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Variability and Host Specificity of *Striga hermonthica* (Del.) Benth. in Response to in-situ Root Exudates of *Sorghum bicolor* (L.) Moench

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ABSTRACT

Striga hermonthica (Del.) Benth., Orobanchaceae, is an obligate root parasite on important cereal crops. The aim of this study is to investigate variability and host specificity in the early developmental stages of *S. hermonthica* parasitism in response to *in-situ* root exudates of sorghum. Field surveys were conducted during the seasons 2013/14 in *Striga* endemic areas in Sudan to collect seeds from the parasite. Fifteen *S. hermonthica* populations were collected. An *in vivo* experiment was conducted at the University of Gezira, Sudan to study the effects of *in-situ* root exudates of three sorghum cultivars on percentage of seed germination, haustorium initiation, attachment and penetration. Treatments were arranged in a factorial completely randomized design with three replicates. Data were subjected to the analysis of variance ($P \leq 0.5$). The results revealed the highest percentage of seed germination (46.9-57.5 %), haustorium initiation (73.8-77.9 %), attachment (38.4–40 %) and penetration (20.7–23.7 %) into sorghum root was induced by *in-situ* root exudates of sorghum cv. Abu-70 and by sorghum cv. Wad Ahmed. While, the lowest percentage of seed germination (53.5 %), haustorium initiation (45.2 %), attachment (5.8 %) and penetration (1.5 %) into sorghum root was induced by *in-situ* root exudates of Hakika. The results also revealed that percentage of seed germination, haustorium initiation, attachment and penetration of *S. hermonthica* populations collected from infected sorghum in response to sorghum *in-situ* root exudates was the highest. While, the percentage of seed germination, haustorium initiation, attachment and penetration of *S. hermonthica* populations collected from infected millet in response to sorghum *in-situ* root exudates was the lowest. This study confirms the existence of two levels of physiological specialization in *S. hermonthica* populations in Sudan. Moreover, two strains of *S. hermonthica* are one specific to sorghum and the other to millet.

Introduction

Striga hermonthica (Del.) Benth., belongs to the family Orobanchaceae, is a noxious, hemi-parasitic weed infecting for several cereal crops in semi-arid, sub-Saharan Africa, Middle East and

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Asia, and is responsible for food shortage and poverty of millions of Africans (Parker, 2012). The main cereal crops parasitized by *S. hermonthica* are sorghum [*Sorghum bicolor* (L.) Moench], millet [*Pennisetum glaucum* (L.) R. Br.), maize [*Zea mays* L.], rice [*Oryza sativa* L.] and sugarcane [*Saccharum officinarum* L.] (Runo and Kuria, 2018). The area infested by *Striga* in sub-Saharan Africa has been estimated to be over 50 million ha of the arable farmland under cereals. Losses in grain yield due to *Striga* infestation vary from 5 to 90 %, according to the host species, the variety grown, climatic conditions, infestation level and nature of the soil. The overall loss in grain production amounts to 4.1 million tons (Gwary et al. 2001; Showemimo, 2006). The annual yield loss has been estimated to exceed US$10 billion (Pennisi, 2015). Farmers have reported losses between 20 and 80%, and are eventually forced to abandon highly infested fields. Moreover, the *Striga* epidemic is going to increase and the parasite is likely going to become a more serious threat to crop production. The parasite also causes indirect losses comprising changes in production strategies, land abandonment and in extreme cases human migrations in response to heavy infestations (Atera and Itoh, 2011; Ronald et al. 2017).

Several *Striga* control methods, including cultural, physical, biological, chemical, host plant resistance and genetically modified crops have been developed. However, the huge seed production, prolonged viability of the seeds, breeding behavior that maintains enormous genetic variability, ability to parasitize a broad host range and the subterranean nature of the early stages of parasitism make control of the parasite by a single method difficult if not impossible (Dawud, 2017; Garba et al. 2017). Resistant varieties have long been proposed as a means of reducing losses due to *Striga* under the low-cost input subsistence farming in Africa. The host/ parasite relationship is governed by a series of steps involving stimulation of germination, haustorium initiation, penetration of the host root, connection to the host xylem and the concurrent growth (Ali et al. 2009). In theory the host could develop resistance to the parasite at any or all of these steps. Development of resistant cultivars has been hindered by the paucity of resistance genes in crop germplasm, specificity of resistance and the existence of morphotypes, physiological strains, ecological variants and races of the parasite. High genetic variability has been observed among different species and ecotypes, i.e. genetically distinct populations within a species of the parasite, making *Striga* management complex as the resistance found in some cultivars may be overcome by a small subset of *Striga* individuals within the seed bank leading to the development of a virulent population over time (Rodenburg and Bastiaans, 2011; Kountche et al. 2013). Koyama (2000) studies indicated high levels of genetic distances between *S. hermonthica* populations collected from Mali, Nigeria and Kenya. In contrast with Koyama (2000) results, Gethi et al. (2005) reported a very low genetic diversity between 24 populations of *S. hermonthica* from Kenya. Existence of physiological strains, ecological variants and races of the parasite together with variability in size of the seed bank offer serious obstacles for the development of simple and effective control measures. Co-evolution of the parasite with its hosts has resulted in both specificity and non-specificity within the genus (Babiker, 2007). Two levels of physiological specialization have been suggested in *Striga*: inter-crop specialization (strain specificity to a crop species) and intra-crop specialization (strain specialization to a cultivar of a crop species) (Dafaallah et al. 2019). Mohamed et al. (2007) suggested the existence of physiological strains of *S. hermonthica*, where it was observed that varieties of *Sorghum* resistant in one location were susceptible in others. Pescott (2013) reported the existence of physiological specialization in S. hermonthica from West Africa following their analysis of parasite virulence on different host crops. Host adaptations, or pre-adaptations, are commonly revealed using tests for differential virulence between *Striga* populations and host genotypes; that is, by demonstrating population-level genotype-by-genotype interactions. Evidence for such interactions was found between three West African populations of *S. hermonthica* and five sorghum cultivars. These interactions were shown to be strongest at the parasite post-attachment life stage, and to depend on the parasite virulence metric used. Environmental influences on host-parasite interactions were strong and variable between years and sites (Pescott, 2013).

Several experiments were undertaken to study variability and host specificity in within *S. hermonthica* populations and its interaction with selected hosts, however, little work has been done in Sudan. Therefore, this study was conducted to investigate variability and host specificity in the early developmental stages of *S. hermonthica* parasitism in response to *in-situ* root exudates of sorghum cv. Abu-70, cv. Wad Ahmed and cv. Hakika.

Materials and Methods

In general, the materials and methods of this study followed the protocol developed by Dafaallah (2006). To achieve the aim of this study, several field surveys were carried out during the rainy season in different endemic areas in Sudan in season 2013/2014 to collect *S. hermonthica* seeds. The study also comprised different laboratory experiments that were carried out at the Faculty of Agricultural Sciences (FAS), University of Gezira, Sudan.

Materials collection

To collect *S. hermonthica* seeds, several field surveys were carried out during the rainy season 2013/2014 in *S. hermonthica* endemic areas in Eastern, Central, and Western Sudan. Five locations were selected randomly in each area (Table 1). Twelve populations of *S. hermonthica* were collected from infected sorghum and three populations were collected from infected millet. Three sites were selected at random in each location. Three *Striga* infested fields were chosen at random in each site. At the time of harvest ten plots (10 x10 m) were selected in each field. Ten quadrates (1 m^2 each) were placed at random in each plot. In each quadrat, the *S. hermonthica* plant and the host plants, sorghum or millet, were identified. From the mature *Striga* plants, several capsules were collected, transferred to the biology laboratory of the FAS. Then, the capsules were air dried on the bench for 30 days in dark at room temperature. About 5 grams of *Striga* seeds were retrieved from capsules in each location. The seeds of Sorghum cv. Abu-70, cv. Wad Ahmed and cv. Hakika, that have a germination percentage of 95-100% and purity of 100%, were obtained from the Sorghum Program, Agricultural Research Corporation (ARC), Sudan. The seeds of the parasite and sorghum were surface sterilized by sodium hypochlorite, (NaOCl) 1% solution, for 3 min with continuous agitation. Subsequently, they were thoroughly washed with sterilized distilled water for several times. Floating seeds were discarded and the remaining ones were stored at room temperature until used.

Table 1. Geographical locations of *Striga hermonthica* collection sites and the hosts employed in this study

Geographical locations		Latitude	Longitude	Host plants
Area	Location			
Eastern Sudan	Galabat	14° 09' N	35° 99' E	Sorghum
	Sumsum	13° 17' N	35° 36' E	Sorghum
	Gadarif	14° 01' N	35° 40' E	Sorghum
	Butana	13° 93' N	35° 12' E	Sorghum
	El Fau	14° 12' N	34° 08' E	Sorghum
Central Sudan	Hasaheisa	14° 74' N	33° 31' E	Sorghum
	Abu-Haraz	14° 12' N	33° 31' E	Sorghum
	Hag-Abdalla	13° 95' N	33° 56' E	Sorghum
	Barakat	14° 23' N	33° 61' E	Sorghum
	Wad-Rabia	14° 32' N	13° 19' E	Sorghum
Western Sudan	Um-Rawaba	12° 39' N	30° 21' E	Sorghum
	El-Rahad	12° 74' N	31° 39' E	Sorghum
	Kadugli	11° 19' N	29° 69' E	Millet
	Khour-Tagat	13° 20' N	30° 30' E	Millet
	El Obied	13° 19' N	30° 21' E	Millet

Seed conditioning

Prior to germination, *Striga* seeds were preconditioned as described by Dafaallah (2015). About 80-100 (0.63 mg) *S. hermonthica* seeds were spread on a sterile disc (0.5 mm diameter) of Glass

Fiber Filter Paper (GFFP) (Whatman GF/C) and sterilized - distilled water (4.5 ml) was added to Striga seeds. The discs were placed one layer of GFFP in a sterile glass Petri-dish and followed by incubation at 30 ˚C for 12 days for pre-conditioning.

In vivo experiment

The technique that described by Dafaallah (2006) was also used in this *in vivo* experiment. Gezira soil was sterilized in an oven at 105 ˚C for 24 h. Gezira soil is typical haplusten, line smectitic, isophyperthemic and characterized by heavy clay soil (clay 60%), with pH 8-8.5, low organic matter and nitrogen, adequate potassium and low available phosphorous (Elbasher, 2016). Five grams of the sterilized soil were placed on Fiber filter paper (Whatman F/C) that placed on disposable petri-dishes (9 cm diameter). Then, sterilized- distilled water (30 ml) was added to each disposable petri dish. On the other hand, Sorghum (cv. Abu-70, cv. Wad Ahmed and cv. Hakika) seeds were raised in paper rolls for 5 days. The 5 days old seedlings transferred and placed on FFP in the disposable petri dishes that contained sterilized soil and has a lateral opening to allow for the emergence of crop shoot. Then, the preconditioned seeds of the parasite were placed underneath the seedling roots in the disposable petri-dish and sterilized distilled water was added to each petri dish as needed. The Petri dishes were covered with a black glass fiber filter paper, sealed with Para film, placed in black polyethylene bags and incubated at room temperature in continuous light. The experiment was laid in a factorial completely randomized design with three replicates. *S. hermonthica* seeds and/or germilings were then examined under a binocular (40 x magnification) for germination, haustorium initiation, attachment and penetration at 24, 72, 144, 192 h after initial incubation, respectively.

Statistical analysis

Data were subjected to descriptive analysis using the following scale (Very low (≤ 20), Low (21 ≤ 40), moderate (40 ≤ 60), high (61 ≤ 80) and very high (≤ 81)) and analysis of variance procedure (P ≤ 0.05). Means were separated for significance using Duncan's Multiple Range Test. The statistical analysis was done using the Statistical Analysis System software v.9.0.

Results and Discussion

Effects of in-situ root exudates of sorghum cultivars on seed germination

S. hermonthica displayed significantly moderate germination (46.9 and 57.5%) when seeds were placed in close proximity to the roots of sorghum cv. Abu-70 and cv. Wad Ahmed, respectively (Figure 1). However, seeds similarly placed in the vicinity of the root of sorghums cv. Hakika displayed significantly low germination (33.5%). The seed germination of *S. hermonthica,* sorghum populations, placed in close proximity to the roots of sorghum cv. Abu-70 was high and ranged between 63.6% in population collected from Wad Rabia and 84.0% in population collected from Gadarif (Table 2). The seed germination of *S. hermonthica,* sorghum populations, placed in the vicinity of the roots of sorghum cv. Wad Ahmed was relatively high and ranged between 57.0% in population collected from Wad Rabia and 73.0% in population collected from Abu Haraz (Table 2). The seed germination of *S. hermonthica,* sorghum populations, placed near the roots of sorghum cv. Hakika, was low to moderate and ranged between 33.0% for seeds collected from Barakat and 47.0% for seeds collected from Sumsum. Moreover, there were significance differences among *S. hermonthica* populations.

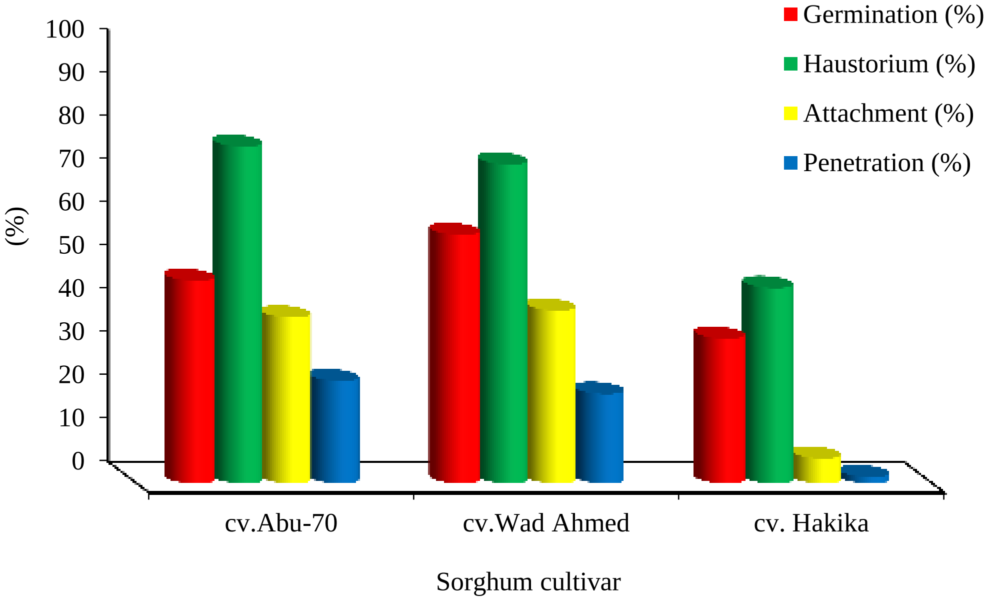

Figure 1. Effects of *in-situ* root exudates of sorghum cultivars on early developmental stages of *S. hermonthica* parasitism.

The seed germination of *S. hermonthica,* millet populations, placed near the roots of sorghum cv. Abu-70 was significantly low and ranged between 29.9% in population collected from Khour-Tagat and 32.7% in population collected from Kadugli (Table 2). The seed germination of *S. hermonthica,* millet populations, placed in close proximity to the roots of sorghum cv. Wad Ahmed was low and ranged between 22.7% for seeds collected from Khour-Tagat and 25.0% for seeds collected from El Obied. The seed germination of *S. hermonthica,* millet populations, placed in the vicinity of the roots of sorghum cv. Hakika, germination was negligible and ranged between 2.3 and 4.3%. There were significance differences among *S. hermonthica* populations. The highest percentage of seed germination that induced by *in-situ* root exudates of sorghum cv. Abu-70 and sorghum cv. Wad Ahmed compared to the lowest germination that induced by *in-situ* root exudates of sorghum Hakika, might be due to a high production of the germination stimulants (strigolactones) exuded by the roots of sorghum cv. Abu-70 and sorghum cv. Wad Ahmed. Jamil et al. (2011) found that a positive relationship between the amount of strigolactones in the *situ* exudate and *Striga* germination, attachment and emergence rates. The cultivars that produced the highest amounts of strigolactones showed the most severe *Striga* infection, while the cultivars that produced the lowest amounts of strigolactones showed the lowest *Striga* infection. Moreover, Ali (2008) studies, on the basis of differential germination, attachment, penetration and genetic distance confirmed clearly the existence of millet and sorghum strains in *S. hermonthica*. The minor differences in virulence and genetic distance observed between the two populations could be attributed to provincial differences.

Table 2. Effects of *in-situ* root exudates of sorghum cultivars on seed germination of *S. hermonthica* populations

S. hermonthica population	Location	Germination (%)		
		cv. Abu-70	cv. Wad Ahmed	cv. Hakika
S. hermonthica populations collected from infected sorghum	Galabat	71.5 cd	67.0 gh	45.3 l
	Sumsum	78.5 b	70.7 de	47.0 l
	Gadarif	84.0 a	68.7 efg	45.7 l
	Butana	67.0 gh	61.3 j	37.0 o
	El Fau	70.3 de	65.0 hi	39.7 mn
	Hasaheisa	73.1 c	65.3 hi	41.0 m
	Abu-Haraz	80.0 b	73.0 c	39.0 mno
	Hag-Abdalla	70.3 de	64.0 i	38.3 no
	Barakat	64.0 i	57.7 k	33.0 pq
	Wad-Rabia	63.6 i	57.0 k	34.0 p
	Um-Rawaba	78.0 b	70.0 def	46.0 l
	El-Rahad	79.3 b	70.3 de	46.0 l
S. hermonthica populations collected from infected millet	Kadugli	32.7 pq	24.3 st	4.3 u
	Khour-Tagat	29.9 r	22.7 t	2.3 u
	El Obied	31.8 qr	25.0 s	3.3 u
SE ±		0.74		
CV %		5.2		

*Means in columns and rows followed by the same letter(s) are not significantly (P ≤ 0.05) different according to Duncan's Multiple Range Test.

Effects of in-situ root exudates of sorghum cultivars on haustorium initiation

S. hermonthica displayed significantly high haustorium initiation (73.8 and 77.9%) when seeds placed in close proximity to the roots of sorghum cv. Wad Ahmed and Abu-70, respectively (Figure 1). Seeds similarly placed in the vicinity of the roots of sorghum cv. Hakika exhibited moderate haustorium initiation (45.2%). On placement of seeds in close proximity to the roots of sorghum cv. Abu-70, haustorium initiation of *S. hermonthica,* sorghum populations, was high and ranged between 69.7 in population collected from El Fau and 84.0% in populations collected from Galabat, Gadarif and Abu-Haraz (Table 3). When seeds of *S. hermonthica,* sorghum populations, placed in close proximity to the roots of sorghum cv. Wad Ahmed, haustorium initiation was high and ranged between 64.7% for seeds collected from Um-Rawaba and 79.3% for seeds collected from Gadarif. On placement of seeds in close proximity to the roots sorghum cv. Hakika, haustorium initiation of *S. hermonthica,* sorghum populations, was moderate and ranged between 32.3% for population collected from Um-Rawaba and 57.3% for population collected from Abu-Haraz. Furthermore, there were significance differences among *S. hermonthica* populations. There were significance differences among *S. hermonthica* populations. When seeds of *S. hermonthica,* millet populations, placed near the root of sorghum cv. Abu-70, haustorium initiation ranged between 72.0% in population collected from Khour-Tagat and 78.0% in population collected from El Obied (Table 3). When seeds of *S. hermonthica,* millet populations placed similarly to the roots of sorghum cv. Wad Ahmed, haustorium initiation ranged between 75.0% for population from El Obied and 78.7% for population from Kadugli. Haustorium initiation of *S. hermonthica,* millet populations, ranged between 2.7% for seeds collected from El Obied and 44.0% for seed collected from Khour-Tagat, when placed near the roots of sorghum cv. Hakika. There were significance differences among *S. hermonthica* populations. There were significance differences among *S. hermonthica* populations.

Table 3. Effects of *in-situ* root exudates of sorghum cultivars on haustorium initiation of *S. hermonthica* populations

S. hermonthica population	Location	Haustorium initiation (%)		
		cv. Abu-70	cv. Wad Ahmed	cv. Hakika
S. hermonthica populations collected from infected sorghum	Galabat	85.0 a	79.0 cde	49.0 op
	Sumsum	80.7 bc	73.0 hi	49.0 op
	Gadarif	85.0 a	79.3 cd	54.7 n
	Butana	76.0 fg	71.7 ijk	39.7 s
	El Fau	69.7 k	65.0 l	34.0 t
	Hasaheisa	80.0 bc	75.0 gh	49.7 o
	Abu-Haraz	85.0 a	78.3 cde	57.3 m
	Hag-Abdalla	78.7 cde	73.0 hi	47.0 p
	Barakat	75.0 gh	71.0 ijk	40.7 rs
	Wad-Rabia	76.7 efg	69.7 k	42.3 qr
	Um-Rawaba	85.0 a	79.0 cde	49.0 op
	El-Rahad	80.7 bc	75.3 g	53.3 n
S. hermonthica populations collected from infected millet	Kadugli	76.0 fg	78.7 cde	43.0 q
	Khour-Tagat	72.0 ij	78.0 cdef	44.0 q
	El Obied	78.0 cdef	75.0 gh	42.7 qr
SE ±		0.74		
CV %		4.4		

*Means in columns and rows followed by the same letter(s) are not significantly (P ≤ 0.05) different according to Duncan's Multiple Range Test.

Haustorium initiation, which represents the switch from the vegetative to the parasitic mode of life, occurs on or near the host root. This process has been shown to depend on a haustorium-imitating substance. The substance responsible for initiating haustorial development has been identified as 2,6-dimethoxy-ρ-benzoquinone (2,6-DMBQ). The 2,6-DMBQ cannot normally be detected in the exudates from sorghum roots, although it is present in its extract (Dafaallah et al. 2014, 2017). Host resistance can be linked to low production of germination stimulants (Yoder and Scholes, 2010). In this case the resistance is known as 'pre-attachment' resistance (Jamil et al. 2011); that is, the resistance operates before the attachment of the haustorium to the host root.

Effects of in-situ root exudates of sorghum cultivars on attachment

S. hermonthica displayed significantly low attachment (38.4, 40.0 and 5.8%) to the roots of sorghum cv. Abu-70, cv. Wad Ahmed and cv. Hakika, respectively (Figure 1). *S. hermonthica,* sorghum populations, showed low to relatively moderate attachment to the roots of sorghum cv. Abu-70 and ranged between 33.7% in population collected from Barakat and 46.0% in population collected from Gadarif (Table 4).

Table 4. Effect of *in-situ* root exudates of sorghum cultivars on attachment of *S. hermonthica.*

S. hermonthica population	Location	Attachment (%)		
		cv. Abu-70	cv. Wad Ahmed	cv. Hakika
S. hermonthica populations collected from infected sorghum	Galabat	41.0 de	42.0 c	8.3 ijk
	Sumsum	41.0 de	40.0 e	8.7 jk
	Gadarif	46.0 b	50.3 a	9.0 j
	Butana	34.0 hi	36.0fg	6.0 m
	El Fau	41.3 cde	40.0 e	7.3 klm
	Hasaheisa	41. de	41.7 cde	7.0 lm
	Abu-Haraz	36.0 fg	35.3 gh	6.0 m
	Hag-Abdalla	40.0 e	40.0 e	8.3 jkl
	Barakat	33. i	37.0 f	6.3 m
	Wad-Rabia	34.0 hi	36.0 fg	6.0 m
	Um-Rawaba	41.0 de	42.0 c	8.3 ijk
	El-Rahad	41.0 de	40.3 de	7.0 lm
S. hermonthica populations collected from infected millet	Kadugli	37.0 f	40.0 e	0.0 n
	Khour-Tagat	35.0 ghi	39.7 e	0.0 n
	El Obied	35.0 ghi	41.3 cde	0.7 n
SE ±		0.53		
CV %		4.7		

* Means in columns and rows followed by the same letter(s) are not significantly (P ≤ 0.05) different according to Duncan's Multiple Range Test.

S. hermonthica, sorghum populations, displayed low to relatively moderate attachment to the roots of sorghum cv. Wad Ahmed and ranged between 35.3% in population collected from Abu-

Haraz and 50.3% in population collected from Gadarif. *S. hermonthica,* sorghum populations, achieved very low attachment to the roots of sorghum cv. Hakika and ranged between 6.07% in populations collected from Butana, Abu-Haraz and Wad-Rabia and 9.0% in population collected from Gadarif. Millet populations displayed low attachment to the root of sorghum cv. Abu-70 and ranged between 35.0% in population collected from El Obied and 37.0% in population collected from Kadugli (Table 4). Millet populations showed low to moderate attachment to sorghum cv. Wad Ahmed and ranged between 39.7% in population collected from Khour-Tagat and 41.3% for population collected from EL Obied. Millet populations, exhibited negligible attachment to the roots of sorghum cv. Hakika. El Obied population displayed extremely low attachment 0.7%, while, Kadugli and Khour-Tagat exhibited no attachment (0.0%). There were significance differences among *S. hermonthica* populations.

As it develops, the haustorium becomes covered in sticky hairs. These hairs on the young haustorium help the parasite germiling to adhere to any surface. After attachment by these hairs, intrusive cells develop at the root tip and penetrate the cortex of the host. The haustorium penetrates the host root, establishes connection with host xylem, guided possibly by host-derived secondary metabolites (Bouwmeetster et al. 2003). Unlike its response to germination stimulants and haustorium initiators, *Striga* is non-specific with the response to the attachment. Attachment frequencies were reported to be similar for host and non-host plant species (Yoshida and Shirasu, 2009). Therefore, the variability and host specificity of *S. hermonthica* might be due to the interaction and incompatibility of the host and the parasite. Incompatible hosts can interfere with the formation of intrusive cells and the subsequent xylem bridge.

Effects of in-situ root exudates of sorghum cultivars on penetration

S. hermonthica displayed low significantly penetration (23.7, 20.7 and 1.5%) into the roots of sorghum cv. Abu-70, cv. Wad Ahmed and cv. Hakika, respectively (Figure 1). *S. hermonthica,* sorghum populations, showed low penetration into the roots of sorghum cv. Abu-70 and ranged between 18.4% in population collected from Wad-Rabia and 39.3% in populations collected from Sumsum (Table 5). *S. hermonthica,* sorghum populations, exhibited low penetration into the roots of sorghum cv. Wad Ahmed and ranged between 16.0% in population collected from El Rahad and 33.0% in population collected from Gadarif. *S. hermonthica,* sorghum populations, displayed extremely low penetration into sorghum cv. Hakika and ranged between 0.0% and 5.7%.

Millet populations showed very low penetration into the roots of sorghum cv. Abu-70 and ranged between 17.0% in population collected from Khour-Tagat and 20.0% in population collected from Kadugli (Table 5). Millet populations showed very low penetration into the roots of sorghum cv. Wad Ahmed and ranged between 14.0% in population collected from Khour-Tagat and 15.0% in populations collected from Kadugli and El Obied. Millet populations were net able to penetrate into the roots of sorghum cv. Hakika. There were significance differences among *S. hermonthica* populations. The highest penetration into roots of sorghum cv. Abu-70 and sorghum cv. Wad Ahmed compared to the lowest penetration into roots of sorghum Hakika, might be due to several resistance mechanisms. These mechanisms have been suggested to be operating in host species including low stimulants production, mechanical barriers, inhibition of germ tube exoenzymes by root exudates, phytoalexins synthesis, post attachment hypersensitive reactions, antibiosis, unfavorable phytohormone supplied by the host, insensitivity to *Striga* toxin and avoidance through root growth habit (Yoshida and Shirasu, 2009). A study, on the basis of penetration and genetic distance, confirms clearly the existence of millet and sorghum strains in *S. hermonthica*. The minor differences in virulence and genetic distance observed between the two populations could be attributed to provincial differences.

Table 5. Effect of *in-situ* root exudates of sorghum cultivars on penetration of *S. hermonthica* populations

S. hermonthica population	Location	Penetration (%)		
		cv. Abu-70	cv. Wad Ahmed	cv. Hakika
S. hermonthica populations collected from infected sorghum	Galabat	29.0 c	28.0c	5.7 j
	Sumsum	39.3 a	27.7 c	0.0 k
	Gadarif	36.0 a	33.0 b	5.7 j
	Butana	19.0 e	18.0 efg	0.0 k
	El Fau	24.0 d	17.0 fgh	0.0 k
	Hasaheisa	30.0 c	24.0 d	0.0 k
	Abu-Haraz	30.0 c	17.7 efg	0.0 k
	Hag-Abdalla	29.0 c	24.0 d	5.7 j
	Barakat	18.6 ef	18.0 efg	0.0 k
	Wad-Rabia	18.4 efg	17.0 efg	0.0 k
	Um-Rawaba	29.0 c	28.0c	5.7 j
	El-Rahad	19.0 7	16.0 ghi	0.0 k
S. hermonthica populations collected from infected millet	Kadugli	20. e	15.0 hi	0.0 k
	Khour-Tagat	17.0 fgh	14.0i	0.0 k
	El Obied	17.7 efg	15.0 hi	0.0 k
SE ±		0.80		
CV %		20.9		

* Means in columns and rows followed by the same letter(s) are not significantly (P ≤ 0.05) different according to Duncan's Multiple Range Test.

In general, the results revealed that *in-situ* root exudates of all sorghum cultivars induced seed germination and haustorium initiation in *S. hermonthica* populations tested. The highest seed germination, haustorium initiation, attachment and penetration into sorghum root was induced by *in-situ* root exudates of sorghum cv. Abu-70 and by sorghum cv. Wad Ahmed, while, *in-situ* root exudates of sorghum cv. Hakika induced the lowest one. The results also revealed that, seed germination, haustorium initiation, attachment and penetration of *S. hermonthica* collected from infected sorghum in response to sorghum *in-situ* root exudates was significantly higher compared to *S. hermonthica* collected from under millet. Moreover, the result showed that there were significant differences among *S. hermonthica* populations collected from different areas in Sudan with respect to seed germination, haustorium initiation, attachment and penetration into the host cultivars. The findings of the present study are in agreement with those of Ali, (2008) who reported that, root extracts and exudates from sorghum, millet and maize were able to induce germination and haustorium initiation, attachment and penetration. However, the magnitude of germination, haustorium initiation, attachment and penetration varied with the parasite population and the host in question. Ali, (2008) suggested that the earlier stages of parasite establishment may have greater importance in determining host specificity. These findings are consistent with those of Dafaallah, (2019) who confirmed that there are that two strains of *S. hermonthica* exist in Sudan, one prevailing in Eastern and Central Sudan and only attacks sorghum while in Western Sudan, both millet and sorghum were attacked. Furthermore, the strain on millet did not attack sorghum and vice versa. Sorghum was usually heavily attacked by *S. hermonthica* in the clay soils of Central Sudan, whereas millet was particularly immune, but the reverse was true on sandy soils.

The observed differential response of the two *Striga* strains to haustorium inducing factor(s) from sorghum and millet may indicate specificity of the haustorium factors. Such specificity may be related to differences in quality, identity and/or quantity of the haustorium factor. The observed differential response is consistent with a previous report by Mbuvi et al. (2017) who reported that the potential number of haustoria is a product of the concentration and/or quality of haustoria inducing factor and the parasite's individual ability to respond. The host specificity and variability of *S. hermonthica* populations might affect the efficiency of introducing new resistant cultivars as a control measure against the parasitic weed. Christopher et al. (2002) reported various *Striga* populations that exhibited different degrees of virulence on susceptible host plants and suggested that different populations of this parasite may well be considered and treated as ecotypes in plant breeding programs developing resistance to the parasite.

Conclusion

The *in-situ* root exudates of all sorghum cultivars induced seed germination, haustorium initiation, attachment and penetration in *S. hermonthica* populations tested. However, there were significant differences among cultivars and among *S. hermonthica* populations. This study confirms the existence of variability and physiological specialization in *S. hermonthica* in Sudan and suggesting genetic variation. These findings are highly relevant to sorghum and millet agronomists and breeders and molecular geneticists working on *S. hermonthica* resistance.

Conflicts of Interest

No conflicts of interest have been declared**.**

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