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BRIEF COMMUNICATION

Gas exchange of root hemi-parasite *Striga hermonthica* and its host *Sorghum bicolor* under short-term soil water stress

T. INOUE[1]*, Y. YAMAUCHI[2], A.H. ELTAYEB[3], H. SAMEJIMA[2], A.G.T. BABIKER[3], and Y. SUGIMOTO[2]

Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan[1]
Graduate School of Agricultural Science, Kobe University, Rokkodai, Nada, Kobe 657-8501, Japan[2]
College of Agricultural Studies, Sudan University of Science and Technology, Shambat, Khartoum, North Sudan[3]

Abstract

The gas exchange of the upper fully expanded leaf of the root parasite *Striga hermonthica* and of its host *Sorghum bicolor* was measured under wet and dry conditions to identify the mechanisms of the devastating effects of the parasite on its hosts under drought. The short-term water stress severely reduced photosynthetic rate in infected sorghum, but less in *S. hermonthica*. Soil water stress did not affect leaf respiration rate in either *S. hermonthica* or infected sorghum. This suggests that under dry conditions both infected sorghum and *S. hermonthica* decreased autotrophic carbon gain. The transpiration rate of *S. hermonthica*, a major driving force for assimilate uptake from the host, was higher and less affected by water stress than that of infected sorghum. Stomatal density on the abaxial surfaces of the leaves was higher in *S. hermonthica* than in sorghum. Both *S. hermonthica* infection and water stress decreased stomatal conductance of the sorghum leaves. *S. hermonthica,* irrespective of soil water status, had greater stomatal aperture on the adaxial and abaxial surfaces of its leaves than infected sorghum. These results indicate that the higher transpiration rate of *S. hermonthica* even under water stress, achieved through higher stomatal density on the abaxial surfaces of the leaves and greater stomatal aperture on both surfaces of the leaves, may induce the maintenance of water and solute transfers from the host to the parasite leading to severe damage to the host under drought.

Additional key words: drought, host-parasite interaction, net photosynthetic rate, relative water content, respiration rate, stomatal conductance, transpiration rate.

Striga hermonthica is an obligate root hemi-parasitic angiosperm and a major biotic constraint on cereal production in Sub-Saharan Africa (Parker 2009). *Striga* infection in crops causes devastating losses in yield (Parker 2009) and the damage is more serious under drought conditions (Ejeta *et al.* 1993). *Striga* species rely upon their hosts for most of their mineral nutrients, saccharides, and water supply (Rich and Ejeta 2007). In *S. hermonthica* infecting sorghum, approximately 35 to 43 % of the parasite carbon is derived from the sorghum (Graves *et al*. 1989). Although photosynthesis and transpiration in *S. hermonthica* and in an infected host under well watered conditions were extensively studied by Press and co-workers in the 1980s and 1990s, the effects of soil drying on leaf water status and stomatal response in *Striga* and its host plants remain to be clarified.

Most parasitic plants, including *Striga*, have very high transpiration rate which helps to maintain a gradient in leaf water potential towards the parasite and thus facilitate the flux of water and solutes to the parasite (Stewart and Press 1990). Press *et al*. (1987) reported that the transpiration rate of *S. hermonthica* is higher than that of its sorghum host throughout the whole day.

S. hermonthica infection reduces both the photosynthetic rate (P_N) and transpiration rate (E) of the sorghum host (Frost *et al*. 1997). The reduction in host P_N

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Abbreviations: c_i - intercellular CO_2 concentration; DAS - days after sowing; E - transpiration rate; F_v/F_m - variable to maximum chlorophyll fluorescence (maximal quantum yield of PS II); g_s - stomatal conductance; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; PS II - photosystem II; R_s - respiration rate; RWC - relative water content.
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* Corresponding author; fax: (+81) 857 296199, e-mail: sapana@alrc.tottori-u.ac.jp

by *S. hermonthica* infection results mainly due to stomatal limitation (Frost *et al*. 1997). However, a recent report has indicated that photosynthetic metabolism and photosystem II (PS II) photochemistry of the host plants are also negatively affected by the parasite (Rodenburg *et al*. 2008).

Growing conditions including soil fertility, rainfall, and irrigation affect the growth of *Striga* and the severity of the damage inflicted by *Striga* upon a crop. However, to our knowledge, there are only three reports on the effects of water stress on host plant response to *Striga* (Andrews 1945, Ogborn 1972, Ejeta *et al.* 1993). Ducarme and Wesselingh (2010) reported that the responses of growth and seed production to water stress differed between root hemi-parasites *Rhinanthus minor* and *R. angustiflolius*. Alleviation of the severe damage caused by *Striga* infection under water stress through improved agronomic practices and/or genetic improvements necessitates proper understanding of the mechanisms mediating the assimilation and distribution of assimilates in host-*Striga* association under different water regimes. Thus, in the present study, the photosynthetic capacity and stomatal response of sorghum and *S. hermonthica* were investigated under wet and dry conditions.

A pot experiments were conducted at the experimental farm of the College of Agricultural Studies, Sudan University of Science and Technology, Khartoum, Sudan, from 23 June to 26 August 2010. A soil mix (clay soil collected from the farm of the College of Agricultural Studies and river sand, 2:1, m/m) was used as a potting medium. In the first pot set, 12 kg of the soil mix was placed in each pot. In the second set, 12 kg of potting medium previously mixed with 10 mg of *Striga hermonthica* (Del.) Benth. seeds was placed in each pot. Urea (0.476 g) was added to the soil in each pot. Six seeds of *Sorghum bicolor* (L.) Moench cv. Dabar, which is highly susceptible to *Striga,* were sown in each pot. Seedlings were thinned to 2 plants per pot at around the four leaf stage. Soil water content at field capacity, as determined in a preliminary experiment, was 30 % (m/m). Initially, the soil water content in each pot was brought to 18 %. When the soil water content eventually dropped to 9 %, loss in water content was replenished by bringing pots back to their initial mass until 17 d after sowing (DAS). Similarly, soil water content was kept between 15 and 24 % from 17 to 58 DAS, and between 18 and 27 % from 58 to 64 DAS. Seedlings of *S. hermonthica* started to emerge at 47 DAS. At 62 DAS, when 2 - 3 seedlings of *S. hermonthica* per pot had emerged and reached the 5 to 10 leaf stage, the pots were divided into two sets. In one set, soil water content was maintained between 18 and 27 %. In the other set, water stress was imposed and soil water content was kept between 12 and 21 %.

Gas exchange, stomatal conductance, chlorophyll fluorescence, and leaf water status were measured on the upper fully expanded leaves of *S. hermonthica* and sorghum from 10:00 to 14:00 h at 63 and 64 DAS. In order to ensure similar soil water stress, pots with similar mass were used for measurements in each water regime (soil water content of 22.5 ± 1.1 and 14.6 ± 0.2 %, respectively). A portable infrared gas analyser (*LCpro+*, *ADC BioScientific*, Great Amwell, UK) was used to measure P_N and intercellular CO_2 concentration (c_i). Gas exchange measurements were recorded when steady state was achieved at photosynthetic photon flux density (PPFD) of 1600 µmol m^{-2} s^{-1}, similar to field conditions. Dark respiration rate (R_s) was determined after a 10-min dark period following the photosynthetic rate measurements. The maximal quantum yield of PS II (variable to maximum chlorophyll fluorescence ratio, F_v/F_m) was measured with a portable pulse amplitude modulated fluorometer fitted with a *2030-B* leaf clip holder (*MINI-PAM*, *Heinz Walz*, Effeltrich, Germany). Stomatal conductance (g_s) and E on the adaxial and abaxial surfaces of the leaves were measured with a transit-time porometer (*AP4*, *Delta-T Devices*, Cambridge, UK). Stomatal replicas of the adaxial and abaxial surfaces of the leaves were made using the stomatal impression method as described by Mehri *et al*. (2009). The stomatal replicas were photographed under an optical microscope (*BX51*, *Olympus*, Tokyo, Japan). The number of stomata in each photograph was counted and converted into stomatal density. The stomatal aperture on those photographs was measured with *ImageJ* software (*v. 1.40g*, National Institutes of Health, Bethesda, MD, USA). Relative water content (RWC) of the leaves was determined as described by Nagasuga *et al*. (2011). Three replications were taken for each treatment. The means were compared by the least significant difference (LSD) test at $\alpha = 0.05$. A two-factorial analysis of variance (*ANOVA*) was also performed to study the effects of plant, water stress, and their interactions.

Leaf RWC of *S. hermonthica* was invariably lower than that of uninfected and infected sorghum under both wet and dry conditions (Table 1). Soil water stress decreased leaf RWC in both uninfected sorghum and *S. hermonthica*, but did not affect significantly leaf RWC in infected sorghum.

For a given moisture treatment, there was no difference in P_N in the leaves between uninfected and infected sorghum (Table 1). Under wet conditions, P_N in the leaves of both uninfected and infected sorghum was 3.5-times higher than that in *S. hermonthica*. Water stress, irrespective of *S. hermonthica* infection, decreased P_N of sorghum leaves about 6-times. Mean P_N in the leaves of *S. hermonthica* was also reduced (1.5-times) by soil water stress but the reduction was statistically non-significant. Water stress did not decrease R_s of sorghum leaves, irrespective of *S. hermonthica* infection, or that of *S. hermonthica* leaves (Table 1). *S. hermonthica* infection did not affect the R_s of sorghum leaves in either wet or dry treatments. The c_i in leaves was higher in *S. hermonthica*, a C_3 plant, than in sorghum, a C_4 plant (Table 1). Soil water stress increased c_i in infected sorghum, but decreased it in *S. hermonthica*.

F_v/F_m was higher in *S. hermonthica* than in uninfected or infected sorghum (Table 1). Water stress decreased F_v/F_m in uninfected sorghum, but did not affect F_v/F_m in *S. hermonthica* or infected sorghum.

Table 1. Relative water content (RWC) [%], net photosynthetic rate (P_N) [μmol m^{-2} s^{-1}], respiration rate (R_s) [μmol m^{-2} s^{-1}], intercellular CO_2 concentration (c_i) [μmol mol^{-1}], maximal quantum yield of photosystem II (F_v/F_m), transpiration rate (E) [mmol m^{-2} s^{-1}], stomatal conductance (g_s) [mol m^{-2} s^{-1}], stomatal density [mm^{-2}], and stomatal aperture [μm^2] on adaxial and abaxial leaf surfaces of uninfected sorghum, *Striga hermonthica*-infected sorghum, and *Striga hermonthica* under wet and dry conditions. The same letters within a column means no significant differences at 95 % probability level; *, **, and *** indicate significance of differences at the $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively; ns - not significant.

Plant	Treat.	RWC	P_N	R_s	c_i	F_v/F_m	E		g_s		Density		Aperture	
							adax	abax	adax	abax	adax	abax	adax	abax
Uninfected	wet	93.7a	28.3a	2.2a	30.0d	0.61b	1.9c	9.6b	0.08cd	0.37b	119a	137b	98.6ab	100.7b
sorghum	dry	87.2b	4.5c	2.4a	60.7cd	0.56c	0.9cd	1.7c	0.04de	0.06c	120a	139b	60.8cd	63.0d
Infected	wet	95.3a	27.5a	2.3a	31.0d	0.57c	3.1b	11.2b	0.11bc	0.39b	118a	137b	79.9bc	79.1c
sorghum	dry	91.4ab	4.7c	2.4a	82.0c	0.59bc	0.4d	1.9c	0.01e	0.05c	114a	139b	53.0d	54.2e
Striga	wet	87.8b	8.0b	1.7a	246.0a	0.69a	7.1a	24.9a	0.29a	0.97a	109a	192a	112.3a	118.5a
hermonthica	dry	72.0c	5.2bc	1.6a	190.3b	0.67a	3.7b	5.6bc	0.14b	0.20b	110a	191a	90.7b	77.5c
Plant		***	***	ns	***	***	***	**	***	***	ns	**	***	***
Treatment		***	***	ns	ns	ns	***	***	***	***	ns	ns	***	***
P × T		*	***	ns	*	ns	*	ns	*	*	ns	ns	ns	*

The E, irrespective of leaf side and soil water status, was invariably higher in *S. hermonthica* than in uninfected or infected sorghum (Table 1). Water stress decreased E on both the adaxial and abaxial surfaces of leaves in sorghum and *S. hermonthica* but this reduction on the adaxial surface of leaves was most severe in infected sorghum. The g_s in sorghum and *S. hermonthica* mostly corresponded to E. The reduction in g_s under dry conditions was more severe in infected sorghum than in *S. hermonthica* on both surfaces of the leaves (Table 1).

Sorghum and *S. hermonthica* leaves displayed approximately equal stomatal densities on their adaxial surfaces (Table 1). On the abaxial surfaces, however, stomatal density was higher in *S. hermonthica* than in sorghum. *S. hermonthica* infection did not affect the stomatal density on either surface of sorghum leaves. As expected, short-term water stress had no effect on stomatal density in either sorghum or *S. hermonthica.* Stomatal aperture, irrespective of leaf side, was greater in *S. hermonthica* than in infected sorghum (Table 1). Water stress decreased stomatal aperture on both the adaxial and abaxial surfaces of leaves in sorghum and *S. hermonthica*. *S. hermonthica* infection, irrespective of soil water status, decreased stomatal aperture on the abaxial surfaces of sorghum leaves.

In the present study, under dry conditions, the P_N of sorghum decreased, and was of the same order of magnitude as its R_s (Table 1). Infection by *S. hermonthica* did not affect the P_N of sorghum under wet or dry conditions. Conflicting results were found in the holoparasite *Cuscuta campestris*-*Mikania micrantha* association, where the decline in P_N of host was apparent already on day 5 after parasitization (Chen *et al.* 2011). Because the measurements in the present study were undertaken when *S. hermonthica* had just emerged above the soil surface, it is expected that the effect of infection on host P_N was not pronounced at the early stages of parasitism in *S. hermonthica* as reported by Frost *et al.* (1997). In contrast to the P_N, water stress-induced reductions in E and g_s were greater in infected sorghum than in uninfected control plants, although the reduction in leaf RWC under dry conditions was more severe in uninfected sorghum than in infected sorghum (Table 1). Taylor and Seel (1998) reported no difference in leaf RWC in maize infected and uninfected with *S. hermonthica* even though g_s was lower in infected than in uninfected plants. The present results corroborate those reported by Taylor and Seel (1998) and support their suggestion that the change in g_s of the host plants under dry conditions was not a response to dehydration of the leaf tissues.

The c_i in uninfected sorghum (Table 1) was lower than that observed by Yan *et al*. (2012). In addition to low soil moisture, high temperature (Zhu *et al*. 2011) and low air humidity (Ohsumi *et al*. 2008) also affect c_i. In this study, photosynthesis measurements were conducted at temperature of 33 - 40 °C and relative humidity of 35 - 40 %. Thus, it seems likely that high temperature and low humidity induced low c_i in uninfected sorghum even under wet conditions.

Most of the previous research on host-*Striga* association has been focused on the host response rather than the physiological characteristics of *Striga*. The present study showed that P_N of *S. hermonthica* was as low as those previously reported (Press *et al*. 1987, Shah *et al*. 1987, Cechin and Press 1993). Water stress did not significantly decreased P_N of *S. hermonthica* (Table 1). The g_s might play an important role in high P_N under mild to moderate water stress but high P_N under severe water stress are related more to the maintenance of photochemical and/or biochemical reactions in the chloroplast (Flexas and Medrano 2002, Lawlor 2002, Ghannoum 2009). Increased c_i accompanied by decreased g_s implies losses in chloroplast activity resulting from altered chloroplast metabolism and consequently a decrease in demand for CO_2 (Graan and Boyer 1990). In the present study, reductions in g_s and P_N decreased c_i in

S. hermonthica but increased it in sorghum (Table 1). Additionally, the F_v/F_m of *S. hermonthica* was higher than that of sorghum under both wet and dry conditions (Table 1). The responses of g_s, c_i, and F_v/F_m to water stress (Table 1) suggest that photochemical and biochemical activity in *S. hermonthica* is less sensitive to water stress than that in sorghum. However, the increased ratio of R_s to P_N in the leaves of *S. hermonthica* under dry conditions (Table 1) may result in negative autotrophic carbon gain.

Water stress increased the ratio in E between *S. hermonthica* and sorghum: under dry conditions, *S. hermonthica* had E around 4 times higher than that of infected sorghum (Table 1). Transpiration is largely controlled by stomata (Kramer and Boyer 1995). Press *et al*. (1987) reported that g_s was higher in *S. hermonthica* than in infected or uninfected sorghum under conditions of both high and low leaf RWC. Yet, leaf RWC was lower in *S. hermonthica* than in sorghum and the reduction in RWC under dry conditions was even greater in *S. hermonthica* than in sorghum (Table 1). It has been reported that abscisic acid concentration in leaf tissue of *S. hermonthica* is an order of magnitude higher than that in infected maize (Taylor *et al*. 1996). Furthermore, g_s in *S. hermonthica* showed little response to exogenously applied abscisic acid (Shah *et al*. 1987). Jiang *et al*. (2003) also reported that the facultative root hemiparasite *Rhinanthus minor* attached to *Hordeum vulgare* showed higher g_s than its host despite extremely high abscisic acid content in the leaves. Thus, it seems likely that the insensitivity of g_s to leaf dehydration and abscisic acid ensures a higher E in *S. hermonthica*.

Stomatal density on the abaxial surfaces of *S. hermonthica* leaves was about 1.3 times higher than that of sorghum leaves (Table 1). Stomatal aperture on the adaxial and abaxial surfaces of the leaves of *S. hermonthica* was higher than that of sorghum which was decreased to 46 % by both *S. hermonthica* infection and water stress (Table 1). As a consequence, *S. hermonthica* maintained higher stomatal aperture on both the adaxial and abaxial surfaces of its leaves under both wet and dry conditions than infected sorghum did. Smith and Stewart (1990) observed similar results in uninfected sorghum and *S. hermonthica*, although they monitored stomatal aperture and RWC of detached leaves.

In conclusion, the high E of *S. hermonthica* under dry conditions, sustained through high stomatal density on abaxial surfaces and high stomatal apertures on both the adaxial and abaxial surfaces of the leaves, may account for the maintenance of water and solute transfers from host sorghum. The maintained host carbon uptake by *S. hermonthica* in addition to the decreased net carbon gain by sorghum under dry conditions may explain the particularly devastating effects of the parasite on its host during drought.

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