



Understanding the Nexus of Genotype, Root Nodulation, and Soil Nutrients for Shoot Biomass Production and Seed Yield in Cowpea (*Vigna unguiculata* L. Walp)

Olawale Mashood Aliyu¹ · Toyeeb Abayomi Abioye¹ · Yusuf Folorunsho Abdulkareem¹ · Abdulqudus Ibrahim¹

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Abstract

To enhance the productivity of cowpea for seeds and shoot biomass yields, the complex interwoven relationships of genotype, soil nutrients, and nodulation were studied. A 4-year field study was conducted with ten cowpea accessions in a randomized complete block design of three replicates and data collected on soil parameters, root nodulation, plant growth, and yield characters were analyzed for variance components and correlation analysis. Genotype and year influenced the rate of nodulation, plant nutrient uptake, shoot biomass, and seed yield. Nodulation and nitrogen uptake increased shoot biomass production but not seed yield. Early maturity was associated with high seed yield, while late maturity enhanced biomass production. Cowpeas differ significantly in nodulation efficiency and soil nutrient utilization for seed yield and biomass production, with IT98K-205–8 being the most efficient. Soils cultivated for cowpea showed reduction in clay content and soil nutrients, but increased in silt content, soil acidity, and phosphorus uptake. Proportion of phosphorus uptake was significantly higher than nitrogen and organic carbon uptakes in cowpea. Increasing uptake of nitrogen and organic carbon is inversely associated to nodulation, growth parameters, and shoot biomass, while phosphorus uptake is directly correlated with seed yield. IT89KD-288 and IT00K-1263 were superior for nodulation and shoot biomass production ($> 28 \text{ tons ha}^{-1}$), while IT08K-150–12 and IT00K-1263 were best for seed yield of $> 2.0 \text{ tons ha}^{-1}$. This study reported the efficiency of root nodulation of native rhizobia and nutrient utilization as among the important elements required for optimum development and yield of cowpea. IT00K-1263 that combines high biomass with seed yield is a candidate for dual-purpose, while IT08K-150–12 could be useful as an early-maturing high-yield variety. Inherent nutrient utilization efficiency of IT98K-205–8 could be explored in future improvement programs.

Keywords Cowpea · Genotype · Nodulation · Soil nutrients · Shoot biomass · Seed yield

1 Introduction

The contribution of cowpea (*Vigna unguiculata* L., Walp.) to food security and food quality for the resource-poor people in developing nations cannot be overemphasized, because of its high-quality protein and resilience to adverse climate conditions. Traditionally, farmers in the West Africa sub-region are known to cultivate cowpea because of its low-cost and high-quality proteins (Iseki et al. 2021). The inherent health benefits and nutritional values of cowpea have led to

a rise in its consumption especially with recent reports of its antidiabetic, anticancer, and antihypertensive properties (Affrifah et al. 2022; Ironi et al. 2021). Cowpea is described as a leguminous crop grown for its highly nutritious grain as food. The protein contents of cowpea leaves and dry seeds ranged from 27 to 43% and 21 to 33%, respectively (Abudulai et al. 2016), which makes it a cheap protein source for poor-resource households (Ajeigbe et al. 2012). Crop residue from cowpea is also a valuable source of fodder for livestock especially during dry seasons (Kamara et al. 2012). Cowpea has become an important component of the traditional cropping system to improve soil fertility in sub-Saharan Africa because of its inherent ability to fix nitrogen into the soil. It is mostly a preferred choice companion crop with cereals among smallholder farmers in dry regions

✉ Olawale Mashood Aliyu
walealiyu@mail.com; olawale.aliyu@kwasu.edu.ng

¹ Department of Crop Production, Kwara State University, Malete, PMB 1530, Ilorin, Nigeria

because of its short growing cycle, and tolerance to drought, high temperature, and soil salinity (Bisikwa et al. 2014).

Cowpea production has been on the increase with current world production of 8.9 million tons in 2020, with Africa producing 8.6 million, i.e., about 96% of total world production (FAO Statistics 2022; <https://www.fao.org/faostat/en/#data/QCL> website accessed 26 July 2022). Nigeria's production in 2020 stood at 3.65 million tons, i.e., about 41% of world production (FAO Statistics 2022; <https://www.fao.org/faostat/en/#data/QCL>). Indeed, recent studies have reported about a sixfold increase in production in West Africa in the last decades. This increase has been largely attributed to a surge in food demand to meet rapid population growth in the region (Iseki et al. 2021). Paradoxically, the average cowpea of 300 kg ha⁻¹ still obtained in farmers' fields (Kebede and Bekeko 2020) is comparably low to the biological potential yield of 4000–5000 kg/ha in the crop (Aliyu and Makinde 2016; Kamara et al. 2018; Aliyu et al. 2019, 2021). This yield vulnerability has contributed partly to food insecurity in the region (Iseki et al. 2021). Problems of low yield have been attributed to factors ranging from the adoption of obsolete agricultural practices including inappropriate planting time, use of poor traditional cultivars, pest and disease attack, and unstable climate conditions to the rapid decline in soil fertility among others (Kyie-Boahen et al. 2017). There are concerted efforts at improving grain yield in the past, with emphasis on varietal development and improvement of pest management strategy, with some levels of yield improvement. However, the current low farm yield is suggestive of other important components that need to be addressed to achieve optimum yield. And the role of soil and plant interaction, especially the uptake and utilization of nutrients for growth and seed production cannot be overemphasized in this context.

Low and/or erratic precipitation, high temperature, and poor soil nutrient fertility are among the major causes of poor growth and grain yield of crops in the Guinea savanna that are inherently deficient in nitrogen and phosphorus (Mohammed et al. 2020). Most of the nitrogen required for crop development in the traditional farming system comes from nitrogen-fixing *Rhizobium spp* that are readily available in tropical soils. Rhizobia-leguminous plant interaction during the nodulation process is complex (Kimiti and Odee 2010) and the efficiency varies with genotype. Nodulation is a host-specific process with each rhizobia having a defined host-plant range (Stacey 2007) and this has been found to vary across cowpea genotypes (Nyaga and Njeru 2020).

Since nodulation plays an important role in the growth and development of cowpea, further knowledge of the nodulation characteristics (size and number) will be vital to improving grain seed yield and overall productivity. The ability to fix atmospheric nitrogen through root nodulation is a unique adaptive trait for legumes especially in regions with highly

deficient soils. The presence of appropriate rhizobia in the soil is critical for the effective nitrogen fixation process and nodule formation (Pepper and Upchurch 1991), and rhizobia are sometimes selective in their symbiotic relationship with legumes (Rending and Taylor 1989). Such selective interaction will bring about intra- and interspecific variation for nodulation in legumes. Cowpea has the potential to fix nitrogen of between 50 and 300 kg/ha per year (Simunji et al. 2019) and this potential could be optimally explored to improve its production. There are studies on genotypic variation for the effectiveness of nitrogen-fixing rhizobia (Leite et al. 2009) and compatibility and interaction of rhizobia with the host crop (Wang et al. 2011). At present, there are very limited studies that have documented the interrelationship between genotype, root nodulation, soil nutrients, biomass production, and seed yield together in a single study in cowpea.

Addressing the problem of low cowpea yield therefore requires innovative approaches away from the traditional practices of the selection of improved varieties only (Aliyu et al. 2021) to the development of precision farming management technologies (genotype requirement-soil-specific selection, time of planting, plant population, nutrient supplementation, and rhizobia inoculation). There are few studies on the efficiency of nodulation and nutrient uptake for cowpea yield (biomass and seed). To this end, this 4-year field study was carried out to evaluate the interaction of genotype, root nodulation (number of root nodules), and soil nutrients, especially nitrogen and phosphorus, on seed yield and shoot biomass production in cowpea. The outcome should elucidate yield (seed and biomass) complexity in the crop and facilitate the development of sustainable improvement technology for cowpea production.

2 Material and Methods

2.1 Planting Materials

Ten (10) genotypes of cowpea collected from the Genetic Resources Unit of the International Institute of Tropical Agriculture (IITA), Ibadan, were used in this study. The ten cowpeas were selected for their medium-large seed size characteristics (0.14–0.22 g) [IT89KD-288 (0.19 g), IT93K-693-2 (0.17 g), IT95-1090-12 (0.14 g), IT96D-610 (0.16 g), IT98K-205-8 (0.18 g), IT98K-503-1 (0.14 g), IT99K-491-7 (0.14 g), IT99K-1245 (0.18 g), IT08K-150-12 (0.17 g), and IT00K-1263 (0.22 g)] and potential high yielding in the previous studies (Aliyu and Makinde 2016; Aliyu et al. 2019).

2.2 Description of Study Site and Soil Characteristics

The field trials were carried out at the Kwara State University Teaching and Research Farms, Malete, located at latitude 08° and 26¹ N and longitude 04° 29¹ E and about

345 m above sea level in the southern Guinea savanna ecological zone of Nigeria. The area is characterized by an average annual temperature of 28.3 °C and average annual rainfall of 1100 mm. The experimental site has been previously used to grow various crops ranging from legumes and cereals in the recent past and was only fallowed for 6 months before being used. The soil is an Afisol, deep (0–150 cm), and well drained with moderate acidity (pH 5.47–6.31) and texture ranging from sandy loam to sandy clay loam (Alabi et al. 2017). The soil is characterized by low macronutrients (nitrogen, phosphorus, and potassium), organic carbon (OC), and cation exchange capacity (CEC) with high base saturation (> 50%) and varying quantities of mottles and Fe–Mn concretions (Alabi et al. 2017).

2.3 Experimental Design, Planting, and Management of Cowpea Field

The field trials were carried out between the months of July and October when the rain was steady and soil precipitation is certain. Each field trial, consisting of 10 cowpea genotypes as treatments, was laid out in a randomized complete block design (RCBD) and replicated thrice. Each treatment was planted on a plot size of 3.0 m × 6.0 m with an intrarow spacing of 0.3 m and interplot spacing of 0.75 m. This gives a sample size of 100 plants per plot/genotype after thinning.

The experimental field was mechanically prepared into ridges to mitigate erosion and allows ease of digging and uprooting of the plant for root nodulation count. Sowing was done by the 3rd week of July in each of the 4-year study period (2016–2019) with two (2) seeds planted per hole and later thinned down to one plant/stand. The fields were maintained weed-free and plants were sprayed with cypermethrin at the rate of 0.02 kg a.i. ha⁻¹ in 150 L of water (Ajeigbe et al. 2012) fortnightly through the period of flowering until pod maturity to prevent insect pest damage.

2.4 Analysis of Soils from the Experimental Plots

Soil samples collected at different times during the trials using a soil auger at the depths of 0–15 cm and 16–30 cm across the experimental fields were processed separately for laboratory analysis following standard procedure. One kilogram (1.0 kg) of the soil samples dispersed on an aluminum foil with 0.5 cm thickness was air-dried at room temperature for 72 h and sieved with a 2 mm sieve and the following were analyzed: textural quality using the Bouyoucos hydrometer method (Gee and Bauder 1986), pH in 1:1 in H₂O, organic carbon by the Walkley–Back method (Olowoake and Ojo 2014), total N by the Kjeldahl method (Ojanuga 1975; Foth 2014), extractable P by the Bray 1 method (Bray and Kutz 1945), and exchangeable bases and acidity and micronutrients by atomic absorption spectrophotometer. Because of the

likely contribution of root nodulation to soil nitrogen (N), phosphorus (P), and organic carbon (OC) and their important roles in the growth and development of the plant, greater attention was paid to these soil parameters, especially N, P, and OC during the data analysis. Two soil samples were collected from each soil profile at the planting stage of the experiment, i.e., at 0–15 cm (top soil) and 16–30 cm depths (sub-soil), since genotype will only be measured later. Only one soil sample was collected in each soil profile at plant maturity, i.e., at 0–20 cm depth (root zone), as cowpea roots do not exceed a depth of 20 cm and no significant change in soil nutrients beyond this depth. Soil samples from different depths at maturity could also be collected in future studies to determine any nutrient change in the sub-soil layer (> 20 cm). Differences between available soil nutrients at planting and at plant maturity, i.e., harvest, were used to compute for nutrient (N, P, and OC) uptakes.

2.5 Collection of Data on Vegetative Growth and Yield Components

Data were collected on the growth parameters of plant height (cm) (PHF), leaf area (cm²) (LAF), number of leaves (NLF), and number of main branches (NBF), using a descriptor for cowpea (IBPGR 1983). For root nodulation, five plants were randomly selected per treatment and were uprooted individually with the aid of a trowel while a buck of the soil was still attached to the roots. The uprooted plant was thereafter washed in 20 l of water (changes for each treatment) and the number of nodules per plant was counted while placing the plants on a white flat board. Plants for root nodulation count were harvested (uprooted) at 4 weeks after sowing (active vegetative growth phase of the plants) (RN4) and at plant maturity (RNM). Five plants sampled for root nodulation at plant maturity were used to determine total plant biomass (wet weight of root, stem, and leaves) (g) (TPB), and oven-dried at 60 °C until constant weight for total dry matter content (g) (TDM).

Data on flowering and pod maturity were collected when at least 50% of the plants per plot had flowered (DTF) and 50% of pods are ready for harvest (DPM), respectively. Yield components data were collected on pod length (cm) (POL), peduncles per plant (NPE), pods per peduncle (NPO), pods per plant (POP), seeds per pod (SPO), seeds per plant (SPP), and seed weight (hundred seed weight) (g) (SWH). Seed yield per hectare (kg) (SYH) was thereafter estimated from seed yield per plant at a population density of 55,555 plants. For brevity, seed yield per hectare (SYH) was used in data analysis. The ratio of seed yield to total plant biomass (RSB) was computed to rank the genotypes in order of seediness and or biomass production for the identification of potential dual-purpose cowpea genotype(s).

Considering the importance of soil nitrogen, phosphorus, and organic carbon to cowpea development, analysis of nutrient uptake of these elements by plants was computed using the relationship below:

$$NU = \frac{IQN - FQN}{IQN}$$

where NU is the Nutrient Uptake, IQN is the Initial Quantity of Nutrient at planting and FQN is the Final Quantity of Nutrient at harvest.

Initial quantity of nutrient at planting is the mean of the respective nutrient from the top layer (0–15 cm) and sub-layer (16–20 cm) of the soil sampled at the point of planting. The final quantity of nutrient at harvest is the amount of nutrients obtained from the root zone (0–20 cm) of the soil sampled after plant maturity. The values were thereafter expressed in %.

The efficiency of nutrients (phosphorus, nitrogen, and organic carbon) utilization for seed yield production was computed as follows:

$$NUE = \frac{SYP}{NNP}$$

where NUE is the nutrient use efficiency, SYP is the weight of seed yield per plant (g) and NNP is the net nutrient uptake per plant.

2.6 Statistical Analyses of Plant and Soil Data

Plant and soil data collected for the 4 years of study (2016–2019) were summarized and analyzed for variance (ANOVA) of randomized complete block design (RCBD) to measure genotypic and environmental (year) variations, the genotype $\times$ year interaction, and Pearson's correlation matrix analysis to determine the relationship among the variables (plant and soil). Additive Main Effects and Multiplicative Interaction (AMMI) model was used to estimate the degree of stability and contributions of genotype and year (environment) to the total variation. The analyses were carried out using Genstat 14.0 version and STATA 16.0 version statistical software packages developed by VSN International (www.vsnl.co.uk/software/genstat) and Stata Corp. USA (www.stata.com), respectively.

3 Results

3.1 Variation in Plant Vigor, Shoot Biomass, Root Nodulation, and Seed Yield in Cowpea

Effects of genotype, year of planting (season), and their interaction were found to significantly influence plant vigor (growth parameters), shoot biomass production, and root nodulation, irrespective of the time of sampling (Table 1). Data across the

4 years indicated that cowpea grown in 2019 were more vigorous in terms of the number of branches, number of leaves, and plant height, producing the highest fresh shoot biomass and total shoot dry matters and with the highest numbers of root nodules.

The highest number of branches was recorded in IT96D-610, with the value not significantly different from IT89KD-288. IT00K-1263 recorded the highest leaf area (Table 1). IT89KD-288 stood out with the highest number of leaves, total fresh shoot biomass, total shoot dry matter, and number of nodules both at juvenile and at maturity. The best 3 accessions (IT89KD-288, IT96D-610, and IT00K-1263) with the highest nodulation gave the highest values for total fresh shoot biomass and total shoot dry matter (Table 1), with shoot biomass of > 28 tons/ha at planting density of 55,555 plants population.

Flowering time and period of pod maturity were significantly influenced by the variation across the years, the nature of the genotypes, and the interaction of genotype $\times$ year (Table 2). Similar patterns of significant variations of year, genotype, and their interaction were obtained for all the yield components, seed yield, and seed yield–shoot biomass ratio. Flowering and pod maturity were earlier in 2018 (7 and 12 days, respectively) than in 2017, with the longest flowering and pod maturity times (Table 2). The highest number of peduncles, pods per peduncle, pods per plant, seeds per pod, seeds per plant, and total seed yield were obtained in the 2019 season. The highest seed yield–shoot biomass ratio of 28% (0.28) was recorded in the same 2019 compared to 16% (0.16) in 2017. The variation in the rainfall, temperature, and relative humidity of the experimental site for the 4 years period is presented in Table 3. The highest rainfall with the lowest temperatures was recorded in 2019 and the reverse was obtained during the 2018 growing season.

3.2 Variation in Soil Properties During Cowpea Development

The variation in the physico-chemical characteristics of the experimental site showed general reductions in clay contents with elevated silts in the cultivated soils both at depth of 0–30 cm at planting and at depth of 0–20 cm at plant maturity (Table 4). The sand content of the soil did not vary significantly with cultivation. There was a slight increase in soil acidity (reduction in pH) and a general reduction in soil nutrients (available P, organic carbon content, total nitrogen, magnesium, and sodium) due to cowpea growth (Table 4). The rate of depletion of available phosphorus (17.83 g kg⁻¹; 77%) was significantly higher than organic carbon (3.2 g kg⁻¹; 16.18%), total nitrogen (0.37 g kg⁻¹; 17.79%), magnesium (1.03 cmol.kg⁻¹; 43.10%), and potassium (0.33 cmol.kg⁻¹; 41.77%) in cultivated soil compared to soil analysis at planting. There was significant

Table 1 Phenotypic variation (mean squares and mean values) of plant vigor indices, fresh shoot biomass, shoot dry matter, and root nodules among 10 cowpea accessions evaluated on a 4-year field trial under a savanna ecological condition

Source of variation	NBF	LAF	NLF	PHF	TDM	TPB	RN4	RNM
Replication	0.68 ns	46.14 ns	317.20 ns	47.98 ns	213.20 ns	816.00 ns	13.58 ns	20.22 ns
Genotype	6.39**	15,078.35**	16,696.80**	1579.72**	115,345.40**	86,830.00**	225.07**	365.23**
Year	4.82**	3450.87**	4179.20**	315.00**	56,977.60**	219,061.00**	137.96**	84.72**
Gen. × year	1.59**	2512.64**	2399.70**	77.35**	15,759.70**	83,538.00**	17.68*	39.45**
Error	0.36	63.50	177.90	34.07	222.00	1931	14.33	5.59
Year								
2016	4.53	72.24	98.50	29.59	128.30	319.70	9.04	6.81
2017	5.00	86.03	122.90	35.56	80.50	238.70	9.70	7.27
2018	4.45	59.86	110.30	32.13	69.90	220.40	9.40	7.50
2019	5.30	71.03	123.30	36.68	163.70	407.10	13.63	10.51
<i>LSD (0.05)</i>	0.31	4.10	6.86	3.00	7.66	22.59	1.95	1.22
<i>S.E.M</i>	0.11	2.30	2.44	1.06	2.72	8.02	0.69	0.43
Genotype								
IT00K-1263	5.67	144.15	143.80	37.70	178.60	519.80	13.67	16.42
IT08K-150–12	4.17	50.43	88.20	25.54	76.70	137.00	11.42	6.67
IT89KD-288	5.58	110.43	181.50	40.21	318.30	903.00	17.08	18.83
IT93K-693–2	4.58	53.44	90.10	25.88	36.30	133.50	6.09	3.67
IT95K-1090–12	4.58	58.72	143.10	47.60	33.10	92.90	12.00	4.00
IT96D-610	6.00	108.18	146.00	20.21	215.50	523.50	12.58	9.83
IT98K-205–8	3.92	54.68	74.90	53.09	46.20	126.40	5.25	2.20
IT98K-503–1	5.04	60.07	108.50	21.72	43.50	147.00	6.08	5.43
IT99K-1245	4.67	38.42	90.70	38.37	125.80	275.90	14.67	7.50
IT99K-491–7	4.00	44.38	70.80	24.60	32.10	105.80	5.58	5.68
<i>LSD (0.05)</i>	0.49	6.48	10.84	4.74	12.11	35.72	3.08	1.92
<i>S.E.M</i>	0.17	1.46	3.85	1.69	4.30	12.69	1.09	0.68
Mean	4.82	72.29	113.70	33.49	110.60	296.50	10.44	8.02

*, **, and ns indicate significance at $p < 0.05$, 0.001, and not significant, respectively. Legend: *LAF*, leaf area, cm²; *NBF*, number of branches at flowering; *NLF*, number of leaves; *PHF*, plant height at maturity, cm; *TDM*, total shoot dry matter, g; *TPB*, fresh shoot biomass, g; *RN4*, number of root nodules at 4 weeks after planting; *RNM*, number of root nodules at plant maturity; *LSD*, least significant different; *S.E.M.*, standard error of means

variation in soil pH, available phosphorus, organic carbon, and total nitrogen across cultivated cowpea soils (Table 4). Soils cultivated to IT00K-1263 recorded the lowest pH and lowest available phosphorus and at the same time with highest organic carbon and total nitrogen contents (Table 4).

3.3 Genotype by Environment Variation in Cowpea

The proportion of contributions of genotype, year, and their interaction to the total variation in each of the plant traits including shoot biomass (fresh & dry matter), number of root nodules and yield components, and the soil nutrients is presented in Table 5. Genotype accounts substantially for variations obtained for plant vigor indices (plant height, leaf area, number of leaves, and stem girth) and shoot biomass (fresh and dry matter) than environment (year),

while variation in most of the seed yield components were largely contributed by the environment (year) (Table 5). Interestingly, variations in seed weight, seed yield per hectare, and ratio of seeds to shoot biomass were largely explained by genotype. Genotype was also found to substantially influence root nodulation and utilization of soil nutrients (nitrogen, organic matter, and phosphorus) in cultivated cowpea soils than the environment.

3.4 Interrelationship of Soil Nutrients and Root Nodulation for Plant Vigor and Yield Components in Cowpea

The quantity of soil total nitrogen and organic carbon content at the time of planting (Fig. 1a, c, and e) or at plant maturity (Fig. 1b, d, and f) have a significant correlation

Table 2 Phenotypic variation (mean squares and mean values) of yield components and seed yield among 10 cowpea accessions evaluated on a 4-year field trial under Guinea savanna ecological condition

Source of variation	DTF	DTP	POL	NPE	NPO	POP	SPO	SPP	SWH	SYH	RSB
Replication	8.56 ns	7.68 ns	0.58	11.06 ns	0.08 ns	4.72 ns	2.78 ns	2975.00 ns	0.00 ns	54,855.00 ns	0.003
Genotype	853.55**	1767.06**	46.35**	175.41**	0.93**	777.52**	15.81**	43,948.00**	0.011**	3,935,907.00**	0.23**
Year	287.09**	967.43**	5.28**	275.40**	3.37**	924.00**	25.88**	47,570.00**	0.003**	1,535,097.00**	0.10**
Gen. × year	76.92**	140.66**	4.15**	81.69**	0.48**	450.43**	7.90**	11,153.00**	0.001**	856,287.00**	0.03**
Error	5.13	7.44	0.58	9.79	0.05	33.91	1.03	1095.00	0.00	73,367.00	0.00
Year											
2016	56.23	67.97	14.81	16.97	1.48	28.73	10.07	163.90	0.15	1341.00	0.17
2017	57.40	70.00	15.50	20.33	1.58	34.93	12.03	186.90	0.17	1804.00	0.16
2018	50.03	58.03	15.53	22.83	1.85	38.80	11.27	233.00	0.16	1635.00	0.23
2019	52.47	60.90	15.78	23.73	2.23	41.53	12.03	249.50	0.16	1836.00	0.28
<i>LSD</i>	1.16	1.40	0.39	1.61	0.12	2.99	0.52	17.01	0.01	139.20	0.03
<i>S.E.M</i>	0.41	0.50	0.14	0.57	0.04	1.06	0.19	6.04	0.02	49.50	0.01
Genotype											
IT00K-1263	62.83	74.08	18.96	26.50	1.83	50.00	11.58	258.80	0.22	2288.00	0.09
IT08K-150-12	45.75	50.75	16.55	20.42	2.08	41.92	13.33	324.30	0.17	2853.00	0.49
IT89KD-288	69.50	83.92	16.81	19.33	1.20	24.67	10.50	91.20	0.19	885.00	0.02
IT93K-693-2	49.00	55.58	14.11	25.42	1.92	36.17	12.00	216.70	0.16	1746.00	0.23
IT95K-1090-12	49.25	58.83	16.48	19.50	2.04	38.42	11.83	207.50	0.14	1592.00	0.36
IT96D-610	58.25	71.33	15.10	24.58	1.50	38.83	10.12	157.00	0.15	1196.00	0.17
IT98K-205-8	44.92	52.33	15.16	20.58	2.04	38.67	12.25	211.80	0.17	1805.00	0.26
IT98K-503-1	46.08	51.42	15.69	20.92	1.83	35.42	11.92	217.40	0.13	1507.00	0.19
IT99K-1245	60.00	78.25	12.78	19.17	1.83	34.00	9.75	187.50	0.14	1494.00	0.09
IT99K-491-7	56.75	65.75	12.43	13.25	1.58	21.92	10.17	209.60	0.12	1175.00	0.19
<i>LSD</i>	1.84	2.22	0.62	2.54	0.19	4.73	0.83	26.89	0.01	220.10	0.05
<i>S.E.M</i>	0.65	0.79	0.22	0.90	0.07	1.68	0.29	9.55	0.003	78.20	0.02
<i>Mean</i>	54.23	64.22	15.41	20.97	1.79	36.00	11.35	208.20	0.16	1654.00	0.21

*, **, and ns indicate significance at $p < 0.05$, 0.001, and not significant, respectively. Legend: *DTF*, days to 50% flowering; *DTP*, days to 50% maturity; *POL*, pod length, cm; *NPE*, peduncles per plant; *NPO*, pods per peduncle; *POP*, pods per plant; *SPO*, seeds per pod; *SPP*, seeds per plant; *SWH*, seed weight (hundred seed weight) (g); *SYH*, seed yield per hectare (kg); *RSB*, ratio of seed yield to shoot biomass; *LSD*, least significant different; *S.E.M.*, standard error of means

with root nodulation than phosphorus. Combination of rich soil with nitrogen and organic carbon contents and a high number of root nodules significantly influenced the growth and better plant vigor (leaf area, number of branches, number of leaves, and plant height), total fresh shoot biomass, and total shoot dry matter (Table 6). Plant vigor and plant biomass were not significantly influenced by the available phosphorus (Table 6). Soil nitrogen, organic carbon, and the number of nodules have significant positive correlations with days to flowering, days to pod maturity, pod length, and seed weight (Table 7). However, root nodulation shows no direct relationship with the number of peduncles, number of pods, pods per plant, seeds per pod, seeds per plant, and total seed yield (Table 7). Importantly, there were significant negative correlations between root nodulation and the number of pods per peduncle and seeds per plant (Table 7). The amount

of available soil phosphorus at the time of planting had no significant correlation with yield components (Table 7). In the contrast, correlations between available soil phosphorus at maturity and all yield components including total seed yield were significantly negative (Table 7). Analysis of the amount of nutrients taken up by each plant (nitrogen, organic carbon, and phosphorus uptakes) showed that phosphorus recorded a highly significant positive correlation with all yield components including seed yield.

Increasing uptake of soil nitrogen and organic carbon negatively correlated ($p < 0.01$) with root nodulation, all plant growth parameters, shoot biomass including dry matter, and plant phenology characters (days to flowering and pod maturity) (Tables 6 and 7). In contrast, increasing uptake of phosphorus positively correlated ($p < 0.001$) with all the yield components including seed yield (Table 7).

Table 3 Weather records (rainfall and temperature) of experimental site for the 4 years (2016–2019)

Months	Rainfall (mm)											
	Years				Temperature (°C)							
	2016	2017	2018	2019	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
January	0.00	2.20	0.00	0.00	21.22	33.68	19.80	34.32	21.60	33.30	21.29	33.67
February	0.00	0.00	13.50	13.50	19.80	34.22	21.07	36.07	19.37	33.93	19.62	34.34
March	49.00	33.50	49.50	94.90	22.54	35.16	23.83	37.51	15.96	34.96	22.00	34.40
April	192.00	38.20	70.40	147.85	23.62	32.33	23.76	35.73	18.13	33.60	23.66	31.26
May	313.30	118.20	323.60	349.60	18.54	33.03	22.41	32.67	17.66	32.93	20.38	31.19
June	184.40	184.90	144.20	235.76	19.64	31.21	22.66	31.40	19.93	31.03	20.03	30.80
July	78.80	42.80	184.10	186.10	21.31	28.49	22.06	30.00	20.83	26.64	20.70	27.70
August	194.40	302.7	126.02	156.72	22.01	28.05	21.32	28.70	20.64	27.14	21.12	27.38
September	332.20	215.90	451.60	281.90	21.32	29.21	21.76	29.23	21.32	28.70	19.57	24.33
October	61.50	38.20	87.02	96.40	22.56	29.51	22.54	30.80	21.76	29.23	23.00	27.66
November	7.80	0.00	0.00	0.00	22.06	32.18	21.83	33.56	22.54	30.80	18.21	34.32
December	0.00	0.00	0.00	0.00	22.21	33.84	21.07	31.21	22.58	34.72	22.02	33.31
Total	1411.40	990.60	1449.94	1562.73	256.83	380.91	264.11	391.20	242.32	376.98	251.60	370.36
Mean	156.82	110.06	161.10	159.19	21.40	31.74	22.00	32.60	20.19	31.41	20.96	30.86

Source: Lower Niger River Basin Development Authority, Ilorin, Nigeria

Table 4 Physical characteristics and nutrients dynamics of the soil of experimental fields sampled at planting and at plant maturity of 10 cowpea accessions

Soil analysis at planting (depth 0–15 cm & 15–30 cm)												
Soil depth (cm)	Clay (g kg ⁻¹)	Silt (g kg ⁻¹)	Sand (g kg ⁻¹)	pH (H ₂ O)	Av. P (mg kg ⁻¹)	O.C (g kg ⁻¹)	T.N (g kg ⁻¹)	Ca (cmol. kg ⁻¹)	Mg (cmol. kg ⁻¹)	K (cmol. kg ⁻¹)	Na (cmol. kg ⁻¹)	
0–15	54	94	852	7.3	17.15	26.60	2.82	3.24	2.70	0.95	0.39	
15–30	54	74	872	7.2	29.05	12.95	1.34	2.50	2.08	0.62	0.28	
<i>Mean</i>	54	84	862	7.3	23.10	19.78	2.08	2.87	2.39	0.79	0.34	
Soil analysis at plant maturity (depth of 0–20 cm)												
Genotype	Clay (g kg ⁻¹)	Silt (g kg ⁻¹)	Sand (g kg ⁻¹)	pH (H ₂ O)	Av. P (mg kg ⁻¹)	O.C (g kg ⁻¹)	T.N (g kg ⁻¹)	Ca (cmol. kg ⁻¹)	Mg (cmol. kg ⁻¹)	K (cmol. kg ⁻¹)	Na (cmol. kg ⁻¹)	
IT00K-1263	24	126	850	5.7	0.48	21.1	2.18	3.84	1.28	0.36	1.22	
IT08K-150–12	36	94	870	5.8	2.21	15.34	1.59	3.49	1.02	0.29	1.36	
IT89KD-288	26	128	846	5.8	7.03	17.81	1.84	4.37	1.33	0.38	1.28	
IT93K-693–2	74	46	880	6.7	3.79	9.32	0.96	3.87	1.30	0.45	1.24	
IT95K-1090–12	57	102	841	6.4	7.99	16.72	1.73	4.74	1.55	0.62	1.13	
IT96D-610	36	106	858	5.8	7.44	15.89	1.64	4.24	1.52	0.69	1.43	
IT98K-205–8	42	86	872	6.2	4.48	18.63	1.93	4.92	1.50	0.53	1.10	
IT98K-503–1	44	84	872	6.1	7.92	18.08	1.87	4.27	1.45	0.41	0.96	
IT99K-1245	48	86	866	6.3	4.06	18.36	1.90	4.07	1.11	0.51	1.36	
IT99K-491–7	58	136	806	6.2	7.30	14.52	1.50	4.22	1.49	0.38	1.33	
<i>Mean</i>	44.5	99.4	856.1	6.1	5.27	16.58	1.71	4.20	1.36	0.46	1.24	

Legend: Av. P, available soil phosphorus; OC, soil organic carbon; TN, soil total nitrogen; Ca, calcium; Mg, magnesium; K, potassium; Na, sodium

Table 5 *F*-values and % total contributions of the genotype ($n=10$), year ($n=4$), and their interaction to variation in plant vigor, total shoot dry matter, seed yield, and soil nutrients

	Genotype		Year		Genotype $\times$ year	
<i>DF</i>	9		3		27	
	<i>F-value</i>	% total	<i>F-value</i>	% total	<i>F-value</i>	% total
NBF	17.71	49.92	13.35	37.64	4.42	12.43
LAF	237.45	71.66	54.34	16.40	39.57	11.94
NLF	93.86	75.56	23.49	17.95	13.49	10.31
PHT	46.37	80.10	9.25	15.98	2.27	3.92
TDM	519.49	61.65	251.65	29.86	71.53	8.49
TPB	460.05	76.05	98.74	16.32	46.18	7.63
RN4	15.71	66.51	6.24	26.41	1.61	6.81
RNM	58.42	79.06	8.94	12.10	6.53	8.84
DTF	166.35	70.10	55.95	23.58	14.99	6.32
DTP	237.65	61.46	130.11	33.65	18.92	4.89
LOP	15.51	45.62	14.53	42.55	4.11	12.04
LPO	79.90	83.16	9.10	9.47	7.08	7.37
NPE	17.93	32.94	28.15	51.71	8.35	15.34
NPO	17.39	19.50	62.83	70.44	8.98	10.07
POP	22.93	36.13	27.25	42.94	13.28	20.93
SPO	15.33	31.88	25.09	52.18	7.66	15.32
SPP	40.14	42.80	43.45	46.33	10.19	10.86
SWH	90.22	75.06	23.75	19.76	6.22	5.18
SYH	53.65	62.21	20.92	24.26	11.67	13.53
RSB	54.07	62.79	24.71	28.70	7.33	8.51
SNM20	670.71	95.83	19.33	2.76	9.84	1.41
OCS20	374.71	77.52	89.56	18.53	19.05	3.94
AVP20	1260.87	99.67	0.20	0.02	3.99	0.32

DF degree of freedom ($n-1$)

LAF, leaf area, cm²; NBF, number of branches at flowering; *NLF*, number of leaves; *PHF*, plant height at maturity, cm; *TDM* total shoot dry matter, g; *TPB* fresh shoot biomass, g; *SNM20*, total nitrogen at plant maturity; *OCS20*, organic carbon content at plant maturity; *AVP20*, available soil phosphorus at plant maturity; *DTF*, days to 50% flowering; *DTP*, days to 50% maturity; *POL*, pod length, cm; *NPE*, peduncles per plant; *NPO*, pods per peduncle; *POP*, pods per plant; *SPO*, seeds per pod; *SPP*, seeds per plant; *SWH*, seed weight (hundred seed weight) (g); *SYH* (seed yield per hectare (kg); *RSB*, ratio of seed yield to shoot biomass

3.5 Variation in Uptake of Soil Nutrients and Efficiency of Utilization in Cowpea

The ten (10) cowpeas showed significant variation in the quantities of nutrient (nitrogen, phosphorus, and organic carbon) uptake from the soil for its development (Fig. 2a–c). There are accessions that showed high uptakes for the three nutrients (e.g., IT93K-693–2 and IT08K-150–12), whereas others combined different levels of uptake of these three elements (Fig. 2a–c). For example, IT00K-1263 combines high uptake of phosphorus with low uptakes of nitrogen and organic carbon.

The cowpeas also exhibited high genotypic variation for utilization efficiency of the nutrients (nitrogen, organic carbon, and phosphorus) and root nodulation for shoot dry matter production and seed yield (Table 8). IT98K-205–8 was most efficient in root nodulation for

both total shoot dry matter and seed yield. TK89D-288, IT00K-1263, and IT96D-610 were, however, most efficient in the utilization of nitrogen, organic carbon, and phosphorus for total shoot dry matter production. Distinctively, IT08K-150–12 was the most efficient in the conversion of nitrogen, organic carbon, and phosphorus for seed yield (Table 8).

Exploring the genotypic variation data, the 10 cowpeas were ranked based on their order of performance across each of the growth and yield parameters, and the best 3 were selected (Table 9). IT89KD-288, IT00K-1263, and IT96D-610 combine superior root nodulation and growth vigor with biomass production (Table 9). IT98K-205–8, IT08K-150–12, and IT98K-503–1 are the best genotypes, in terms of earliness for flowering and pod maturity. These accessions flowered within 6 weeks of planting and their pods matured 10 days after. IT00K-1263

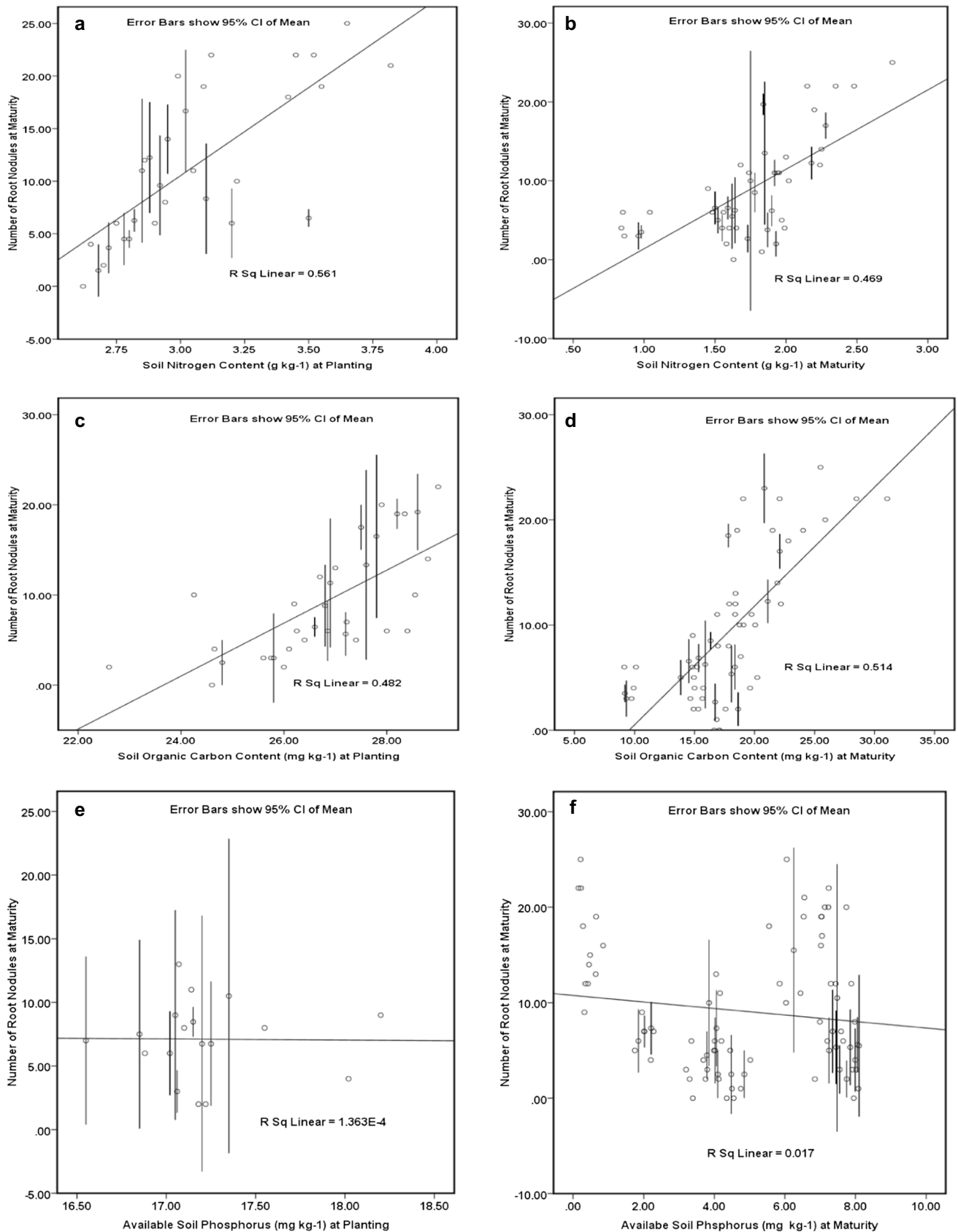


Fig. 1 Correlation analysis of soil nutrients and root nodulation of 10 cowpea accessions evaluated at the time of planting (sowing) (**a** nitrogen, **c** organic carbon, and **e** phosphorus) and at plant maturity period (**b** nitrogen, **d** organic carbon, and **f** phosphorus)

Table 6 Pearson's correlation between soil organic carbon content, total nitrogen, and root nodulation and plant vigor and plant biomass (fresh shoot biomass and dry matter) of 10 cowpea accessions grown on 4-year field trial

	LAF	NBF	NLF	PHF	TDM	TPB
NR4	0.41**	0.39**	0.53**	0.22**	0.54**	0.51**
NRM	0.69**	0.50**	0.63**	0.04 ns	0.79**	0.83**
OCS20	0.58**	0.38**	0.45**	0.31**	0.55**	0.53**
OCS15	0.45**	0.51**	0.43**	0.12 ns	0.45**	0.49**
SNM20	0.43**	0.31**	0.40**	0.39**	0.41**	0.42**
SNS15	0.44**	0.41**	0.56**	0.27**	0.47**	0.51**
AVP15	.041 ns	0.027 ns	0.021 ns	0.028 ns	−0.03 ns	−0.02 ns
AVP20	0.20*	0.02 ns	0.12 ns	−0.11 ns	−0.06 ns	−0.04 ns
P-UP%	0.20*	−0.02 ns	−0.12 ns	0.11 ns	0.06 ns	0.04 ns
N-UP%	−0.29**	−0.16 ns	−0.21*	−0.32**	−0.25**	−0.25**
OC-UP%	−0.53**	−0.31**	−0.40**	−0.31**	−0.50**	−0.48**

Degree of freedom = ($n = 120 - 2 = 118$), $p = 0.05$; 0.164; $p = 0.01$, 0.230. ns, *, and **: not significant, significant at $P < 0.05$, and significant at $P < 0.001$

Legend: *LAF*, leaf area, cm²; *NBF*, number of branches at flowering; *NLF*, number of leaves; *PHF*, plant height at maturity, cm; *TDM*, total shoot dry matter, g; *TPB*, fresh shoot biomass, g; *NR4*, number of root nodules at 4 weeks after planting; *NRM*, number of root nodules at plant maturity; *OCS20*, organic carbon content at plant maturity; *OCS15*, organic carbon content planting; *SNM20*, total nitrogen at plant maturity; *SNS15*, total nitrogen at planting; *AVP15*, available soil phosphorus at planting; *AVP20*, available soil phosphorus at plant maturity; *P-UP%*, percentage of phosphorus content uptake at maturity; *N-UP%*, percentage of soil nitrogen content uptake at maturity; *OC-UP%*, percentage of soil organic carbon at maturity

Table 7 Pearson's correlation between soil organic carbon content, total nitrogen, and root nodulation and yield components including seed yield among cowpea accessions ($n = 10$) grown on a 4-year field trial under Guinea savanna ecology

	DTF	DTP	POL	NPE	NPO	POP	SPO	SPP	SWH	SYH	RSB
NR4	0.48**	0.52**	0.28**	0.07 ns	−0.11 ns	0.07 ns	0.02 ns	−0.04 ns	0.36**	0.09 ns	−0.26**
NRM	0.70**	0.65**	0.45**	0.02 ns	−0.33**	−0.07 ns	−0.07 ns	−0.21*	0.52**	−0.03 ns	−0.51**
OCS20	0.43**	0.45**	0.48**	−0.03 ns	−0.18 ns	0.11 ns	−0.05 ns	−0.14 ns	0.44**	0.03 ns	−0.37**
OCS15	0.36**	0.35**	0.31**	0.16 ns	−0.07 ns	0.06 ns	0.17 ns	−0.04 ns	0.40**	0.12 ns	−0.34**
SNM20	0.36**	0.37**	0.47**	0.00 ns	−0.08 ns	0.15 ns	−0.02 ns	−0.08 ns	0.42**	0.05 ns	−0.33**
SNS15	0.43**	0.40**	0.39**	0.07 ns	−0.14 ns	−0.03 ns	0.20*	−0.20*	0.46**	0.04 ns	−0.33**
AVP15	−0.03 ns	−0.05 ns	0.10 ns	0.00 ns	0.15 ns	0.05 ns	0.06 ns	0.16 ns	0.07 ns	0.16 ns	0.10 ns
AVP20	−0.03 ns	−0.02 ns	−0.31**	−0.27**	−0.19*	−0.35**	−0.21*	−0.38**	−0.57**	−0.56**	−0.08 ns
P-UP%	0.03 ns	0.02 ns	0.31**	0.27**	0.19*	0.35**	0.21*	0.39**	0.57**	0.56**	0.05 ns
N-UP%	−0.21*	−0.24**	−0.35**	0.02 ns	0.03 ns	−0.17 ns	0.09 ns	0.02 ns	−0.27**	−0.04 ns	0.29**
OC-UP%	−0.39**	−0.41**	−0.45**	0.05 ns	0.18 ns	−0.10 ns	0.08 ns	0.14 ns	−0.39**	−0.01 ns	0.34**

Df = ($n = 120 - 2 = 118$), $p = 0.05$; 0.164; $p < 0.01$, 0.230. ns, *, and **: not significant, significant at $P < 0.05$, and significant at $P < 0.001$

Legend: *DTF*, days to 50% flowering; *DTP*, days to 50% maturity; *POL*, pod length, cm; *NPE*, peduncles per plant; *NPO*, pods per peduncle; *POP*, pods per plant; *SPO*, seeds per pod; *SPP*, seeds per plant; *SWH*, seed weight (hundred seed weight) (g); *SYH*, seed yield per hectare (kg); *RSB*, ratio of seed yield (g) to shoot biomass yield (g); *NR4*, number of root nodules at 4 weeks after planting; *NRM*, number of root nodules at plant maturity; *OCS20*, organic carbon content at plant maturity; *OCS15*, organic carbon content planting; *SNM20*, total nitrogen at plant maturity; *SNS15*, total nitrogen at planting; *AVP15*, available soil phosphorus at planting; *AVP20*, available soil phosphorus at plant maturity; *P-UP%*, percentage of phosphorus content uptake at maturity; *N-UP%*, percentage of soil nitrogen content uptake at maturity; *OC-UP%*, percentage of soil organic carbon at maturity

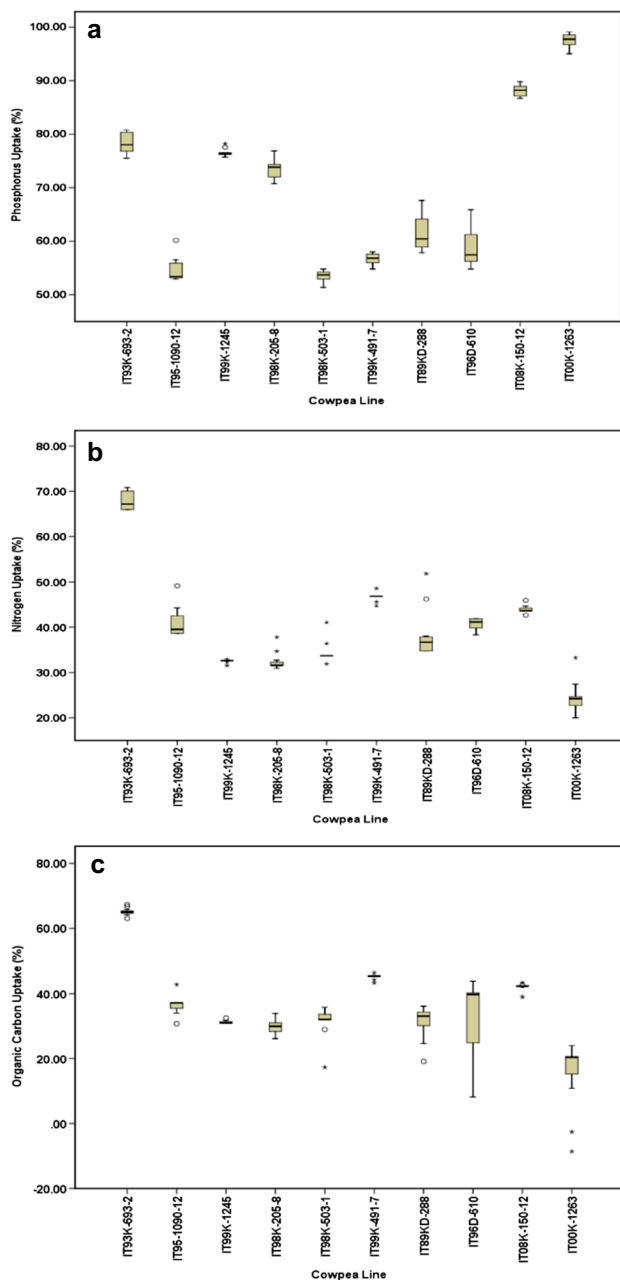


Fig. 2 Boxplots with percentiles of ten (10) cowpea accessions from a 4-year field trial showing genotypic variation for rate of different soil nutrient uptake (%), **a** phosphorus, **b** nitrogen, and **c** organic carbon uptake

shared quality podding attributes with IT08K-150-12, which translated to high seed yield (> 2000 kg/ha) in these 2 accessions (Table 9). The highest rate of nitrogen and organic carbon uptake was obtained in IT93K-693-2, IT99K-491-7, and IT08K-150-12. IT00K-1263, IT08K-150-12, and IT93K-693-2 ranked highest in the utilization of phosphorus for growth and seed development (Table 9).

4 Discussion

Climate change and food insecurity remain important current global issues in the face of increasing human population and low yield of food crops, especially in developing countries. These interwoven social and environmental variables are the primary factors driving the increase in hunger and conflicts in sub-Saharan Africa today. This has continuously thrown a challenge to plant breeders to explore the available genetic resources to improve plant yield. To further explore the inherent potential of cowpea for improved productivity, ten (10) cowpea accessions were evaluated for growth, nodulation, shoot biomass production, seed yield, and efficiency of soil nutrients uptake, over a 4-year period, with a goal to understand the interaction of genotype, nodulation, and soil nutrients, which is critical to improvement in biomass production and/or grain yield of cowpea in the savanna ecology.

The ten cowpeas exhibited wide variation in performance across all the studied traits. Significant genotypic variation in growth, biomass production, and seed yield obtained in this data further underscore the important role of selecting adaptable planting materials to achieve better yield in cowpea. The wide variation is an indication of the difference in the genetic background, breeding history, and selective adaptation of the accessions (Aliyu et al. 2019). The variation grouped the ten cowpeas into different maturity groups, viz, early, intermediate, and late maturity. The variations in flowering and maturity are important components for delineating cowpea into different morpho-types (Aliyu et al. 2019; Ongom et al. 2021) that are explored as an adaptive measure for dehydration avoidance and/or shortening the growth cycle. Earliness is an important trait mostly selected for in dry ecology where cowpea is predominantly cultivated and available. IT08K-150-12, IT98K-503-1, IT98K-205-8, and IT93K-693-2 are characterized by early-maturing, high seed yield but low shoot biomass production. Genotypes that produced higher plant biomass (IT89KD-288, IT96D-610, and IT00K-1263) are late maturing and low in seed production, except IT00K-1263 that combines high yield of shoot biomass and seed yield. This is unexpected that the elongation of the growth phase will lead to the production of more plant biomass, but not commensurate in seed yield except IT00K-1263 that balances biomass production with seed yield. Agele et al. (2018) reported variations in the efficiency of dry matter partitioning to reproductive sinks and assimilate utilization between cowpea of different maturity groups. In terms of nodulation, genotypes like IT89KD-288 and IT-00 K-1263 produced more than eightfold of root nodules obtained compared to less nodule's productive genotypes like IT98K-205-8. Host plant (genotypic) differences in nitrogenase activity, nodule number, and plant biomass in response to rhizobia has been reported in cowpea (Miller

Table 8 Efficiency of nodules and soil nutrients (nitrogen, organic carbon, and phosphorus) contributions to total shoot dry matter and seed yield in 10 cowpea accessions

Genotype	Root nodule to shoot dry matter	Nitrogen uptake (mg g ⁻¹) to shoot dry matter	Organic carbon (mg g ⁻¹) to shoot dry matter	Phosphorus (mg g ⁻¹) to shoot dry matter	Root nodule to seed yield	Nitrogen uptake (mg g ⁻¹) to seed yield	Organic carbon (mg g ⁻¹) to seed yield	Phosphorus (mg g ⁻¹) to seed yield
IT00K-1263	10.20	249.50	17.00	10.69	2.70	56.79	0.22	2.46
IT08K-150-12	11.10	63.00	6.90	5.05	8.70	41.34	4.65	3.38
IT89KD-288	17.90	269.30	38.40	30.11	0.90	13.92	1.88	1.52
IT93K-693-2	38.30	18.10	2.10	2.70	26.40	15.71	1.78	2.34
IT95K-1090-12	14.50	27.70	3.50	3.55	13.60	23.67	3.04	3.04
IT96D-610	20.00	192.70	23.20	21.60	5.10	18.65	3.04	2.15
IT98K-205-8	156.00	50.90	5.90	3.65	138.30	35.88	4.22	2.57
IT98K-503-1	68.40	44.50	5.40	4.76	51.70	28.03	3.27	2.96
IT99K-1245	26.10	136.20	15.10	9.61	5.10	29.11	3.22	2.05
IT99K-491-7	26.00	24.60	2.70	3.30	12.40	16.14	1.77	2.17
<i>LSD</i>	64.44	19.07	9.26	1.24	50.71	4.50	4.83	0.35
<i>S.E.M</i>	22.89	6.77	3.29	0.44	18.01	1.60	1.72	0.122
<i>Mean</i>	38.80	107.60	12.00	9.50	26.50	27.92	2.71	2.47

LSD, least significant difference; *S.E.M.* standard error of means

Table 9 Selection of best 3 accessions for growth, biomass production, seed yield, root nodulation, and nutrients mining among 10 cowpeas evaluated over a 4-year trial. Legend: *NBF*, number of branches at flowering; *LAF*, leaf area, cm²; *NLF*, number of leaves; *PHF*, plant height at maturity, cm; *TDM*, total shoot dry matter, g; *TPB*, fresh shoot biomass (g); *DTF*, days to 50% flowering; *DTP*, days to 50% maturity; *POL*, pod length, cm; *NPE*, peduncles per plant; *NPO*, pods

per peduncle; *POP*, pods per plant; *SPO*, seeds per pod; *SPP*, seeds per plant; *SWH*, seed weight (hundred seed weight) (g); *SYH*, seed yield per hectare, kg; *RSB*, ratio of seed yield (g) to shoot biomass (g); *NRM*, number of root nodules at plant maturity; *N-UP%*, percentage of soil nitrogen content uptake at maturity; *OC-UP%*, percentage of soil organic carbon at maturity; *P-UP%*, percentage of phosphorus content uptake at maturity

Rank	NBF		LAF		NLF		PHF		TDM		TPB	
	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean
1 st	IT96D-610	6.00	IT00K-1263	144.15	IT89KD-288	181.50	IT98K-205-8	53.09	IT89KD-288	318.30	IT89KD-288	903.00
2 nd	IT00K-1263	5.67	IT89KD-288	110.43	IT96D-610	146.00	IT95K-1090-12	47.60	IT96D-610	215.50	IT96D-610	523.50
3 rd	IT89KD-288	5.58	IT96D-610	108.18	IT00K-1263	143.80	IT89KD-288	40.21	IT00K-1263	178.60	IT00K-1263	519.80

Rank	DTF		DTP		POL		NPE		NPO	
	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean
1 st	IT98K-205-8	44.92	IT08K-150-12	50.75	IT00K-1263	18.96	IT00K-1263	26.50	IT08K-150-12	2.08
2 nd	IT08K-150-12	45.75	IT98K-503-1	51.42	IT89KD-288	16.88	IT93K-693-2	25.42	IT98K-205-8	2.04
3 rd	IT98K-503-1	46.08	IT98K-205-8	52.33	IT08K-150-12	9.83	IT96D-610	24.58	IT95K-1090-12	2.04

Rank	POP		SPO		SPP		SWH		SYH	
	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean
1 st	IT00K-1263	50.00	IT08K-150-12	13.33	IT08K-150-12	324.30	IT00K-1263	0.22	IT08K-150-12	2853.00
2 nd	IT08K-150-12	41.92	IT98K-205-8	12.25	IT00K-1263	258.80	IT89KD-288	0.19	IT00K-1263	2288.00
3 rd	IT96D-610	38.83	IT93K-693-2	12.00	IT98K-503-1	217.40	IT08K-150-12	0.17	IT98K-205-8	1805

Rank	RSB		RNM		N UPTAKE		OC UPTAKE		P UPTAKE	
	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean	Acc	Mean
1 st	IT08K-150-12	0.49	IT89KD-288	18.83	IT93K-693-2	67.93	IT93K-693-2	65.09	IT00K-1263	97.56
2 nd	IT95K-1090-12	0.36	IT00K-1263	16.42	IT99K-491-7	46.68	IT99K-491-7	45.22	IT08K-150-12	88.12
3 rd	IT98K-205-8	0.26	IT96D-610	9.83	IT08K-150-12	43.91	IT08K-150-12	41.86	IT93K-693-2	78.36

et al. 1982) and this was attributed to inherent differences in root elongation (Kahn and Stoffella 1991). The variation in abiotic stress tolerance could account for differences in root nodulation among the cowpea genotypes. Moisture has been found to be a major factor in the nodulation success of leguminous crops (Kasper et al. 2019). This study therefore

identifies early-maturing cowpeas that are only luxuriant for seed yield (IT08K-150-12), and late maturing cowpea that combines high seed yield with high biomass production (dual purpose) (IT-00 K-1263). A combination of prolific nodulation, high seed yield, and high biomass production

with late maturity could suggest inherent tolerance for moisture stress (Kasper et al. 2019).

A phenotype is a product of genotype and environment. And the latter is equally as important as the former to achieve optimum plant performance. This study revealed that fluctuations in environmental (climatic) variables led to a significant difference in plant performance across the 4 years of study. The 2019 season produced the highest biomass production and seed yield, which could partly be attributed to higher moisture and better adaptation of the accessions to the environment. Smith et al. (2020) reported a similar variation in seed yield and biomass production of different cowpea cultivars between the 2015 and 2016 growing seasons in the USA. A significant variation across the years further corroborates the previous submission that climatic variables play important role in the production of cowpea in the Guinea savanna (Aliyu et al. 2019). Iseki et al. (2021) recorded a significant variation in cowpea yield among the years than soil types in a 2-year study using different cowpea varieties across different soil types in Sudan savanna. It was evident from that study that soil precipitation was the major factor responsible for annual yield variation (Iseki et al. 2021). The degree of agricultural drought is often determined by available precipitation and the soil type (Sileshi et al. 2010). In addition to precipitation, a rise in air temperature especially during the reproductive phase can cause infertility, poor dehiscence, and non-adherence of pollen grains and finally fluctuation in annual yield in cowpea. 2017 with the lowest rainfall and highest temperature recorded the lowest seed yield. This increasing evidence of the significant effect of climate (environment) on agricultural production underscores the need to develop highly resilient and water-nutrient-use-efficient crops through a sustainable approach (Rivero et al. 2022). This could only be achieved by identifying the biological mechanisms regulating the plant performance in changing environments. A significant interaction of genotype and environment obtained in this study indicates differences in genotypic response to the environmental variables of moisture and temperature across years. Notwithstanding, IT08K-150-12 and IT00K-1263 exhibited greater stability in seed yield than other accessions. Iseki et al. (2021) opined that unstable climatic conditions, low precipitation, and high temperature are major constraints to cowpea yield in the savanna. Soil temperature could affect plant growth, nodulation efficiency, and N_2 fixation under a changing environment (Aranjuelo et al. 2014). Suffice to say that environmental (climatic and edaphic) factors are critical to the optimal phenotypic expression (performance) of cowpea and should be optimally managed through the use of early-maturing and stress tolerant genotypes, moisture conservation, and/or supplementation.

The genotypic variation in root nodulation as obtained in this study indicates differences in the adaptation of these

cowpeas across the ecologies where the materials were originally collected as germplasm and this could influence nutrient uptake and water use efficiency. Such inherent variation could however be exploited for biomass and seed yield improvement in cowpea. Kasper et al. (2019) have reported the association between soil moisture and nodulation in N_2 plants with increasing frequency of watering resulting in a significant increase in nodulation. Root architecture and compatibility of soil native rhizobia strains are biological factors driving such phenotypic variation (Leite et al. 2009) and these could in a way determine the effectiveness of the nodulation process and plant adaptation in a nutrient-limited environment (Nyaga and Njeru 2020). Studies had shown a relationship between nodulation and distribution and morphology of adventitious roots in cowpea genotypes (Kahn and Stoffella 1991). Cowpea with efficient capacity for absorption and utilization of nutrients (especially phosphorus) could add to a sustainable solution to improve productivity and reduce the cost of production (Araujo et al. 2012).

Concordance between root nodulation and shoot biomass production in this study indicated a strong relationship between the duo and that root nodulation promotes cowpea growth and vigor, including shoot biomass. Suffice that the best 3 accessions with the highest biomass production (IT89KD-288, IT00K-1263, and IT96D-610) produced the highest number of root nodules (nodulation). Thus, suggesting that increasing the root nodulation process would enhance growth performance in cowpea. Carter and Tegeder (2016) reported improved shoot nutrition and seed number in soybean plants through increased nodule nitrogen production.

Surprisingly, data obtained in this study did not show a strong direct relationship between the nodulation process and total seed yield. Nevertheless, increasing nodulation led to improved seed size and pod length. It is obvious from the data that root nodulation contributed more to soil nitrogen content and shoot biomass than phosphorus, which is more critical for seed development. It is apparent that beyond the number of nodules, other important factors like quantity of available native rhizobia, efficiency of root rhizobia infection, and effectiveness of the symbiosis would determine the contribution of nodulation to yield. Negative correlation between nodulation at maturity and seed yield components like the number of pods per peduncle and seeds per plant demonstrate higher efficiency of nodulation among genotypes with fewer nodules but produced higher seeds. Kyie-Boahen et al. (2017) have reported that available soil phosphorus levels often limit the effective nodulation ability of the indigenous rhizobia population in cowpea and the number of nodules tends to reduce with plant maturity. It therefore appears that the factors controlling seed yield in a plant are complex and require multiple approaches to dissecting them into simple utilizable components (Cai et al.

2016). Thus, it is suggestive that increasing the availability of nitrogen through nodulation and biological fixation would enhance growth but may not translate to a significant increase in total seed yield in cowpea and that phosphorus is a limiting factor in cowpea seed improvement. Low soil phosphorus availability is known to limit nitrogen fixation and cowpea productivity (Kye-Boahen et al. 2017) and should be factored into the management of cowpea fields. Contrasting relationship of root nodulation with a positive correlation with seed size, and a negative correlation with seed number, partly explains the biological mechanisms behind seed size and number trade-off reported in cashew (Aliyu 2006) and cowpea (Aliyu and Makinde 2016; Aliyu et al. 2019, 2021).

Soil nutrient analysis through plant developmental phases, i.e., from planting to maturity, showed that increasing nodulation enhances nitrogen fixation and subsequently increases total soil nitrogen and organic carbon contents (Carter and Tegeder 2016; Leptin et al. 2021). A non-significant correlation was however recorded between available phosphorus and root nodulation. This non-direct relationship is not unexpected, because the end product of increased P uptake through nodulation will lead to improved nitrogen fixation (Yang 1995; Míguez-Montero et al. 2020). This scenario became clearer with available phosphorus at maturity recording a negative significant correlation with seed yield, therefore suggesting that the efficiency of phosphorus utilization is perhaps more important to cowpea for seed development than the amount available in the soil at the time of planting. Reduction of P in the soil (i.e., depletion) accelerates biological nitrogen fixation thereby enhances phosphorus and nitrogen uptake efficiencies in legumes (Míguez-Montero et al. 2020). Suffice that higher P uptake (depletion from soil) enhances seed yields, which perhaps accentuate the importance of phosphorus for fruit-set and seed development in cowpea. Phosphorus is known to play an important role in the nodulation, nitrogen fixation, and plant growth processes, which include improved root development, formation of root hair, initiation, and growth of nodules and serve as an energy source for nitrogen fixation (Nziguheba et al. 2016). A study of different cowpea varieties has shown that phosphorus deficiency negatively affected the aboveground production of dry mass (shoot biomass) (Araujo et al. 2012). Optimum cowpea production will therefore require a balance between nitrogen and phosphorus to ensure adequate growth with high yield.

Phenotypic stability remains an important selection index in varietal development and as such was examined in this study. It was evident that vegetative growth parameters exhibited high phenotypic stability, driven majorly by genotype, as compared to seed yield and yield components with high environmental influence (Aliyu and Makinde 2016; Aliyu et al. 2019; Nassir et al. 2021; Mbeyagala et al. 2021).

Apparently, abiotic factors of soil moisture, temperature, light radiance, and soil nutrients have a substantial effect on the yield components and total seed yield than on vegetative parameters. Besides, insect pest and disease could further compound the effect of abiotic factors on seed yield and this could also account for high environmental variation being recorded. Cowpea is mostly cultivated towards the end of the rainy season and seed development could extend to the dry period in case of late maturing varieties, or early cessation of rain. This study further underscores the significant effects of the annual variation in climatic factors (erratic rainfall, high temperature, and severe drought) on crop farming in the Nigerian savanna ecology (Aliyu et al. 2019; Sufiyan et al. 2020). With increasing global warming and the attendant climate change, there is a need to focus more resources to develop more resilient and adaptive varieties with stable seed yield. It is important to note that variation exhibited by the cowpea in terms of root nodulation and soil nutrients (available phosphorus, nitrogen, and organic carbon matter) as explained by the GxE model was driven largely by genotype than the environment. It is therefore possible to select cowpea genotypes with different levels of root nodulation and soil nutrient improvement for better adaptation and to mitigate the effect of climatic instability. IT00K-1263 with prolific nodulation and high phosphorus uptake efficiency will be a good candidate for the development of variety with better adaptation and high yield.

The nature of cowpea yield (seed and biomass) was demonstrated through the complex interaction of root nodulation and soil nutrients (nitrogen, phosphorus, and organic carbon) uptake. In comparison, soil phosphorus uptake was higher than nitrogen and organic carbon uptakes across the cowpea accessions. This high degree of phosphorus mining could not be unconnected to the significance of this nutrient to growth, as an energy source and contribution to nitrogen fixation in cowpea (Nziguheba et al. 2016). High phosphorus uptake could be linked to high utilization for nitrogen production through nodulation and nitrogen fixation for plant growth and development and at the same time for seed development. In other words, phosphorus is contributing substantially to biomass production through enhancing nitrogen fixation and indirectly to seed yield. High uptake of phosphorus has been reported in P-deficient soil of savanna ecology particularly in Nigeria (Pypers et al. 2006).

Phosphorus is also known to have the capacity to mitigate the adverse effect of abiotic stress. It is therefore not impossible that a significant quantity of soil available P has been utilized to minimize the effect of abiotic stress especially water stress (Jemo et al. 2017). Incidentally, cowpea is mostly cultivated as a late-season crop in the savanna region of sub-Saharan Africa and a significant proportion of soil phosphorus will be utilized to mitigate moisture stress. This result emphasizes the importance of phosphorus to cowpea

production and the need to encourage farmers to supplement soil with phosphorus fertilizer where the P-requirement of the plant cannot be met naturally. More importantly, a better understanding of the variability of cowpea for phosphorus nutrition may facilitate the breeding of improved varieties for regions with limited access to synthetic fertilizers.

In terms of nitrogen and organic carbon uptakes, the cowpeas exhibited significant negative correlations with increasing root nodulation. Increasing nodulation with less nitrogen uptake implies that some genotypes with high nitrogen fixation activity (nodulation) could have more nitrogen for their photosynthetic and metabolic activities and still have a high net balance of nitrogen in the soil after harvest (less uptake). This is in addition to nitrogen being produced through available soil phosphorus earlier discussed. Looking at the genotypic variation data on root nodulation vs. nitrogen uptake, the cowpea grouped into different classes of (i) low nodulation–low nitrogen uptake, (ii) high nodulation–low nitrogen uptake, and (iii) low nodulation–high nitrogen content. Also considering the association between nitrogen and phosphorus uptakes, the cowpeas grouped into clusters of (i) low nitrogen–low phosphorus uptakes, (ii) low nitrogen–moderate phosphorus uptakes, (iii) high nitrogen–moderate phosphorus uptake, and (iv) low nitrogen–high phosphorus uptakes. And these classes of cowpeas could be further explored for improvement of the crop. Fageria et al. (2014) have reported inherent variation in the efficiency of root uptake of N and P and their implications on crop plant productivity. As such, the genetic attributes leading to differences in growth habit, morphology, and/or photosensitivity, among other factors, could account for the variation in nutrient utilization and nodulation efficiency (Abaidoo et al. 2017; Míguez-Montero et al. 2020). In addition, root length, root hair, and rhizosphere activity are also known to affect phosphorus uptake in cowpea (Krasilnikoff et al. 2003). Importantly, phosphorus uptake of between 51 and 99% recorded in this study was comparatively higher than the 6 to 50% reported by Krasilnikoff et al. (2003). Differences in the breeding history of the genotypes (phenotypic plasticity), heterogeneity of agroecological locations, and/or nature of the experiment (pot or field) could account for the disparity between studies. Study location and season are also known to influence the performance of native rhizobia (Nyaga and Njeru 2020).

Since soil nutrient is critical to growth and yield in the crop and very central to the goal of this study, the identification of individual genotypes for their nutrient utilization efficiency will enrich resources for the genetic improvement of cowpea. Availability, absorption, and distribution of nutrients are critical determinants in shoot biomass production and overall crop yield (Epstein and Bloom 2006). With this in mind, further evaluation of soil nutrient (nitrogen, phosphorus, and organic carbon) utilization efficiency

by individual genotype was carried out for the selection of efficient genotypes for seed yield and biomass production. Nutritional utilization efficiency is the ability of the genotype to absorb the nutrient from the soil and distribute and use it internally (Mengel and Kirkby 2001). IT00K-1263 and IT08K-150–12 stood out for efficient utilization of nitrogen (N) and phosphorus (P) for seed yield, while IT89KD-288 was the most efficient for utilization of the nitrogen (N), organic carbon (OC), and phosphorus (P) for shoot biomass production. This set of cowpeas can be selected for further evaluation and/or introgression for the development of dual-purpose cowpea to combat the issue of hunger and provision of fodder for the animals in dry savanna ecology. Kostadinova et al. (2016) submitted that barley genotypes differ in uptake efficiencies of nitrogen and phosphorus elements. It is possible that the variation in the efficiency of nodulation and biological nitrogen fixation processes account for such differences in the nutrient uptake and their contributions to seed yield. IT98K-205–8 with the highest nodulation efficiency for shoot biomass and seed yield is a candidate for further study and future introgression into the breeding program.

There are many studies that have reported the contribution of phosphorus to the growth and yield of cowpea (Okeleye and Okelana 1997; Kolawole et al. 2002; Owolade et al. 2006), and that nitrogen and phosphorus remain the main limiting nutrients for the production of cowpea in the tropics. In the submission of Prasad et al. (2014), nitrogen and phosphorus play an important role in root development and nutrient acquisition and utilization for economic yield in plants. It is therefore evident from this study that nutrient requirement and supplementation for cowpea will vary across genotypes and/or agroecologies. Henceforth, farmers should pay attention to this during the cultivation and management of cowpea fields.

5 Conclusion

The data presented here had shown the degree of genotypic variation in nutrient uptake efficiencies and root nodulation for seed and biomass production in cowpea crops. The interrelationship of these factors as reported in this study has further elucidated the complex nature of yield in the plant as a biological trait with many regulatory pathways. It is evident that the contribution of root nodulation to seed yield is not linear (indirect), but through improved nitrogen fixation and growth indices (shoot biomass). The data reemphasize the importance of soil phosphorus to seed yield than other nutrients and, thus, underscore the need to supplement P-deficient soils with phosphorus fertilizer to increase production. Cowpea exhibited significant variation in nodulation, nodulation

efficiency, nutrient uptake, and efficiency of utilization, and above all, stability across seasons, which can be explored for improvement in seed yield and shoot biomass. IT08K-150–12 combines high seed yield with earliness in maturity, very good traits for developing high seed yield. IT00K-1263, though late in maturity, combines high seed yield with high shoot biomass production. This genotype therefore stood out as a candidate for dual-purpose variety. Most of the biological fixation activity in IT89KD-288 was however mobilized for plant biomass rather than seed yield, and could be useful for fodder production and/or soil replenishment.

This study has shed light on the spectrum of interaction between nodulation and nutrient mobilization and/or utilization for seed yield and shoot biomass production in cowpea. These pieces of information should be considered as part of the important determinants of productivity in cowpea plant. The results presented here will add to available genetic/agronomic tools that could facilitate the development of sustainable crop improvement technology for cowpea production in the Guinea savanna region and serve as additional knowledge on soil nutrients and plant development interaction.

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Data Availability The data for the 4 years field trial and outputs of the statistical analysis is available.

Declarations

Conflict of Interest The authors declare no competing interests.

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