


Performance of cowpea varieties under *Striga gesnerioides* (Willd.) Vatke infestation using biplot analysis

Lucky O. Omoigui  · Alpha Y. Kamara · Hakeem A. Ajeigbe ·
Richard O. Akinwale · Michael P. Timko · Muhyideen Oyekunle ·
Lateef L. Bello

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Abstract *Striga gesnerioides* (Willd) Vatke, is a major destructive parasitic weed of cowpea (*Vigna unguiculata* (L.) Walp.) which causes substantial yield reduction in West and Central Africa. The presence of different virulent races within the parasite population contributes to significant genotype × environment interaction, and complicates breeding for durable resistance to *Striga*. A 3-year study was conducted at three locations in the dry savanna agro-ecology of Nigeria, where *Striga gesnerioides* is endemic. The primary objective of the study was to identify cowpea genotypes with high yield under *Striga* infestation and yield stability across test environments and to assess suitability of the test environment. Data collected on grain yield and yield components were subjected to analysis of variance (ANOVA). Means from ANOVA were subjected to the genotype main effect plus

genotype × environment (GGE) biplot analysis to examine the multi-environment trial data and rank genotypes according to the environments. Genotypes, environment, and genotypes × environment interaction mean squares were significant for grain yield and yield components, and number of emerged *Striga* plants. The environment accounted for 35.01%, whereas the genotype × environment interaction accounted for 9.10% of the variation in grain yield. The GGE biplot identified UAM09 1046-6-1 (V7), and UAM09 1046-6-2 (V8), as ideal genotypes suggesting that these genotypes performed relatively well in all study environments and could be regarded as adapted to a wide range of locations. Tilla was the most repeatable and ideal location for selecting widely adapted genotypes for resistance to *S. gesnerioides*.

L. O. Omoigui (✉) · L. L. Bello
Department of Plant Breeding and Seed Science, College
of Agronomy, University of Agriculture Makurdi,
P.M.B. 2373, Makurdi, Nigeria
e-mail: luckyomoigui@gmail.com;
lomoigui@cgiar.org

L. O. Omoigui · A. Y. Kamara
International Institute of Tropical Agriculture (IITA),
Ibadan, Oyo State, Nigeria

H. A. Ajeigbe
International Crops Research Institute for the Semi-Arid
Tropics (ICRISAT), Kano, Kano, Nigeria

R. O. Akinwale
Department of Crop Production and Protection, Obafemi
Awolowo University, Ile-Ife, Nigeria

M. P. Timko
Department of Biology, University of Virginia,
Charlottesville, USA

M. Oyekunle
Department of Plant Science, Faculty of Agriculture,
Ahmadu Bello University, Zaria, Nigeria

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Introduction

Cowpea [*Vigna unguiculata* (L.) Walp.] is a legume of vital importance to the livelihood of millions of people in West and Central Africa (WCA), for food, income generation and nutritional security. More than 5.59 million tons of dried cowpeas are produced on 12.61 million ha worldwide, with sub Saharan Africa producing nearly 5.3 million tons with West Africa producing over 84% of the production (FAOSTAT 2017). Nigeria, the largest producer and consumer, accounts for 61% of production in Africa and 58% worldwide. It provides nutritious grain and an inexpensive source of protein for both rural and urban consumers (Bressani 1985). Its haulms are also an important source of nutritious fodder for the livestock in the dry savannas (Bressani 1985; Singh and Emechebe 1997; Tarawali et al. 1997). However, the average yield of cowpea is low because of numerous biotic and abiotic constraints. Among the biotic constraints, two parasitic flowering weed species, *Striga gesnerioides* (Willd.) Vatke and *Alectra vogelii* (Benth), cause considerable yield reduction in cowpea (Emechebe et al. 1991). *Striga gesnerioides* is the most widespread parasitic weed and poses a serious threat to cowpea production in the WCA region. Parasitism by *S. gesnerioides* alone is a major constraint to achieving the potential cowpea yield in the savannas of WCA, especially in areas with sandy soils, low fertility, and low rainfall. The parasite is difficult to control because it produces a large number of seed and up to 75% of the crop damage is caused before *Striga* emergence. The *Striga* seed germinates in response to specific stimulants exuded by the host's roots (Worsham 1987). Cowpea varieties with complete resistance to *Striga* can stimulate *Striga* seed germination and permit attachment of *Striga* radicles to their roots, but the haustorium development is inhibited. On the other hand, there is normal development of haustorium on roots of susceptible varieties. Successful parasite establishment creates a strong sink for nutrients to the detriment of the host, leading to drastic growth reduction (Keyes et al. 2001; Joel et al. 2007). Because several parasitic plants attach to a

single cowpea plant, their impact on host-plant biomass and grain yield can be devastating, and can cause 100% yield loss under severe infestation (Ransom et al. 1990; Haussmann et al. 2000; Kim et al. 2002). The levels of infestation are often so high that cowpea can suffer total yield loss and farmers may be compelled to abandon their fields (Singh and Emechebe 1997). This leads to problems of food insecurity and malnutrition because of scarcity of a leguminous crop that is high in protein.

Striga gesnerioides is estimated to infest severely 97% of cowpea fields in north-east Nigeria where cowpea is a major crop (Dugje et al. 2006). The *Striga* problem is intimately associated with intensification systems and the reduced fallow periods, resulting in low levels of soil fertility (Vogt et al. 1991). Effective control of *Striga* is extremely difficult, because the parasite produces millions of tiny seeds that can remain viable in the soil for up to 20 years (Ouedraogo 2012). Methods available to control the parasite include hand-pulling, crop rotation, high amount of phosphorus fertilizer use, fallow, and host-plant resistance (Bebawi et al. 1984; Odhiambo and Ransom, 1994; Shaxson and Riches, 1998). Among the control measures, the use of genetic resistance is the most appropriate, safe and cost-effective way to control the parasite (DeVries 2000). Under field conditions, both *Striga* parasitism and drought stress occur simultaneously and the combined effect is more devastating than drought alone. It is, therefore, desirable to deploy *Striga*-resistant cowpea genotypes in the *Striga*-endemic areas of the dry savannas agroecology of Nigeria.

During the last two decades, national and international research centers have devoted increased attention and resources to developing improved varieties with resistance to *S. gesnerioides*, high yield potential, and stable performance across a broad range of growing conditions in the Sudan and Sahelian regions of Nigeria. Host-specific virulence has been observed in *S. gesnerioides* (Lane et al. 1997). Several cowpea genotypes have been identified that show race-specific resistance to *S. gesnerioides*. Based on qualitative differential host reactions and genetic diversity analysis, seven races of *S. gesnerioides* have been identified within the cowpea-growing regions of WCA (Lane et al. 1997; Botanga and Timko 2006). This has led to breakdown of resistance in the host plant because of an increase either in the

aggressiveness of the *Striga* races or the presence of new races. Omoigui et al. (2012) reported differential responses of cowpea breeding lines to *S. gesnerioides* in the dry savanna agro-ecology of Nigeria. Some lines that were reported previously to be resistant to *Striga*, such as IT90K-76, IT90K-59-2, and IT98K-503-1, in one region, were found to be susceptible when grown in other regions such as Borno, leading the authors to speculate the presence of other races or ecotypes within the *S. gesnerioides* population in the agro-ecology. In that study, the authors suggested that the occurrence of new races could complicate breeding genotypes with stable resistance, unless genotypes can be developed with broad-based resistance to multiple races of the parasitic weed.

Host-specific virulent parasite populations may contribute to significant genotype \times environment interaction, which is frequently observed in multi-location field trials conducted to characterize genotypes for resistance to *S. gesnerioides* (Hausmann et al. 2001). Understanding such complex host \times parasite interaction patterns such as chemical defense mechanism is therefore important for designing an effective breeding strategy to develop and deploy resistant cowpea genotypes against *S. gesnerioides* (Lane et al. 1997). In addition to these, other factors, such as location-to-location differences in soil physical and chemical properties, climatic conditions, fertilizer application, other crop management practices, and the presence of biological enemies that affect aggressiveness of the parasite populations, may contribute to the genotype \times environment (GE) interaction (King and Zummo 1977; Hausmann et al. 2001; Madden et al. 2007). The GE interaction, defined as the variation in relative performance of genotypes in different environments (Cooper and Byth 1996), is challenging to plant breeders because it complicates the selection of superior genotypes. If GE interactions are present, breeders need to identify stable genotypes with relatively consistent performance across a range of environments. Limited studies have been conducted to validate stability of monogenic resistance in cowpea genotypes under natural *S. gesnerioides* infestation across locations and seasons. Multilocation evaluation of cowpea genotypes with varying levels of resistance to *S. gesnerioides* at hotspot under heavy *Striga* infestation helps to achieve a more effective screening methodology with intense parasite pressure under which effective selection to

tolerant genotypes can be made. In addition, such conditions can lead to better understanding of the host–parasite interaction patterns and allow identification of broadly adapted cowpea genotypes for areas infested with *S. gesnerioides* in West and Central Africa where the private seed delivery system is poorly developed and farmers still rely largely on recycled seeds of cowpea genotypes that are often susceptible to the parasite.

The use of genetic resistance is the most appropriate, safe and cost-effective way to control the parasite. Several methods have been used to analysis genotype \times environment interaction and yield stability of different crops in Nigeria. For instance, Menkir et al. (2012) and Badu-Apraku et al. (2011) used GGE biplot analysis to determine grain yield performance and stability of maize genotypes under *Striga*-infested conditions and induced drought stress in Nigeria and their results identified genotypes that combined tolerance/resistance across the stresses with high grain yield under different stress conditions. The present study was, therefore, conducted to (i) determine the performance of newly developed *Striga*-resistant medium-maturity cowpea genotypes under natural *Striga* infestation using GGE biplot, (ii) examine the reaction patterns of cowpea genotypes with varying levels of resistance to *S. gesnerioides* under natural infestation, (iii) identify cowpea genotypes with stable resistance to the parasite across varying growing environments, and (iv) assess the repeatability of the test locations so as to identify ideal test location.

Materials and methods

Genetic materials and experimental procedures

Eighteen medium-maturity cowpea genotypes along with resistant (IT03K-338-1) and susceptible (Borno Brown) checks were evaluated during the main cropping season in three locations representative of the major cowpea producing areas in northern Nigeria, where *Striga* is endemic and infestation is severe. The study was conducted during three cropping seasons in three locations from 2012 to 2014, resulting in 7 environments (location–year combination). The three locations were Tilla, located in the southern part of Borno State at 12°56.4'N, 09°88.8'E (2012, 2013 seasons), Minjibir located in the northern part of Kano

State at 12°10.4'N, 08°39'E (2012, 2013, 2014 seasons), and Suletankakar located in the eastern part of Jigawa State at 11°50'N, 10°25'E (2013, 2014 seasons) of Nigeria. Climatic variables including soil type, rainfall, temperature, relative humidity at the experimental sites are given in Table 1. The 18 medium-maturity cowpea genotypes developed for *Striga* resistance at University of Agriculture, Makurdi, from diverse sources of germplasm, along with the checks used in this study are presented in Table 2. Some of the genetic materials that constituted the new improved genotypes were developed using marker-assisted selection (MAS) and have been found to consistently offer resistance to *Striga* parasitism, produce higher grain yields than the local genotypes under *Striga* infestation, and possess most of the farmer-preferred characteristics (seed size, color and plant type). One of the check genotypes, Borno Brown, possessed farmer-preferred characteristics but was highly susceptible to *Striga*. The genotypes were evaluated under natural conditions in fields previously identified to be heavily infested with *S. gesnerioides*.

In each environment, the experimental layout was a randomized complete-block design (RCBD) with

three replications. Depending on the weather conditions, the genotypes were planted from mid-June to the first week of July and harvested 70–80 days after planting (Table 2). Each genotype was grown in a four-row plot, each row 4 m long, spaced 0.75 m apart, with 0.25 m between plants within the row. Three cowpea seeds were sown per hill and later thinned to two plants per hill two weeks after planting to obtain a final population density of about 106,666 plants ha⁻¹. In addition, 2 weeks after planting, a compound fertilizer (15–15–15 NPK) was applied at the rate of 15 kg ha⁻¹. Weeds, other than *Striga*, were controlled manually throughout the cropping season.

Determination of soil fertility status

From each site, soil samples were collected from the top to a depth of 20 cm at each of 10 points, using a soil auger and the 10 samples were later bulked together to give a composite sample. All soil samples taken from the field were air-dried on trays. After drying, the clods were broken using a porcelain mortar and the ground soil sieved through a 2 mm mesh sieve. Soil samples were analyzed for physical and chemical

Table 1 Description of the cowpea testing environments under natural *Striga* infestation and soil type at the experimental locations

Environment	Coordinate			Temperature (°C)		Rainfall (mm)	Sunshine	Soil physio-chemical properties
	Latitude	Longitude	Altitude	Max	Min			
Minjibir								
2012–2014	12°10.4'N	08°39.3'E	453	36	23	650	21.04	Loamy sandy, organic C (g/kg) = 6.9, total N (g/kg) = 0.3, available P (mg/kg) = 3.1, available K (Cmol/kg) = 0.42, pH = 7.1
Tilla								
2012–2013	12°56.4'N	09°88.8'E	749	35	22	888	22.15	Sandy clay, organic C (g/kg) = 5.6, total N (g/kg) = 0.8, available P (mg/kg) = 1.6, available K (Cmol/kg) = 0.51, pH = 5.65
Suletankaka								
2013–2014	11°50'N	10°25'E	380	38	24	550	23.91	Sandy loam, organic C (g/kg) = 2.73, total N (g/kg) = 0.17, available P (mg/kg) = 1.29, available K (Cmol/kg) = 0.3, pH = 6.4

Max maximum temperature, *Min* minimum temperature, *RH* relative humidity

Table 2 Description of the medium-maturing cowpea genotypes used in the study

Entry	Genotypes	Pedigree	Source	Reaction to <i>Striga</i>	Selection methods
V1	Borno Brown	N/A	Land race	S	Local
V2	IT03K-338-1	IT87D-941-1 × IT 95K-1088-4	IITA	R	Conventional
V3	UAM09 10039	Borno Brown × IT97K-499-35	UAM	R	Conventional
V4	UAM09 10039-2	Borno Brown × IT97K-499-35	UAM	R	Conventional
V5	UAM09 1040-2	Borno Brown × IT97K-499-35	UAM	R	Conventional
V6	UAM09 1046-2	Borno Brown × IT97K-499-35	UAM	R	Conventional
V7	UAM09 1046-6-1	Borno Brown × IT97K-499-35/Borno Brown	UAM	R	MAS
V8	UAM09 1046-6-2	Borno Brown × IT97K-499-35/Borno Brown	UAM	R	MAS
V9	UAM09 1051-1	Borno Brown × IT97K-499-35/Borno Brown	UAM	R	MAS
V10	UAM09 1051-4	Borno Brown × IT97K-499-35	UAM	R	MAS
V11	UAM09 1062-1	Borno Brown × IT97K-499-35	UAM	R	MAS
V12	UAM09 2078-2	Borno Brown × IT97K-499-35	UAM	S	Conventional
V13	UAM09 2078-3	Borno Brown × IT97K-499-35	UAM	S	Conventional
V14	UAM09 2078-4	Borno Brown × IT97K-499-35	UAM	S	Conventional
V15	UAM09 2079-1	Borno Brown × IT97K-499-35	UAM	S	Conventional
V16	UAM09 2079-4	Borno Brown × IT97K-499-35	UAM	R	Conventional
V17	UAM09 2079-7	Borno Brown × IT97K-499-35	UAM	R	Conventional
V18	UAM09 2105-9	Borno Brown × IT97K-499-35	UAM	S	Conventional

R Resistant, S susceptible, N/A not available, IITA International Institute of Tropical Agriculture, UAM University of Agriculture Makurdi, MAS Marker-assisted selection

properties using the automated and semi-automated methods for soil and plant analysis (IITA 1982).

Data collection

Observations were made on the two middle rows. At 9 weeks after planting, *Striga* emergence data were recorded as the number of emerged *Striga* plants per plot. Days to maturity were determined when senesced plants had reached harvest maturity and pods had turned brown. Grain yield was determined by harvesting the two middle rows (6 m²) in each plot, drying the pods in open air after which the pods were threshed, weighed and moisture content was measured using Farmex MT-16 grain moisture tester. The grain yield was then adjusted to 13% moisture. Fodder weight after harvesting was determined by weighing fresh fodder samples (minimum of 300 g fresh weight) randomly collected from each plot, oven-dried at 60°C for 48 h to constant weight, and weighed. The moisture percentage was used to adjust the dry weight to determine the fodder weight per plot and converted

to kg/ha. One-hundred-seed weight (seed size) was determined and adjusted to 13% moisture content.

Statistical analysis

Analysis of variance (ANOVA) was carried out for data collected in each location and a combined ANOVA across locations was performed after Levene's test for homogeneity of variance had confirmed that data from individual environments (E) could be pooled. The ANOVA was done using the PROC MIXED procedure of SAS (SAS Institute, 2001). The variance of *Striga* counts increases with the mean; therefore, a natural logarithm transformation (LN (count + 1)). In the combined ANOVA, genotypes were considered fixed effects, whereas environments, replicates within the environment and the genotype × environment interaction were treated as random effects. The significance of the mean squares for the main and interaction effects was tested using the appropriate mean squares from the ANOVA obtained from the type-3 mixed model analysis.

Subsequently, grain yield mean values adjusted for block effects were subjected to genotype main effect plus genotype \times environment (GGE) biplot analysis (Yan and Hunt 2002). The GGE biplot analysis was used to partition significant genotype and genotype \times environment interaction into its Eigen values to obtain information on the average performance and stability of the cowpea genotypes, and to examine the discriminating power and representativeness of the test environments. The biplot analyses were done using GGE-biplot software, a Windows application that fully automates biplot analysis [Yan 2001, www.ggebiplot.com (verified 31 Dec. 2015)], represented in the following statistical model:

$$Y_{ij} - Y_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \varepsilon_{ij}$$

where, Y_{ij} is the mean yield of genotype i in environment j , Y_j is the mean yield across all genotypes in environment j , λ_1 and λ_2 are the singular values for PC1 and PC2, ξ_{i1} and ξ_{i2} are the PC1 and PC2 scores, for genotype i , η_{j1} and η_{j2} are the PC1 and PC2 scores, for environment j , ε_{ij} is the residual of the model associated with the genotype i in environment j .

The GGE-biplot software (Yan 2001) was employed to generate graphs showing (i) ‘which-won-where’ pattern, (ii) ranking of genotypes on the basis of mean yield and stability, and (iii) an evaluation of test environments (Yan et al. 2007). To visualize correlations between locations, a vector-view biplot was made. The data were not transformed (‘Transform = 0’), nor standardized (‘Scale = 0’), and were environment-centered (‘Centering = 2’).

Results

Combined analysis of variance for grain yield and other agronomic traits

Results of the combined analysis of variance showed highly significant ($P \leq 0.01$) genotype mean squares for all traits evaluated across environments and year of evaluation (Table 3). The presence of significant genotype mean squares for all traits indicated variability in the response of the cowpea genotypes to *Striga* infestation and possibility of making progress through selection. Environment effect was highly significant for all the traits indicating distinctiveness

of the environments in terms of differences in the amount of rainfall, soil fertility, mean temperature, *Striga* pressure, and length of the growing period. The $G \times E$ interaction mean squares was significant for all traits except for days to 95% pod maturity. Grain yield was the only trait where significant mean squares was observed for all the sources of variation. Partitioning $G \times E$ into the different environments, highly significant differences were observed among the environments except for pod maturity in E1, E4, and E5 that were not significant. Non-significant difference was also observed for *Striga* count in E1, and 100-seed weight in E4. The significant $G \times E$ interaction effects observed for *Striga* shoot count, grain yield and 100-seed weight justified the use of GGE biplot for the genotype plus genotype-by-environment analysis to identify stable genotypes with consistent performance across a range of environments under natural *Striga* infestation.

Mean yields varied from 294 to 1962 kg ha⁻¹ across the 7 diversified environments, indicating large variation in yield potential of genotypes (Table 4). The mean yield for an individual location ranged from 374 to 1962 kg ha⁻¹ in Minjibir, 294 to 1664 kg ha⁻¹ in Suletankakar and 455 to 1762 kg ha⁻¹ in Tilla (Table 4). Mean grain yield of the cowpea genotypes in environment under severe *Striga* infestation was 845 kg ha⁻¹, a value close to the mean yield reported by Singh and Emechebe (1997) in northern Nigeria where soils are sandy, with low fertility, and heavily infested with *S. gesnerioides*. The results indicated that in moderately favorable environments (Minjibir and Tilla), where rainfall was relatively higher, the yield potential of most of the *S. gesnerioides*-resistant lines ranged between 374 and 1962 kg ha⁻¹ in Minjibir, and 454–1762 kg ha⁻¹ in Tilla compared with Suletankakar (296–1646 kg ha⁻¹) where rainfall is low, soils are sandy and less fertile (Table 4). Significant genotype differences were observed in Suletankakar. At this location, the *Striga*-resistant lines yielded between 471 and 1646 kg ha⁻¹, whereas *Striga*-susceptible lines gave mean yield of 296 kg ha⁻¹ (Table 5). It is interesting to note that a few *Striga*-resistant lines, such as V7 (UAM09 1046-6-1), V8 (UAM09 1046-6-2), and V9 (UAM09 1051-1), yielded between 1179 and 1962 kg ha⁻¹ of grain even at Suletankakar, indicating their adaptability to poor soils and their ability to make efficient use of limited soil nutrients. There were no significant

Table 3 Mean squares from combined analysis for grain yield and other traits of cowpea genotypes evaluated under *Striga* stress across seven environments from 2012 to 2014

Source	df	Pod maturity	<i>Striga</i> damage	Grain yield	100 seed weight
Environment (E)	6	1626.96**	1459.32**	6283106.06**	29.44**
Rep (E)	14	57.81**	188.07ns	207464.40**	6.41ns
Genotype (G)	17	52.63**	1883.71**	3268638.77**	99.03**
G * E	102	15.44ns	316.01**	250588.78**	6.02**
G * E1	17	25.46ns	98.06ns	854569.40**	32.14**
G * E2	17	21.05**	101.70**	760121.70**	30.82**
G * E3	17	33.97**	786.86**	923066.70**	19.98**
G * E4	17	20.35ns	261.70**	325194.20**	8.80ns
G * E5	17	26.55ns	1882.41**	378364.20**	13.58**
G * E6	17	15.49**	552.52**	1042432.00**	26.61**
G * E7	17	5.97*	152.22**	616871.40**	13.76**
Error	195	9.32	130.74	92263.60	4.20

*, ** Significant at $p < 0.05$, and 0.01 respectively, *ns* = not significant

Table 4 Range, mean and standard deviation for the tested five (5) morphological traits evaluated in 2012–2014

Variables	Minjibir			Suletankakar			Tilla		
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Seed weight (g)	18–25	20.7	2.1	17–24	20.6	2.1	17–24	20.7	2.2
Maturity (days)	80–86	83.1	1.8	69–84	74.1	3.0	76–82	78.8	1.5
Fodder yield (kg ha ⁻¹)	1478–1921	1680.2	143.3	1374–1914	1632.6	133.0	1569–1971	1755.6	117.8
Grain yield (kg ha ⁻¹)	374–1962	1191.6	393.1	294–1646	844.9	354.6	454–1762	1072.2	407.6
Emerged <i>Striga</i> (6 m ⁻²)	0–30	5.1	7.7	0–41	8.4	14.5	0–31	7.2	9.9

differences among the top five genotypes based on grain and fodder yields, but significant differences did exist for the number of emerged *Striga* plants. The three highest-yielding genotypes were V7, V8, and V9 in that order; these genotypes did not support *Striga* plants. The three-best top-ranking *Striga*-resistant genotypes, i.e., UAM09-1046-6-1 (1689 kg ha⁻¹), UAM09-1046-6-2 (1664 kg ha⁻¹), and UAM09-1051-1 (1488 kg ha⁻¹), out-yielded the susceptible genotype, Borno Brown (374 kg ha⁻¹) by 331%. This is an indication of the impact of the severe parasitic pressure on grain yield of the susceptible cowpea genotypes. Plants with higher number of emerged *Striga* plants per plot also recorded lower grain yield on the susceptible local genotype under severe *Striga* infestation.

Biplot analysis of performance and stability of the genotypes

The GGE biplot was constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component (PC2). The PC1 explained 73.2% of the total variation in the sum of squares, while PC2 explained 10.3%; thus, PC1 and PC2 together accounted for 83.5% of the G + G × E variation for the grain yield of the cowpea genotypes evaluated under severe *Striga* infestation at seven environments (Figs. 1 and 2). This result indicated the environments accounted more for the variability observed and that the biplot was effective in explaining both the genotype and G × E interaction variation for grain yield of the cowpea genotypes.

Table 5 Mean grain yield and resistance reaction to *S. gesnerioides* of 18 medium maturing cowpea genotypes and checks evaluated under natural *Striga* stress at Tilla, Minjibir and Suletankakar from 2012 and 2014

Code	Genotypes	Grain yield (kg ha ⁻¹)				Emergenced <i>Striga</i> ⁺ per plot (6 m ²)			
		Min.	Sul.	Til.	Mean	Min.	Sul.	Til.	Mean
V1	Borno Brown	374	296	454	375	16.3	40.3	25.8	27.5
V2	IT03K-338-1	941	778	903	874	0	0.2	0.2	0.1
V3	UAM09 10039	1494	1260	1419	1391	1.9	0	0.9	0.9
V4	UAM09 10039-2	1316	1068	1303	1229	4.8	3.7	3.3	3.9
V5	UAM09 1040-2	1348	850	1279	1159	2	9.7	4.3	5.3
V6	UAM09 1046-2	1278	1156	1236	1223	2.9	11.2	13.4	9.2
V7	UAM09 1046-6-1	1681	1646	1742	1690	0	0	0	0.0
V8	UAM09 1046-6-2	1962	1270	1762	1665	0	0	0	0.0
V9	UAM09 1051-1	1710	1179	1577	1489	0	0	0	0.0
V10	UAM09 1051-4	1476	936	1349	1254	0	0	0.1	0.0
V11	UAM09 1062-1	1026	471	860	786	0	0	0.1	0.0
V12	UAM09 2078-2	840	554	674	689	29.7	34.7	31.3	31.9
V13	UAM09 2078-3	935	565	736	745	7.6	4.4	6.9	6.3
V14	UAM09 2078-4	822	487	627	645	14	41.3	22.4	25.9
V15	UAM09 2079-1	1332	666	966	988	3.3	4.8	4.5	4.2
V16	UAM09 2079-4	1021	738	823	861	5.1	0	2.4	2.5
V17	UAM09 2079-7	785	557	725	689	2.6	0	1.2	1.3
V18	UAM09 2105-9	1108	732	764	868	1.8	0.2	12.1	4.7
	Grand mean	1192	845	1067	1034	5.1	8.4	7.2	6.9
	LSD	382	345	388	362	8	14	10	10
	CV	22.07	21.6	21.6	17.6	8.7	9.2	7.7	8.05

Locations are abbreviated as *Min.* Minjibir, *Sul.* Suletankakar, and *Til.* Tilla

Polygon view of the GGE biplot

In the polygon view (Fig. 1), the vertex genotype in each sector represents the highest yielding genotype in the location that falls within that particular sector. Thus, groups of sites that share the same best performers can be graphically identified. In the biplot, V3 (UAM09 10039) and V15 (UAM09 2079-1) were the vertex genotypes for the environments STK14 and MJ14, indicating that genotype V3 and V15 were the highest-yielding genotypes in the two environments. Similarly, V7 (UAM09 1046-6-1), and V8 (UAM09 1046-6-2), were vertex genotypes in the sector where MJ13, STK13 and TIL12 fell, signifying that the V7 and V8 were the highest-yielding genotypes in the three environments (Fig. 1). Similarly, V4 (UAM09 10039-2) was the best genotype at MJ12 and TIL13. Although, V1 (Borno Brown), V17 (UAM09 2079-7)

and V14 (UAM09 2078-4) were vertex genotypes in their respective sectors, no environment fell within their sectors, indicating that these genotypes were the least-yielding in all or most of the test environments. Genotypes that fell within the polygon, they were less responsive than the vertex genotypes. Similarly, genotypes located close to the origin of the axes are less responsive to the environment.

Mean grain yield and stability

Figure 2 represents the 'mean vs. stability' view of the GGE biplot, which show performance and stability of the genotypes and ultimately facilitated the identification of an ideal genotype. In the GGE biplot display, the thick single-arrow red line that passes through the biplot origin and the average environment is regarded as the average-tester axis (ATC abscissa), on which

Fig. 1 The “which-won-where” view of the GGE biplot based on a $G \times E$ yield data of 18 cowpea genotypes evaluated at 7 environments from 2012 to 2014. The data were not transformed (Transform = 0), not scaled (Scaling = 0), and were environment-centered (Centering = 2). The biplot was based on environment-focused singular value partitioning (SVP = 2) and therefore is appropriate for visualizing the relationships among environments. See Tables 1 and 2 for environments and genotypes legends, respectively. *MJ* Minjibir, *STK* Suletankarka, *TIL* Tilla

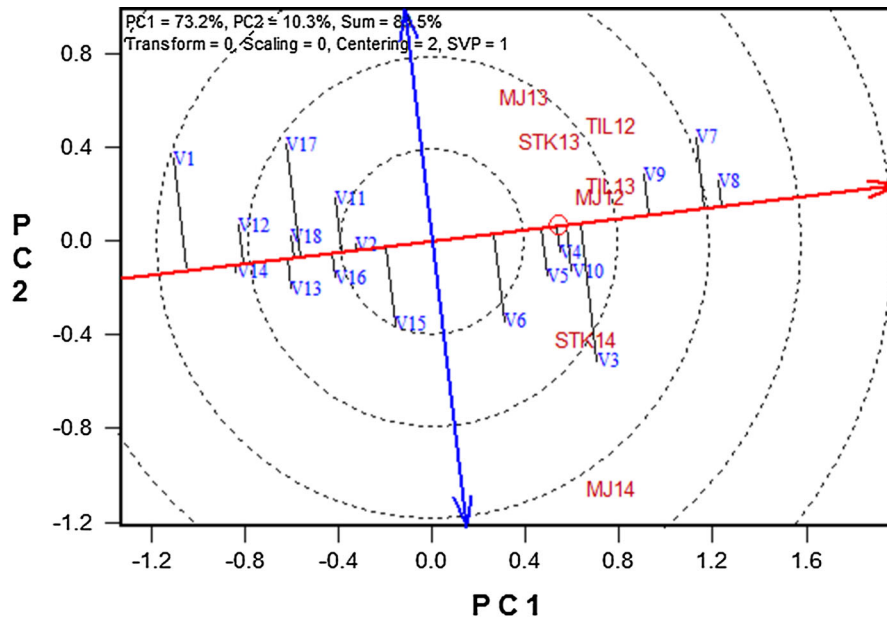
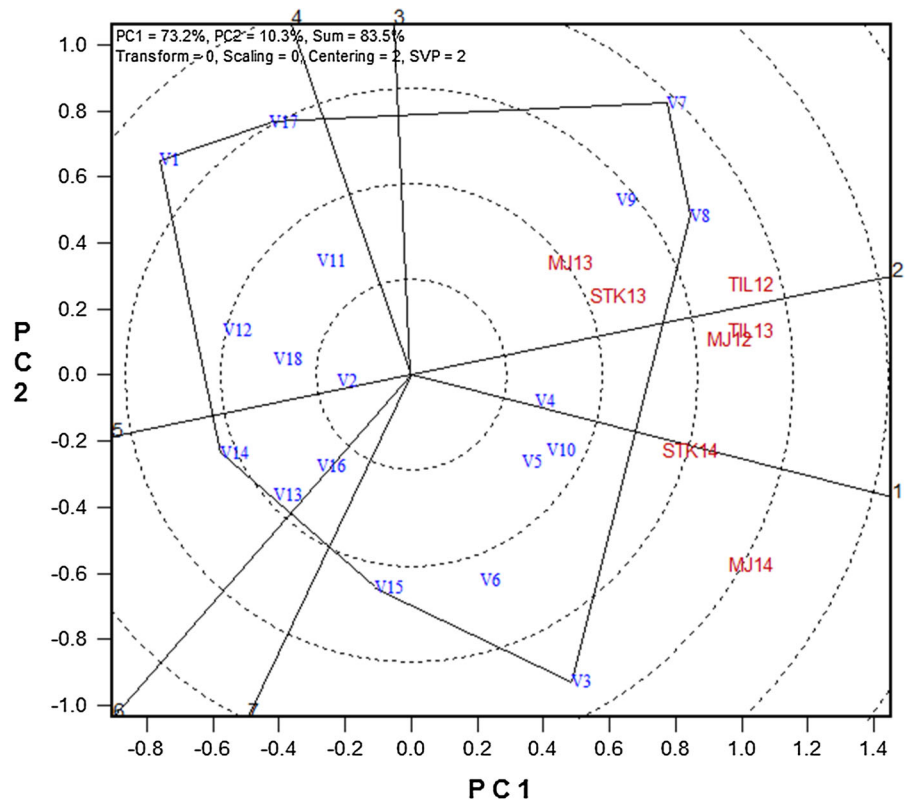


Fig. 2 The “mean vs. stability” view of the GGE biplot based on a $G \times E$ yield data of 18 cowpea genotypes evaluated at 7 environments (locations plus year) from 2012 to 2014. The data were not transformed (Transform = 0), not scaled (Scaling = 0), and were environment-centered (Centering = 2).

The biplot was based on cultivar-focused singular value partitioning (SVP = 1) and therefore is appropriate for visualizing the similarities among genotypes. See Tables 1 and 2 for environments and genotypes legends, respectively. *MJ* Minjibir, *STK* Suletankarka, *TIL* Tilla

the performances of the genotypes were ranked. Furthermore, the blue vertical double-arrow line called the ATC ordinate, divides the abscissa at the biplot origin, separating the genotypes into above-average genotypes at the right-hand side and below-average genotypes at the left. Based on this, eight of the eighteen genotypes, UAM09 1046-6-2 (V8), UAM09 1046-6-1 (V7), UAM09 1051-1 (V9), UAM09 10039 (V3), UAM09 1051-4 (V10), UAM09 10039-2 (V4), UAM09 1040-2 (V5) and UAM09 1046-2 (V6) produced yields higher than the mean grain yield of all genotypes. Genotype V1 had the lowest yield across test environments. Furthermore, the stability of the genotypes was measured by their projection onto the average-tester coordinate (ATC) y-axis double-arrow line. On this basis, genotypes V8, V9, V10, V4 and V5 had short projections onto the ATC ordinate and thus, the most stable genotypes across the environments. Genotypes V7, V3 and V6 were high yielding but less stable.

GGE biplot evaluation of test environments

The GGE biplot also allows for assessment of the suitability of the test environments for evaluating the set of genotypes. Results from the vector view of biplot provided information on the relationship among the test environments, thereby identifying the core testing sites as well as redundant environments based on their discriminating power and representativeness. The relationship among environments was determined by the size of the angle between the vectors of any two environments. The larger the angle, the less correlated the environments. If the angle is acute ($<90^\circ$), it indicates a strong positive correlation between the environments, suggesting that the same information about the genotypes could be obtained from correlated test environments without sacrificing precision. If the angle is a right angle ($=90^\circ$), no relationship was indicated, if the angle was obtuse ($>90^\circ$), it indicated a strong negative correlation and an indication of the presence of a strong crossover GE, and if the angle was on a straight line ($=180^\circ$), it indicated a perfect negative correlation. In Fig. 3, all the vectors had acute angles between any two vectors indicating that they were all positively correlated. Thus, Tilla had the highest repeatability as TIL12 and TIL13 had the closest angle between them. All the three environment vectors of MJ had large acute angles between them,

indicating weak positive relationship between them and therefore performance of the cowpea genotypes at Minjibir was less repeatable. Similarly, STK13 and STK14 were less correlated, indicating that Sule-tankakar had less repeatability.

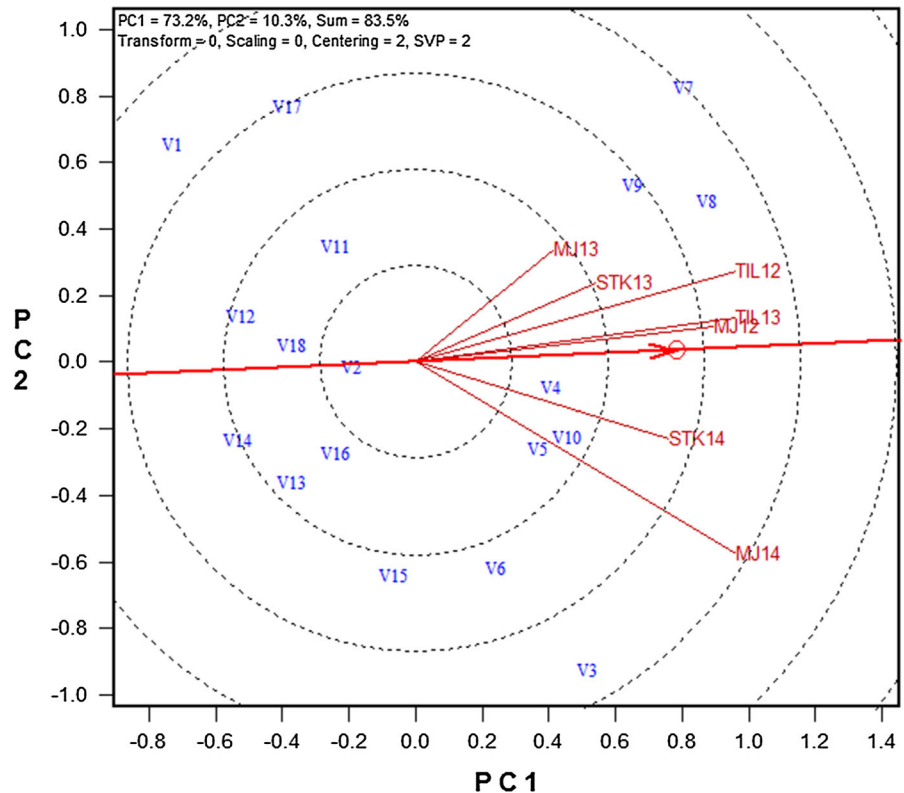
Parasite variability

Significant genotype-by-environment effect observed in this study for *Striga* damage scores may suggest variation in the agro-ecologies used for this study, differences in parasite population, ecotypes or strains of the parasitic weeds in the different locations. Stability analysis also showed that resistant genotypes had consistently no emerged parasites and produced higher grain yields even under heavily infested fields. Among the 18 cowpea genotypes, the most promising candidates for stable resistance to *S. gesnerioides* were UAM09 1046-6-1(V7), UAM09 1046-6-2 (V8), and UAM09 1051-1 (V9). These genotypes had the highest mean yield, did not support emerged parasites, and could therefore, be recommended for commercial cultivation in *S. gesnerioides* endemic areas in the dry savannas of Nigeria. The resistant genotypes also had, been tested for consistency of performance in the Republic of Niger in areas where *S. gesnerioides* is endemic (data not provided). These genotypes were also free of *Striga* infestation. Genotypes with a high level of stable resistance to *S. gesnerioides* can reduce the buildup of the parasite seed bank in the soil for subsequent legume crops and could be used as an important component to develop integrated *S. gesnerioides* control strategies. Resistant genotypes can also be invaluable sources of resistance alleles in breeding programs to increase the level of resistance to *S. gesnerioides*.

Discussion

The approaches to GE interaction analysis are important for enhancing the value of Multi-environment trials (METs) and gaining an understanding of causes of GE interactions (Yan and Hunt 2001, Fox and Rosielle 1982). The techniques used to interpret GE interactions involve the characterization of trial sites according to environmental factors, using either direct measurements, calculated indices, or variables derived from crop growth models. These covariates can then

Fig. 3 The “discriminating power vs. representativeness” view of the GGE biplot based on a genotype \times environment yield data of 18 cowpea genotypes evaluated at 7 environments (location plus year) from 2012 to 2014. Genotype of the G \times E data in Table 4. The data were not transformed (Transform = 0), not scaled (Scaling = 0), and were environment-centered (Centering = 2). The biplot was based on cultivar-focused singular value partitioning (SVP = 2) and therefore is appropriate for visualizing the relationship among environments. See Tables 1 and 2 for environments and genotypes legends, respectively. *MJ* Minjibir, *STK* Suletankarka, *TIL* Tilla



be analyzed in combination with modern multivariate techniques such as pattern analysis, AMMI (additive main effect and multiplicative interaction) or GGE (G + GE) biplots to identify patterns of GE interactions and identify critical factors driving the interactions (Yan and Hunt 2001; Fox and Rosielle 1982). These methods have been demonstrated successfully in a range of other crops. In addition, the GGE biplot also has a usage in selecting superior cultivars and test environments for a given environment.

The significant G \times E interaction effects observed for *Striga* shoot count, grain yield and 100-seed weight justified the use of GGE biplot for the genotype plus genotype-by-environment analysis to identify stable genotypes with consistent performance across a range of environments under natural *Striga* infestation. Our results indicated that The PC1 explained 73.2% of the total variation in the sum of squares, while PC2 explained 10.3%; thus, PC1 and PC2 together accounted for 83.5% of the G + G \times E variation for the grain yield of the cowpea genotypes evaluated under severe *Striga* infestation at seven environments resulting in crossover GE interaction

and leading to inconsistent yield performance of genotypes across environments. Thus, indicated that the biplot was effective in explaining both the genotype and G \times E interaction variation for grain yield of the cowpea genotypes. Both PC1 and PC2 scores had both positive and negative values, resulting in crossover GE interaction and leading to inconsistent yield performance of genotypes across environments. Most of the environmental and genotypic covariables were more highly correlated with PC1 than with PC2 scores, indicating that the contribution of most covariables can be defined in relation to PC1 scores. This indicated that the environment was largely responsible for the wide variability observed. According to Yan et al. (2000), ideal genotypes could be considered those that have a large PC1 score (high yielding ability) and small or absolute PC2 score (high yielding ability), similarly, the ideal test environment should have a large PC1 score, which means that it is more discriminating of the genotypes in terms of the genotypes main effect and small or absolute PC2 score (more representative of the overall environment). However, when PC1 and PC2 were considered

together, rainfall, soil fertility and *Striga* pressure contributed most to GE interaction. The results confirmed that *Striga* pressure is an important trait responsible for observed GE interaction and suggest that GE interaction could be reduced by optimizing the environment (by selecting *Striga* resistant plants with moderate *Striga* infested fields). In this strategy, extremely susceptible genotypes can produce yields.

Among the environmental covariables, rainfall was the main contributor to GE interaction and may be the most effective in identifying superior genotypes under *Striga* infestation for different environments. The significant $G \times E$ interaction effects observed for *Striga* shoot count, grain yield and 100-seed weight justified the use of GGE biplot for the genotype plus genotype-by-environment analysis to identify stable genotypes with consistent performance across a range of environments under natural *Striga* infestation.

The GGE biplot was constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component (PC2). The PC1 explained 73.2% of the total variation in the sum of squares, while PC2 explained 10.3%; thus, PC1 and PC2 together accounted for 83.5% of the $G + G \times E$ variation for the grain yield of the cowpea genotypes evaluated under severe *Striga* infestation at seven environments. This result indicated that the biplot was effective in explaining both the genotype and $G \times E$ interaction variation for grain yield of the cowpea genotypes.

In the polygon view, the vertex genotype in each sector represents the highest yielding genotype in the location that falls within that particular sector. Thus, groups of sites that share the same best performers can be graphically identified. In the biplot, V3 (UAM09 10039) and V15 (UAM09 2079-1) were the vertex genotypes for the environments STK14 and MJ14, indicating that genotype V3 and V15 were the highest-yielding genotypes in the two environments. Similarly, V7 (UAM09 1046-6-1), and V8 (UAM09 1046-6-2), were vertex genotypes in the sector where MJ13, STK13 and TIL12 fell, signifying that the V7 and V8 were the highest-yielding genotypes in the three environments (Fig. 1). Although, V1 (Borno Brown), V17 (UAM09 2079-7) and V14 (UAM09 2078-4) were vertex genotypes in their respective sectors, there was no environment fell within their

sectors, indicating that these genotypes were the least-yielding in all or some of the test environments. Genotypes that fell within the polygon, indicating that they were less responsive than the vertex genotypes. Similarly, V4 (UAM09 10039-2) was the best genotype at MJ12 and TIL13. Genotypes located close to the origin of the axes are less responsive to the environment (Yan et al. 2000).

In the GGE biplot display, the thick single-arrow red line that passes through the biplot origin and the average environment is regarded as the average-tester axis (ATC abscissa), on which the performances of the genotypes were ranked. Furthermore, the blue vertical double-arrow line called the ATC ordinate, divides the abscissa at the biplot origin, separating the genotypes into above-average genotypes at the right-hand side and below-average genotypes at the left. The stability of the genotypes was measured by their projection onto the average-tester coordinate (ATC) y-axis double-arrow line. The greater the absolute length of the projection of a genotype, the less stable it is (Yan et al. 2007). Genotypes V8, V9, V10, V4 and V5 had short projections onto the ATC ordinate and thus, the most stable genotypes across the environments. Genotypes V7, V3 and V6 were high yielding but less stable. An “ideal genotype” was defined as the genotype that combined high yielding ability (rank high on ATC abscissa) with good stability across test environments (short genotype projection onto the ATC ordinate) (Kang 2002; Yan and Kang 2003). The genotypes V8 and V7 were identified to be closest to the ideal genotype (data not shown). This result suggests that V8 and V7 are the best genotypes because it combined high yield with high stability across environments, and it had broad adaptation to the test environmental conditions.

The GGE biplot also allows for assessment of the suitability of the test environments for evaluating the set of genotypes. The relationship among environments was determined by the size of the angle between the vectors of any two environments. The larger the angle, the less correlated the environments. If the angle is acute ($<90^\circ$), it indicates a strong positive correlation between the environments, suggesting that the same information about the genotypes could be obtained from correlated test environments without sacrificing precision. If the angle is a right angle ($=90^\circ$), no relationship was indicated, if the angle was obtuse ($>90^\circ$), it indicated a strong negative

correlation and an indication of the presence of a strong crossover GE, and if the angle was on a straight line ($=180^\circ$), it indicated a perfect negative correlation (Yan and Tinker 2006). All the vectors had acute angles between any two vectors indicating that they were all positively correlated. Furthermore, the GGE biplot revealed the discriminating power of a test environments based on the length of its vector (Yan and Holland 2010). Hence, the discrimination ability of a test location identifies the best genotypes for a specific location, desirability of the environment and discrimination power on genotypic differences (Xu et al. 2013; Zhang et al. 2010). Based on this, TIL12, TIL13, MJ12, and MJ14 had long vectors and thus had high discriminating ability whereas MJ13, STK13 and STK14 had moderate discriminating power. The representativeness of a test environment was determined by its closeness to the average tester axis (a small circle located on the abscissa with an arrow pointing to it) (Yan et al. 2007). Thus, MJ12, TIL12 and TIL13 were closest to the average tester axis and therefore were the most representative of all the environments. This result indicated that Tilla had high discriminating power and high representativeness and could therefore be considered as an ideal test location for selection of high yielding and *Striga*-resistant cowpea genotypes.

An important objective of the present study was to assess the repeatability of the test locations. The combination of year-location as an environment provided the opportunity to assess the repeatability of the test locations. A location was said to be repeatable when the vectors of their respective years had close angles between them (i.e., when they were closely correlated). In other words, the wider the angle between vectors of a location for different years, the less repeatable was the location and by implication, the less reliable the information provided by the location (Yan and Holland, 2010). Thus, Tilla had the highest repeatability as TIL12 and TIL13 had the closest angle between them. All the three environment vectors of MJ had large acute angles between them, indicating weak positive relationship between them and therefore performance of the cowpea genotypes at Minjibir was less repeatable. Similarly, STK13 and STK14 were less correlated, indicating that Sule-tankakar had less repeatability.

The broad range of values of the five traits recorded for each genotype under *Striga* infestation provided a

clear indication of variable parasite pressure in different test environments. However, the complete resistance demonstrated that monogenic resistance had a strong effect on reactions of genotypes to *S. gesnerioides* and its effect was stable across environments as exhibited by the reactions of genotypes V7 and V8. The mechanism for the broad adaptation could be explained as activation of a very effective arsenal of inducible defense responses, which comprised genetically programmed suicidal of the infected cells (the hypersensitive response, HR), as well as tissue reinforcement and antibiotic production at the site of infection. These local responses can, in turn, trigger a long-lasting systemic response (systemic acquired resistance, SAR) that primes the plant for resistance against a broad spectrum of pathogens (Conrath 2011). Thus, defenses are kept under tight genetic control and are activated only if the plant detects a prospective invader.

The fact that the resistant genotype did not show differential responses in the contrasting environments in this study implied that the parasite population could be the same. Cowpea varieties with complete resistance to *Striga* stimulate germination and permit attachment of *Striga* radicles to their roots but the haustorium development is inhibited (Singh and Emechebe 1997). Six of the 18 genotypes included in the present study met these criteria and were therefore classified as immune to *S. gesnerioides*. It appears that these genotypes carry resistance alleles, which were specific to a virulence gene of the parasite population, which prevailed during field-testing. Several studies have shown that genes with dominant effects confer vertical resistance to *S. gesnerioides* in cowpea (Singh et al. 1991; Atokple et al. 1993; Omoigui et al. 2012). Lane et al. (1997) also identified wild relatives of maize that restricted the penetration and establishment of haustorium to host roots and impaired the development and survival of parasites. The genotypes included in the present study are new cowpea lines developed from improved *Striga*-resistant dual-purpose variety \times local adapted genotype cross.

Significant genotype-by-environment effect observed in this study for *Striga* damage scores may suggest variation in the agro-ecologies used for this study, differences in parasite population, ecotypes or strains of the parasitic weeds in the different locations. However, further study is needed to confirm and

identify the different ecotypes that may be present in these different locations. This information is needed to plan the development of multilines selection or gene pyramiding in order to improve on the durability of resistance of cowpea genotypes to the parasitic weed. Although host–parasite interaction may occur for monogenic resistance under such circumstances, its effect on rank changes for resistance reactions of the genotypes can be minimal (Turkensteen 1993). Stability analysis also showed that resistant genotypes had consistently no emerged parasites and produced higher grain yields even under heavily infested fields. Among the 18 cowpea genotypes, the most promising candidates for stable resistance to *S. gesnerioides* were UAM09 1046-6-1(V7), UAM09 1046-6-2 (V8), and UAM09 1051-1 (V9). These genotypes had the highest mean yield, did not support emerged parasites, and could therefore, be recommended for commercial cultivation in *S. gesnerioides* endemic areas in the dry savannas of Nigeria. The resistant genotypes also had, been tested for consistency of performance in the Republic of Niger in areas where *S. gesnerioides* is endemic. These genotypes were also free of *Striga* infestation. Genotypes with a high level of stable resistance to *S. gesnerioides* can reduce the buildup of the parasite seed bank in the soil for subsequent legume crops and could be used as an important component to develop integrated *S. gesnerioides* control strategies. Resistant genotypes can also be invaluable sources of resistance alleles in breeding programs to increase the level of resistance to *S. gesnerioides*.

The study also revealed that two environments Suletankaka and Tilla were close to the ideal environment; therefore, they should be regarded as the most suitable locations for selecting superior genotypes for resistance to *S. gesnerioides* because these locations have high *Striga* pressure. This finding supports the earlier work of Yan and Kang (2003), who reported that an ideal genotype should have the highest mean grain yield and must be stable across environment. The most stable genotypes were UAM09 1046-6-1(V7), UAM09 1046-6-2 (V8) and UAM09 1051-1 (V9) because they had the shortest distance from the average environment suggesting adaptation to a wide range of environments. This finding is consistent with the results of Ito et al. (2016), who found that genotypes that were close to the polygon origin had high stability and yield

performance. Asfaw et al. (2009) reported that genotypes placed far away from the origin of the vector had strong interactions and were adapted to specific environments.

Conclusions

The present study has demonstrated that UAM09 1046-6-1 and UAM09 1046-6-2 were the best cowpea genotypes under the study conditions and are therefore, recommended as promising genotypes for commercial release to farmers for cultivation or as invaluable sources to introgress *Striga* resistance into new cowpea populations. The study also revealed that in good environments (Minjibir and Tilla), the yield potential of most of the *S. gesnerioides*-resistant lines was between 1026–1962 kg ha⁻¹ in Minjibir and 860–1762 kg ha⁻¹ in Tilla. However, significant genotype differences were observed in the poor environment (Suletankakar). The *Striga*-resistant genotypes yielded between 471 and 1646 kg ha⁻¹, whereas the *Striga*-susceptible genotypes yielded 296 kg ha⁻¹. Tilla was identified as the ideal testing site for cowpea genotypes.

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Compliance with ethical standards

Conflict of interest The authors declared that they have no conflict of interest

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