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Host specificity of Sudan Witchweed (*Striga hermonthica* [Del.] Benth.) Seed Germination and Haustorium Initiation in Response to Millet Root Exudates and Extracts

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Abstract: *Witchweed [Striga hermonthica (Del.) Benth.] is obligate root-parasitic plants belonging to the Orobanchaceae family are deadly pests for major crops all over the world. The aim of this study is to investigate host specificity of Sudan witchweed (S. hermonthica) seed germination and haustorium initiation in response to millet [Pennisetum glaucum (L.) R. Br.] root exudates and extracts. Field surveys were conducted during the seasons 2013/2014 in Striga endemic areas in Sudan to collect seeds from the parasite. Fifteen S. hermonthica populations were collected. Tow in vitro experiments were conducted at the University of Gezira, Sudan to study the effects of root exudates and root extracts of millet cv. Ugandi, cv. Ashana and cv. Sudan II on percentage of seed germination and haustorium initiation. 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 showed that there were significant differences in seed germination and haustorium initiation of witchweed in response to root exudates and root extracts among millet cultivars and among the witchweed populations. Moreover, the highest seed germination (61.7 – 76.4 %) and haustorium initiation (55 – 58%) percentages attained by S. hermonthica collected from parasitized millet. While the lowest seed germination (35.3 -37.1%) and haustorium initiation (14.3 -17%) percentages attained by S. hermonthica collected from parasitized sorghum. This study confirms the existence of two levels of physiological specialization in S. hermonthica populations in Sudan. Moreover, two strains of S. hermonthica are suggested, one specific to sorghum and the other to millet. The existence of host specificity within witchweed populations are suggested to be based almost entirely on differential response of Striga isolates to root exudates and root extracts from the host.*

Keywords: exudates; germination; haustorium; specificity; *Striga*; witchweed

1. INTRODUCTION

Witchweed [*Striga hermonthica* (Del.) Benth.], belongs to the family Orobanchaceae, is annual obligate root parasites of grasses. It is native to semi-arid areas of northern tropical Africa, from Senegal to Ethiopia and the Democratic Republic of Congo, and into south-west Arabia and southern tropical Africa, including Angola, Namibia, Madagascar and Tanzania. *S. hermonthica* is responsible for food shortage and poverty of millions of Africans [1]. The primary hosts of the parasite include sorghum [*Sorghum bicolor* (L.) Moench], millet [*Pennisetum glaucum* (L.) R. Br.), maize [*Zea mays* L.], rice [*Oryza sativa* L.] and sugarcane [*Saccharum officinarum* L.] [2]. It is estimated that the area infested by *Striga* in sub-Saharan Africa to be over 50 million ha of the arable farmland under cereals [3]. Infection by *S. hermonthica* causes grain yield losses ranging from 5 to 90%, depending on the host species, the variety grown, climatic conditions, the level of infection and the soil nature. The total loss in cereal production is 4.1 million tons [4, 5]. The annual yield loss was estimated at more than US $ 10 billion [6]. Farmers reported losses between 20% and 80%, and eventually had to abandon highly infested fields. Moreover, the *Striga* epidemic will increase and the parasite is likely to become a more serious threat to crop production. The parasite also causes indirect losses, including changes in production strategies, land abandonment, and in extreme cases of human migration in response to severe infection [7, 8].

Many measures have been developed to control *S. hermonthica*, including cultural, physical, biological, chemical, host plant resistance and genetically modified crops. However, mass seed production, prolonged seed viability, reproductive behavior that maintains tremendous genetic variation, the ability to parasitize a wide range of host, and the subterranean nature of the early stages of parasitism, make control of the parasite by a single method difficult if not impossible [9, 10]. Resistance varieties have long been proposed as a means of reducing losses caused by *Striga* under low-cost subsistence agriculture in Africa. The host / parasite relationship undergoes a series of steps that include germination stimulation, initiation of haustorium, host root penetration, contact with host tissue and

simultaneous growth [11]. Resistant varieties have long been proposed as a means of reducing losses caused by *Striga* under the low-cost input subsistence agriculture in Africa. The host/ parasite relationship undergoes a series of steps that include germination, haustorium initiation, penetration of the host root, connection to the host xylem and the concurrent growth [11]. 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 lack of resistance genes in crop germplasm, specificity of resistance and the presence of morphotypes, physiological strains, ecological variants and races of the parasite. The significant genetic variation 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 [12, 13]. Studies of [14] indicated high levels of genetic distances between *S. hermonthica* populations collected from Mali, Nigeria and Kenya. Contrary to the results of [14], [15] reported a very low genetic diversity between 24 populations of *S. hermonthica* from Kenya. The presence of physiological strains, ecological variants and races of the parasite together with variability in size of the seed bank are 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 [16]. Two levels of physiological specialization have been proposed in *Striga*: inter-crop specialization (strain specificity to a crop species) and intra-crop specialization (strain specialization to a cultivar of a crop species) [17]. Reference [18] 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. Reference [19] 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 usually detected using differential virulence tests 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 varieties of sorghum. 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 locations [19].

Several experiments were undertaken to study 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 the host specificity of *S. hermonthica* populations collected from different locations in Sudan with respect seed germination and haustorium initiation in response to millet root exudates and extracts.

2. MATERIALS AND METHODS

In general, the materials and methods of this study followed the protocol developed by [20]. 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.

2.1 Material collection

To collect *S. hermonthica* seeds, several field surveys were carried out during the rainy season of the 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 (10X10 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 five 5 grams of *Striga* seeds were retrieved from capsules in each location.

The seeds of millet cv. Ugandi, cv. Ashana and cv. Sudan II, that have a germination percentage of 95-100% and purity of 100%, were obtained from the Millet Program, Agricultural Research Corporation (ARC), Sudan. The seeds of the parasite and millet 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.

2.2 Seed conditioning

Prior to germination, *Striga* seeds were preconditioned as described by [21]. About 80-100 (0.63 mg) *S. hermonthica* seeds were spread on a sterile disc (0.5 mm internal 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 30^0C for 12 days for pre-conditioning.

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

2.3 Effects of millet root exudates on germination and haustorium initiation of S. hermonthica

Tow *in vitro* experiment were designed to study the effects of millet root exudates on germination and haustorium initiation of *Striga*. Millet cultivars (cv. Ugandi, cv. Ashana and cv. Sudan II) were used in this experiment. Crops seedlings, grown in Petri dishes for 24 hours, were transferred each to rockwool in plastic pots. In each case rockwool was moistened with 200 ml of sterilized-distilled water and incubated in a growth chamber for 10 days prior to collection of root exudates under suction using a suction pump. Aliquots of each root exudates (30 µl) were applied to each pair of discs containing conditioned *Striga* seeds placed on glass fiber discs (8 mm internal diameter). The Petri dishes were sealed with Para film, placed in black polyethylene bags and incubated at 30°C in the dark. Treatments were arranged in a factorial completely randomized design with three replicates. The seeds were examined under a binocular (40 × magnification) for germination and haustorium initiation 24 and 72 hours (h) after incubation, respectively. The experiment was repeated twice.

2.4 Effects of millet root extract on germination and haustorium initiation of S. hermonthica

Tow *in vitro* experiments were designed to study the effects of millet root extracts on germination and haustorium initiation of *Striga*. Millet cv. Ugandi, cv. Ashana and cv. Sudan II were sown on filter paper rolls placed in plastic pots and watered daily for 6 days. Root samples (1g) each were obtained from crop seedlings and placed in a mortar. Five ml of sterilized-distilled water were added and the roots were crushed using a mortar and pestle, subsequently centrifuged and the supernatant was collected. Conditioned *Striga* seeds were treated with aliquots of the root extract (30µl each). Treatments were arranged in a factorial completely randomized design with three replicates. Seeds were examined under a binocular (40 × magnification) for germination and haustorium initiation 24 and 72 h after incubation, respectively. The experiment was repeated twice.

2.5 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 (SAS) Software v.9.0.

3. RESULTS

3.1 Effects of millet root exudates on germination

Witchweed, populations collected from different geographical locations, exhibited significance (P ≤ 0.05) variations in response to millet root exudates (Fig. 1). Root exudates from millet cv Ashana, cv. Ugandi and Sudan II induced relatively moderate germination (45.0, 46.8 and 44.7%, respectively).

On treatment with root exudates from millet cv. Ashana, seed germination of *S. hermonthica* collected from parasitized millet at Khour-Tagat, Kadugli and El Obied was significantly high (74.3, 74.8 and 76.4%, respectively) (Table 2). On treatment with root exudates from millet cv. Ugandi, seed germination of *S. hermonthica* collected from parasitized millet at Khour-Tagat, Kadugli and El Obied was moderate (64.0, 65.0 and 65.7%, respectively). On treatment with root exudates from millet cv. Sudan II, seed germination of *S. hermonthica* collected from parasitized millet at El Obied, Khour-Tagat and Kadugli was moderate (58.7, 59.7 and 60.0%, respectively). There were no significant differences among the parasite populations.

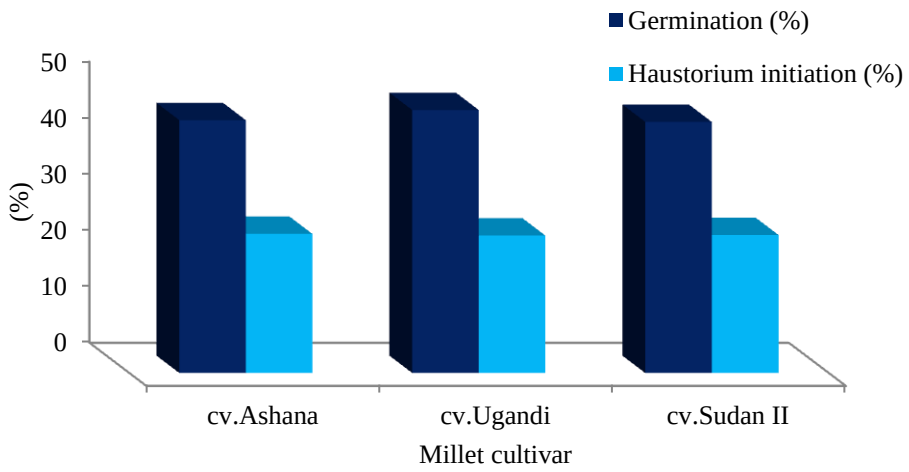

Fig. 1. Effect of root exudates of millet cultivars on germination and haustorium initiation of witchweed

Table 2. Effects of millet root exudates on germination of *Striga* seed populations

S. hermonthica population	Location	Germination (%)		
		cv. Ashana	cv. Ugandi	cv. Sudan II
S. hermonthica populations collected from infected sorghum	Galabat	39.8 jklmn	39.0 klmnop	41.0 hijk
	Sumsum	38.9 klmnop	38.0 nop	42.0 ghi
	Gadarif	40.6 ijkl	40.0 ijklmn	43.3 fg
	Butana	40.1 ijklmn	41.3 ghij	45.0 ef
	El Fau	40.0 ijklmn	41.0 hijk	46.0 e
	Hasaheisa	37.1 p	38.0 nop	40.0 ijklmn
	Abu-Haraz	41.2 ghij	43.0 gh	40.0 ijklmn
	Hag-Abdalla	41.0 hijk	42.0 ghi	40.0 ijklmn
	Barakat	40.2 ijklm	38.7 lmnop	40.3 ijklm
	Wad-Rabia	38.2 mnop	40.3 ijklm	37.3 op
	Um-Rawaba	38.7 lmnop	39.3 jklmno	39.3 jklmno
	El-Rahad	39.8 jklmn	39.0 klmnop	38.3 mnop
S. hermonthica populations collected from infected millet	Kadugli	74.8 ab	65.0 c	60.0 d
	Khour-Tagat	74.3 b	64.0 c	59.7 d
	El Obied	76.4 a	65.7 c	58.7 d
	SE ±	0.6636		
	CV %	5.03		

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

On treatment with root exudates from millet cv. Ashana, seed germination of *S. hermonthica* collected from parasitized sorghum was ranged between 37.1% for population from Hasaheisa and 41.2% for population from Abu-Haraz and Barakat (Table 2). On treatment with root exudates from millet cv. Ugandi, seed germination of *S. hermonthica* collected from parasitized sorghum was ranged between 38.0% for population collected from Sumsum and Hasaheisa to 40.0% for population collected from Hag-Abdalla. On treatment with root exudates from millet cv. Sudan II, seed germination of *S. hermonthica* collected from parasitized sorghum was slightly low. The germination ranged between 37.3% for seeds collected from Wad-Rabia and 46.0% for seeds collected from El Fau. Moreover, there were significant differences among the parasite populations.

3.2 Effects of millet root exudates on haustorium initiation

Root exudates from millet cultivar cv. Ashana, cv. Ugandi, cv. and Sudan II induced comparable low haustorium initiation (24.8, 24.5 and 24.6%, respectively) (Fig. 1). On treatment with root exudates from millet cv. Ashana, haustorium initiation of *S. hermonthica* collected from parasitized millet was ranged between 47.6% for population

collected from El Obied and 49.9% for population collected from Khour-Tagat, with no significant differences (Table 3). When *Striga* germilings were challenged with root exudates from millet cv. Ugandi, haustorium initiation of *S. hermonthica* collected from parasitized millet was moderate and ranged between 49.0% for population collected from Khour-Tagat and 50.3% for population collected from El Obied with significant differences. On treatment with root exudates from millet cv. Sudan II, haustorium initiation of *S. hermonthica* collected from parasitized millet was low to moderate and ranged between 34.0% for population collected from Kadugli and 55.0% for population collected from El Obied.

Table 3. Effect of millet root exudates on haustorium initiation of *Striga* populations

S. hermonthica population	Location	Germination (%)		
		cv. Ashana	cv. Ugandi	cv. Sudan II
S. hermonthica populations collected from infected sorghum	Galabat	18.9 fghij	18.0 ghijk	18.3 fghijk
	Sumsum	18.9 fghij	19.0 fghij	20.0 fghi
	Gadarif	17.5 ijkl	16.0 klm	18.7 fghij
	Butana	18.0 ghijk	19.0 fghij	20.0 fghi
	El Fau	19.7 fghij	17.7 hijk	15.0 lm
	Hasaheisa	17.4 ijkl	18.0 ghijk	19.7 fghij
	Abu-Haraz	20.6 efg	20.0 fghi	22.0 e
	Hag-Abdalla	14.3 m	19.7 fghij	21.0 ef
	Barakat	20.0 fghi	20.3 efgh	18.0 ghijk
	Wad-Rabia	18.3 fghijk	18.0 ghijk	17.0 jkl
	Um-Rawaba	19.7 fghij	19.0 fghij	19.0 fghij
	El-Rahad	18.1 ghijk	17.3 ijkl	17.0 jkl
S. hermonthica populations collected from infected millet	Kadugli	48.8 bc	50.0 bc	34.0 d
	Khour-Tagat	49.9 bc	49.0 bc	53.3 a
	El Obied	47.6 c	50.3 b	55.0 a
	SE ±		0.7755	
	CV %		12.69	

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

On treatment with root exudates from millet cv. Ashana, haustorium initiation of *S. hermonthica* collected from parasitized sorghum was ranged between 14.3% for population collected from Hag-Abdalla and 20.6% for population collected from Abu-Haraz (Table 3). When witchweed germilings were challenged with root exudates from millet cv. Ugandi, haustorium initiation of *S. hermonthica* collected from parasitized sorghum was significantly low and ranged between 17.3% for seeds collected from El- Rahad and 20.3 for seeds collected from Barakat. On treatment with root exudates from millet cv. Sudan II, haustorium initiation of *S. hermonthica* collected from parasitized sorghum was poor and ranged between 15.0% for seeds collected from El Fau and 22.0% for seeds collected from Abu-Haraz. Furthermore, there were significant differences among the parasite populations.

3.3 Effects of millet root extract on germination

Regardless of witchweed collection, root extracts from millet cv. Ashana, cv. Ugandi and cv. Sudan II induced moderate germination (43.9, 45.7 and 43.2%, respectively) with significance differences (Fig. 2). On treatment with root extracts from millet cv. Ashana, seed germination of *S. hermonthica* collected from parasitized millet was relatively high and ranged between 60.2% for population collected from Kadugli and 61.2% for population collected from El Obied (Table 4). Seed germination of *S. hermonthica* collected from parasitized millet when treated with root extracts from millet cv. Ugandi was moderate and ranged between 59.3% for population collected from Kadugli and 61.0% for population collected from Khour-Tagat and from El Obied. On treatment with root extracts from millet cv. Sudan II, seed germination of *S. hermonthica* collected from parasitized millet was moderate to high and ranged between 59.0% for population collected from Khour-Tagat and 61.7% for population collected from El Obied.

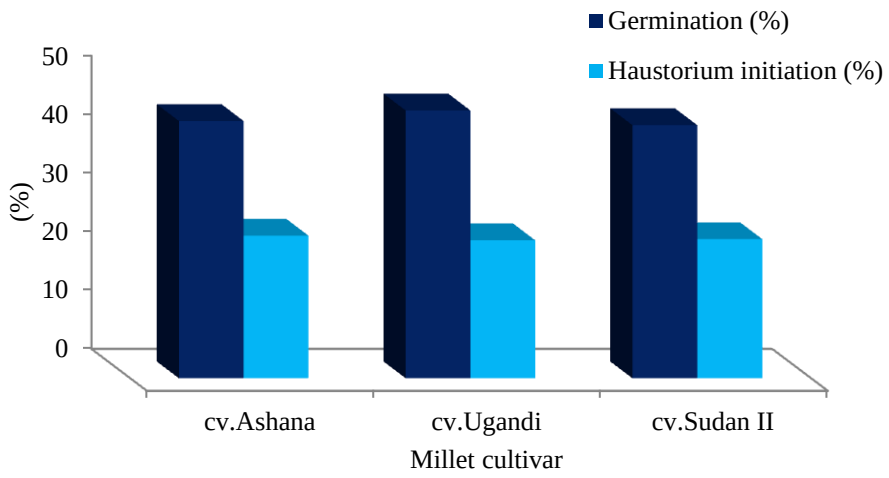

Fig. 2. Effect of root extracts of millet cultivars on germination and haustorium initiation of witchweed

Table 4. Effect of millet root extracts on germination of *Striga* seed populations

S. hermonthica population	Location	Germination (%)		
		cv. Ashana	cv. Ugandi	cv. Sudan II
S. hermonthica populations collected from infected sorghum	Galabat	44.9 d	43.3 defg	40.7 ijklmn
	Sumsum	44.1 de	42.0 efghij	41.3 ghijkl
	Gadarif	45.0 d	42.7 efghi	43.0 defgh
	Butana	43.3 defg	40.0jklmno	39.0 lmnop
	El Fau	43.3 defg	36.3 qr	35.3 r
	Hasaheisa	43.6 def	40.3 jklmn	38.3 opq
	Abu-Haraz	40.3 jklmno	37.3 pqr	37.3 pqr
	Hag-Abdalla	40.0 jklmn	40.0 jklmn	41.0 hijklm
	Barakat	38.2 opq	36.3 qr	39.7 klmno
	Wad-Rabia	39.1 mnop	37.3 pqr	38.7 nop
	Um-Rawaba	42.7 efghi	40.0 jklmno	40.7 ijklmn
	El-Rahad	47.2 c	41.7 fghijk	41.0 hijklm
S. hermonthica populations collected from infected millet	Kadugli	60.2 ab	59.3 b	60.3 ab
	Khour-Tagat	60.2 ab	61.0 ab	59.0 b
	El Obied	61.2 ab	61.0 ab	61.7 a
	SE ±		0.6655	
	CV %		5.17	

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

On treatment with root extracts from millet cv. Ashana, seed germination of *S. hermonthica* collected from parasitized sorghum was low to moderate and ranged between 38.3% for population collected from Barakat and 47.3% for population collected from El-Rahad (Table 4). Seed germination of *S. hermonthica* collected from parasitized sorghum when treated with root extracts from millet cv. Ugandi was low and ranged between 36.3% for population collected from EL Fau and 43.3% for population collected from Galabat. Seed germination of *S. hermonthica* collected from parasitized sorghum was low and ranged between 35.3% for seeds collected from El Fau and 43.0% for seeds collected from Gadarif. In addition, there were significant differences among the parasite populations.

3.4 Effects of millet root extract on haustorium initiation

Witchweed collected from different geographical locations, displayed low haustorium initiation when *Striga* germilings were challenged with root extracts from millet cultivars (Fig. 2). Root extracts from millet cv. Ashana, Ugandi and cv. Sudan II showed 24.4, 23.6 and 24.8% haustorium initiation, respectively. However, there were significance differenct among the parasite populations.

On treatment with root extract from millet cv. Ashana, haustorium initiation of *S. hermonthica* collected from

parasitized millet was moderate (57.0 – 58.0%) (Table 5). When *S. hermonthica* collected from parasitized millet treated with root extracts from millet cv. Ugandi, haustorium initiation ranged between 49.7% for population collected from Kadugli and 55.3% for population collected from El Obied. When *S. hermonthica* germilings were challenged with root extracts from millet cv. Sudan II, haustorium initiation *S. hermonthica* collected from parasitized millet was ranged between 43.0% for population collected from Khour-Tagat and 46.3% for population from El Obied. Moreover, there were significance differenct among the parasite populations.

Table 5. Effect of millet root extracts on haustorium initiation of *Striga* populations

S. hermonthica population	Location	Germination (%)		
		cv. Ashana	cv. Ugandi	cv. Sudan II
S. hermonthica populations collected from infected sorghum	Galabat	15.1 pqrs	18.0 klmn	24.0 f
	Sumsum	16.9 mno	19.0 jkl	22.0 gh
	Gadarif	16.7 nop	17.0 mno	23.0 fg
	Butana	14.1 rs	16.0 pq	13.7 s
	El Fau	13.9 rs	14.3 qrs	14.0 rs
	Hasaheisa	16.0 opq	18.3 jklmn	20.0 ij
	Abu-Haraz	15.1 pqrs	17.3 mno	17.0 mno
	Hag-Abdalla	15.1 pqrs	16.7 nop	18.0 klmn
	Barakat	13.3 s	14.3 qrs	15.0 pqrs
	Wad-Rabia	14.1 rs	15.0 pqrs	15.0 pqrs
	Um-Rawaba	17.0 mno	19.7 ijk	19.7 ijk
	El-Rahad	15.5 opqr	18.7 jklm	21.0 hi
S. hermonthica populations collected from infected millet	Kadugli	58.2 a	49.7 c	45.3 d
	Khour-Tagat	57.0 ab	56.3 ab	43.0 e
	El Obied	57.0 ab	55.3 b	46.3 d
	SE ±	0.5715		
	CV %	7.09		

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

On treatment with root extract from millet cv. Ashana, haustorium initiation of *S. hermonthica* collected from parasitized sorghum was low and not exceeded 17.0% (Table 5). When *S. hermonthica* collected from parasitized sorghum treated with root extracts from millet cv. Ugandi, haustorium initiation was low and ranged between 14.3% for seeds collected from El Fau and likewise from Barakat and 19.0% for seeds collected from Sumsum. There were significanct differences among the parasite populations.

4. DISCUSSION

The results showed that, there were significant differences in seed germination and haustorium initiation of witchweed in response to root exudates and root extracts from millet cultivars and among the parasite populations. Also, the results revealed that, seed germination and haustorium initiation of witchweed collected from under millet in response to millet root exudates and root extracts was significantly high. However, germination and haustorium initiation of witchweed collected from under sorghum in response to millet root exudates and root extracts was significantly low.

These finding are in consist with the previous studies made [17] who conducted an *in vivo* experiment to study the effects of *in situ* root exudates of the three millet varieties on percentage of seed germination, haustorium initiation, attachment and penetration. The results revealed that *in situ* root exudates of all millet cultivars induced seed germination and haustorium initiation in *S. hermonthica* tested populations. Seed germination, haustorium initiation, attachment and penetration of *S. hermonthica* collected from parasitized millet in response to millet *in situ* root exudates were significantly higher compared to *S. hermonthica* collected from parasitized sorghum.

These findings also agreed with those of [11] who reported that, root extracts and exudates from sorghum, millet and maize were able to induce germination and haustorium initiation, attachment and penetration of sorghum, millet and maize. However, the magnitude of germination, haustorium initiation, attachment and penetration varied with the parasite population and the host in question. These findings are, also, in agreement with the results of [22] who suggested that the earlier stages of parasite establishment may have greater importance in determining host specificity.

These findings are consistent with those of [20] 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 variations in the effect of the root exudates from millet cv Ashana, cv. Ugandi and Sudan II on the percentage of seed germination might be due to the variations in the germination stimulants (strigolactones) exuded by the roots of different millet cultivars. Reference [23] 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, reference [11] 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.

The variations in the effect of the root exudates from millet cv Ashana, cv. Ugandi and Sudan II on the percentage of haustorium initiation might be due to the variations in the haustorium-imitating substances presence the roots of different millet cultivars. 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 [24, 25].

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 [26]. 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 [27]. 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.

The observed differential response of the two *Striga* strains to haustorium inducing factor(s) from 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 [28] 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. [29] 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.

5. CONCLUSION

The root exudates and extracts of all sorghum cultivars induced seed germination and haustorium initiation in *S. hermonthica* populations tested. However, there were significant differences among millet 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.

6. REFERENCES

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