > 300 μmol m^{-2} s^{-1}*

Predicted WUE for *Striga*-infected sorghum plants are calculated from *Tn*, using the relationship between Tn and WUE from uninfected plants. Means of n measurements and 95% confidence limits are reported. (Although measurements at PPFD > 300 μmol m^{-2} s^{-1} were not all at saturated-light photosynthesis for uninfected plants (Fig. 3), WUE at PPFD > 900 μmol m^{-2} s^{-1} did not differ statistically from that reported here.)

Species	Treatment	n	Mean Tn	Mean Measured WUE	Mean Predicted WUE
			mmol m^{-2} s^{-1}	*mmol CO$_2$ mol^{-1} H$_2$O*	
Sorghum	Uninfected	51	5.4 (4.8–6.1)	3.38 (3.17–3.58)	3.38 (3.17–3.58)
	+ S. hermonthica	46	3.6 (3.2–4.0)	2.62 (2.34–2.90)	3.74 (3.67–3.81)
	+ S. asiatica	44	2.7 (2.4–3.0)	3.16 (2.79–3.54)	3.90 (3.85–3.95)
S. hermonthica		86	13.2 (12.4–14.0)	0.44 (0.39–0.49)	
S. asiatica		34	21.6 (19.3–24.0)	0.20 (0.13–0.28)	

Gs of both *Striga* spp. exceeded that of the host, and the ratio of host to parasite *Gs* was greater than that commonly observed in mistletoe associations (21). Mistletoes do not share the lack of stomatal response to PPFD of *Striga*, observed here during daily (24 h) measurements (17, 21). In the sorghum-*Striga* association, a large and continuous flux of H$_2$O from the parasite leaf may be necessary to maintain diversion of host transport fluids given the difference in evaporative surface areas of the two plants. Although this ratio can vary widely, our measurements show that it is often in the order of 50 to 1 in favor of sorghum in adult plants. The high *Gs* in *Striga* will also have a large cooling effect on the leaf, and this will play an important role in the plant's energy budget.

Although high *Tn* values have been generally associated with parasitism (9), only the mistletoes have until now received close attention. A high *Tn* is certainly not a universal feature of parasitic angiosperms, since low rates have been calculated for the achlorophyllous plants *Cuscuta* and *Orobanche* (13). In the latter, as in *Odontities* (6), guttation and the excretion of solutes via leaf glands may play a similar role to a high *Tn* in the abstraction of host water and solutes.

Despite the capacity of *Striga* for independent C fixation, rates of *Wd* lead to a negligible net C gain over 24 h. Thus, the parasite is largely reliant on the host for supply of photosynthate. The low rates of net C fixation in *Striga* may result from losses concealed by high rates of light respiration and photorespiration. However, measurements of the latter (N. Shah, personal communication) suggest that the ratio of photorespiration to photosynthesis in *S. hermonthica* is within the range typically found in barley. A more likely explanation of the reduced ability of *Striga* to fix CO$_2$ results from structural and biochemical modifications in the leaf. Although the ultrastructure of *S. hermonthica* chloroplasts is normal, the leaves have a poorly differentiated paliside layer and there are relatively low numbers of chloroplasts per cell (20). There is also evidence to suggest lower concentrations of Chl and lower activities of ribulose bis phosphate carboxylase-oxygenase in *Striga* compared to autotrophic Scrophulariaceae (12). The abundance of mitochondria in haustoria of *Striga* spp. (JM Tuohy, unpublished data) suggest that respiration from below-ground parts of the plant could exacerbate C losses.

Infection of sorghum by both *Striga* spp. results in a large reduction in the host's capacity to fix CO$_2$. *Striga* also predisposes the host to water stress, arising from the parasite's high *Tn*. Consequent reductions in the *Gs* of infected sorghum plants are not adequate to account for reductions in the CO$_2$ fixation rate. Our data (Fig. 5, Table III) suggest that *Striga* has a specific effect on the processes affecting C acquisition in the leaves of infected plants. Together with losses of water and solutes from sorghum to the parasite (10, 16), this reduction in CO$_2$ fixation rate may account for the dramatic effect that *Striga* has on sorghum growth (1, 3). In this experiment *S. hermonthica* and *S. asiatica* reduced shoot yields of sorghum by 86 and 77%, respectively.

Mistletoes have also been reported to reduce the photosynthetic capacity of their host, although to a lesser extent than reported here for *Striga* (4). The reduced value of A_{max} reported in *Juniperus osteosperma* infected with the mistletoe *Phoradendron juniperinum* can be accounted for in terms of a reduced *Gs* (4); mistletoe infection had little effect on the relationship between *Ci* and *A*. In addition, mistletoe infection tended to increase WUE in *J. osteosperma*. These data suggest that, in contrast to *Striga*, *P. juniperinum* does not have an effect on C acquisition processes in *J. osteosperma*, the host.

In this paper we demonstrate that *S. hermonthica* and *S. asiatica* reduce photosynthetic capacity in sorghum and in addition predispose the plant to water stress. These modifications, together with loss of resources to the parasite may be responsible for the large effect *Striga* has on the productivity of sorghum. Both *Striga* spp. have low rates of CO$_2$ fixation and high *Tn*. The lack of coupling of *Gs* to environmental conditions seen in *Striga*, together with low values of WUE, appear inconsistent with a water conserving strategy often employed for growth during the dry season in the semiarid tropics. As such they are more likely to reflect an adaptation to the parasitic lifestyle. In comparison with another group of parasitic angiosperms, the mistletoes, *Striga* appears to demonstrate a more extreme form of parasitism, both in terms of its reliance on the host for resources and with regard to its effects on host plant growth and physiology.

LITERATURE CITED

1. AYENSU ES, H DOGGETT, RD KEYNES, J MARTON-LEFEVRE, LJ MUSSELMAN, C PARKER, A PICKERING 1984 *Striga* Biology and Control. ICSU/IDRC, Paris
2. BEADLE CL, MM LUDLOW, JL HONEYSET 1985 Water Relations. *In* J Coombs, DO Hall, SP Long, JMO Scurlock, eds, Techniques in Bioproductivity and Photosynthesis, Ed 2. Pergamon Press, Oxford, pp 50–61
3. DOGGETT H 1982 Factors reducing sorghum yields-Striga and birds. *In* Sorghum in the Eighties, Vol 1. ICRISAT, Patancheru, India, pp 313–320
4. EHLERINGER JR, CS COOK, IL TIESZEN 1986 Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68: 279–284
5. EHLERINGER JR, E-D SCHULZE, H ZIEGLER, OL LANGE, GD FARQUHAR, IR COWAN 1985 Xylem-tapping mistletoes: water or nutrient parasites? Science 227: 1479–1481
6. GOVIER RN, JGS BROWN, JS PATE 1968 Hemiparasitic nutrition in angiosperms. II. Root haustoria and leaf glands of *Odontities verna* (Bell.) Dum and their relevance to abstraction of solutes from the host. New Phytol 67: 963–972
7. HULL RJ, OA LEONARD 1964 Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*) I. The carbohydrate nutrition of mistletoe. Plant Physiol 39: 996–1007
8. HULL RJ, OA LEONARD 1964 Physiological aspects of parasitism in mistletoes (*Arceuthobium* and *Phoradendron*). II. The photosynthetic capacity of mistletoe. Plant Physiol 39: 1008–1017
9. MUSSLEMAN LJ 1980 The biology of *Striga*, *Orobanche* and other root-parasitic weeds. Annu Rev Phytopathol 18: 463–489

10. OKONKWO SNC 1966 Studies on *Striga senegalensis*. II. Translocation of C^{14}-labeled photosynthate, urea-C^{14} and sulphur-35 between host and parasite. Am J Bot 53: 142–148

11. PARKINSON KJ 1985 A simple method for determining the boundary layer resistance in leaf cuvettes. Plant Cell Environ 8: 223–226

12. PRESS MC, N SHAH, GR STEWART 1986 The parasitic habit: trends in metabolic reductionism. *In* SJ ter Borg, ed, Biology and Control of *Orobanche*. LH/VPO Wageningen, The Netherlands, pp 96–106

13. RAVEN JA 1983 Phytophages of xylem and phloem: A comparison of animal and plant sap-feeders. Adv Ecol Res 13: 135–234

14. REED KL, ER HAMERLY, BE DINGER, PG JARVIS 1976. An analytical model for field photosynthesis. J Appl Ecol 13: 925–942

15. RICHARDSON SG, KJ MCCREE 1985 Carbon balance and water relations of sorghum exposed to salt and water stress. Plant Physiol 79: 1015–1020

16. ROGERS WE, RR NELSON 1962 Penetration and nutrition of *Striga asiatica*. Phytopathology 52: 1064–1070

17. SCHULZE E-D, JR EHLERINGER 1984 The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. Planta 162: 268–275

18. SCHULZE E-D, NC TURNER, G GLATZEL 1984 Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant Cell Environ 7: 293–299

19. SHAH N, N SMIRNOFF, GR STEWART 1987 Photosynthesis and stomatal characteristics of *Striga hermonthica* in relation to its parasitic habit. Physiol Plant 69: 699–703

20. TUOHY JM, EA SMITH, GR STEWART 1986 The parasitic habit: Trends in morphological and ultrastructural reductionism. In SJ ter Borg, ed, Biology and Control of *Orobanche*, LH/VPO. Wageningen, The Netherlands, pp 86–95

21. ULLMANN I, OL LANGE, H ZIEGLER, JR EHLERINGER, E-D SCHULZE, IR COWAN 1985 Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in central Australia. Oecologia 67: 577–587

22. VON CAEMMERER S, GD FARQUHAR 1981 Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153: 376–387