

Research Article

Genetic and Environmental Effects on Nodulation and Yield Among Selected Cowpea (*Vigna unguiculata* [L.] Walp) Genotypes in Uganda

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Received 13 July 2024; Accepted 6 December 2024

Academic Editor: Othmane Merah

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Cowpea (*Vigna unguiculata* [L.] Walp) is among the most important legume crops grown especially in the Eastern and Northern regions of Uganda. It is a climate-resilient and protein-rich legume crop that also serves as a soil fertility restorer. This crop is a mainstay across Africa, Southeast Asia, and certain areas in America. Nevertheless, the productivity of the Ugandan-cultivated cowpea varieties remains relatively low compared to improved cultivars when subjected to optimal field management. The objective of this study was to evaluate the performance of selected cowpea genotypes with a specific focus on analyzing the effect of the interaction between genotype and environment on nodulation capacity and yield performance in Uganda field conditions. The research evaluated 35 cowpea genotypes using a 5 × 7 alpha lattice design, with three replicates across seven test environments in Uganda. The additive main effect and multiplicative interaction (AMMI) for the number of nodules (NN) per plant and seed yield per plot showed significant differences for genotypes, environments, and genotype-by-environment interaction. However, the environmental effect was the largest contributor to the total variation in NN and seed yield compared with genetic and G × E interactions. MUARIK 2023A was the most favorable environment while Ngetta (Lira23B) was the most unfavorable for all the studied traits. Kitgum 2023A was the most discriminant environment for NN and seed yield. Across environments, genotypes UCR_5280 (G43) and TVu-13958 (G2) were more stable for nodulation ability while TVu-6439 (G23) and CB3 (G6) were the most stable for seed yield. Overall, genotypes TVu-14691 (G13) and TVu-1477 (G27) combined relative performance for the two studied traits. The findings of this study show the potential of using the current genetic material in breeding for high yield and nodulation capacity in cowpea through intensive selection and introgression. However, further evaluation of the cowpea germplasm in diverse growing regions would make selection more effective and accelerate genetic gains.

Keywords: cowpea accessions; G × E; nodulation capacity; seed yield; Uganda field conditions

1. Introduction

Cowpea (*Vigna unguiculata* [L.] Walp), also known as “black-eyed pea,” is a staple leguminous crop that is crucial to food security [1] and to small-scale agriculture with diverse benefits including resilience in changing climate [2]. Cowpea has diverse uses, including human consumption [3], animal feed [4], green manure, fodder, vegetable production, and industrial applications [3, 5]. Cowpea is grown on more than 15.2 million hectares in Africa, Southeast Asia, and some countries in America [6]. The bulk of cowpea production and consumption is in sub-Saharan Africa, especially in the Sudano-Sahelian zone [7]. Just around 9.8 million metric tons of dry cowpeas were produced worldwide in 2022 [6], with Africa producing nearly 9.5 million of which, and western Africa accounts for 90.3% of African production [6]. Cowpea farming is essential to the sustenance of livelihoods and the fulfillment of nutritional demands [5] in many Ugandan communities, as a key source of protein and essential nutrients [3]. In addition, food from leaves, immature pods, and grains of cowpeas is rich in micronutrients, including iron and vitamin A [8], a good source of potassium, fiber, and protein [9] which are essential for addressing major deficiencies in the human body. In Uganda, especially in northern and eastern regions where 90% of the country's cowpea is grown, cowpea is the fourth most widely consumed grain legume food after soybean, groundnuts, and beans [10, 11].

However, cowpea productivity in Uganda is still low with an average yield of up to 412.3 kg/ha [6]. The use of outdated varieties, insufficient input application, and inappropriate agronomic techniques are some of the factors contributing to Uganda's low productivity in cowpea cultivation [5]. Additional challenges include pest and disease problems, climate change effects, drought, salinity, and the costly use of synthetic pesticides [3]. According to Omomowo and Babalola [3], improving cowpea production requires assisting farmers with improved varieties adapted to their agroecological conditions. An important component of cowpea production is nodulation efficiency, which has a direct effect on the plant's capacity to fix atmospheric nitrogen (N_2) [12] and, in turn, affects total yield performance [13]. Thus, to improve soil fertility, crop yields, and food security, it is important to optimize nodulation efficiency in sub-Saharan Africa [14] where smallholder farmers mostly depend on cowpea as a food and cash crop.

Legume crops such as cowpea can transform atmospheric N_2 into ammonia, a form of N_2 that plants can use, through their symbiotic relationship with N_2 -fixing bacteria like rhizobia [12]. Research on the ability of legumes to efficiently nodulate could lead to improvement in soil health [15], food security and environmental sustainability [3], biodiversity preservation [16], and agricultural productivity [17].

The dynamic interaction between the environmental and the genetic composition of various cowpea cultivars [18, 19] has significant effect on nodulation and cowpea yield and yield-related traits. Understanding the genotype by

environment ($G \times E$) interaction is essential to maximizing nodulation capacity in cowpea production, guaranteeing high-yield performance [20]. The nodulation capacity is crucial in preserving soil fertility, particularly in areas where crop productivity may be constrained by nutrient availability [21]. The evaluation of $G \times E$ interaction in cowpea nodulation in Uganda entails analyzing how various cultivars react to various environmental factors across agroecological zones. However, the knowledge of the impact of nodulation on yield characteristics in cowpea plants, including biomass production, pod development, and seed yield, is still limited [22]. In addition, the influence of agronomic techniques, genetic variants, and environmental factors on this relationship has not yet been investigated [23]. In this study, the main objective was to assess the relationship between cowpea genotypes and the environments in which they are cultivated in Uganda with emphasis on the effect of $G \times E$ interaction on nodulation capacity and seed yield performance.

2. Materials and Methods

2.1. Genetic Materials. In this study, a total of thirty five (35) genotypes were used. Out of these, thirty three (33) genotypes were selected from the cowpea minicore collection [24]. Two released varieties from the National Agricultural Research Organization (NARO), Uganda, were included as positive checks (Table 1). The 35 genotypes were selected after screening 241 cowpea genotypes from the minicore collection for biological nitrogen fixation (BNF) efficiency [25]. Out of the 35 genotypes, 4 genotypes (11.4%) were highly efficient, 16 (45.7%) were efficient, 12 (34.3%) were moderate, and 3 (8.6%) were the least efficient for BNF used as negative controls (Table 1) [25].

2.2. Experiment Sites and Cropping Seasons. The experiments were conducted for 2 cropping seasons, 2023A (May–August 2023) and 2023B (October 202–January 2024), in 3 sites including Makerere University Agricultural Research Institute Kabanyolo-MUARIK, National Semi-Arid Resources Research Institute-NaSARRI-(Serere), Kitgum, and in Ngeta ZARDI (Lira) for one cropping season 2023B. Each cropping season and location was considered as a single environment giving a total of seven test environments (Table 2).

2.3. Experiment Design and Trial Management. The trials were laid out in a 5×7 alpha lattice design with three replications. In each replication, a two-row plot of 2 m comprising 16 plants was established at a spacing of 75 cm between rows and 25 cm within rows. Weeding was done three times, but no fertilizer was added in all the experiments.

2.4. Soil Sampling and Analysis. Before planting, at a depth of 30 cm, composite soil samples from all the test environments were collected using the zigzag sampling pattern and

TABLE 1: List of the cowpea genotypes used in this study.

Genotype	Genotype code	Type	BNF status*	Origin
FN-2-13-04	G1	Landrace	Highly efficient	Mozambique
TVu-13958	G2	Landrace	Highly efficient	USSR
TVu-16408	G4	Landrace	Highly efficient	Benin
INIA-72	G5	Landrace	Highly efficient	Mozambique
CB3	G6	Breeding line	Efficient	USA-UCR
TVu-1000	G7	Landrace	Efficient	Ghana
TVu-13485	G9	Landrace	Efficient	Kenya
Massava-11	G10	Landrace	Efficient	Mozambique
TVu-14691	G13	Landrace	Efficient	Botswana
VAR-3A	G16	Landrace	Efficient	Mozambique
TVu-8641	G17	Landrace	Efficient	Togo
TVu-8883	G19	Landrace	Efficient	Benin
TVu-6439	G23	Landrace	Efficient	South Africa
TVu-132	G25	Landrace	Efficient	Uganda
TVu-1477	G27	Landrace	Efficient	Mali
IT93K-503-1	G28	Breeding line	Efficient	IITA-Nigeria
TVu-6644	G30	Landrace	Efficient	Liberia
TVu-15661	G32	Breeding line	Efficient	IITA-Nigeria
TVu-1583	G33	Landrace	Efficient	Nigeria
UCR_5329	G36	Landrace	Efficient	Kenya
TVu-14190	G37	Breeding line	Moderate	IITA-Nigeria
INIA-5E	G38	Landrace	Moderate	Mozambique
TVu-15411	G39	Landrace	Moderate	Lesotho
TVu-4545	G40	Breeding line	Moderate	IITA-Nigeria
UCR_5280	G43	Landrace	Moderate	Sudan
TVu-15114	G44	Landrace	Moderate	Malawi
UCR_5279	G45	Landrace	Moderate	Ghana
TVu-9393	G48	Landrace	Moderate	India
TVu-7684	G49	Landrace	Moderate	Mali
NAROCOW 4	G54	Cultivar (+control)	Moderate	NARO-Uganda
Par18	G55	Landrace	Moderate	Ghana
NAROCOW 2	G56	Cultivar (+control)	Moderate	NARO-Uganda
IT97K-207-21	G57	Landrace (–control)	Low efficient	IITA-Nigeria
IT97K-499-35-1-1	G58	Landrace (–control)	Low efficient	IITA-Nigeria
NamuesseD	G59	Landrace (–control)	Low efficient	Mozambique

*The BNF status was based on the percentage of efficient nodules and the nodule dry weight after screening 241 genotypes from the minicore cowpea collection [25].

TABLE 2: Geographical characteristics of the environments used in the study.

Environment	Code	District	Region	Latitude	Longitude	Altitude (m.a.s.l)	Cropping season
MUARIK ^a	Kab23A	Wakiso	Central	0° 28' 02"N	32° 36' 28"E	1189	2023A
MUARIK	Kab23B	Wakiso	Central	0° 28' 02"N	32° 36' 29"E	1188	2023B
NaSARRI ^b	Ser23A	Serere	Eastern	1° 32' 22"N	33° 26' 49"E	1147	2023A
NaSARRI	Ser23B	Serere	Eastern	1° 32' 20"N	33° 26' 49"E	1148	2023B
Kitgum	Kit23A	Kitgum	Northern	3° 17' 12"N	32° 53' 17"E	943	2023A
Kitgum	Kit23B	Kitgum	Northern	3° 17' 20"N	32° 53' 27"E	935	2023B
Ngetta ZARDI ^c	Lira23B	Lira	Northern	0° 03' 32"N	32° 28' 43"E	1170	2023B

Abbreviation: m.a.s.l, meter above the sea level.

^aMakerere University Agricultural Research Institute Kabanyolo.

^bNational Semi-Arid Resources Research Institute.

^cNgetta Zonal Agricultural Research and Development Institute.

analyzed in the Soil Sciences Laboratory of Makerere University. The soil texture was determined using the hydrometer method [26], and soil pH was determined using a soil–water solution at a ratio of 1 g:2.5 mL with a pH meter [27]. Organic matter was analyzed by the Walkley–Black method (wet oxidation method) [28]. The model PFP7

Flame Photometer Jenway was used to read the emission of exchangeable K, Na, and Ca from the ammonium acetate extract [29]. At a wavelength of 880 nm, the available phosphorus (P) was measured using the Bray 1 method [28] with a Jenway model 6705UV/V spectrophotometer. Salicylic acid, concentrated sulfuric acid, and selenium powder

were used to digest the total nitrogen (N), which was then measured using a distillation unit model Keltec™ from the Kjeldahl method [30]. The soil analysis was performed using the routine procedures as outlined by Okalebo, Gathua, and Woomer [31].

2.5. Traits Measurement. Nodulation count was determined at the pod formation stage [32], in each site per season, one row (8 out of the 16 plants per plot) was randomly selected and uprooted, the root system from each plant was carefully washed, and all nodules were collected and counted to determine the number of nodules (NN). Pods in the remaining row per plot were harvested at 90% maturity, dried then threshed to determine the grain yield per plot. Details on how data were collected are captured in Table 3.

2.6. Data Analysis. The data were analyzed using *lmer* function under the *lme4* package [33] in R software Version 4.3.2 [34] with genotypes and blocks treated as fixed terms and environment as random. Before mean comparison and other downstream analyses, violation assumptions (normality and homogeneity) of analysis of variance were tested. Means were separated using Fisher's protected least significant difference (LSD) at a 5% probability level.

Additive main effects and multiplicative interaction (AMMI) analysis was performed using “*metan*” (Version 1.18.0) package [35] in R statistical software, Version 4.3.2 [34] to determine the contribution of the genotypes, environments, as well as their interaction to the total variation following the AMMI linear model as stated in the following equation (1):

$$Y_{ijk} = \mu + g_i + e_j + \sum_{n=1}^N \lambda_n \gamma_{in} \delta_{jn} + \rho_{ij}, \quad (1)$$

where

- Y_{ij} is the observation of the i th genotype in the j th environment;
- μ is the grand mean; g_i and e_j are the genotype and environment deviations from the grand mean, respectively;
- λ_n is the square root of the eigenvalue of n th interaction principal component (IPCA);
- γ_{in} and δ_{jn} are the principal component scores for IPCA axis n of the i th genotype and j th environment, respectively;
- n is the number of principal components retained in the model;
- ρ_{ij} is the deviation of i th genotype on j th environment from the model.

The GGE biplot was performed based on singular value decomposition (SVD) of the principal components according to Yan and Tinker [36]. The GGE model used is detailed in the following equation:

$$Y_{ij} = \mu + \beta_j + \sum_{n=1}^N \lambda_n \gamma_{in} \delta_{jn} + \epsilon_{ij}, \quad (2)$$

where

- Y_{ij} is the performance of i th genotype in j th environment,
- μ is the grand mean, and β_j is the main effect of j th environment,
- n is the number of principal components (PCs),
- λ_n is the singular value of the n th PC,
- γ_{in} and δ_{jn} are the scores for PC of i th genotype and j th environment, respectively, and
- ϵ_{ij} is the residual associated with i th genotype and j th environment.

The mega-environments were demarcated using a “*which-won-where*” scatter plot as described by Yan and Tinker [36]. AMMI's stability value (ASV) proposed by [37, 38] was used and its formula is described in the following equation:

$$ASV = \sqrt{\frac{\text{IPCA1 Sum of Square}}{\text{IPCA2 Sum of Square}}} (\text{IPCA1})^2 + (\text{IPCA2})^2. \quad (3)$$

3. Results

3.1. Soil and Weather Conditions Prevailing in the Locations Used in the Study. Soil nutrient composition determined before planting in each field trial is presented in Table 4. Except for two environments (MUARIK 2023B and Kitgum 2023B), the soil pH was in the range for cowpea normal growth (6.0–7.5) [39]. However, soil organic matter (OM), N_2 , and phosphorous contents were less than the optimum levels across all the environments. On the other hand, soil potassium and calcium (Ca) levels were excessive [39] in all the environments except in MUARIK season 2023A (Kab23A) for potassium. The soil texture classes varied from sandy clay, clay loam, and sandy clay loam to sandy loam (Table 4). Weather conditions across the environments are shown in Table 4. During the growing cycle, there was much more rain in MUARIK 2023A (Kab23A) (1301.58 mm/growing cycle), followed by MUARIK 2023B (Kab23B) (1247.68 mm/growing cycle), and Lira 23B (1194.73 mm/growing cycle). In terms of temperature, the variation between minimum and maximum temperatures was high in Kitgum 2023A (10.24°C) followed by Kitgum 2023B (10.06°C) and it was low in Lira 23B (3.37°C). However, the relative humidity was almost similar across the test environments varying from 78.5% to 83.9% (Table 4).

3.2. AMMI. AMMI analysis showed a significant effect ($p < 0.05$) of genotypes, environments, and interaction between genotypes and environment on all the studied traits (Table 5). Genotype, environment, and genotype-by-

TABLE 3: Description of traits measured during the genotype evaluation.

Trait	Description	Stage
Number of nodules	$N = (\text{Total count of nodules per plot}) / (\text{number of plants harvested per plot})$	At 90% of pod formation
Seed yield	Weight of seeds per plot (grams)	After harvesting

TABLE 4: Soil and weather characteristics of seven environments in the study.

Parameter	Critical range (*)	Kab23A ^a	Kab23B ^b	Ser23A ^c	Ser23B ^d	Kit23A ^e	Kit23B ^f	Lira23B ^g
Soil texture		SC	CL	SCL	SL	SCL	SL	SCL
pH ^h	6–7.5	6.5	5.25	6.54	6.65	6.23	5.09	6.06
Organic matter (%)	2–5	1.18	1.62	1.51	0.4	1.97	1.08	0.27
N ₂ (%) ⁱ	1.0–2.0	0.14	0.18	0.05	0.18	0.05	0.18	0.12
P (ppm) ^j	15–30	6.32	2.34	4.44	2.34	4.54	8.4	2.05
K (cmols/mol) ^k	0.099–0.198	0.34	0.17	0.18	0.24	0.21	0.24	0.29
Na (cmol/mol) ^l		0.12	0.07	0.08	0.09	0.09	0.06	0.09
Ca (cmols/mol) ^m	0.33–0.99	4.2	6.1	4.8	6.1	4.8	9.15	15.25
TR (mm/GC) (**)		290.70	1301.58	324.40	1247.68	429.76	613.71	1194.73
AMinT (°C/day) (**)		18.58	18.47	19.27	19.08	18.96	18.45	21.14
AMaxT (°C/day) (**)		26.19	25.67	28.37	28.32	29.20	28.51	24.51
ARelH (%RH) (**)		78.50	83.06	83.87	80.73	83.90	81.63	80.68

Note: Source: [40, 41]. GC: Growing cycle of 3 months. Ca: Calcium, N₂: Nitrogen, P: Phosphorus, Na: Sodium.

Abbreviations: AMaxT, Average maximum temperature; AMinT, Average minimum temperature; ARelH, Average Relative humidity, (**); CL, Clay Loam; SC, Sandy Clay; SCL, Sandy Clay Loam; SL, Sandy Loam; TR, total rainfall.

^aMUARIK 2023A.

^bMUARIK 2023B.

^cSerere 2023A.

^dSerere 2023B.

^eKitgum 2023A.

^fKitgum 2023B.

^gLira/Ngetta 2023B.

^hpotential hydrogen.

ⁱNitrogen content in the soil.

^jPhosphorus content in the soil.

^kPotassium content in the soil.

^lSodium content in the soil.

^mCalcium content in the soil.

(*): [39].

environment interactions contributed 7.28%, 50.19%, and 15.25%, respectively, to total observed variations in the NN per plant. For seed yield per plot, genotypes, environment, and genotype by environment interactions contributed 5.65%, 62.29%, and 14.13%, respectively (Table 5).

Based on ASVs, the most stable genotype was G43 (0.649) followed by G2 (0.699) with their lowest ASV score for the NNs per plant (Table 6 and Figure 1(b)), indicating that they were more stable across environments while the genotypes G28 (3.77) and G9 (3.175) had the highest ASV scores, implying that those genotypes were unstable across the test environments (Table 6 and Figure 1(b)). Similarly, for seed yield per plot, the genotypes G23 (0.234) and G6 (0.297) were the most stable across environments while the genotypes G4 (11.07) and G9 (10.02) were the most unstable for that trait with their highest ASV score (Table 6 and Figure 2(b)).

The first two principal components (IPCA1 and IPCA2) were the only significant ($p < 0.01$) for all the traits studied, contributing 39.8% and 26.0%, respectively, in the $G \times E$ interaction for NN and 31.1% and 26.9%, respectively, in the

$G \times E$ interaction for seed yield (Table 5). Based on the biplot (Figure 1(b)) for NN, the genotypes G43 and G2 were still the most stable while for seed yield per plot; the biplot (Figure 2(b)) indicates that the genotypes G23 and G6 are the most stable across the environments.

For the NN per plant, MUARIK 2023A (Kab23A) was the most favorable for the genotypes evaluated with the lowest absolute IPCA1 score of 0.67 and a mean of 25.28 nodules per plant while Kitgum 2023B (Kit23B) was the most favorable for seed yield per plot with an absolute IPCA1 score of 0.05 and a mean of 341.1 g per plot (Table 7). In contrast, Kitgum 2023A (Kit23A) was unfavorable for the NN per plant and seed yield per plot (Table 7). Considering both traits, Kitgum 2023B (Kit23B) was relatively favorable for both NN and seed yield with the absolute IPCA score of 1.07 and 0.05, respectively (Table 7).

3.3. Performance of Cowpea Genotypes Evaluated in Seven Test Environments. The NN per plant ranged from 6 to 17, averaging 9 nodules per plant across the test environments

TABLE 5: AMMI analysis of 35 cowpea genotypes in seven environments of Uganda.

Source	d.f. ^a	NN ^b			Seed_yield ^c (g/plot)		
		SS	MS	%TV	SS	MS	%TV
Total	720	80,673			17,183,500		
Genotypes (G)	34	5877	172.9***	7.28	971,446	28,572***	5.65
Environments (E)	6	40,493	6748.9***	50.19	10,703,133	1,783,855***	62.29
G × E	204	12,303	60.3***	15.25	2,427,214	11,898***	14.13
IPCA 1	39	4897	125.6***	39.8	756,009	19,385***	31.1
IPCA 2	37	3197	86.4**	26.0	652,258	17,629***	26.9
Error	476	22,000	46.2		3,081,707	6474	

Note: %TV: contribution in percentage out total variation.

Abbreviations: MS, mean squares; SS, sum of square.

^aDegree of freedom.

^bNumber of nodules per plant.

^cSeed yield in gram per plot.

Level of significance **: $p < 0.01$.

***: $p < 0.001$.

TABLE 6: The AMMI stability value (ASV) of the top five and bottom five genotypes evaluated in seven environments of Uganda for number of nodules per plant (NN) and seed yield per plot.

NN ^a				Seed_yield ^b (g/plot)			
Genotype	Mean	ASV	Rank_ASV	Genotype	Mean	ASV	Rank_ASV
G43	8.81	0.649	1	G23	170.6	0.234	1
G2	10.24	0.699	2	G6	179.3	0.297	2
G19	8.14	0.787	3	G17	179.3	1.306	3
G56	7.81	0.824	4	G16	194	1.618	4
G25	9.19	0.871	5	G28	193.5	1.662	5
G10	8.81	2.564	31	G10	262.2	9.124	31
G30	16.9	2.733	32	G59	207.9	9.557	32
G4	17	2.88	33	G7	240.8	9.948	33
G9	17.38	3.175	34	G9	229.7	10.022	34
G28	11.52	3.772	35	G4	222.9	11.071	35

Note: The first five genotypes in each column are the top five whereas the last five genotypes are the bottom five for the corresponding trait. The full table of ASV for all the genotypes is presented in Supporting Information SM1 and SM2 for NN and seed yield, respectively.

^aNumber of nodules per plant.

^bSeed yield in grams per plot.

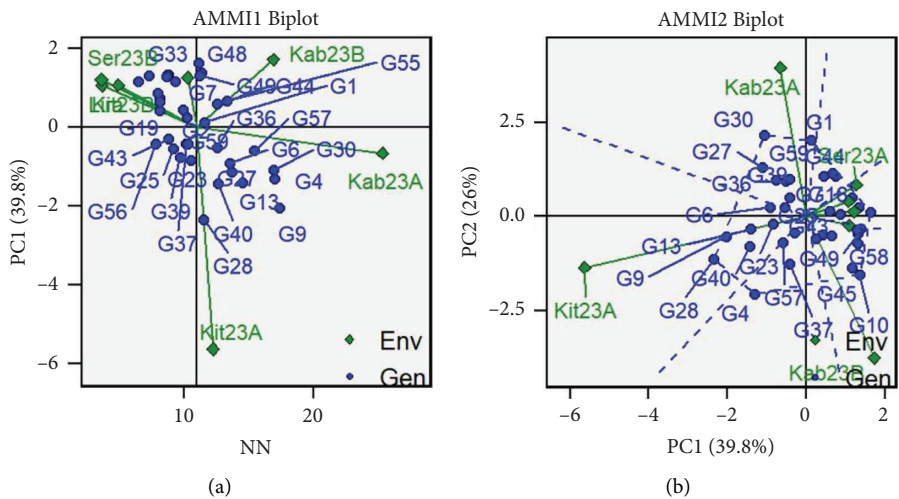


FIGURE 1: AMMI1 biplot (a) and biplot of PCA1 and PCA2 (b) scores of 35 cowpea genotypes evaluated in seven test environments for the number of nodules (NN) per plant.

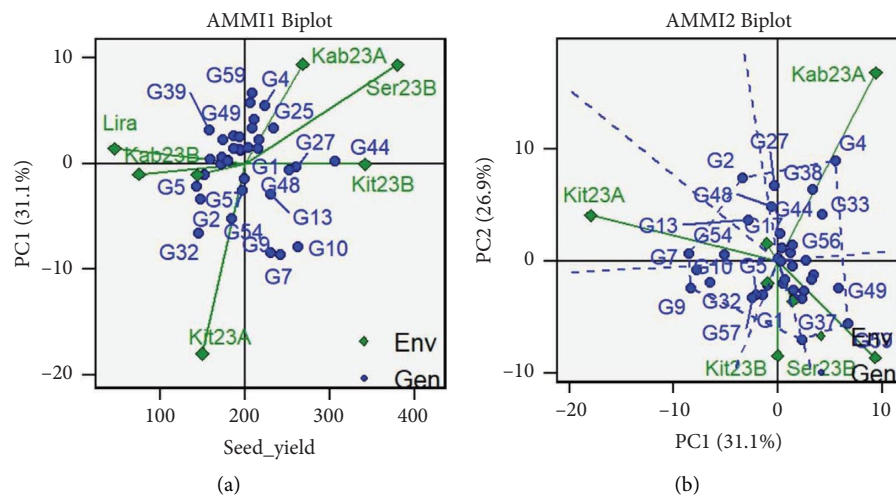


FIGURE 2: AMMI1 biplot (a) and biplot of PCA1 and PCA2 scores (b) of 35 cowpea genotypes evaluated in seven test environments for the seed yield per plot.

TABLE 7: Classification of environments based on their stability index (IPCAe1) scores.

Environment	NN/plant ^a			Seed yield (g/plot) ^b		
	Mean	IPCAe1	Rank	Mean	IPCAe1	Rank
Kab23A	25.28	-0.67	1	267.6	9.37	6
Kab23B	16.88	1.71	6	74.4	-1.02	2
Ser23A	10.29	1.26	5	143.6	-1.06	3
Ser23B	3.61	1.20	4	379.4	9.33	5
Kit23A	12.23	-5.63	7	149.3	-17.97	7
Kit23B	4.91	1.07	3	341.1	-0.05	1
Lira23B	3.68	1.06	2	45.9	1.41	4

^aNumber of nodules per plant.

^bSeed yield in grams per plot.

(Table 8). The best-performing genotypes were G4 and G9 each with 17 nodules per plant while genotypes G45, G58, the check NAROCOW 2 (G56) and G17 with 6, 7, 7, and 7 nodules per plant, respectively, were the worst-performant ones (Table 8).

In terms of seed yield per plot, the overall performance of the evaluated genotypes across the environments ranged from 142.90 g/plot to 305.55 g/plot with an average of 200.18 g/plot (Table 9). The genotype G44 had the highest seed yield of 305.55 g/plot across test environments whereas seed yields of 142.4 g/plot, 144.59 g/plot, and 147.04 g/plot, respectively, for the genotypes G5, G32, and G2 were obtained as the lowest (Table 9). In terms of environmental performance, Kitgum 2023B (341.11 g/plot) had the highest seed yield per plot while Lira (45.88 g/plot) was the poorest environment (Table 9).

3.4. Stability and “Which-Won-Where” Pattern of Genotypes for Studied Traits

3.4.1. NN per Plant. For NN per plant, the first two PCs in the GGE analysis accounted for 67.06% (PC1 (49.12%) and PC2 (17.94%)) of the total variations (Figure 3). The genotype outcomes and G × E interactions for NN are visually shown by the “which-won-where” GGE ranking biplot and stability (Figures 3(a) and 3(b)). For this trait, the seven

environments were subdivided into two megaenvironments. The first mega environment comprised MUARIK 2023B (Kab23B) and Kitgum 2023A (Kit23A) with the genotypes G4 and G9 as the best performers. The second mega-environment was constituted by MUARIK 2023A (Kab23A), Serere 2023A (Ser23A), Serere 2023B (Ser23B), Kitgum 2023B (Kit23B), and Lira 2023B with genotype G30 as the best-performing genotype (Figure 3(a)). The GGE biplot shows that Kitgum 2023A (Kit23A) was the most discriminating of the environments for NN as its environment vector is longer than the rest of the environments while Kitgum 2023B (Kit23B) was the most representative due its closest angle to the average environment axis (Figure 3(b)).

3.4.2. Seed Yield per Plot. For seed yield per plot, the GGE biplot accounted for 61.81% of the total variation with 39.61% of PC1 and 22.2% of PC2. The seven environmental conditions were grouped into two megaenvironments. The first megaenvironment was composed of MUARIK 2023A (Kab23A), MUARIK 2023B (Kab23B), Serere 2023A (Ser23A), Serere 2023B (Ser23B), Kitgum 2023B (Kit23B), and Lira23B with the genotype G4 as the best performer and the second one was composed by Kitgum 2023A (Kit3A) with genotype G7 and G10 as the best performers (Figure 4(a)). The genotypes G1 and G16 were stable across environments but with low yield performance (Figure 4(a)). Kitgum 2023A (Kit23A) was the most discriminating environment followed by MUARIK 2023A while the lowest discriminating environment was seen to be Lira23B (Figure 4(b)). The environment seen as the most representative one was Kitgum 2023B (Kit23B) as its angle from the AEC axis was the smallest (Figure 4(b)).

3.5. Pearson Correlation Among Studied Traits and Environmental Factors. The evaluation of the 35 genotypes across seven environments found a weak to moderate positive correlation between NN and environmental factors.

TABLE 8: Mean of number of nodules per plant for 35 cowpea genotypes evaluated in seven environments in Uganda.

Genotype	Kab23A ^a	Kab23B ^b	Ser23A ^c	Ser23A ^d	Kit23B ^e	Kit23B ^f	Lira23B ^g	Mean + SE
G1	37.3 a	13.3 a	8.7 a-d	3.7 bcd	8.7 e-i	2.7 cde	6.7 abc	11.6 ± 2.0
G2	23.3 c-g	20 a	7 a-d	2.3 cd	10.7 c-i	3.7 cde	4.7 cdef	10.2 ± 1.6
G4	28.3 a-e	32.7 a	13 a-d	5 bcd	27.7 ab	10 ab	2.3 def	17 ± 2.2
G5	22.7 d-g	16 a	13.3 a-d	1.3 cd	2.3 hi	4 b-e	1.3 ef	8.71 ± 1.7
G6	31 a-e	18.7 a	13.3 a-d	1 d	19.3 a-f	7.7 abc	3.7 c-f	13.5 ± 2.1
G7	30.7 a-e	14 a	7 a-d	3 cd	6.7 f-i	7 a-e	1 f	9.9 ± 1.7
G9	30 a-e	20.7 a	11.7 a-d	10.3 a	31 a	8 abc	10.0 a	17.4 ± 1.8
G10	14 g	21 a	9.3 a-d	3 cd	5 f-i	3.7 cde	5.7 bcd	8.8 ± 1.3
G13	29.7 a-e	21.3 a	15.3 a-d	0.7 d	24 abc	5.3 a-e	5 cde	14.4 ± 2.1
G16	27.7 a-f	11.7 a	3.3 d	4.7 bcd	3.3 ghi	4.3 b-e	1.7 ef	8.1 ± 1.6
G17	22.7 d-g	15.3 a	4.7 cd	4 bcd	4 ghi	2.3 cde	2.7 def	7.9 ± 1.6
G19	20.3 efg	16.3 a	5.3 bcd	1.7 cd	7.7 e-i	3 cde	2.7 def	8.1 ± 1.5
G23	24 a-g	15.7 a	10.3 a-d	2 cd	17 a-g	1 e	3.7 c-f	10.5 ± 1.7
G25	23.7 b-g	11.7 a	6 bcd	4.7 bcd	13.3 b-i	2.7 cde	2.3 def	9.12 ± 1.7
G27	36.7 abc	15.7 a	10.7 a-d	4.7 bcd	19 a-f	2.3 cde	6.7 abc	13.6 ± 2.1
G28	22 efg	16.3 a	4.7 cd	4.7 bcd	27.7 ab	3 cde	2.3 def	11.5 ± 1.9
G30	37 ab	9.7 a	20.7 a	7.7 ab	22 a-e	11.0 a	10.0 a	16.9 ± 2.0
G32	21.7 efg	12.3 a	13.7 a-d	4 bcd	4 ghi	6.7 a-e	3 c-f	9.3 ± 1.6
G33	23.7 b-g	19 a	18 abc	2.7 cd	3.3 ghi	7.3 a-d	3.7 c-f	11.1 ± 1.9
G36	29.3 a-e	12.3 a	15 a-d	1.3 cd	15.7 b-i	11.0 a	3 c-f	12.5 ± 1.8
G37	14 g	14.7 a	12 a-d	3.7 bcd	16.7 a-h	6.3 a-e	3.7 c-f	10.1 ± 1.3
G38	20.3 efg	17 a	5 bcd	2.7 cd	6.3 f-i	2.7 cde	3 c-f	8.1 ± 1.5
G39	29.3 a-e	11.0 a	4.7 cd	5.7 bc	13.7 b-i	1.3 de	2 def	9.6 ± 1.8
G40	22 efg	16.7 a	13.7 a-d	3.7 bcd	23.7 a-d	7 a-e	1.7 ef	12.6 ± 1.9
G43	19.3 efg	13 a	5 bcd	2.3 cd	12.7 c-i	5.7 a-e	3.7 c-f	8.8 ± 1.5
G44	31.7 a-e	16.3 a	14.7 a-d	7.7 ab	9.3 d-i	4.3 b-e	9.3 ab	13.3 ± 1.7
G45	14.7 fg	19 a	2.7 d	1.7 cd	3 ghi	3 cde	1.3 ef	6.5 ± 1.2
G48	25.7 a-g	23.7 a	13 a-d	5.7 bc	5 f-i	2 cde	4.3 c-f	11.3 ± 1.7
G49	20.7 efg	20 a	18.7 ab	5 bcd	6.3 f-i	5 a-e	2.6 def	11.2 ± 1.7
G54	21 efg	18 a	7.7 a-d	4.7 bcd	3 ghi	4 b-e	2 def	8.6 ± 1.6
G55	30 a-e	22 a	12.7 a-d	1.7 cd	9.7 c-i	7.7 abc	4 c-f	12.5 ± 2.0
G56	18.3 efg	5.7 a	13.3 a-d	1.7 cd	12 c-i	2.7 cde	1 f	7.8 ± 1.4
G57	36 a-d	31 a	8 a-d	2.3 cd	19.3 a-f	6.3 a-e	5 cde	15.4 ± 2.3
G58	18.3 efg	18 a	4.7 cd	2.3 cd	2 i	4.3 b-e	1.7 ef	7.3 ± 1.7
G59	27.7 a-f	11.0 a	13.3 a-d	3.3 bcd	13 c-i	3 cde	1 f	10.3 ± 1.7
GM	25.28	16.88	10.29	3.61	12.23	4.91	3.68	9.55
LSD (5%)	13.37	12.27	13.68	4.58	14.51	6.29	3.81	4.18
CV (%)	32.34	44.11	81.22	76.95	72.47	77.61	62.8	62.90

Note: Within a column, means followed by the same letters are not significantly different at 5% significance level.

Abbreviations: CV, coefficient of variation; GM, Grand mean; LSD, Least significant difference.

^aMUARIK 2023A.

^bMUARIK 2023B.

^cSerere 2023A.

^dSerere 2023B.

^eKitgum 2023A.

^fKitgum 2023B.

^gLira/Ngetta.

Thus, the NN had a moderate positive relationship ($r=0.54$ and $r=0.55$) with OM content and soil sodium content, respectively. On the other hand, the NN was moderately negatively correlated ($r=-0.43$ and $r=-0.49$, respectively) with the total rainfall and the average minimum temperature and strongly negatively correlated ($r=-0.6$) with the Ca content in the soil (Figure 5). Likewise, seed yield was moderately positively correlated ($r=0.45$) with the N_2 content in the soil. In addition, seed yield showed a moderate negative correlation ($r=-0.42$ and $r=-0.5$) with the average relative humidity and the average minimum temperature, respectively (Figure 5).

4. Discussion

4.1. Genotype Performance. The evaluation of 35 cowpea genotypes in seven environments targeted mainly the assessment of the performance of the genotypes vis-a-vis different environments of Uganda in terms of nodule formation and seed yield. Results showed a significant difference (Table 5), implying genetic variability among the genotypes used in the study. Genetic diversity plays a key role in cultivar development targeting resilience to biotic and abiotic stress and yielding productivity [43]. Similarly, this study revealed a significant effect of the interaction

TABLE 9: Mean of seed yield per plot for 35 cowpea genotypes assessed in seven environments of Uganda.

Genotype	Kab23A ^a	Kab23B ^b	Ser23A ^c	Ser23A ^d	Kit23B ^e	Kit23B ^f	Lira23B ^g	Mean $\pm$ SE
G1	225 d-i	37.7 gh	90.7 d-g	389.7 b-j	178 d-h	419.7 a-d	52 b-f	198.9 $\pm$ 25.6
G2	277 b-i	91.7 b-g	142.6 b-g	175 l	143 d-i	142.7 l	57.3 b-f	147.0 $\pm$ 15.7
G4	495 a	83.3 b-h	140.8 b-g	424.7 a-h	136.3 d-i	246.7 jkl	33.3 c-f	222.8 $\pm$ 31.2
G5	106.7 hi	37.3 gh	197.3 a-d	295.7 i-l	77.5 hi	268.3 h-k	14 f	142.4 $\pm$ 21.0
G6	230.3 d-i	98 a-g	187.4 a-e	299 i-l	77.5 hi	312.7 c-k	50 b-f	179.2 $\pm$ 24.9
G7	257 c-i	81 b-h	151.4 b-g	407 a-i	393.5 a	384 a-g	11.3 f	240.7 $\pm$ 29.6
G9	201.7 f-i	160 a	89.1 d-g	364 d-j	338.3 abc	425.3 abc	29.3 c-f	229.6 $\pm$ 27.2
G10	243.7 d-i	115.3 abc	189.5 a-d	444 a-f	387.5 ab	368 b-h	87.3 ab	262.2 $\pm$ 26.9
G13	346.3 a-g	42.7 fgh	203.8 abc	347 e-j	249 cde	410.3 a-e	12 f	230.1 $\pm$ 28.4
G16	304.3 a-g	51d e-h	99.7 c-g	361 d-j	127.7 e-i	382 a-g	32 c-f	193.9 $\pm$ 28.2
G17	265.7 b-i	68.7 c-h	138.6 b-g	274.3 jkl	87.5 ghi	327 c-k	93 ab	179.2 $\pm$ 22.8
G19	293.3 b-h	50.3 d-h	80.7 efg	352.7 d-j	82.7 hi	363 b-i	77.3 bc	185.6 $\pm$ 30.8
G23	245.7 d-i	35 gh	80.7 efg	351 d-j	129.7 e-i	297 e-k	55.3 b-f	170.6 $\pm$ 23.9
G25	304.7 a-g	108.3 a-e	200.1 abc	469.3 a-e	116.5 f-i	371.7 b-h	60.7 b-f	233.0 $\pm$ 27.6
G27	443.7 abc	79.7 b-h	255.5 a	374 c-j	239.7 c-f	395.7 a-f	28.7 c-f	259.5 $\pm$ 28.5
G28	255 c-i	87 b-g	169.0 a-f	372.3 c-j	98.5 ghi	321.7 c-k	50.7 b-f	193.4 $\pm$ 23.6
G30	200.7 f-i	47.3 e-h	71.5 fg	349 d-j	90.7 ghi	319 c-k	30.7 c-f	158.4 $\pm$ 22.8
G32	100.7 i	22.3 h	153.6 a-g	222.3 kl	166.5 d-h	289.3 f-k	57.3 b-f	144.5 $\pm$ 17.0
G33	399.7 a-e	53.3 c-h	126.1 b-g	412.3 a-i	119.3 f-i	333 c-j	30 c-f	210.5 $\pm$ 28.45
G36	231.7 d-i	37 gh	106.7 c-g	424.3 a-h	116 f-i	360 b-j	26 def	185.9 $\pm$ 27.9
G37	174.7 ghi	87.7 b-g	176.7 a-f	529 a	113.3 f-i	369 b-h	58 b-f	215.4 $\pm$ 29.6
G38	411.7 a-d	94.7 b-g	194.5 a-d	309.7 g-k	89.5 ghi	331.3 c-j	25.3 def	208.1 $\pm$ 30.9
G39	227.3 d-i	39.3 gh	72.9 fg	353 d-j	33.3 i	308 d-k	64.7 b-e	156.9 $\pm$ 23.0
G40	172 ghi	113.7 a-d	54.6 g	301 h-k	89.3 ghi	302.7 e-k	25.3 def	151.2 $\pm$ 19.2
G43	233.3 d-i	59.7 c-h	170.5 a-f	429 a-g	83.7 hi	358.3 b-j	12.7 f	192.4 $\pm$ 27.2
G44	450.7 ab	138.7 ab	141.2 b-g	507.3 ab	308 abc	466 ab	127 a	305.5 $\pm$ 31.3
G45	172.3 ghi	93.7 b-g	150.3 a-g	451 a-f	72.5 hi	214.7 kl	55.7 b-f	172.8 $\pm$ 23.1
G48	391 a-f	75.7 b-h	232.8 ab	447 a-f	259.5 bcd	324 c-k	31.3 c-f	251.6 $\pm$ 27.8
G49	291.3 b-i	92.7 b-g	107.1 c-g	473.3 a-d	51.3 hi	358 b-j	69.3 bcd	206.1 $\pm$ 31.7
G54	219.3 e-i	39.3 gh	137.5 b-g	273 jkl	214 c-g	363.3 b-i	36 c-f	183.2 $\pm$ 22.8
G55	186.7 ghi	35.7 gh	205.7 abc	407.3 a-i	101.5 ghi	250.3 i-l	17.3 ef	172.1 $\pm$ 23.9
G56	313.3 a-g	104 a-f	133.8 b-g	465 a-f	176.5 d-h	273.3 g-k	37.3 c-f	214.7 $\pm$ 25.1
G57	192.7 ghi	116 abc	126.8 b-g	341.7 f-k	157 d-i	408 a-e	32 c-f	196.3 $\pm$ 24.7
G58	223 d-i	104.3 a-f	167.2 a-f	391.3 b-j	87 ghi	380 b-h	69.3 bcd	203.1 $\pm$ 24.2
G59	279 b-i	22.7 h	79.5 efg	490.7 abc	32.3 i	495 a	56 b-f	207.8 $\pm$ 37.3
GM	267.59	74.42	143.61	379.37	149.26	341.11	45.88	200.18
LSD (5%)	191.79	63.87	108.72	124.64	128.60	113.60	49.67	52.71
CV (%)	43.82	52.05	46.23	19.92	52.61	20.20	65.66	43.42

Note: Within a column, means followed by the same letters are not significantly different at 5% significance level.

Abbreviations: CV, coefficient of variation; GM, Grand mean; LSD, Least significant difference.

^aMUARIK 2023A.

^bMUARIK 2023B.

^cSerere 2023A.

^dSerere 2023B.

^eKitgum 2023A.

^fKitgum 2023B.

^gLira/Ngetta.

between genotype and environment on the overall genotype performance of the evaluated genotypes for studied traits (Table 5). A substantial $G \times E$ interaction suggests that the environment affects a genotype's contribution to a phenotype and vice versa [44]. Therefore, by considering the $G \times E$ interaction, plant scientists can improve cultivars' stability and adaptability, which are primary concerns in plant breeding. In previous studies on cowpea genotype evaluated under multienvironmental conditions, nodule formation [45] and seed yield [46, 47] as quantitative traits are highly affected by $G \times E$ interactions. Similarly, in the

current study, the significant effect of $G \times E$ interactions on the number of NN per plant and the seed yield per plot suggests that there is always a need to evaluate the germplasm in contrasting environmental conditions before releasing it for use by farmers any new variety. In addition to being complex traits, other factors such as environmental variability, genetic variation, adaptation to local conditions, stress responses, interactions among genes within a particular genotype, and geographical and ecological differences contribute to this interaction effect [48, 49].

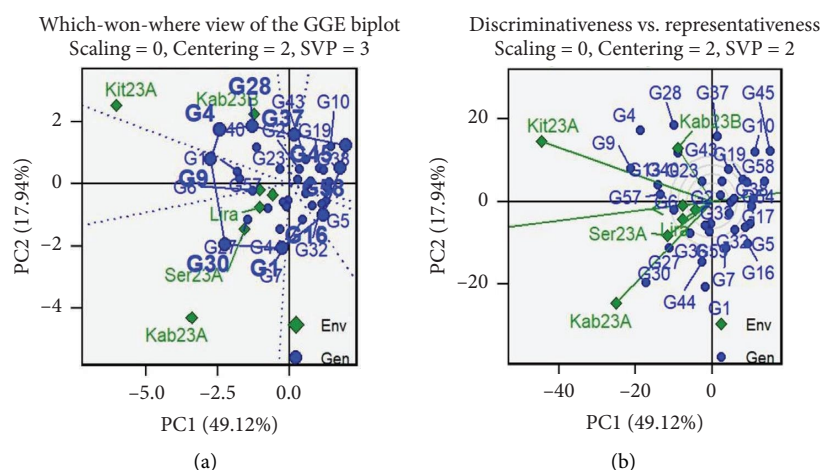


FIGURE 3: A symmetrical scaling-based GGE scatter plot representing the “which-won-where” pattern (a) and the discriminative versus representativeness power (b) of environments using the 35 cowpea genotypes assessed for the number of nodules per plant in seven environments. Discriminative environments are those with long vectors (as they can discriminate the genotypes) while representative environments are those with small angle from the average environment axis (AEA).

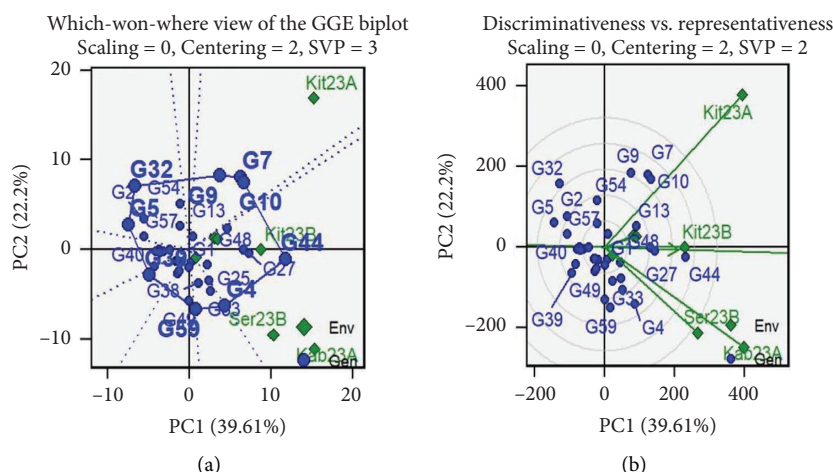


FIGURE 4: A symmetrical scaling-based GGE scatter plot representing the “which-won-where” pattern (a) and the representativeness and discriminative power (b) of environments for the 35 cowpea genotypes assessed for seed yield (g/plot) in seven environments. Discriminative environments are those with long vectors (as they can discriminate the genotypes) while representative environments are those with small angle from the average environment axis (AEA).

Moreover, one of the features of the GGE biplot is the capacity to visualize the relationship between genotypes and environments known as the “which-won-where” pattern [50]. Hence, the genotype main effect plus $G \times E$ interaction illustrated by the GGE biplot are both based on the statistical model of principal component analysis [51]. While AMMI analysis is referred to as double-centered principal component analysis, GGE biplot analysis is based on environment-centered principal component analysis [52]. Likewise, in this work, GGE biplot was used to visualize the relationship between the environment and the performance of the genotypes evaluated regarding their genetic parameters including NN per plant and seed yield per plot (Figures 3 and 4).

It was shown that genotypes G9, G4, G30, G57, G13, and G27 were the most performing for NN per plant but were all unstable across environments (Table 8 and Figure 3(a)). Regarding stability for this trait, genotypes G43, G2, and G56 (NAROCOW 2 used as a check) were the most stable in nodulating but their nodulating capacity remained low across environments (Table 8 and Figure 3(a)). The stability of the genotype used as a check is not surprising since it was an already released variety in Uganda.

In terms of seed yield, the most performing and adapted genotypes were G44 followed by G10 and G27 but were usually unstable across environments. The genotype G23 followed by G6 and G17 were broadly stable but with a low yield across environments (Table 9 and Figure 4(a)).

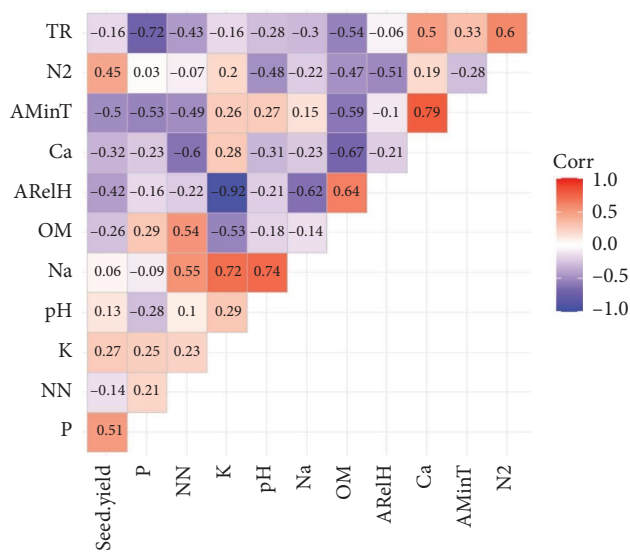


FIGURE 5: Correlation among studied traits (number of nodules per plant [NN] and seed yield per plot) and environmental factors prevailing in seven test environments for 35 cowpea genotypes evaluated. N₂: nitrogen, P: phosphorus, Na: sodium, Ca: calcium, TR: total rainfall per growing cycle, AMinT: Average minimum temperature, ARelH: average relative humidity. The gradation of this scale is as follows: (1) 0–0.19, very weak association; (2) 0.2–0.39, weak association; (3) 0.40–0.59, moderate association; (4) 0.6–0.79, strong association; and (5) 0.80–1.0, very strong association [42].

Previous studies have also found that different genotypes may be stable across locations or seasons but not necessarily perform better for seed yield [46, 53] and for nodulation capacity [45] in cowpea. It has been recommended that to increase cowpea production and provide food security, it is essential to evaluate both the yield and yield stability of cowpea genotypes across environments and seasons [54]. Overall, G13 and G27 were the most genotypes with the combined ability to nodulate with high yield.

4.2. Environment Clustering. The agroclimatic conditions recorded in the test environments during the experimentation influenced differently the performance of the evaluated genotypes. For instance, the ideal annual rainfall for cowpea normal growth ranges from 1000 mm to 1200 mm (2.7 mm–3.9 mm per day) while the temperature should remain between 28 and 30°C [55]. In our test environments, the minimum temperature was quite low (18°C) and the precipitation was only close to the range in MUARIK 2023A (Kab23A), Serere 2023A (Ser23A), Kitgum 2023A (Kit23A), and Kitgum 2023B (Kit23B) (Table 4). This explains why the performance of the evaluated genotypes was better in the abovementioned locations, making those environments favorable for the studied traits. Among those environments, Kitgum 2023A (Kit23A) with relatively less rain and the highest maximum temperature compared with the rest was found to be the most discriminative environment for the positively correlated studied traits including the NN per

plant and seed yield per plot. This result is in agreement with the report of Mbeyagala et al. [46] who also found Kitgum region to be the most discriminative environment for cowpea yield in their evaluation of 29 cowpea genotypes for yield stability in 13 cowpea growing areas of Uganda. On the other hand, the low temperatures and high rainfall increase fungal disease incidence decreasing, therefore, the ability to nodulate and seed yield [55]. This scenario explains why MUARIK 2023B (Kab23B) with the highest level of rain (1301.58 mm/GC) was the worst discriminative for the NN per plant and seed yield. However, high temperatures can also negatively impact cowpea production, especially at the flowering stage [56, 57] and seed filling [58]. Various factors including the cropping season, precipitation, temperature patterns, relative humidity, and light intensity have been reported by previous researchers to have an impact on GEI in sorghum forage [59] and cowpea yield [46]. In terms of representativeness, Kitgum 2023B (Kit23B) remains the most representative environment for the correlated traits including the NN per plant and seed yield (Figures 3(b) and 4(b)). This result makes again the Kitgum region more suitable for cowpea production in Uganda as it can even represent the rest of the environmental conditions.

Regarding soil element composition, P and the OM content were not in range in all environments but with various amounts which may have influenced the respective performance observed. Generally, the low N₂ content is not a problem because the cowpea crop has the capacity for BNF; that is why cowpea crops are more tolerant to infertile and acid soils, can adapt to low fertility levels, and do not need the addition of N₂ fertilizers [60]. However, the recorded average yield of 200.18 gr/plot (1333.3 kg/ha) remained small compared with the potential yield of 3000 kg/ha in a well-managed field [61]. On the other hand, potassium and Ca contents were in the range across all the environments but could not boost the cowpea genotypes under evaluation. This is probably because their action is effective when the rest of the required soil elements are also at a certain level. The evaluation of the 35 cowpea genotypes in 7 test environments identified the existence of certain mega environments. According to Bakare et al. [62], a megaenvironment is defined as a group of environments that share a common performing genotype, suggesting that genotypes vary more between megaenvironments than within them and that various genotypes are adapted to different megaenvironments. Overall, in this work, the existence of identified megaenvironments for each of the studied traits including NN and seed yield suggests that certain genetic adaptations to specific megaenvironments occurred, leading to the beneficial selection of suited genotype adapted for each megaenvironment by exploitation of the G×E interaction [63]. However, as this work evaluated the performance of genotypes for only 2 consecutive seasons, it is important to better identify and utilize the identified mega environments by conducting more evaluation trials for multiseasons and multiyears to adjust shifting environmental conditions.

4.3. Correlation and Effect of Environmental Factors on the Studied Traits. The NN per plant was positively correlated with soil OM content (Figure 5). These results agree with Allito et al. [64] who found that nodulation and biomass production of Faba bean genotype depends on, among other factors, rhizobium strain and its interaction with soil biophysical conditions. The positive correlation found in this report between NN and K (Figure 5) agrees with that of [65] and between NN and P agree with that of [66]. This explains why, in this work, MUARIK 2023A with high K, P, and OM contents in the soil performed better in regards to the nodulation ability as those elements were positively correlated to the NN per plant (Figure 5). However, the positive correlation between NN and Na found in this report disagrees with previous studies such as those of Rao et al. [67] and Swaraj and Bishnoi [68] who found that legume nodulation and N_2 fixation are adversely affected by high soil salt and sodicity levels. Although, the host plant's ability to nodulate is the main influencing factor, the rhizobial strains present in the different test environments might have influenced this scenario [68].

On the other hand, the NN per plant being negatively correlated with minimum temperature in this report (Figure 5) and those of Hungria and Vargas [69] for the minimum temperature, of Brauer, Ritchey, and Belesky [70] for soil Ca content, of Zahran [71] for N_2 content, and of Ferguson et al. [72] for high levels of rain explain why Lira 2023B performed poorly regarding nodulation ability.

Likewise, adequate K content in the soil improves seed yield in crops by increasing root growth and improving water stress tolerance [73]. This was confirmed in Serere 2023A and Serere 2023B as well as in MUARIK 2023A where the K content in the soil positively influenced the recorded seed yield (Table 4). The present results agree with those previously reported by Islam et al. [74]. The N_2 content in the soil positively influenced the recorded high seed yield in Kitgum 2023B which corroborates the findings of Reinprecht et al. [75]. In addition, as previously reported by Nord et al. [76] and Sita et al. [57] for high temperatures, by Brauer, Ritchey, and Belesky [70] for high Ca content in the soil and by Zhelyazkova, Delchev, and Stoyanova [77] for high levels of rain, crop seed yield being negatively affected by those factors also justifies why Lira 2023B yielded poorly in this cowpea genotype evaluation.

Soil OM content affects nodulation capacity by enhancing nutrient availability such as N_2 [78] and P [79, 80]. On the other hand, the effect of a high concentration of Ca in the soil was reported to be decreasing the nodule number and nodule dry mass per plant, especially when combined with a high level of aluminum [81]. Likewise, due to preferential usage in the lateral roots and a reduction in the transfer of photoassimilates to the nodules, supplying more nitrate, a major form of inorganic N_2 in the soil, was found to inhibit the growth of soybean nodules [82]. Furthermore, nodulation in kidney beans and soybeans was found to be 73% inhibited by acidic "simulated rain" with a pH of 3.2, suggesting that heavy rains that cause the soil to become acidic could potentially hinder the development of nodules [83].

5. Conclusion

This study shows that cowpea genotypes are sensitive to environmental factors and possess significant genetic variation for the improvement of traits such as nodulation capacity and seed yield. The study identified, in Ugandan field conditions, genotypes UCR_5280 (G43), TVu-13958 (G2), and TVu-8883 (19) as the most stable across environments with a high ability to nodulate. Those genotypes can be good candidates for breeding for nodulation capacity through cowpea breeding programs. In terms of yield performance, the study identified genotypes TVu-6439 (G23), CB3 (G6), and TVu-8641(G17) as the most stable with relatively high yields across locations. Among the test environments, MUARIK 2023A was the most favorable for all the studied traits. However, overall, Kitgum was the most suitable region for cowpea production and could therefore be targeted by seed companies or other agricultural development projects aiming at cowpea production enhancement in Uganda. In general, genotypes with multipurpose performance were not many in this study. However, genotypes such as TVu-14691 (G13) and TVu-1477 (G27) had a combined relative performance for the two studied traits including nodulation capacity and seed yield. Among the released varieties used as checks, the variety NAROCOW 2 (G56) was more stable for nodulation capacity despite its overall low performance. Those genotypes identified as high performing and stable across the test environments could be recommended for further testing in other cowpea-growing regions with the active participation of farmers before release. Cowpea breeding programs could also use the findings of this study for future selection and introgression in other genetic materials targeting cowpea productivity enhancement.

Data Availability Statement

The data used to support the findings of this study are included within the article and as Supporting Information.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

G.N., E.K.M., T.L.O., I.O.D., and J.B.T.: conceptualization; G.N.: methodology, investigation, data curation, and writing the original draft; G.N. and E.A.A.: formal analysis; E.K.M., T.L.O., E.A.A., R.A., I.O.D., R.E., and A.B. M.O.-S.: reviewing and editing; E.K.M., T.L.O., I.O.D., and J.B.T.: supervision. All authors have read and agreed to the submitted version of the manuscript.

Funding

This study was jointly funded by the Regional Universities Forum for Capacity Building in Agriculture (RUFORUM), Makerere University-Research Innovation Fund (MakRif, 4 Edition), Makerere University Regional Center for Crop

Improvement (MaRCCI), and the Institute of Agricultural Sciences of Burundi (ISABU).

Acknowledgments

We acknowledge the support of individuals from MaRCCI, Kitgum, and the National Agricultural Research Organization-National Semi-Arid Research Institute (NARO-NaSARRI) and Ngeta ZARDI for their technical support, especially in daily-type data collection.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

Supporting Information 1. Table SM1: Ranking of 35 selected cowpea genotypes according to ASV_based on their NN per plant.

Supporting Information 2. Table SM2: Ranking of 35 selected cowpea genotypes according to ASV_based on their seed yield per plot.

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