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Influence of Sorghum Genotype on Germination, attachment and Survival of *Striga hermonthica* (Del.) Benth.

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Abstract

The root parasitic weed *Striga hermonthica* constitutes a major constraint to cereals production in sub-Saharan Africa. Several control measures have been recommended, however, incompatibility with the prevalent low inputs production systems precludes their adoption. Resistant genotypes could provide an ideal solution; however, durable resistance necessitates pyramiding of resistance mechanisms. The present investigation was undertaken at the College of Agricultural Studies Sudan University of Science and Technology to study *in situ* germination of *S. hermonthica* seeds, seedlings attachment and subsequent development, over a three weeks duration, on three sorghum genotypes, Wad-Ahmed, *Striga* tolerant, and Tetron and Hakika *Striga* resistant, using an *in vitro* system (the Rhizotron technique) for sorghum and *Striga* co-culture. *Striga* germination progressively increased with time and was 66.9-92.1%, 61.1-85.5% and 52.6-74.1% for Wad-Ahmed, Tetron and Hakika, respectively. *Striga* seedlings affected comparable attachment (53.6-68.8%) to the roots of the three genotypes. However, development and survival of the seedlings were genotype dependent. At 1-3 weeks post-inoculation *Striga* seedlings at stage 3 were 19.1-24.7%, 2.9-7.1% and 6.3-12.6% on Wad-Ahmed, Tetron and Hakika, respectively. Seedlings mortality was 0-1.2%, 3.0-8.1% and 2.5-29.6% on Wad -Ahmed, Hakika and Tetron, respectively. The strong developmental arrest noted beyond stage 2, where xylem-to-xylem connection between the parasite and the host was established, coupled with the notable seedling mortality on Tetron and Hakika suggest that *Striga* resistance in these genotypes is attributed, in part, to impairment of diversion of nutrients, water and carbon compounds from the host to the parasite.

Keywards: - *Striga*-resistant, Root exudates, *Striga* seedlings, xylem-xylem connection.

Introduction

Sorghum [*Sorghum bicolor* (L) Moench) is the main staple food crop in rural areas of the Sudan and most of the neighboring countries in sub- Saharan Africa (Babiker, 2000). The crop is well adapted to harsh environments characterized by drought, high temperatures and fitful rains (Yohannes, 2017). Sorghum grows over a wide range of agro-ecological zones extending between latitudes 45° North and 45° South (ICRISAT, 1991). It requires less water than most cereals, hence it offers a great potential for supplementing food and feed resources especially in dry lands where rainfall is limited (KARI, 2000). However, sorghum production is besieged by an array of biotic and a biotic stresses (Yohannes, 2017). Among the biotic stresses the root hemi parasitic weeds of the genus *Striga*, Orobanchaceae, are considered to be the most important (Parker and Riches, 1993). The intensity of infection, time of infection relative to crop emergence and the tripartite interaction between the parasite, the host and the environment are determinant factors in the outcome which could reach a complete crop failure (Taylor *et al*., 1996). Among *Striga* species "Striga *hermonthica* (Del.) Benth., which is predominant in sub Saharan Africa, is the most important (Parker and Riches, 1993). In Sudan, *S. hermonthica* affects the wellbeing of the majority of farmers especially in the rain-fed sector where the parasite is pandemic, drought spells are frequent, low soil fertility is prevalent, mono cropping of sorghum is practiced and low input crop production systems are in vogue (Yousif, *et al*., 2018). Annual crop losses due to the parasite damage were estimated to be 1,060,000 tones in Sudan and 30,000-90, 000 tons in neighboring Eritrea, Ethiopia and Kenya (Yohannes, 2017).

S. hermonthica is an out crosser and accordingly existence of strains and ecophysiological variants which differ in genetic composition and/or virulence as revealed by the distinct host specificity of the parasite on pearl millet and sorghum is incontestable (Parker and Riches, 1993). A successful *Striga* parasitism entails an orderly sequence of events starting with seeds germination in response to a stimulant, mostly a strigolactone (SL), exuded by the host roots (Yoneyama *et al*, 2012) and in response to a second host-derived signal a haustorium is formed (Westwood, 2013). The haustorium attaches, penetrates the host roots and establishes connection with the host xylem (Hood *et al*, 1998). The parasite subsequently develops and stays subterranean for 6-8 weeks prior to emergence (Babiker, *et al*., 2000). Disruption and/or interruption of any of the events within the sequence abort parasitism and indicate resistance (Timko and Scholes, 2013). Resistance is defined as the ability to avoid, reduce or prevent infection and reproduction. Resistance is used on a continuous scale with susceptibility on the one end and complete resistance or immunity on the other (Rodenburg and Batiaans, 2011).

Resistance is broadly classified as pre- or post-attachment. Pre-attachment resistance resides on reduced production of germination stimulants, production of germination inhibitors and/or reduced production of a haustorium initiation factor (Michael *et al*., 2013). Post-attachment resistant comes into play once a haustorium is formed and the parasite attempts to attach, penetrate the host root and establish connections with the host xylem (Hood, *et al*., 1998; Michael *et al*., 2013). The xylem-to-xylem connection is the start of the parasitic mode where further development is dependent on the ability of the parasite to act as an active sink for withdrawal of water, nutrients and carbon compounds from the host. A report by Hood *et al*. (1998) showed that establishment of xylem-to-xylem connection in *Striga. statica* (L) Kuntze is followed by enlargement of the cotyledons and breakdown of the seed coat.

For post-attachment resistance constitutive or induced incompatibility or host resistance mechanisms may be activated (Timko and Scholes, 2013). The challenged roots may release cytotoxic compounds, undergo lignifications and suberization of cell walls or vascular occlusion. Delineation of resistance mechanisms together with associated molecular basis may help in stacking resistance genes and pyramiding resistance mechanisms to ensure consistent spatiotemporal performance and a durable resistance against ecotypes and variants of a difficult to control weed which threatens food security of over 300 million Africans in sub-Saharan Africa.

The present investigation was therefore designed to study *in situ* germination and subsequent development of *S. hermonthica* on three sorghum genotypes Wad-Ahmed, *Striga* tolerant improved local cultivar (Hamad, *et al*, 2019), Tetron *Striga* resistant local landrace (Gobena *et al*., 2017) and Hakika, *Striga* resistant exotic genotype (Hamad, *et al*, 2019).

Material and Methods:

In-situ germination and subsequent development of *S. hermonthica* on three sorghum genotypes. Wad-Ahmed (*Striga* tolerant improved variety), Tetron (*Striga* resistant local landrace), and Hakika (*Striga* resistant exotic genotype) differing in their reaction and/or origin to the parasite were studied. The investigation was undertaken at the College of Agricultural Studies, Sudan University of Science and Technology (SUST) at Shambat, (Lat 22-27°N, Long 8-20°E). The sorghum genotypes seeds were obtained from the Agricultural Research Corporation (ARC), Wad-Madni, Sudan. *S. hermonthica* seeds were collected from under sorghum at the Gaderif state in 2014.

An *in vitro* system (the Rhizotron technique) for sorghum and *Striga* co-culture, adapted from Vasey *et al*., (2005) for wheat (*Triticum asetivum*) and *S. hermonthica* ,was used. Briefly surface disinfected sorghum seeds were germinated on filter paper for 3 days at 30ºC.The seedlings were subsequently transferred to glass test-tubes filled with 40% long Ashton solution. The tubes were wrapped with aluminum foil to exclude roots from light. Plants were allowed to grow for 10 days in a controlled environment with a 12 h photoperiod, a temperature of 30ºC and subsequently transferred, each, to a rhizotron. The rhizotron comprised of a 150 mm diameter plastic Petri- dish with a sheet of rock wool at the bottom overlaid by a glass fiber filter paper. The rhizotron had a hole at the top to allow for shoot growth. S. *hermonthica* seeds surface sterilized and conditioned in distilled water, as described by Babiker, *et al*., (2000), were sprinkled in close proximity of the roots. The rhizotron, placed in a black jacket, each, were incubated in a controlled environment with a 12 h photoperiod and a temperature of 30 ºC prior to examination for *Striga* germination, attachment and seedling development at 7, 14 and 21 days post inoculation. Treatments were arranged in a complete randomized design with 4 replicates. Germination counts and seedling development were based on 200 seeds, randomly selected, in each rhizotron. Attachments were classified according to their stage of development from stage 1 (least advanced) to stage 3 (most advanced): stage 1 = parasite plumule emerged from seed coat, cotyledons visible, stage 2 shoot formed two leaf pairs, stage 3 = shoot formed 3 or more leaf pairs. Dead seedlings were counted at each observation date.

Statistical analysis:

Data on *Striga* germination, transformed to arcsine, and subsequent development were analyzed by analysis of variance and means were separated for significance by the Least Significant Difference Test (LSD) at 5% probability level using Statistixd., 8 (PC/Windows 7),VSN International Ltd., UK staistical package (Rothamsted Experimental Station).

Results:

In the first week Wad-Ahmed root exudates induced 66.9% germination (Table 1). Of the total parasite seedlings (133.8) 66.6 % were attached (Fig. 1). Of the attached seedlings 52.1, 28.7 and 19.2 % were at stage 1, 2 and 3, respectively. None of the seedlings was dead. Tetron root exudates induced 61.1% germination (Table 1). Of the total parasite seedlings (122.2) 57.7% were attached (Fig. 2). Of the attached seedlings 66.7, 27.9 and 2.9 % were at stage 1, 2 and 3, respectively and 2.5% of the seedlings were dead. Hakika root exudates induced 52.6 % germination (Table 1). Of the total parasite seedlings (105.2) 53.6% were attached (Fig. 3). Of the attached seedlings 54.2, 36.3 and 6.3 % were at stage 1, 2 and 3, respectively and 3.0% were dead. In the second week cumulative germination induced by Wad-Ahmed root exudates was 80.8 % (Table 1). Of the total parasite seedlings (161.6) 56.8% were attached (Fig. 1). Of the attached seedlings 41.2, 35.4 and 23.4 % were at stage 1, 2 and 3, respectively and none of the seedlings was dead. Cumulative germination induced by Tetron, roots exudates was72.3 % (Table 1). Of the total parasite seedlings (144.6) 65.9% were attached (Fig. 2). Of the attached seedlings 51.2, 24.4 and 6.7 % were at stage 1, 2 and 3, respectively and 17.7 % were dead. Cumulative germination induced by Hakika root exudates was 64.1 % (Table 1). Of the total parasite seedlings (128.2) 64.5% were attached (Fig. 3). Of the attached seedlings 45.8, 29.8 and 17.1% were at stage 1, 2 and 3, respectively and 7.2% were dead.

In the third week cumulative germination induced by Wad-Ahmed root exudates was 92.1% (Table 1). Of the total parasite seedlings (184.2) 65.8 % were attached (Fig. 1). Of the attached seedlings 54.0, 19.9 and 24.0 % were at stage 1, 2 and 3, respectively and 1.2 % were dead. Cumulative germination induced by Tetron roots exudates was 85.5 % (Table 1). Of the total parasite seedlings (171) 64.9% were attached (Fig. 2). Of the attached seedlings 33.4, 29.9 and 7.1 % were at stage 1, 2 and 3, respectively and 29.6 % were dead. Cumulative germination induced by Hakika roots exudates was 74.1 %. (Table 1) Of the total parasite seedlings (148.2) 68.8% were attached (Fig. 3). Of the attached seedlings 50.2, 29.1 and 12.6 % were at stage 1, 2 and 3, respectively and 8.2 % were dead.

Discussion:

The results showed clearly that *Striga* germination progressively increased with time over the 3 weeks ‘period and that it was invariably maximal for Wad-Ahmed, intermediate for Tetron and minimal for Hakika. However, the differences in germination inducing activity between the genotypes were often not significant. The notable staggered and/or progressive germination indicates that not all seeds were at the same physiological status and may thus be a survival mechanism as reported for seeds displaying physiological dormancy which possess several embryonic blocks inhibiting radicle protrusion (Baskin and Baskin, 2014; Brun, *et al*., 2018). *Striga* germination is a complex phenomenon. Germination stimulants, natural or synthetic, induce germination through elicitation of ethylene biosynthesis and ethylene triggers a series of biochemical reactions that influence abscisic acid/gibberellins balance in seeds leading to release of embryo dormancy and subsequently to germination (Babiker, *et al*., 2000). The high germination inducing activity of root exudates of Wad-Ahmed is consistent with the reported high contents of 5-deoxystrigol in the strigolactones blend in its roots exudates (Nasreldin *et al*., 2016). *S. hermonthica* seeds, sorghum strain, are renowned for their high response to 5-deoxystrigol which is a strigol type strigolactones and for their low response to the orobancol-type strigolactones (Nasreldin *et al*., 2018; Gobena *et al*. 2017). The relatively high germination inducing activity of roots exudates of the genotype Hakika and Tetron is difficult to explain and is not consistent with the reported low germination inducing capacity of their root exudates which is claimed to account for their high levels of resistance to the parasite (Nasreldin *et al*., 2016; Gobena *et al*. 2017). Hakika and Tetron were reported to produce orobancol, a less active strigolactone than the more active 5-deoxystrigol (Nasreldin *et al*., 2016; Gobena *et al*. 2017). The discrepancy between the results reported in this paper and those reported by others (Nasreldin *et al*., 2016; Gobena *et al*. 2017) may be attributed, as recently reported by Yoneyama (2020) to differences in assay protocols. Yoneyama (2020) reported that *Striga* resistant sorghum cultivars that produce orobanchol under the standardized assay procedure could produce similar germination levels to their susceptible congeners under a different assay protocol. Such change may suggest an alteration in strigolactones profile. Typical strigolactones, designated as canonical strigolactnes, have carlactone as immediate precursor, whereas the recently discovered non-canonical strigolactones have methyl-carlactonic acid as immediate precursor. Non-canonical strigolactones lack the ABC ring, the core in their canonical congeners, but retain the enol-ether–D ring moiety which is claimed to be essential for germination inducing activity (Burn *et al*, 2018; Yoneyama, 2020). However, bearing in mind that *S. hermonthica* is an obligate out crosser variability in response to germination stimulants due to parasite ecotypes and/or strains cannot be ruled out without further investigations.

Comparison of attachment expressed as percentage of the total number of germinated seeds for each of the genotypes across time showed little to negligible differences between genotypes and this is consistent with the notion that haustorium initiation and attachment are not specific as haustoria could attach to inert soil constituents (Riopel and Timko, 1995). The haustorium initiation factor in sorghum (2,6-DMBQ) is a lignin degradation product which results from activation of peroxidases in sorghum roots in response to a chemical signal (H_2O_2) released from the tip of the parasite radicle in close proximity of the host roots (Wada *et al*., 2019). However, based on number of attached seedlings sorghum cultivar Wad-Ahmed displayed the highest attachment followed in descending order by Tetron and Hakika. Further, irrespective of genotype attachment progressively increased with time and was maximal at 3 weeks..

Due to the different assay protocols adopted the rhizotron assay in this study, versus the standard agar gel assay (Ejeta, 2003; Vasey *et al*. 2005), the results, albeit do not refute previous reports, showed clearly that *Striga* resistance in Hakika and Tetron may not be due, solely, to low germination inducing activity of their roots exudates and/ or due to failure of the parasite to attach to the roots. The abrupt developmental arrest of the parasite at stage 2, which is an advance stage of parasitism as indicated by formation of two leaf pairs which indicate that the xylem-to-xylem connection had already been established (Hood *et al*., 1998), suggest, as previously reported for Framida (Arnaud, 1999), involvement of physiological mechanisms which impair nutrients and carbon acquisition by the parasite. This notion is substantiated by the notable death of the parasite seedlings attached to Hakika and Tetron. Striga seedlings mortality was maximal and highly significant on Tetron. However, on Hakika seedlings mortality

albeit high, was at par with that on Wad-Ahmed. Curtailment of nutrients transfer from the host to the parasite could be attributed to low haustorial competence and/or a physiological process that increases water and nutrient retention in host root and shoot tissues. *S. hermonthica* is reported to perturb the hormonal balance of its host. The parasite stimulates abscisic acid (ABA) accumulation and decreases that of gibberellins (GAs) in its host (Taylor *et al*., 1996; Westwood, 2013). An increase in ABA concentration leads to a decrease in stomatal aperture, stomatal conductance, photosynthesis, host growth and increase in flow of the xylem sap from the host to the parasite (Taylor *et al*., 1996; Westwood, 2013). Equally well a decrease in GA leads to stunted growth of the host and lessen it competitive ability (Taylor *et al*., 1996). Accordingly, it is plausible that differences in magnitude of the perturbation of the hormonal balance and/or differential sensitivity to the attained changes in hormonal balance between genotypes may alter the xylem flow from the host to the parasite. However, the possibility of vascular occlusion as noted for some sorghum genotypes (Timko and schools, 2013) cannot be refuted. In nature juvenile *S. hermonthica* plants at 6-8 weeks post-infection are subterranean and are totally dependent on their hosts for nutrients, water and carbon compounds essential for growth and survival. The results attained in this study is consistent with a model in which the sorghum genotypes Tetron and Hakika resistance to *S. hermonthica* could be accounted for, at least in part, by physiological reactions which impair transfer of water, nutrients and carbon compounds from the host to the parasite.

Conclusion:

S. hermonthica attached, displayed rapid development and low mortality on the tolerant genotype Wad-Ahmed, while slow development and high mortality were exhibited on the resistant congeneers Tetron and Hakika. In contrast to previous reports which claimed that pre-attachment resistance residing on low stimulant production is the principal mechanism of resistance of the sorghum genotypes Tetron and Hakika to the parasite the present study showed, for the first time, that post-attachment resistance subsequent to establishment of xylem-to-xylem connection, is a key component of the overall resistance of the two genotypes to the parasite. Further, the study clearly demonstrates the need to use more than one assay procedure to fully delineate the mechanisms conferring resistance to *S. hermonthica*

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Table1. *Striga hermonthica* germination as influenced by **sorghum genotype** and time in weeks post inoculation

Sorghum genotypes	**Time in weeks**		
	first	**second**	**third**
Hakika	**52.6 (** 46.7) e	**64.1** (53.7) cde	**74.1** (60.1) bcd
Tetron	**61.1** (52.2) de	**72.3** (59.0) bcd	**85.5** (68.6) ab
Wad-Ahmed	**66.9 (**54.9) cde	**80.8 (**64.4) abc	**92.1** (74.3) a
Mean	51.3 c	59.0 b	67.7 a
SE± Cultivars		3.24	
SE± Dates		3.24	
SE± Cultivars*dates		5.62	
		F value	
Cultivars		0.0085**	
Dates		0.0002***	
Cultivars*dates		0.9594NS	
CV		**13.39**	

Data within parenthesis are arcsine transformed. Data not within parenthesis are the actual germination data.

Table and Figures legends:

Table.1.*Striga hermonthica* germination as influenced by **sorghum genotype** and time in days post inoculation. Data within parenthesis is arcsine transformed. Data not within parenthesis is the actual germination data.

Fig 1. *Striga hermonthica* development and survival on Wad-Ahmed as influenced by time. A) 7, B) 14 and C) 21 days post inoculation. Bars, each, represent a mean of 4 replicates. Vertical bars represent standard error of the means.

Fig1.

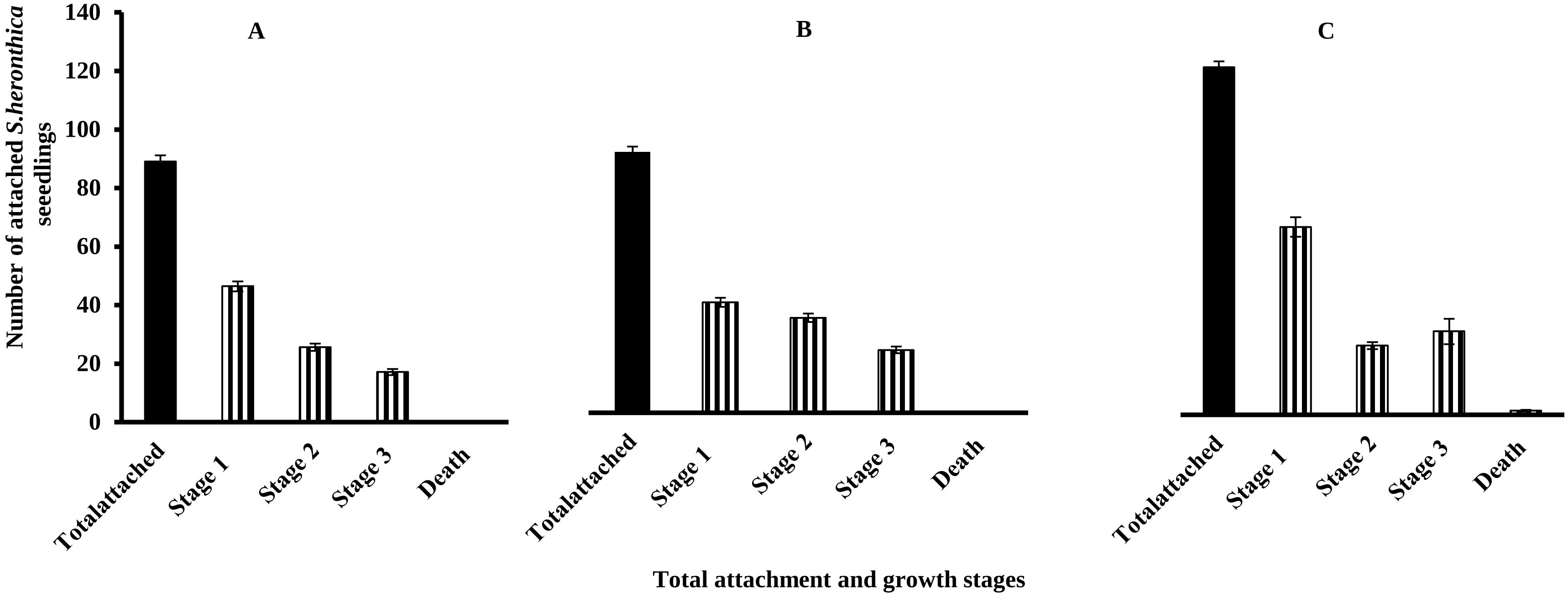

A
B
C
Number of attached *S.heronthica* seedlings
140
120
100
80
60
40
20
0
Totalattached
Stage 1
Stage 2
Stage 3
Death
Total attachment and growth stages

Fig 2 .

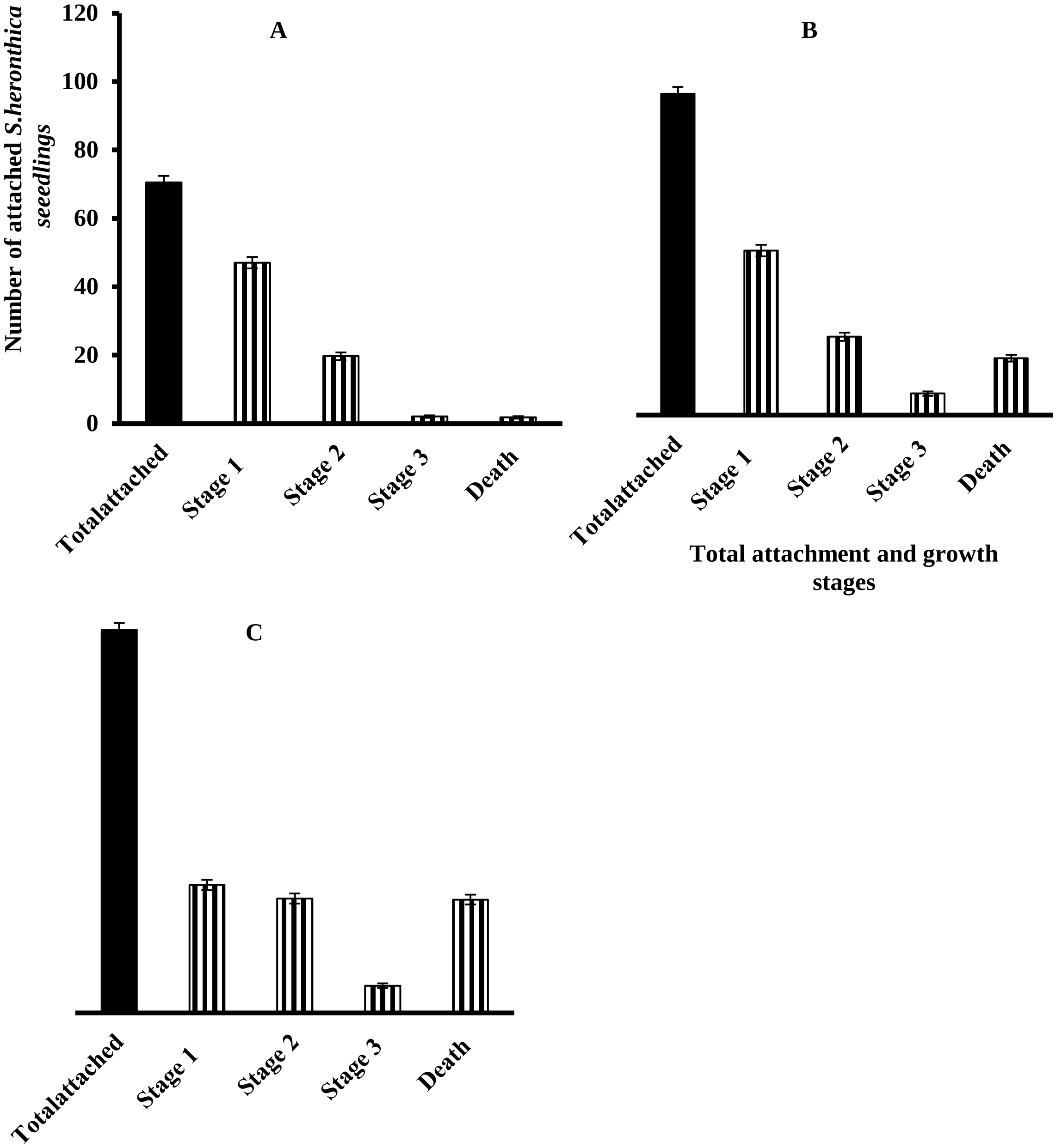
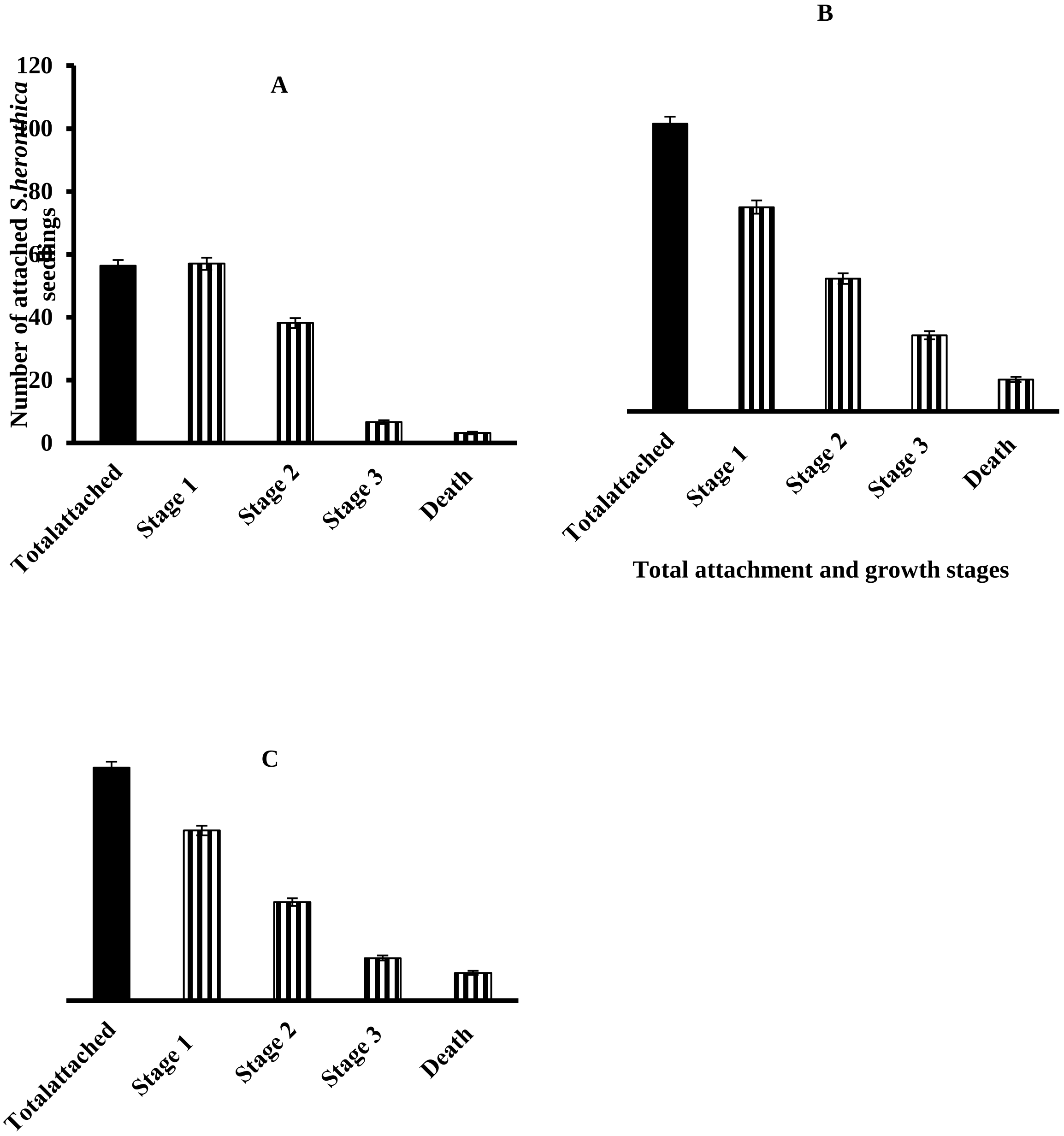

A
B
C
120
100
80
60
40
20
0
Number of attached S.heronthica seeedlings
Totalattached
Stage 1
Stage 2
Stage 3
Death
Total attachment and growth stages

Fig 3.


B
120
100
80
60
40
20
0
A
Number of attached S.heronthica seedlings
Totalattached
Stage 1
Stage 2
Stage 3
Death
Totalattached
Stage 1
Stage 2
Stage 3
Death
Total attachment and growth stages
C
Totalattached
Stage 1
Stage 2
Stage 3
Death

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تأثير النمط الجيني للذرة الرفيعة على الإنبات والتعلق والبقاء على قيد الحياة للبودا

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المستخلص

تشكل حشيشة البودا(*Striga hermonthica*) المتطفلة جذريا معوقًا كبيرًا أمام إنتاج الحبوب في أفريقيا جنوب الصحراء. وقد تمت التوصية بالعديد من تدابير التحكم ، ومع ذلك ، فإن عدم التوافق مع أنظمة إنتاج المدخلات المنخفضة السائدة يحول دون اعتمادها. يمكن أن توفر الأنماط الجينية المقاومة حلًا مثاليًا ؛ ومع ذلك ، تتطلب المقاومة الدائمة وجود آليات متعددة للمقاومة.تم إجراء البحث الحالي في كلية الدراسات الزراعية بجامعة السودان للعلوم والتكنولوجيا لدراسة الإنبات لبذور البودا(*S. hermonthica*) ، وربط البادرات والتطور اللاحق ، لمدة ثلاثة أسابيع ، على ثلاثة أنواع وراثية من الذرة الرفيعة ، وداحمد، صنف متحمل للبودا ، و تترون بري محلي مقاوم ، و حقيقة ، نمط وراثي مقاوم غريب ، وذلك باستخدام نظام مخبري (تقنية رايزوترون) للذرة الرفيعة المشتركة. ازداد انبات البودا بشكل تدريجي مع مرور الوقت وكان 92.1-66.9٪ و 85.5-61.1٪ و 74.1-52.6٪ لود أحمد وتترون وحقيقة على التوالي. أثرت البودا على ارتباط مماثل (68.8-53.6 ٪) بجذور الأنماط الجينية الثلاثة. ومع ذلك كان نمو وبقاء البودا يعتمد على النمط الجيني. في 1-3 أسابيع بعد تلقيح البودا في المرحلة 3 كانت 24.7-19.1٪ و 7.1-2.9٪ و 12.6-6.3٪ في ود أحمد وتترون وحقيقة على التوالي. وبلغ معدل موت للبودا 0-1.2٪ و 8.1-3.0٪ و 29.6-2.5٪ في ود أحمد وحقيقة وتترون على التوالي. تطور النمو بعد المرحلة 2 ، حيث تم تأسيس علاقة ارتباط طبقة الخشب بين الطفيل والمضيف (xylem-to-xylem) ، إلى جانب الموت البارز للبودا على تترون وحقيقة تشير إلى أن مقاومة البودا في هذه الأنماط الجينية تُعزى جزئيًا إلى ضعف تحويل المواد الغذائية والمياه ومركبات الكربون من العائل إلى الطفيل