

Genetic Variation for *Striga hermonthica* Resistance and Yield Among Sorghum Accessions in Nigeria

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Abstract

Striga hermonthica (Delile) Benth., commonly referred to as witch weed, is a major constraint to sorghum (*Sorghum bicolor* (L.) Moench) production in the Northern region of Nigeria because of high yield losses due to infestation. To identify parental lines useful in breeding for *S. hermonthica* resistant sorghum genotypes adapted to Nigeria, twenty-five sorghum accessions were evaluated in Nigeria across three test environments. Both phenotypic and genetic components influenced the variation observed in the sorghum accessions. The estimates for the genetic coefficient of variation, heritability and genetic advance for the area under *Striga* number progress curve (ASUNPC), *Striga* emergence counts, yield and other agronomic traits, obtained in this study revealed that genetic gain for resistance to *S. hermonthica* could be realized through selection. Based on the performance of the 25 sorghum accessions SRN39, Danyana, Sepon82, and SAMSORG40 were the top four accessions found to be most resistant to *S. hermonthica*. Assessment of resistance was based on the low *Striga* emergence counts and the ASUNPC values. These accessions can be used as donor sources of *S. hermonthica* resistant genes for introgression into cultivars adapted to Nigeria, followed by recombination breeding for pyramiding the different resistance mechanisms.

Keywords: ASUNPC, constraints, infestation, *Striga*, witch weed

1. Introduction

Sorghum (*Sorghum bicolor* (L.) Moench) is essential for food security in sub-Saharan Africa (SSA), due to its relative drought tolerance as compared with other cereals (Senthilvel et al., 2008). This is evident from breeding programs in the region that are directing their efforts in developing sorghum varieties that are high yielding, resistant to insect pests and diseases, *Striga hermonthica* and can also survive in drought-prone environments (Obilana, 2004). These breeding efforts through hybridization and successful selection have led to the development of pure-line cultivars from progenies with suitable adaptation (plant height and maturity), disease resistance and higher yield (Rooney, 2004).

Despite all efforts aimed at the improvement in breeding programs, sorghum yield still remains very low (0.83 t/ha) in sub-Saharan Africa (SSA) (Tadele, 2017), with approximately 1.2 t/ha in Nigeria (FAOSTAT, 2018). This is attributable to several biotic and abiotic production constraints. The parasitic weed, *Striga hermonthica* is one of the major biotic constraints to sorghum production in SSA. *Striga hermonthica* causes damage to its host by extracting water, nutrients and assimilates, thus affecting the host water relations and carbon fixation (Press et al., 1996). *Striga hermonthica* depends mainly on the host for its survival with its life cycle closely revolving around that of the host plant. The development and deployment of effective host-plant resistance (HPR) is the most feasible option against this parasite (Kountche et al., 2013).

Several differential resistance mechanisms to *S. hermonthica* by sorghum genotypes, based on field/ glasshouse conditions, have been described by (Hausmann et al., 2000a). Such mechanisms include the production of low germination stimulant, the mechanical prevention of host cell penetration in the form of cell wall lignification, the inhibition of exo-enzymes in the germ tube by root exudates and the synthesis of phytoalexin. Likewise, as described by (Lane et al., 1993), there could be hypersensitive reactions after *S. hermonthica* attachment or incompatibility which may result into the reduction of further growth once the haustorial connection is established. The reduction of *Striga* development through; antibiosis which is the supply of unsuitable phytohormone by the host, insensitivity to *Striga* toxin by maintaining the stomatal aperture, photosynthetic efficiency and the inhibition of haustorial formation are other mechanisms of reducing *Striga* development in host plants (Hausmann et al., 2000a; Ejeta et al., 2000).

The resistance of the various sorghum genotypes can be defined based on field or pot observations with different *Striga* infection measures indicating the level of resistance. Such measures as described by (Hausmann et al., 2000a) include: (i) number of emerged *Striga* plants per pot or m² at n days after sowing (Sn). Such counts could be done at 2-week intervals starting from 2-3 weeks after the first *Striga* plant has emerged in the trials. (ii) Number of above-ground *Striga* plants at harvest (NSharvest); (iii) mean *Striga* vigor score (Vn). The score is based on the morphological characteristics of the *Striga* plant by evaluating the mean *Striga* height and number of branches and is scored at each counting date on a 1-9 scale. The score is important because the effect of *Striga* plants of 5 cm height may differ significantly from that of fully-developed 40 cm *Striga* plants with numerous branches, flowers, and seed capsules. Another measure is *Striga* severity index at n days after sowing (SVn) which is estimated by multiplying the emerged *Striga* by its respective mean *Striga* vigor. This resistance measure helps to have a relative assessment of the total *Striga* biomass in a plot because the evaluation of *Striga* biomass is a destructive measure that is generally painstaking and commonly has a high error variance (Omanya et al., 2004). Area Under the Above-ground *Striga* Number Progress Curve (AUSNPC) is another measure. This trait is calculated from the successive emerged *Striga* counts by adapting the formula for Area Under the Disease Progress Curve, AUDPC (Hausmann et al., 2000a). The AUSNPC accounts for the intensity and speed of the *Striga* epidemic and the higher the AUSNPC the more susceptible the genotype is. Finally, another measure for resistance evaluation is (iv) the Area Under the *Striga* Severity Progress Curve (AUSNPC) which can also be estimated using the severity value.

Narrow genetic variability range among accessions of a crop is always disadvantageous because it limits the crop's ability to adapt to or tolerate/resist environmental stresses and epidemics which result in yield loss (Govindaraj et al., 2015). However, there are many wild relatives (National Research Council, 1993), landraces and some improved varieties of crop plants which possess genes influencing resistance to both biotic and abiotic stresses which when introgressed into economically important varieties, could help avert or lessen the issue of yield loss through appropriate breeding schemes. Identification of *S. hermonthica* resistant sorghum accessions will lead to the development of varieties suitable for different agro-ecological zones in Nigeria. Improvement in yield will, in turn, have a significant impact on the livelihoods of farmers thus helping them to reduce poverty as yield security is guaranteed in *Striga* infested conditions (Rodenburg et al., 2017). In the present study, different African landraces, uncharacterized sorghum accessions which have never been screened for resistance to *S. hermonthica* as well as released sorghum varieties available in Nigeria's national gene bank, farmers preferred varieties and documented *S. hermonthica* resistant sorghum varieties were evaluated to; i) characterize genetic variation for *S. hermonthica* resistance, and ii) identify diverse germplasm in *S. hermonthica* resistance breeding.

2. Materials and Methods

2.1 Experimental Material

Experimental materials consisted of 25 sorghum accessions, including two *S. hermonthica* resistant lines (N13 and SRN 39) with known resistant mechanisms and validated QTLs (Table 1).

2.2 Experimental Sites

These accessions were evaluated at the Institute for Agricultural Research (IAR) Samaru, Zaria (11.17, 7.62, altitude 688 m), farmers' fields at Karaukarau, Giwa local government area Kaduna (11.32, 7.38, altitude 679 m) and Farmers' field at Mokwa, Niger state (9.20, 5.47, altitude 331 m). These environments are *Striga* sick plots in high sorghum producing areas.

2.3 Experimental Methods

The accessions were arranged in 5×5 alpha lattice design with three replications. An individual variety was grown on two 5 m rows per plot with 0.75 m spacing between rows and a 0.3 m in row spacing. Plots were demarcated by an empty row of 1 m and a 1.25 m alley was used to separate each replicate.

The experiments were carried out on *S. hermonthica* infested fields that were ascertained to be highly infested and which had been used repeatedly for *S. hermonthica* research. However, to avoid the case of heterogeneity of natural field infestations, artificial *S. hermonthica* infestation of each planting hill was done at a depth of 10cm. *S. hermonthica* seeds used was mixed with finely sieved soil at 30 g of *Striga* seeds per 2000 g of soil and 2.5 g of the mixture was used for infestation per planting hill. In each of the trials, sorghum was sown at 6 seeds per planting hill and was thinned to 2 plants per hill, 25 days after sowing (DAS). Throughout the experiments, all trials were frequently hand weeded between 2 to 3 weeks to eliminate all weeds except *S. hermonthica*. Fertilizer application was done at the rate of 60 kg/ha of NPK 15-15-15 at 4 weeks after sowing and all agronomic practices for sorghum were carried out.

2.4 Collection of Agronomic and Striga Resistant Data

Data were recorded on days to 50% flowering (DTF), Plant height (PH), number of panicles harvested per plot (Head count: HC), the weight of harvested panicle (HW) after drying, grain weight after threshing (GW) and grain yield (GY). The number of *Striga* plants per plot was obtained by counting all the emerged *Striga* plants in each plot, *Striga* emergence counts (STC) were taken at two weeks intervals starting from 45 days after sowing. Emerged *Striga* counts at 45, 59 and 73 days after sowing were recorded at the three environments.

2.5 Data Analysis

Analysis of variance (ANOVA) was conducted on plot means for all traits measured for each of the environment separately followed by combined analysis across environments using the PROC GLM in SAS (K. A. Gomez & A. A. Gomez 1984; SAS Institute, 2010). The analysis from the three environments shows moderate heritability estimates and low coefficient of variation for all traits measured (data not shown) thereby justifying the analysis across the environments. In order to satisfy the rule of the normal distribution, a logarithmic transformation $[\log_{10}(X + c)]$, where, X is the original, individual count and $c = 1.0$, according to (Rodenburg, 2005) was applied to the emerged *Striga* count data before conducting ANOVA. The Area Under *Striga* Number Progress Curve (AUSNPC) which is a degree of the total *Striga* emergence during the growing season, as defined by (Rodenburg, 2005) was estimated with the transformed data as

$$\text{AUSNPC} = \sum_{i=0}^{n-1} \left[S_i + \frac{S_{(i+1)}}{2} \right] [t_{(i+1)} - t_i] \quad (1)$$

where, n = the number of days at which *Striga* was counted, S_i = the *Striga* number at the i^{th} assessment date, t_i = the number of days after sowing at the i^{th} assessment date.

Entry means adjusted for block effects according to the lattice design (Cochran & Cox, 1960) were generated for each trait across environments. A rank summation index (RSI) (Mulumba & Mock, 1978) was constructed to create the aggregate trait by ranking the lines with regard to high grain yield, *S. hermonthica* resistance, and improved agronomic performance. The 25 accessions were ranked from lowest to highest for each trait and RSI was calculated by summing the ranks. The ranks were summed for each accession to select the top ten outstanding sorghum accessions. An accession with the least number for days to 50% flowering, AUSNPC, *Striga* emergence count at 45, 59 and 73 DAS and the highest number for grain yield, ranks first for RSI.

Expectations of mean squares (EMS) from analysis of variance were used to estimate phenotypic (σ^2_p) and genotypic (σ^2_g) variances according to (Keneni & Jarso, 2009). Phenotypic (PCV) and genotypic (GCV) coefficients of variation were derived using the formula of (Allard, 1960):

$$\text{PCV} = \frac{\sqrt{\sigma^2_p}}{\text{Grand mean}} \times 100 \quad (2)$$

and,

$$\text{GCV} = \frac{\sqrt{\sigma^2_g}}{\text{Grandmean}} \times 100 \quad (3)$$

Broad sense heritability (h^2) was estimated according to (Johnson et al., 1955) by the formula:

$$h^2 = \frac{\sigma^2_g}{\sigma^2_p} \quad (4)$$

where, σ^2_p = phenotypic variance and σ^2_g = genotypic variance.

The heritability percentage was categorized as low, moderate and high, similar to that of (Robinson et al., 1949) as follows: < 50% = low; 50% = moderate and > 50% = high. Genetic advance expressed as a percent of the mean supposing a selection intensity of 5% were also calculated using the formula of (Robinson et al., 1949) as follows:

$$GA = K \frac{\sigma_g^2}{\sqrt{\sigma_p^2}} \quad (5)$$

$$GA\% \text{ (GA as \% of the mean)} = \frac{GA}{\text{grandmean}} \times 100 \quad (6)$$

where, k represents the standardized selection differential which was 2.06 at 5% selection differential and it was 2.06 as defined by (Lush, 1949), σ_g^2 is the genetic variance, and $\sqrt{\sigma_p^2}$ denotes phenotypic standard deviation. Pearson's correlation analysis was done to determine the associations among grain yield and other measured agronomic traits with SAS (SAS Institute, 2010).

3. Results

3.1 Performance of Sorghum Accessions Across Test Environments

The combined ANOVA for data collected under artificial *S. hermonthica* infestation evaluated across three environments showed that the environment was an important source of variation for all traits measured except for grain weight and yield (Table 2). The 25 sorghum accessions and accessions \times environment interaction mean squares were highly significant ($P < 0.001$) for yield-related traits, number of days to 50% flowering and plant height, except for *Striga* emergence counts at 45, 59 and 73 days after sowing and AUSNPC. Across the environments, average grain yield and other yield-related traits values were highest at IAR-Zaria. The sorghum accessions grew taller at Giwa-Kaduna and flowered earliest at Mokwa-Niger. The range of *Striga* emergence counts at 45, 59 and 73 days after sowing across environments was 0.17 to 2.43 and Mokwa-Niger had the highest average count of 1.40 at 73 days after sowing (Table 3). Average AUSNPC of the accessions ranged from 0.41 to 60.92. Higher *Striga* infestation was observed at IAR-Zaria with an average AUSNPC of 34.10.

3.2 Performance of Outstanding Sorghum Accessions Across the Test Environments

The mean grain yield of the 25 sorghum accessions evaluated under artificial *S. hermonthica* infestation ranged from 1065.60 kg ha⁻¹ for Sariaso 14 to 4233.84 kg ha⁻¹ for SAMSORG 14 (Appendix A). From the list of the outstanding sorghum accessions, lowest *Striga* emergence count was recorded across environments for SRN39 and Sepon82, but with low grain yield (Table 4). Also, farmers' preferred variety (SAMSORG 40) and NGJD0511063 an accession collected from the national gene-bank of Nigeria had low *Striga* emergence count. Danyana was ranked as the most promising accession with a lower level of *Striga* emergence count combined with high grain yield. The AUSNPC being one the most discriminative measure of resistance gives a degree of the entire *Striga* growth and the level of infestation on its hosts over the growing season. On average, the accessions SRN39 and Sepon82 had the lowest AUSNPC across the environments.

3.3 Genetic Variability Among Sorghum Accessions

The phenotypic variances were larger than the genotypic variances for all the traits measured (Table 5). Grain yield and plant height had the highest phenotypic and genotypic variances. *Striga* emergence count at 45, 59 and 73 days after sowing and AUSNPC had low values for phenotypic and genotypic variances with heritability estimates ranging from 21-32%. Broad sense heritability estimates were high (*i.e.*, > 50%) for head weight, grain weight, grain yield, plant height and days to 50% flowering. However, *Striga* resistance traits reflect lower broad-sense heritability estimates. The Genetic advance as a percentage of the mean ranged from 0.30% for head count to 39.63% for grain yield.

3.4 Phenotypic Correlation

Traits with similar physiology were highly correlated; grain weight was significantly ($P < 0.001$) correlated with head count and height weight. Grain yield had strong positive correlation ($P < 0.001$) with head count, head weight, and grain weight. There was a strong and positive ($P < 0.001$) relationship between AUSNPC and *Striga* emergence count at 45, 59 and 73 days after sowing (Table 6). The significant ($P < 0.01$) correlations between *Striga* emergence count after sowing with head count, number of days to 50% flowering and plant height were rather weak. A negative significant correlation ($P < 0.05$) was recorded between *Striga* emergence count at 73 days after sowing and plant height. There was no significant correlation between grain yield and *Striga* emergence count at 45, 59 and 73 days after sowing and AUSNPC.

Table 1. Description of sorghum accessions evaluated

S. no.	Accession	Source	Comment
1	NGAA0311016	NACGRAB, Nigeria	Local collections, unknown resistance
2	NGOJMAY09009	NACGRAB, Nigeria	Local collections, unknown resistance
3	NGSA07143	NACGRAB, Nigeria	Local collections, unknown resistance
4	NGSA07103	NACGRAB, Nigeria	Local collections, unknown resistance
5	NGJD0511063	NACGRAB, Nigeria	Local collections, unknown resistance
6	NGAO1108001	NACGRAB, Nigeria	Local collections, unknown resistance
7	SAMSORG 14	Nigeria	Improved variety, tolerant to <i>Striga</i>
8	SAMSORG 40	Nigeria	Improved variety, Susceptible to <i>Striga</i>
9	Danyana	Nigeria	Farmers variety, late maturing, unknown resistance
10	CSR-01	Nigeria	Improved variety, High malting quality, unknown resistance
11	CSR-02	Nigeria	Improved variety, High malting quality, unknown resistance
12	SAMSORG 39	Nigeria	Improved variety, Susceptible to <i>Striga</i>
13	SRN 15401	Nigeria	Improved variety, unknown resistance
14	N13	ICRISAT, Mali	<i>Striga</i> resistance
15	SRN39	ICRISAT, Mali	<i>Striga</i> resistant-LGS-Sudan
16	White Kaura	ICRISAT, Mali	Unknown resistance
17	MaceDaKunya	ICRISAT, Mali	Late-season dune sorghum-Niger, unknown resistance
18	Wassa	ICRISAT, Mali	Food-grade guinea-Mali, unknown resistance
19	Malisor 84-7	ICRISAT, Mali	Food-grade-Mali, unknown resistance
20	CSM-63	ICRISAT, Mali	Popular Guinea-Mali, unknown resistance
21	Grinkan	ICRISAT, Mali	Food Grade Guinea-Mali, unknown resistance
22	Framida	ICRISAT, Mali	<i>Striga</i> resistant-Burkina Faso
23	Sepon82	ICRISAT, Mali	Food-grade-Niger, unknown resistance
24	Sariaso14	ICRISAT, Mali	<i>Striga</i> resistant-LGS-Burkina Faso
25	Seguetana	ICRISAT, Mali	Food-grade guinea-Mali, unknown resistance

Note. NACGRAB = National Center for Genetic Resources and Biotechnology Nigeria; ICRISAT = International Crop Research Institute for the Semi-Arid Tropics Mali.

Table 2. Mean squares of *S. hermonthica* resistance and other agronomic traits of sorghum accessions evaluated across three environments in Nigeria

Source	df	Head-Count	Head Weight (kg)	Grain Weight (Kg)	Grain Yield (kg ha ⁻¹)	Days to 50% flowering	Plant Height (cm)	<i>Striga</i> emergence count at 45 DAS	<i>Striga</i> emergence count at 59 DAS	<i>Striga</i> emergence count at 73 DAS	AUSNPC
Environment (Env)	2	1530.59***	4.04*	0.20	1778403	5064.23***	189033.83***	5.55***	1.73*	2.51**	1107.41**
Replication (Rep) (Env)	6	106.63	0.42	0.27	2390860	145.83	3254.02	0.24	0.13	0.16	105.63
Block (Rep × Env)	36	111.63*	0.54*	0.18	1573857	73.65	2825.07**	0.31***	0.30***	0.23**	209.96**
Accessions	24	175.03	1.33**	0.71**	6306471***	845.39**	24911.87***	0.22	0.29	0.24	189.47
Accessions x Env	48	176.40***	0.57**	0.30***	2602801**	326.63***	6673.38***	0.15	0.20	0.15	128.65
Error	102	73.41	0.32	0.14	1260528	99.35	1504.53	0.14	0.14	0.12	90.11
CV		36.14	45.55	43.93	43.93	11.25	17.21	41.48	33.14	27.68	31.62

Note. *, **, *** Significant at 0.05, 0.01 and 0.001 probability levels, respectively. AUSNPC = Area Under *Striga* Number Progress Curve, DAS = Days after sowing.

Table 3. Mean performance of the sorghum accessions for grain yield, *S. hermonthica* emergence counts, AUSNPC and other agronomic traits at three different environments in Nigeria

Environments	Head Count			Head Weight (kg)			Grain Weight (Kg)			Grain Yield (kg ha ⁻¹)			Plant Height (cm)		
	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
IAR-ZARIA	10.46	40.96	28.71	0.43	3.10	1.51	0.27	1.95	0.93	807.83	5805.08	2771.83	124.75	332.08	236.51
GIWA-KADUNA	1.79	46.55	19.51	0.02	2.64	1.20	0.11	1.83	0.82	337.66	5450.28	2454.37	133.25	480.51	269.67
MOKWA-NIGER	0.26	42.64	22.84	0.34	1.44	0.99	0.03	1.40	0.81	100.88	4178.39	2420.48	73.88	334.75	169.88
LSD (5%)			12.73			0.96			0.64			1892.45			62.45
Environments	Days to 50% flowering			<i>Striga</i> emergence count at 45 DAS			<i>Striga</i> emergence count at 59 DAS			<i>Striga</i> emergence count at 73 DAS			AUSNPC		
	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
IAR-ZARIA	77.29	121.41	95.55	1.01	1.41	1.17	1.10	1.48	1.28	1.16	1.50	1.32	29.61	39.6	34.10
GIWA-KADUNA	76.34	126.06	91.08	0.69	1.11	0.91	0.78	1.09	0.96	0.91	1.16	1.04	21.38	30.09	26.18
MOKWA-NIGER	38.27	106.66	79.03	0.29	1.87	0.62	0.17	2.20	1.12	0.50	2.43	1.40	0.41	60.92	29.79
LSD (5%)			9.93			0.30			0.24			0.22			6.30

Note. Min = Minimum, Max = Maximum, AUSNPC = Area Under *Striga* Number Progress Curve, DAS = Days after sowing

Table 4. Means of outstanding sorghum accessions and rank summation index of grain yield and its agronomic components

Accession	Grain Yield (kg ha ⁻¹)	Days to 50% flowering	<i>Striga</i> emergence count at 45 DAS	<i>Striga</i> emergence count at 59 DAS	<i>Striga</i> emergence count at 73 DAS	AUSNPC	Rank summation index
SRN39	1689.08±451.25	70.56±3.88	0.60±0.14	0.68±0.14	0.93±0.13	19.53±3.68	31
Danyana	4077.76±468.95	92.96±3.85	0.68±0.14	0.94±0.14	0.91±0.13	23.59±3.67	32
Sepon82	2083.17±498.38	94.09±4.25	0.57±0.15	0.63±0.15	0.92±0.14	18.63±3.73	36
SAMSORG40	1589.17±455.70	80.45±3.91	0.65±0.15	0.88±0.14	1.00±0.14	23.18±3.70	42
Grinkan	2640.10±449.33	87.47±3.89	0.80±0.15	1.01±0.14	1.09±0.13	26.67±3.69	49
CSM63	1871.81±498.18	89.95±3.91	0.79±0.15	1.00±0.15	1.09±0.14	26.44±3.72	52
NGJD0511063	2898.24±475.42	102.53±3.87	0.67±0.14	0.97±0.14	1.14±0.13	25.52±3.66	53
MaceDaKunya	3971.42±438.90	94.56±3.84	0.82±0.14	1.04±0.14	1.20±0.13	27.95±3.65	58
Framida	2292.50±435.07	78.28±3.83	0.86±0.14	1.17±0.14	1.26±0.13	30.54±3.64	61
NGSA07103	1998.14±441.06	90.63±3.86	0.86±0.14	1.02±0.14	1.18±0.13	27.90±3.67	63

Note. AUSNPC = Area Under *Striga* Number Progress Curve, DAS = Days after sowing.

Table 5. Means, estimates of genetic variance, phenotypic variance, genotypic and phenotypic coefficient of variation, broad-sense heritability and genetic advance for grain yield and its agronomic components

Traits	Mean	Variances		%			
		σ^2_g	σ^2_p	PCV	GCV	H ² (%)	GA
Head Count	23.71	0.15	19.45	18.60	1.64	0.78	0.30
Head Weight (kg)	1.24	0.08	0.15	31.00	23.43	57.14	36.49
Grain Weight (Kg)	0.86	0.05	0.08	32.66	24.82	57.75	38.85
Grain Yield (kg ha ⁻¹)	2555.49	411518.82	700718.96	32.76	25.10	58.73	39.63
Days to 50% flowering	88.60	57.64	93.93	10.94	8.57	61.36	13.83
Plant Height (cm)	225.35	2026.50	2767.99	23.35	19.98	73.21	35.21
<i>Striga</i> emergence count at 45 days after sowing	0.90	0.01	0.02	17.37	8.28	22.73	8.13
<i>Striga</i> emergence count at 59 days after sowing	1.12	0.01	0.03	16.03	7.29	20.69	6.83
<i>Striga</i> emergence count at 73 days after sowing	1.25	0.01	0.03	13.06	6.53	25.00	6.73
Area Under <i>Striga</i> Number Progress Curve	30.02	6.76	21.05	15.28	8.66	32.11	10.11

Note. σ^2_g = genotypic variance, σ^2_p = phenotypic variance, GCV = genotypic coefficient of variation, PCV = phenotypic coefficient of variation, H² (%) = heritability in the broad sense given as a percentage, GA = genetic advance as percentage of mean.

Table 6. Correlation coefficients of grain yield and its agronomic components across environments

	HC	HW	GW	GY	DTF	PH	STC45	STC59	STC73	AUSNPC
HC		0.66***	0.68***	0.68***	0.14*	0.03	0.17**	0.18**	0.16*	0.18**
HW			0.92***	0.92***	0.36***	0.29***	0.12	0.07	0.00	0.06
GW				1.00***	0.30***	0.29***	0.05	0.07	0.04	0.06
GY					0.30***	0.29***	0.05	0.07	0.04	0.06
DTF						0.38***	0.14*	0.03	-0.09	0.02
PH							0.16**	-0.01	-0.14*	-0.01
STC45								0.75***	0.60***	0.83***
STC59									0.89***	0.98***
STC73										0.92***
AUSNPC										

Note. *, **, *** Correlation coefficient (r) significant at 0.05, 0.01 and 0.001 probability levels, respectively. HC = head count: number of sorghum panicles harvested per plot, HW = head weight: weight of harvested sorghum panicles after drying, GW = grain weight of harvested sorghum panicles; GY = grain yield, DTF = number of days to 50% flowering; PH = plant height, STC45, STC59, STC73 = *Striga* emergence count at 45, 59 and 73 days after sowing, AUSNPC = Area Under *Striga* Number Progress Curve.

4. Discussion

The large and significant environment mean squares for *Striga* resistance indices in this study depict variability in the test environments. Thus, testing of the sorghum accessions in several environments will help in identifying *Striga* resistance and high yielding varieties. Diverse genetic background accounts for the significant differences observed in yield related traits, number of days to 50% flowering and plant height. The non-significant difference for *Striga* emergence count at 45, 59 and 73 days after sowing and AUSNPC confirms tolerance to *Striga* in most of the sorghum accessions evaluated. Additionally, N13 and SRN 39 have been reported as resistant to *S. hermonthica* (Hausman et al., 2004; Satish et al., 2012). Highly significant accessions x environment interactions identified in this study for studied traits with exception of *Striga* resistance traits, indicates the ability of the experimental sites to discriminate the accessions evaluated. As the performance of the accessions were not consistent under the three environments, possibly because of the differences in the environmental factors. Our result is in agreement with Robert (2011) who reported non-significant genotype by environment interaction effect for all *Striga* resistance parameters measured in spite of the highly significant differences between the environments of evaluation for Uganda sorghum accessions.

Following the equation given by (Rodenburg et al., 2005), the individual *Striga* emergence counts were converted into the area under *Striga* number progress curve (AUSNPC) which is an excellent measure used in describing the degree of *Striga* emergence on the field throughout the growing season. According to (Hausmann et al., 2001), genotypes having low values for AUSNPC are classified as resistant to *Striga* while on the other hand, those with high values are susceptible. The performance of the 25 sorghum accession under artificial *Striga* infestation shows that SRN 39, Danyana, Sepon 82 and SAMSORG 40 combined lower values for *Striga* emergence counts and AUSNPC which are a useful index for *Striga* resistance. SRN39 was selected as most resistant to *Striga* infestation based on the low AUSNPC but had a relatively low yield. This corroborates the findings of (Press et al., 1996; Robert, 2011). However, the resistance nature of SRN39 in the present research was expressed more under low *Striga* pressure. The resistance of SRN39 has been described to be in the production of low germination stimulant which is conferred by a single major gene, *lgs* with a recessive mode of inheritance (Gobena et al., 2017). Nevertheless, such single-gene mechanism of *Striga* resistance is not enough to prevent infestation when the amount of *Striga* seed present in the soil is very high. Therefore relying on resistance conferred by a single mechanism and single gene is likely to prove risky when using host plant resistance to control a highly variable and allogamous noxious weed such as *Striga hermonthica* (Rodenburg & Bastiaans, 2011; Yoder & Scholes, 2010). On the other hand, the resistance nature of these outstanding sorghum accessions may be exploited in backcross breeding.

Gobena et al. (2017) and Satish et al. (2012) have tagged and validated microsatellite markers linked to the *lgs* gene in different sorghum accessions including SRN39. Since the low *Striga* germination stimulant activity is a unique resistance mechanism in sorghum, it shows that such markers could be successfully used for marker-assisted breeding to boost *Striga* resistance in sorghum. This suggests that SRN39 could be used as a

donor parent to successfully introgress the low stimulant resistance trait into new and existing sorghum varieties in Nigeria.

The difference between phenotypic and genotypic coefficient of variation expressed in percentage for all traits measured ranged between 14-91%, which is a reflection of high environmental influence on the traits measured. This trend was earlier reflected in the ANOVA by the high environment mean squares. Lower phenotypic and genotypic coefficient of variation and genetic advance observed for *Striga* emergence counts at 45, 59 and 73 days after sowing and AUSNPC in comparison to other traits measured in this study implies low genetic variation among the sorghum accessions for those traits. High broad-sense heritability estimates observed for head weight, grain weight, grain yield, plant height and days to 50% flowering depicts that these traits were quantitatively inherited, indicating the presence of additive gene action. Thus, there is adequate variation for further improvement of these traits, which may be exploited to obtain further breeding gains. The lower broad-sense heritability estimates for AUSNPC and *Striga* emergence counts at 45, 59 and 73 days after sowing indicate that the genetic variation was a small and genetic gain for those traits will be slow because both genetic and phenotypic constituents of the accessions are affected by *Striga* infestation stress. Moderate genetic advance for yield-related traits and plant height indicate the possibility for progress from the selection. Similarly, Robert (2011) reported low heritability estimate and genetic advance for *Striga* resistance related traits. However, high estimates of broad-sense heritability and genetic advance for all measured traits in sorghum has been reported previously by (Warkad et al., 2008; Haussmann et al., 2000b). Thus, the results of this study showed that genetic variation exists among the African sorghum accessions, indicating the opportunities to explore these differences through genetic crop improvement with the intention of reducing yield losses obtained from biotic stresses such as *Striga*. According to (Dhliwayo & Pixley, 2003), such genetic variability is normally used for the introgression of important traits that are deficient in elite crop varieties via conventional breeding and molecular breeding approaches.

Furthermore, our results showed that traits with similar basic physiology were highly associated. The significantly high association between grain yield and head count, head weight, grain weight implies that may be considered as a secondary trait when selecting for improved grain yield in sorghum breeding. In contrast, *Striga* emergence counts at 45, 59 and 73 days after sowing and AUSNPC were not correlated with grain yield, suggesting that they are not reliable parameters for the detection of improved grain yield. The negative and weak correlation between *Striga* emergence counts at 73 days after sowing and plant height suggested that taller plants gave lower *Striga* emergence count. Similarly, Omanyia et al. (2004) reported a negative correlation between the AUSNPC and plant height, thus revealing the impact of *Striga* infestation on sorghum plant resulting in stunted growth which could, in turn, affect the entire crop yield. The strong correlation between *Striga* emergence count and AUSNPC indicate that either of the parameters will be sufficient as a selection criterion. Information on the correlation of traits among the sorghum accessions will aid selection index in sorghum varietal improvement programs.

In conclusion, the genetic variability observed among the 25 sorghum accessions evaluated could be exploited by sorghum breeders to boost the efficiency of sorghum improvement programs. Nonetheless, further studies are needed to identify stable and high yielding sorghum accessions resistant to *S. hermonthica* across multiple environments over years. These accessions may then be selected as parental lines which are useful in sorghum improvement programs in Nigeria.

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References

- Allard, R. W. (1960). *Principles of Plant Breeding*. John Willey and Sons, New York.
- Cochran, W. C. & Cox, C. K. (1960). *Experimental Design*. John Wiley and Sons, Incorporated New York, USA.

- Dhliwayo, T., & Pixley, K. V. (2003). Divergent selection for resistance to maize weevil in six maize populations. *Crop Science*, *43*, 2043-2049. <https://doi.org/10.2135/cropsci2003.2043>
- Ejeta, G., Mohammed, A., Rich, P., Melake-Berhan, A., Housley, T. L., & Hess, D. E. (2000). Selection for specific mechanisms of resistance to *Striga* in sorghum. *Breeding for Striga resistance in cereals* (pp. 29-37). Margraf Verlag, Weikersheim.
- FAOSTAT. (2018). Retrieved May 26, 2019, from <http://www.fao.org/faostat/en/#data/QC>
- Gobena, D., Shimels, M., Richa, P., Ruyter-Spirab, C., Bouwmeesterb, H., Kanugantia, S., ... Ejeta, G. (2017). Mutation in sorghum low germination stimulant alters strigolactones and causes *Striga* resistance. *PNAS*, *114*(17), 4471-4477. <https://doi.org/10.1073/pnas.1618965114>
- Gomez, K. A., & Gomez, A. A. (1984). *Statistical Procedures for Agricultural Research* (pp. 8-76). New York: John Wiley & Sons.
- Govindaraj, M., Vetriventhan, M., & Srinivasan, M. (2015). Importance of genetic diversity assessment in crop plants and its recent advances: an overview of its analytical perspectives. *Genetics Research International*, *2015*, Article ID 431487. <https://doi.org/10.1155/2015/431487>
- Hausmann, B. I. G., Hess, D. E., Omany, G. O., Folkertsma, R. T., Reddy, B. V. S., Kayentao, M., ... Geiger, H. H. (2004). Genomic regions influencing resistance to the parasitic weed *Striga hermonthica* in two recombinant inbred populations of sorghum. *Theoretical and Applied Genetics*, *109*(5), 1005-1016. <https://doi.org/10.1007/s00122-004-1706-9>
- Hausmann, B. I. G., Hess, D. E., Omany, G. O., Reddy, B. V. S., Welz, H. G., & Geiger, H. H. (2001). Major and minor genes for stimulation of seed germination in sorghum, and interaction with different *Striga* populations. *Crop Science*, *45*, 1507-1512. <https://doi.org/10.2135/cropsci2001.4151507x>
- Hausmann, B. I. G., Hess, D. E., Reddy, B. V. S., Mukuru, S. Z., Kayentao, M., Welz, H. G., & Geiger, H. H. (2000b). Diallel studies on *Striga* resistance in sorghum. In B. I. G. Hausmann, D. E. Hess, M. L. Koyama, L. Grivet, H. F. W. Rattunde, & H. H. Geiger (Eds.), *Breeding for Striga resistance in cereals Workshop Proceeding* (pp. 41-57). Margraf Verlag, Weikersheim, Germany.
- Hausmann, B. I. G., Hess, E., Welz, H. G., & Geiger, H. H. (2000a). Improved methodologies for breeding *Striga*-resistant sorghums. *Field Crops Research*, *66*, 195-211. [https://doi.org/10.1016/S0378-4290\(00\)00076-9](https://doi.org/10.1016/S0378-4290(00)00076-9)
- Johnson, H. W., Robinson, H. F., & Comstock, R. E. (1955). Estimation of genetic and environmental variability in soybeans. *Agronomy Journal*, *47*, 314-318. <https://doi.org/10.2134/agronj1955.00021962004700070009x>
- Keneni, G., & Jarso, M. (2009). Comparison of Two Approaches for Estimation of Genetic Variation for Two Economic Traits in Faba Bean Genotypes Grown under Waterlogged Verisols. *East African Journal of Sciences*, *3*, 95-101. <https://doi.org/10.4314/eajsci.v3i1.42793>
- Kountche, B. A., Hash, C. T., Dodo, H., Oumarou, L., Sanogo, M. D., Amadou, T., ... Hausmann, B. I. G. (2013). Development of a pearl millet *Striga*-resistant gene pool: response to five cycles of recurrent selection under *Striga*-infested field conditions in West Africa. *Field Crops Research*, *154*, 82-90. <https://doi.org/10.1016/j.fcr.2013.07.008>
- Lane, J. A., Bailey, J. A., Butler, R. C., & Terry, P. J. (1993) Resistance of cowpea [*Vigna unguiculata* (L.) Walp.] to *Striga gesnerioides* (Willd.) Vatke, a parasitic angiosperm. *New Phytologist*, *125*(2), 405-412. <https://doi.org/10.1111/j.1469-8137.1993.tb03893.x>
- Lush, J. L. (1949). Heritability of quantitative characters in farm animals. *Hereditas* *35*(S1), 356-375. <https://doi.org/10.1111/j.1601-5223.1949.tb03347.x>
- Mulumba, N. N., & Mock, J. J. (1978). Improvement of yield potential in the Eto Blanco maize (*Zea mays* L.) population by breeding for plant traits. *Egyptian Journal of Genetics and Cytology*, *7*, 40-51.
- National Research Council. (1993). *Managing global genetic resources: Agricultural crop issues and policies*. National Academies Press.
- Obilana, A. B. (2004). Research process, dissemination and impacts. In M. C. S. Bantilan, U. K. Deb, C. L. L. Gowda, B. V. S. Reddy, A. B. Obilana, & R. E. Evenson (Eds.), *Sorghum genetic enhancement*. Patancheru, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics.

- Omanya, G. O., Haussmann, B. I. G., Hess, D. E., Reddy, B. V. S., Kayentao, M., Welz, H. G., & Geiger, H. H. (2004). Utility of indirect and direct selection traits for improving *Striga* resistance in two sorghum recombinant inbred populations. *Field Crops Research*, *89*, 237-252. <https://doi.org/10.1016/j.fcr.2004.02.003>
- Press, M., Gurney, A. L., Frost, D. L., & Scholes, J. D. (1996). How does the parasitic angiosperm *Striga hermonthica* influence host growth and carbon relations? In M. T. Moreno, J. I. Cubero, D. Berner, D. Joel, L. J. Musselman, & C. Parker (Eds.), *Advances in parasitic plant research* (pp. 303-310). Sixth International Parasitic Weed Symposium, Cordoba, Spain.
- Robert, O. J. (2011). *Genetic analysis of Striga hermonthica resistance in sorghum (sorghum bicolor) genotypes in Eastern Uganda* (Ph.D. Thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa). Retrieved from <http://hdl.handle.net/10413/9981>
- Robinson, H., Comstock, R. E., & Harvey, P. (1949). Estimates of heritability and the degree of dominance in corn. *Agronomy Journal*, *41*, 353-359. <https://doi.org/10.2134/agronj1949.00021962004100080005x>
- Rodenburg, J., & Bastiaans, L. (2011). Host-plant defence against *Striga* spp.: Reconsidering the role of tolerance. *Weed Research*, *51*, 438-441. <https://doi.org/10.1111/j.1365-3180.2011.00871.x>
- Rodenburg, J., Bastiaans, L., Weltzien, E., & Hess, D. E. (2005). How can field selection for *Striga* resistance and tolerance in sorghum be improved? *Field Crops Research*, *93*, 34-50. <https://doi.org/10.1016/j.fcr.2004.09.004>
- Rodenburg, J., Cissoko, M., Kayongo, N., Dieng, I., Bisikwa, J., Irakiza, R., ... Scholes, J. D. (2017). Genetic variation and host-parasite specificity of *Striga* resistance and tolerance in rice: the need for predictive breeding. *New Phytologist*, *214*(3), 1267-1280. <https://doi.org/10.1111/nph.14451>
- Rooney, W. L. (2004). Sorghum improvement—Integrating traditional and new technology to produce improved genotypes. *Advances in Agronomy*, *83*, 37-109. [https://doi.org/10.1016/S0065-2113\(04\)83002-5](https://doi.org/10.1016/S0065-2113(04)83002-5)
- Satish, K., Gutema, Z., Grenier, C., Rich, P. J., & Ejeta, G. (2012). Molecular tagging and validation of microsatellite markers linked to the low germination stimulant gene (lgs) for *Striga* resistance in sorghum [*Sorghum bicolor* (L.) Moench]. *Theoretical and Applied Genetics*, *124*, 989-1003. <https://doi.org/10.1007/s00122-011-1763-9>
- Senthilvel, S., Jayashree, B., Mahalakshmi, V., Sathish, K. P., Nakka, S., Nepolean, T., (2008). Development and mapping of simple sequence repeat markers for pearl millet from data mining of expressed sequence tags. *BMC Plant Biology*, *8*, 119. <https://doi.org/10.1186/1471-2229-8-119>
- Tadele, Z. (2017). Raising crop productivity in Africa through Intensification. *Agronomy*, *7*, 22. <https://doi.org/10.3390/agronomy7010022>
- Warkad, Y. N., Potdukhe, N. R., Dethé, A. M., Kahate, P. A., & Kotgire, R. R. (2008). Genetic variability, heritability and genetic advance for quantitative traits in sorghum germplasm. *Agricultural Science Digest*, *28*, 165-169.
- Yoder, J. I., & Scholes, J. D. (2010). Host plant resistance to parasitic weeds; recent progress and bottlenecks. *Current Opinion in Plant Biology*, *13*(4), 478-484. <https://doi.org/10.1016/j.pbi.2010.04.011>

Appendix A

Means for grain yield and its agronomic components of the 25 sorghum accessions evaluated across environments

Accession	Head Count	Head Weight (kg)	Grain Weight (Kg)	Grain Yield (kg/ha)	Days to 50% flowering	Plant Height (cm)	Striga Count at 45 DAS	Striga count at 59 DAS	Striga count at 73 DAS	AUSNPC
NGAA0311016	24.23	1.35	0.91	2698.39	92.07	279.10	1.14	1.49	1.55	38.94
NGOJMAY09009	23.40	0.98	0.65	1930.96	98.79	350.76	0.96	1.17	1.39	32.26
NGSA07143	28.57	1.50	1.33	3958.64	97.05	251.90	0.92	1.23	1.45	33.07
NGSA07103	12.90	1.21	0.67	1998.14	90.63	284.49	0.86	1.02	1.18	27.90
NGJD0511063	26.02	1.28	0.97	2898.24	102.53	323.23	0.67	0.97	1.14	25.52
NGAO1108001	22.13	1.08	0.56	1653.07	67.39	191.31	0.99	1.23	1.30	32.59
SAMSORG40	17.08	0.72	0.53	1589.17	80.45	180.62	0.65	0.88	1.00	23.18
SAMSORG14	29.95	1.87	1.42	4233.84	100.13	246.61	1.11	1.27	1.40	34.61
N13	18.34	0.87	0.72	2144.77	92.06	234.08	0.95	1.23	1.27	31.98
SRN39	17.52	0.90	0.57	1689.08	70.56	152.44	0.60	0.68	0.93	19.53
SRN15401	20.12	1.50	1.20	3570.55	98.41	321.14	0.87	1.22	1.30	31.57
Danyana	24.75	1.95	1.37	4077.76	92.96	259.21	0.68	0.94	0.91	23.59
CSR-01	28.01	1.97	1.10	3276.64	107.96	229.10	1.00	1.37	1.52	36.01
CSR-02	22.67	1.49	1.27	3781.26	99.08	234.69	0.89	1.11	1.27	30.02
SAMSORG39	29.52	1.34	0.90	2684.54	86.59	157.63	0.98	1.20	1.34	32.28
White kaura	18.91	1.04	0.71	2126.13	81.16	228.86	0.96	1.11	1.33	30.86
MaceDaKunya	27.99	1.95	1.33	3971.42	94.56	174.41	0.82	1.04	1.20	27.95
Wassa	23.29	0.82	0.59	1758.20	79.18	216.71	1.36	1.48	1.61	40.84
Malisor84-7	23.68	0.82	0.57	1686.22	67.95	194.53	1.14	1.40	1.44	36.91
CSM63	23.78	0.85	0.63	1871.81	89.95	198.18	0.79	1.00	1.09	26.44
Grinkan	31.82	1.56	0.89	2640.10	87.47	136.09	0.80	1.01	1.09	26.67
Framida	26.28	1.25	0.77	2292.50	78.28	187.06	0.86	1.17	1.26	30.54
Sepon82	28.82	1.07	0.70	2083.17	94.09	130.50	0.57	0.63	0.92	18.63
Sarioso14	14.05	0.64	0.36	1065.60	86.52	192.09	0.90	1.05	1.09	27.90
Seguetana	16.13	0.54	0.49	1454.98	78.50	263.66	1.03	1.12	1.31	31.30

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