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Induction of *Striga hermonthica* germination and haustorium initiation by allelochemicals produced by millet cultivars

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Abstract Allelopathy, Millet cultivars, *Striga*, Residue, germination, haustoria.

Laboratory experiments were conducted to evaluate the allelopathic potential of 16 millet cultivars on early developmental stages of *Striga*. Millet leaves and roots residue dry matter powder with different level was used for the bioassays on *Striga* germination and haustorium using Fuji techniques. Result revealed that leaves residue of the cultivar DST displayed the highest germination (26.3%), followed in descending order by Ashana (24.0%), SADCL (23.2 %) and KMV221 (22.1%). However, leave residue from Sudan III was completely inhibited germination. Generally, the depressive effects of the leaves powder decreased with increasing concentration, irrespective to cultivars. With respect to root residue, result revealed that DM sustained the highest germination (54.83%). However, root residue from KMV155 and MCSRC displayed negligible germination. Germilings from seeds induced to germination by millet, irrespective of cultivars and plant parts showed pre-mature haustoria. A further increase in amount of leaves residue to 100 mg or more increased haustorium formation, but not significantly (68.2-70.9%). The leaves residue of KMV221, SADCL and Ashana cultivars displayed the highest haustoria. However, *Striga* inoculated with Sudan III leaves powder completely inhibited haustorium. Root powder of SADCL, UGANDI and Sudan III cultivars induced between 70.1 - 75.9% haustoria. However, KMV155 and OK-ashana cultivars sustained the lowest haustoria initiation (5-6.4%). The use of millet residue could diminish the global soil seed bank of *Striga* and reduce our reliance on synthetic herbicides.

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Introduction

Allelopathy is the ability of plant to inhibit the germination of other plants through the production of allelochemicals which may be present in any parts of the plants, i.e. leaves, roots, fruits, stems, rhizomes and seeds, from where they are released to the soil through volatilization, root exudation, leaching and decomposition of plant residues (Alam *et al*., 2001). Allelopathic interactions are primarily based on the synthesis and release of secondary metabolites by higher plants that initiate a wide array of biochemical reactions, which induce several biological changes, however, many of these are yet to be understood. In nature, many plant species grow together and interact with each other by inhibiting or stimulating the growth and development through allelopathic interactions. The research and development in allelopathy is of extreme urgency for the improvement of agriculture, forestry and the global environment (Reigosa and Pedrol, 2002), because allelopathy majorly deals with invasive/ exotic and native weeds, allelopathic crops that keep hampering agricultural practices and bring about environmental degradation (Inderjit, 2005).

Because of their obligate parasitic nature, the life cycle of *Striga* spp. is modulated by exchange of signals between the host, the biotic environment and the parasite (Ransom and Njorage, 1991). *Striga* seeds need an after - ripping period after shedding from the parent plant followed by a pre- treatment (conditioning) period in moist warm environments (25 to 30°C) for 1 to 2 weeks. *Striga* seeds germinate only in the presence of an exogenous germination stimulant exuded by the roots of host plants or some non- host plants. Chemicals from the host root trigger *Striga* germilings to form haustoria, in which modified roots are used to transfer water, minerals, and a diverse collection of carbon compounds from a host to the parasite (Press and Graves, 1995). Following haustorium formation, the parasite attach and penetrates the tissue of the host root and establishes connection with the host xylem. Certain allelochemicals possessing novel modes of action can be utilized as herbicide templates, especially those natural products which are inhibitors of plant specific processes, such as photosynthesis or chlorophyll synthesis (Gonzalez *et al*., 1997). The discovery of allelochemicals, their mode of action and identification of new herbicide chemistry may be helpful tools for increasing the role of allelopathy in crop production as well as weeds control (Duke *et al*., 2001). Present knowledge of plant biochemistry, physiology, morphology, inter and intra plant interactions and chemistry of natural products have proved that weed suppressing crops and their allelochemicals may be manipulated in weed management strategies to minimize herbicides use. Germination and root length of weed *Parthenium hysterophorus* L. was significantly reduced by extracts of sunflower, sorghum and rice (Javaid *et al*., 2006), they further indicated that 50 and 100% extract concentrations of sunflower and sorghum significantly reduced the root biomass of *Parthenium* plants. Sunflower varieties resistant to broomrape (*Orobanche cernua* Loefl.) release 7- hydroxylated simple coumarins which prevent germination and penetration of *O. cernua* parasitism to the host vascular system (Serghini *et al*., 2001).

Allelopathy holds promise for the environmentally friendly weed management. Numerous plants are reported to possess allelopathic potential and efforts have been made to apply them for weed control. The objective of the present study was to investigating the allelopathic effects of millet cultivars on germination, radical length and haustorium of *S. hermonthica*.

Material s and methods

Series of laboratory experiments were undertaken to investigate the efficacy of different millet cultivars on two species of early developmental stages of *Striga* germination and haustorium initiation.

Plant materials

Millet collection

Allelochemicals

The allelopathic potential against *Striga* spp. seed germination and seedling development was evaluated on sixteen millet genotypes (10 local genotypes in

addition to 6 imported varieties). The local genotypes were, Dembi (D), Dembi millit (DM), Dembi Alfasher (DF), Dembi Shangil Tobaya (DST), SudanII, Um-Garfa, Wad-Eldaw, OK-ashana, Sudan III and Ashana, while the imported varieties were UGANDI (Vcand), MCNELC, KMV155, MCSRC, SADCL and KMV221. All these genotypes were obtained from Agricultural Research Corporation (ARC), Sudan.

Sample preparation

Healthy plant parts (leaves and roots) of millet were collected from sixteen mature individuals during the winter season in the Shambat area. The dried plant materials were ground into fine powder with a household blender for 10 minutes and stored in a black plastic bag at room temperature until use.

Striga hermonthica seeds collection, surface disinfection

Striga hermonthica seeds, used in this study, were collected from parasitic plants growing under sorghum in 2010 at the Gezira Research Station Farm in Wad Medani. *S. hermonthica* seeds were cleaned by placement in a measuring cylinder (1000 ml) containing tap water. Tween 20 was added and the seeds were agitated for 5 minutes. Floating materials containing debris and immature light seeds were discarded. The seeds were washed several times with tap water to free them of sand and Tween 20. The seeds were surface sterilized by soaking in 1% sodium hypoclorite (NaOCl) solution for 3 minutes with continuous agitation. Subsequently the seeds, thoroughly washed with sterilized distilled water and plotted dry on Whatman No. 1 filter paper, were allowed to dry under a laminar flow hood. The seeds were stored in sterile glass vials and kept at room temperature until used.

Tests solutions

GR24 stock solution

GR24 was provided by Professor B. Zwanenberg, the University of Nimijhen, the Netherlands. A stock solution of the stimulant was prepared by dissolving 1 mg in 1 ml of acetone and completing to volume (100 ml) with sterile distilled water. The solution was kept in a fridge at 5 ^{o}C till used.

Agar medium preparation

Low nutrient agar medium (gelling temperature 30-31 ^{o}C) was prepared by adding 7.5 g to one liter of distilled water and subsequent autoclaving at 15 bar and121 ^{o}C for 15 min. The autoclaved agar was cooled in a room temperature.

Striga hermonthica seeds conditioning

Striga seeds (collected from infested millet) were conditioned as described by Babiker *et al.*, (1993). Briefly glass fiber filter papers (GF/C) discs (8 mm diameter) were cut, wetted thoroughly with water and placed in an oven at 100 ^{o}C for 1 h to be sterilized and ready for further use. The sterilized discs, placed in 9 cm Petri dishes lined with glass fiber filter papers (GF/C), were moistened with 5 ml distilled water. About 25-50 surface disinfected *S. hermothica* seeds were sprinkled on each of the glass fiber discs in each petri dish. The dishes, sealed with para film, placed in black polythene bags were incubated at 30 ^{o}C in the dark for 10 days.

Effects of millet leave powder on Striga germination and haustorium initiation

Sandwich method as previously described by Fujii *et al.*, (2004) used in this study. Millet leaves, dried, were powdered and kept till used. Low nutrient agar medium was autoclaved as described above. The autoclaved agar was cooled at a room temperature. Aliquots of the autoclaved agar (5ml each) were pipetted into each well of a multi-well plate. Subsequent to gelatinization, samples of millet leaves cultivars (40, 60, 80, 100, 120 and 10 mg/well) were added and distributed evenly by hand. Another 5ml Agar was added to each well on top of the sample, and allowed to solidify. Glass fiber discs, containing conditioned *Striga* seeds, were placed on top of the second agar layer and pressed gently (4/well). Glass fiber discs containing conditioned *Striga* seeds, (4/well) were placed on top of the second agar layer. Discs containing conditioned *Striga* seeds, placed on the top of agar, applied with GR24 at 0.1 ppm or distilled water, were included as control for

comparison. The multi-well-plates were sealed with Parafilm, wrapped with aluminum foil and incubated in the dark at 30 ºC for 48 h. The seeds were subsequently examined for germination and haustorium initiation.

Data were checked for normality using Shapiro-Wilks-W-Test prior to analysis of variance (ANOVA).The data were subsequently subjected to ANOVA using Statistix 8 program. Mean separation was made by Tukey honestly significance difference test at P> 5%

Results

Effects of Millet leave powder on S. hermonthica germination

Generally, *Striga* seeds conditioned in water and subsequently treated with GR24 at 0.1ppm displayed high germination. Leaves powder of sixteen millet cultivars were evaluated on *Striga* germination. Millet residues, irrespective of plant parts and powder level induced germination of *Striga*, the germination varied with millet cultivars. Millet leaves powder at 40mg/well induced about 10% seeds germination, irrespective to cultivars. Among the millet cultivars tested DST leaves powder displayed the highest germination (26.3%), followed in descending order by Ashana (24.0%), SADCL (23.2 %) and KMV221 (22.1%). Powder from Sudan II, Um-Garfa and MCSRC induced 19.2, 13.8 and 11.3% germination, respectively. Cultivars D, DST and UGANDI displayed the lowest germination. However, Powder from Sudan III was completely inhibited germination (100%) (Table 1). Generally, the depressive effects of the leaves powder decreased with increasing concentration, irrespective to cultivars.

Table 1. Effects of Millet leave powder on *S. hermonthica* germination.

	Strigaseeds germination%						
Millet leaves powder levels (mg)							
Cultivars	40	60	80	100	120	140	Mean (cultivars)
DM	0	0	0.9	1.4	9.6	4.4	2.7 ef
DF	7.3	1.0	1.0	10.9	13.5	11.8	7.6 def
KMV221	21.6	28.2	27.7	13.7	15.4	26.0	22.1 ab
D	2.2	10.8	10.6	5.6	12.0	4.9	7.7 def
DST	25.3	23.6	28.0	29.0	27.1	24.7	26.3 a
SADCL	18.4	19.1	22.2	32.3	20.1	27.3	23.2 ab
UGANDI	4.8	3.5	4.9	3.6	1.0	0.0	3.0 def
Sudan II	19.0	22.3	23.2	10.5	26.0	14.2	19.2 abc
MCNELC	7.1	0.0	10.7	2.5	8.6	10.6	6.6 def
KMV155	3.2	3.0	0.0	12.8	12.5	15.1	7.7 def
MCSRC	25.1	7.7	8.7	8.6	3.3	14.2	11.3 cde
Ashana	16.3	24.3	27.3	17.5	32.1	26.6	24.0 a
Wad-Eldaw	7.7	14.9	6.0	7.4	9.3	10.3	9.3 def
OK ashana	6.6	0.0	1.0	3.3	6.0	5.8	3.8 ef
Sudan III	0.0	0.0	0.0	0.0	0.0	0.0	0.0 f
Um-Garfa	0.0	9.0	16.3	19.8	24.1	13.3	13.8 bcd
Mean (levels)	10.3 a	10.5 a	11.8 a	11.2 a	13.8 a	13.1 a	
Standard error for Cultivars	±1.3						
Standard error for level	±2.1						
Standard error for cultivars* level	±5.0						

Means in rows or Colum's followed by the same letters were not significantly different at P≤ 0.5 (Tukey-Test).

Effects of Millet root powder on S. hermonthica germination

Millet residues, irrespective of root powder level induced germination of *Striga*, the germination varied with millet cultivars. The germination of *Striga* seed was increased with increasing the amount of millet powder (Table 2). Among the millet cultivars tested DM root powder displayed the highest germination (54.83%), followed in descending order by Um-Garfa (36.41%), DST (35.51%), DF (33.89) and KMV221 (32.69%). DM millet root powder at 80mg/well induced about 61.53% seeds germination. However, Powder from KMV155 and MCSRC displayed negligible germination.

Table 2. Effects of Millet root powder on *S. hermonthica* germination.

	*Striga*seeds germination%					
Millet root powder levels (mg)						
Millet cultivars	20	40	60	80	100	Mean (cultivars)
DM	48.06	52.57	58.12	61.53	53.85	54.83 a
DF	29.57	31.28	34.40	32.36	41.86	33.89 b
KMV221	42.28	30.61	31.69	32.78	26.07	32.69 b
D	11.19	14.55	5.95	10.78	5.01	9.49 ef
DST	37.64	33.12	31.17	37.82	36.52	35.25 b
SADCL	10.09	22.04	26.19	17.10	24.63	20.01 cde
UGANDI (Vcand)	9.35	20.61	31.65	21.52	25.35	21.70 cd
Sudan II	13.53	16.66	7.23	11.62	5.57	10.92 def
MCNELC	16.65	20.83	9.17	9.50	10.18	13.27 def
KMV155	3.80	16.35	2.08	4.32	1.19	5.55 f
MCSRC	10.30	16.35	2.08	4.32	1.19	6.85 f
Ashana	33.17	34.70	23.88	28.56	27.35	29.53 bc
Wad-Eldaw	22.83	36.46	23.95	27.12	19.82	26.03 bc
OK ashana	0.00	21.44	17.94	12.33	9.81	12.30 def
Sudan III	7.25	9.79	8.00	19.72	9.32	10.81 def
Um-Garfa	30.20	43.36	47.69	23.03	37.76	36.41 b
Mean (levels)	20.37 b	26.29 a	22.57 ab	22.15 ab	20.97 b	
Standard error for Cultivars			±3.19			
Standard error for level			±1.79			
Standard error for cultivars* level			±7.14			

Means in rows or Colum's followed by the same letters were not significantly different at P≤ 0.5 (Tukey-Test).

Effects of Millet leave powder on S. hermonthica haustorium

Generally, germilings from seeds induced to germination by millet, irrespective of cultivars and plant parts showed pre-mature haustoria. A further increase in amount of leaves powder to 100mg or more increased haustorium formation, but not significantly (68.2-70.9%). The introduced cultivars ICMV221, SADCL, MCNELC and MCSRC recorded the highest number of haustoria (70.8-91.7%), while Ugandi cultivar had the lowest 44%. The local cultivars DST, Sudan II, Ashana, Wad-Eldaw and Umgirfa induced 84.8, 76.4, 93.1, 86.1 and 75 haustoria initiation, respectively (Table 2). However, DF, D and Ok-ashana displayed 50-68.8%. However, *Striga* inoculated with Sudan III leaves powder was completely inhibited haustorium (100%).

Effects of Millet root powder on S. hermonthica haustorium

The results showed that SADCL, UGANDI and Sudan III cultivars induced 70.1, 75.9 and 75.4% haustoria, respectively (Table 4). However, KMV155 and OK ashana cultivars sustained the lowest haustoria initiation (5-6.4%). The rest of cultivars displayed moderate effects. The receiver *Striga* plants show varied types of responses to the allelochemicals released from donor plants (millet).

Table 3. Effects of Millet leave powder on haustorium initiation of *S. hermonthica*.

Haustorium initiation%							
Millet leaves powder levels (mg)							
Cultivars	40	60	80	100	120	140	Mean (cultivars)
DM	0.0	0.0	0.0	50.0	25.0	25.0	16.7 de
DF	75.0	0.0	25.0	50.0	100	100.0	58.3 bc
KMV221	100.0	100.0	75.0	100.0	75.0	100.0	91.7 ab
D	25.0	100.0	100.0	62.5	75.0	50.0	68.8 abc
DST	91.7	56.3	98.3	87.5	100	75.0	84.8 ab
SADCL	100.0	100.0	94.2	75.0	72.2	100.0	90.2 ab
UGANDI	75.0	75.0	41.7	50.0	25.0	0.0	44.4 cd
Sudan II	77.5	64.9	84.4	91.7	72.5	67.3	76.4 abc
MCNELC	75.0	0.0	100.0	50.0	100.0	75.0	66.7 abc
KMV155	75.0	50.0	0.0	100.0	75.0	66.7	61.1 abc
MCSRC	100.0	62.5	75.0	75.0	50.0	100.0	77.1 abc
Ashana	91.7	91.7	100.0	75.0	100.0	100.0	93.1 a
Wad-Eldaw	75.0	100.0	75.0	75.0	91.7	100.0	86.1 ab
OK ashana	75.0	0.0	25.0	50.0	75.0	75.0	50.0 cd
Sudan III	0.0	0.0	0.0	0.0	0.0	0.0	0.0 e
Um-Garfa	0.0	75.0	100.0	100.0	75.0	100.0	75.0 abc
Mean (levels)	64.7 a	54.7 a	62.1 a	68.2 a	69.5 a	70.9 a	
Standard error for Cultivars				±7.2			
Standard error for level				±4.4			
Standard error for cultivars* level				±17.5			

Means in rows or Colum's followed by the same letters were not significantly different at P≤ 0.5 (Tukey-Test).

Discussion

Allelochemicals are present in almost all plants and in many plant tissues including leaves, stems, flowers, fruits, seeds and roots. Allelopathic suppression of weeds is caused by biologically active allelochemicals that are actively released from living plants into the environment through root exudation, leaching, and volatilization, and passively liberated through decomposition of plant residues (Wu *et al.*, 2000). This experiment was conducted to compare effects of allopathic crops on the germination and haustorium of *Striga*. The allelopathic effect of Sudan III leaves powder was completely inhibited germination and haustorium of *Striga* (100%). Furthermore, *Striga* treated with leaves powder of DM, UGANDI and OKaashana cultivars reduced germination and haustorium significantly. However, *Striga* inoculated with leaves powder of Ashana and SADCL were significantly induced germination and haustorium initiation of the parasite.

The difference between the cultivars may be related to

differential stimulants contents of the respective powders. Millet cultivars, which failed to stimulate germination of *Striga* seeds, may not be conclusively ruled out as a stimulant producer. These results are in agreement with the findings of (Gbèhounou and Adango, 2003) who reported that crops which stimulate more *Striga* seeds to germinate possibly produce more germination stimulant. Breeding programs focused on selection of host genotypes for high root exudation levels of germination or radicle growth inhibitors could identify better candidates for intercrops to be used in a control strategy. Allelophatic potential of cereal crops can be enhanced by classical or marker-assisted breeding provided that genetic variation and proper screening methods exist. In addition, understanding the genes responsible for the biosynthesis and release of allelochemicals will allow their incorporation in high yielding cultivars by genetic manipulation.

Table 4. Effects of Millet root powder on haustorium initiation of *S. hermonthica*.

Haustorium initiation%						
Millet leaves powder levels (mg)						
Millet cultivars	20	40	60	80	100	Mean (cultivars)
DM	40.91	83.82	57.01	67.74	74.54	64.80 abc
DF	27.50	52.38	60.94	38.12	30.00	41.79 bcde
KMV221	0.00	2.08	30.08	40.17	40.79	22.62 efg
D	0.00	10.00	0.00	62.50	0.00	14.50 efg
DST	36.67	54.24	70.42	73.69	77.68	62.54 abcd
SADCL	50.00	82.29	51.73	83.33	83.33	70.14 ab
UGANDI (Vcand)	71.88	79.73	73.33	71.25	83.33	75.90 a
Sudan II	25.00	54.17	100.00	75.00	75.00	65.83 ab
MCNELC	4.17	39.46	54.17	35.00	10.00	28.56 efg
KMV155	0.00	0.00	0.00	25.00	0.00	5.00 g
MCSRC	16.67	55.42	3.57	41.82	66.25	36.74 cde
Ashana	14.58	34.41	33.33	44.22	50.30	35.37 def
Wad-Eldaw	5.00	36.97	45.30	30.17	28.33	29.15 efg
OK ashana	0.00	16.39	0.00	15.83	0.00	6.44 fg
Sudan III	75.00	91.67	62.50	60.50	87.50	75.43 a
Um-Garfa	12.50	61.01	97.73	100.00	44.62	63.17 abcd
Mean (levels)	23.74 b	47.13 a	46.26 a	54.02 a	46.98 a	
Standard error for Cultivars			±8.48			
Standard error for level			±4.74			
Standard error for cultivars* level			±18.96			

Means in rows or Colum's followed by the same letters were not significantly different at P≤ 0.5 (Tukey-Test).

It is difficult to understand the exact mechanism of action of allelochemicals. After release, allelochemicals cause both inhibitory and stimulatory effects and various factors like concentration, inhibition and stimulation of specific enzymatic activities, flux rate, age, metabolic state and environmental conditions determine their toxicity (Gallet and Pellissier, 1997). Their amount and production varies in quality and quantity with age, cultivars, plant organ, and time of the year (Cambier *et al.*, 2000). Biological activities of receiver plants in response to allelochemicals are known to be

concentration dependent. It is widely believed that seeds of *Striga* require a conditioning period of 10 days under suitable temperature and moisture conditions before germinating in response to GR24 (Hassan *et al.*, 2013). Most of the germination stimulants isolated and identified so far possess the same basic molecular structure, and are collectively known as strigolactones. To date, more than 14 strigolactones have been identified, mainly from plant root exudates (Yoneyama *et al.*, 2010). Ma *et al.*, (2004) suggested that not all plants produce sufficient amounts of strigolactones to induce germination of *Striga*. In addition, chinese medicinal herb extracts may contain substances that inhibit the germination-promoting activities of strigolactones. In the present study, only a very small number of millet cultivars induced germination of *Striga* seeds (Tables 1 and 3). However, introduction of species that can induce germination of *Striga* spp. into affected cropping systems may result in 'suicidal germination' of the weed. Thus, the depletion of its soil seed bank by inducing "suicidal germination" would be an efficient way to control *Striga*. Nie *et al.* (2004) reported the inhibitory effect of aqueous extract of *Wedelia trilobata* on *Brassica parachinensis*. They claimed that these negative effects were due to inhibited activities of peroxidase, superoxide dismutase, nitrate reductase and disruption of nitrogen metabolism. Similar was the finding of Penna (2003) who reported that the inhibitory effects of aqueous extracts of *Chenopodium ambrosioides* on seed germination of *Bidens pilosa*. A range of host resistance strategies to prevent parasite infection have been documented, each interrupting specific stages of the parasite biological cycle (Labrousse *et al.*, 2001). Several phenolic acids, flavonoids, and the quinone 2, 6-dimethoxy-*p*-benzoquinone induced haustoria in *Striga*. The ability of millet cultivars, irrespective to their parts to stimulate germination could be of practical use in inducing germination of witchweed seeds which leads to a reduction in witchweed seed bank in the soil.

Strigol, a germination stimulant for the parasitic plant *Striga asiatica,* has been found in the root exudates of many cereals (Siame *et al.*, 1993). A variety of plants produce herbicidal allelochemicals that may inhibit growth and germination of neighboring plants (Friebe *et al.*, 1995). In addition, root secreted compounds called phytosiderophores may be involved in the acquisition of essential plant nutrients from soils and in defense against toxic metals such as aluminum (de la Fuente *et al.*, 1997). Intuition and limited published data (Gagnon and Ibrahim, 1997) suggest that root secreted compounds should have a wide spectrum of biological activities including protection against biotic and abiotic stresses. Survival of delicate and physically unprotected root cells may depend on their continuous "underground chemical warfare" against a hostile and constantly changing environment teeming with bacteria and fungi preying on any organic material in soil.

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