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# Effect of Rust (*Uromyces Phaseoli* Var. *Vignae*) Infection on Photosynthetic Efficiency, Growth and Yield Potentials of Cowpea (*Vigna Unguiculata* L. Walp) in an Open Field System

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**Keywords:** cowpea; rust pathogen; disease severity; photosynthetic rate; growth; yield.

**GJSFR-C Classification:** FOR Code: 069999



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**Keywords:** cowpea; rust pathogen; disease severity; photosynthetic rate; growth; yield.

## I. INTRODUCTION

Cowpea (*Vigna unguiculata* L. Walp) is an important leguminous food crop and plays a critical role in sustenance of about 194 million people in Africa (Abate et al., 2012; Dugje et al., 2009). In Ghana, cowpea is both food security and a cash crop (Rusike et al., 2013). More than 95% of the dry matter content of cowpea is obtained from photosynthesis (Bate and Carvin, 1971; Chapin III and Eviner, 2003; Ho, 1976). Cowpea is typically a C3 plant and therefore follows the C3 photosynthesis pathway (Kassman et al.,

1991). Cowpea belongs to the crop stability group II of C3 plants and operates under warm conditions with a potential rate of photosynthesis ( $40\text{--}50 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-2}$ ) greater than group I C3 crops ( $20\text{--}30 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-2}$ ) such as common bean, barley, wheat, and oat (Kassman et al., 1991). C3 photosynthesis is a multi-step process and occurs in virtually all leaf mesophyll cells (Ehleringer and Cerling, 2002). The photosynthetic process is largely dependent on stomatal regulation and the amount of chlorophyll present (Brito et al., 2012; Evans, 2013). However, the concentration of chlorophyll may be influenced by responses to biotic and abiotic stresses (Hailemichael et al., 2016; Lobato et al., 2010; Sheikh et al., 2017). Variation in chlorophyll content of healthy and stressed plants provide valuable information about the physiological condition of the plant (Kamble et al., 2015; Sims and Gamon, 2002; Steele et al., 2008).

Cowpea rust fungus (*Uromyces phaseoli* var. *vignae*) is the most important biotic constraint to high yield and production of cowpea (Deshpand et al., 2010; Honnur et al., 2016; Uma et al., 2016). The fungus infects host leaves and is disseminated through the airborne urediniospores (Uma et al., 2016). The pathogen reduces foliar area and photosynthetic activity considerably in cowpea through destruction and reduction of most of the photosynthetic surface area, and interference with the photosynthetic activity of the healthy green parts of the host plant (Honnur et al., 2016; Newcombe, 2004; Singh, 2011). Toxins such as tentoxin and tabtoxin produced by rust fungus inhibit the activities of some enzymes involved directly or indirectly in photosynthesis in cowpea (Agrios, 2004). Cowpea rust fungus consumes photosynthetic products of host leaves and causes premature defoliation and mortality of young and mature plants, leading to reduced seed size and severe yield loss of 60–80% (Deshpand et al., 2010; Leonard and Szabo, 2005; Uma et al., 2016; Voegelé and Mendgen, 2003). The effects of rust disease on cowpea is more severe in the tropical and subtropical regions of the world, particularly Africa, due to the dry, warm, and high humid conditions that are

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conductive for rust disease development and spore dissemination (Kumar and Narain, 2005).

Despite these, knowledge about the photosynthetic metabolism of cowpea cultivars infected with cowpea rust fungus is limited. Determination of the amount of chlorophyll is often employed by scientists to assess photosynthetic performance in vegetative plants. Destructive techniques have been conventionally used to determine leaf chlorophyll content in crops (Brito et al., 2012). The chlorophyll content of various plant species have been determined using 80% acetone (C<sub>3</sub>H<sub>6</sub>O) and magnesite (MgCO<sub>3</sub>) powder followed by spectrophotometric analysis (Kamble et al., 2015; Sheikh et al., 2017). Makeen et al. (2007) estimated chlorophyll content in Black gram (*Vigna mungo* L.) using methanol and dimethyl sulfoxide (DMSO). Diethyl ether (DEE) and dimethylformamide (DMF) are highly recognized as best solvents for chlorophyll extraction (Etemadian et al., 2017; Stiegler et al., 2005; Sumanta et al., 2014). However, these techniques are very laborious, expensive, time-consuming, and involve destructive sampling, various procedural steps, and a high volume of solvent which leads to dilute or poor yield of chlorophyll (Kamble et al., 2015; Makeen et al., 2007). Complete extraction of chlorophyll is difficult to achieve in etiolated plants due to the presence of a low concentration of chlorophyll (Makeen et al., 2007). Besides, the use of solvents such as methanol, DMF, and DMSO is not recommended for chlorophyll extraction as the solvents are toxic to humans and easily absorbed by the skin (de Abreu Costa et al., 2017; Kadam et al., 2018; Long et al., 2001).

Chlorophyll fluorescence meters have been extensively used in research and agricultural applications to determine chlorophyll content of leaves because they are non-destructive to leaf tissue, portable, quick, and easy to use. They also have high accuracy and do not require specially trained personnel (Cate and Perkins, 2003; Chapman and Barreto, 1997; Ling et al., 2011). The plant photosynthesis meter (mini PPM-300, EARS) was used to determine leaf photosynthesis in this work. The meter uses a light emitting diode to elicit and recognize the fluorescence of chlorophyll (EARS, 2009; Fernandez-Jaramillo et al., 2012). The mini PPM-300 instantaneously measures fluorescence yield, photosynthesis yield, photosynthetically active radiation and photosynthetic rate of plant leaves based on quantification of light intensity wavelengths between 300 nm and 800 nm. The data generated is stored in the meter and can easily be assessed.

Although crop productivity is mainly determined by the efficiency of photosynthesis under a specific environmental condition and available resources, measurement of leaf photosynthesis does not necessarily predict improvement in crop growth and yield since the individual leaves used are not

representative of the photosynthetic behavior of the entire crop canopy (Dutton et al., 1988; Elmore, 1980; Singh, 2011). A positive correlation between photosynthesis and productivity in crops, therefore, require a considerable sampling and assessment of various plant parts (Ambavaram et al., 2014; Jiang et al., 2017; Long et al., 2015; Silva et al., 2017). Components for determining cowpea growth and yields such as plant height, number of branches per plant, number of seeds per pod, pod length, and 100-seed weight have been adjudged as important selection traits for genetic improvement of the crop since they are moderate to highly heritable (Adigun et al., 2014; Nwofia et al., 2014).

Several studies have reported variability in cowpea growth and yield components, but the relationship of these parameters with photosynthetic performance in rust-infected leaves is limited (Afutu et al., 2016; Agyeman et al., 2014; Sharma et al., 2017; Shweta and Singh, 2018). The study showed the effect of cowpea rust infection on the efficiency of the net photosynthetic rate of cowpea genotypes based on the virtual lesion concept by Bastiaans (1991) and described the relationship between net photosynthetic efficiency and seed yield. The identification of promising cowpea genotypes with high yield potentials amidst rust infection is necessary to establish the appropriate agronomic manipulations for obtaining high yields in cowpea production, particularly in endemic rust areas in producing countries.

## II. MATERIALS AND METHODS

### a) Study area

The study was conducted at the University of Cape Coast Teaching and Research Farm during the minor cropping season of 2017 because rust disease development in the area is generally higher in the minor season compared with the major season. The study area falls within the coastal savannah agro-ecological zone of Ghana and coordinated on latitude 05°08' N and longitude 01°18' W. The area was characterized by a mean temperature of 28.5 °C and rainfall of 545.50 mm during the study period.

### b) Sowing of cowpea seeds

Twenty-four (24) cowpea genotypes comprising two local lines from the Savanna Agriculture Research Institute (SARI), six accessions from the International Institute of Tropical Agriculture (IITA), and 16 recombinant inbred lines (RILs) from the University of Cape Coast (UCC) were obtained from the Department of Molecular Biology and Biotechnology, UCC for the study (Table 1). The selected cowpea genotypes have different responses to rust infection (Mensah et al., 2019), maturity periods (55–75 days), and usage (grown for seeds and leaves). The genotypes have flower color of either violet, cream, violet-pink, or white. The seed coat color ranges from white, red, brown, cream,

mottled red, rough brown to speckled white. The experimental plot was cleared, demarcated, and divided into blocks at 1 m intervals. The blocks were further divided into subplots of 3 m x 3 m at 1 m interval between two subplots. The plot was sprayed with a 2% solution of Roundup weedicide (Monsanto Europe N.V.) after two weeks of weed emergence. One cowpea

genotype was sowed in a subplot. The cowpea seeds were sowed at two seeds per hole at a spacing of 40 cm within rows and 60 cm between rows. The experiment was set up in a randomized complete block design outlay with three replications and was manually weeded at 3 and 6 weeks after seed germination.

Table 1: Cowpea genotypes used for evaluation of rust disease

Sl. No.	Genotype	Source	Response to rust	Sl. No.	Genotype	Source	Response to rust
1	UCC-11	UCC	Moderately resistant	13	UCC-490	UCC	Moderately resistant
2	UCC-24	UCC	Moderately resistant	14	UCC-513	UCC	Resistant
3	UCC-32	UCC	Moderately resistant	15	UCC-523	UCC	Resistant
4	UCC-153	UCC	Resistant	16	UCC-Early	UCC	Resistant
5	UCC-221	UCC	Resistant	17	Padi-Tuya	SARI	Moderately resistant
6	UCC-241	UCC	Moderately resistant	18	Apagbaala	SARI	Resistant
7	UCC-328	UCC	Resistant	19	IT08K-125-107	IITA	Resistant
8	UCC-366	UCC	Resistant	20	IT08K-193-14	IITA	Resistant
9	UCC-445	UCC	Moderately resistant	21	IT10K-817-3	IITA	Moderately susceptible
10	UCC-466	UCC	Resistant	22	IT10K-819-4	IITA	Moderately resistant
11	UCC-473	UCC	Resistant	23	IT10K-832-3	IITA	Resistant
12	UCC-484	UCC	Resistant	24	IT97K-499-35	IITA	Resistant

c) *Assessment of leaf photosynthetic rate in cowpea genotypes*

Net photosynthetic rates of cowpea genotypes at six weeks germination were determined with the miniPPM-300 photosynthesis system at mean light intensity of 400  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ , photosynthetically active radiation (PAR) of 400–700 nm, temperature of 31 °C and relative humidity of 53%. Rust-infected and uninfected intact leaves in the uppermost layers of five cowpea plants excluding border plants were randomly selected per subplot. Rust-infected leaves showed the presence of pustules with different levels of severities while uninfected leaves showed absence of pustules on both abaxial and adaxial leaf surfaces. Three photosynthetic measurements were taken at 5 min intervals on each leaflet with an area of 7 cm<sup>2</sup>. The net photosynthetic rate was calculated according to the model:  $(1 - (F / F_m)) \times \text{PAR}$ , where F is fluorescence yield, F<sub>m</sub> is maximum fluorescence yield, and PAR is photosynthetically active radiation (Genty et al., 1989; van der Tol et al., 2014).

d) *Assessment of rust disease severity in cowpea genotypes*

The severity of rust disease on the infected leaves were measured to determine the effect of rust infection on photosynthetic rates of the genotypes. Rust severities were assessed by direct estimation using a diagrammatic scale by Godoy et al. (1997), where 0 = 0%, 1 = 1–10%, 2 = 11–25%, 3 = 26–50%, 4 = 51–75%, and 5 = 76–100% of the leaf area covered by pustules on the adaxial and abaxial leaf surfaces.

e) *Measurement of growth and yield parameters in cowpea genotypes*

The relationship between growth and yield parameters and mean  $\beta$  value of cowpea genotypes

were assessed during the cropping season. The growth parameters were determined by measuring plant height and canopy diameter at six weeks germination. The number of branches per plant was obtained by a numerical count of individual branches emerging from the main stem of each sampled plant.

The yield parameters measured were the number of days to 50% flowering, number of pods per peduncle, pod length, number of seeds per pod, 100-seed weight, and seed yield. The number of days to 50% flowering for each cowpea genotype was determined by counting the number of days from seed sowing to 50% flowering of the plants. A numerical count of the number of pods per peduncle was done for each sampled plant at eight weeks germination. The dried cowpea pods on each subplot (excluding border plants) were harvested and air-dried. Fifteen pods were randomly selected from each subplot, and the lengths and number of seeds per pod were determined. All the pods were threshed, and 100 seeds of each cowpea genotype were randomly counted and weighed. The total seed yield of each cowpea genotype ( $\text{kg ha}^{-1}$ ) was estimated.

f) *Data analysis*

The relationships between rust disease severities and photosynthetic rates were determined by Bastiaans (1991) model:  $P_x / P_o = (1 - x)^\beta$ , where  $P_x$  is net photosynthetic rate of a leaf with disease severity x,  $P_o$  is net photosynthetic rate of a healthy leaf, and  $\beta$  (Beta) is a ratio between virtual lesion area and visual lesion area. The value of  $\beta$  was determined using nonlinear regression in GenStat v16.1.0 (VSN International Ltd, UK). Two-sided t-test was used to compare  $\beta$  values with 1, and significant differences in  $\beta$  values were determined among cowpea genotypes.

Analyses of variance (ANOVA) were conducted to test variation in growth and yield components of cowpea genotypes, and significant differences in seed yield were separated with the Tukey test. The relationships between the relative net photosynthetic rates and seed yield of cowpea genotypes were performed by linear regression. Principal component analysis (PCA) biplot of the estimated  $\beta$  values, growth and yield traits was constructed to assess relatedness among the variables and distribution of cowpea genotypes under rust infection.

### III. RESULTS

#### a) Relationships between rust disease severity and leaf photosynthesis

Rust disease severity differed significantly ( $P < 0.001$ ) with an average of  $21.50 \pm 7.33\%$  among the cowpea genotypes. The highest disease severity ( $75.40 \pm 3.97\%$ ) was observed in IT08K-817-3 (Table 2). In contrast, UCC-11 showed the lowest severity of  $10.20 \pm 3.34\%$ . The net photosynthetic rate of healthy leaves and rust-infected leaves did not differ significantly ( $P = 0.91$ ). In healthy leaves, the net photosynthetic rate ranged from  $29.53 \mu\text{mol m}^{-2}\text{s}^{-1}$  (IT08K-193-14) to  $98.12 \mu\text{mol m}^{-2}\text{s}^{-1}$  (Apagbaala). UCC-Early recorded the highest net photosynthetic rate of  $78.80 \mu\text{mol m}^{-2}\text{s}^{-1}$ , whereas IT08K-193-14 recorded the lowest net

photosynthetic rate of  $28.74 \mu\text{mol m}^{-2}\text{s}^{-1}$  in rust-infected leaves. Eleven cowpea genotypes (IT97K-499-35, IT10K-819-4, IT10K-832-3, UCC-221, UCC-241, UCC-366, UCC-473, UCC-490, UCC-513, UCC-523, and UCC-Early) showed higher net photosynthetic rates in rust-infected leaves compared with healthy leaves.

The model by Bastiaans (1991) effectively characterized the effect of rust disease on photosynthesis of the cowpea genotypes (Table 2). The estimated  $\beta$  values differed significantly ( $P < 0.001$ ) from 1 with coefficient of determination ( $r^2$ ) ranging between 0.88 and 0.98 (average of 0.94). Rust infection considerably reduced relative net photosynthetic rate ( $\beta > 1$ ) than expected in all the cowpea genotypes except IT08K-817-3 ( $\beta = 0.93 \pm 0.23$ ,  $r^2 = 0.95$ ). The reduction was severest in IT97K-499-35 ( $\beta = 9.94 \pm 1.74$ ,  $r^2 = 0.93$ ). Similar observations were made in UCC-490 ( $\beta = 9.53 \pm 1.08$ ,  $r^2 = 0.97$ ), UCC-366 ( $\beta = 9.52 \pm 1.56$ ,  $r^2 = 0.92$ ), and UCC-473 ( $\beta = 9.31 \pm 1.34$ ,  $r^2 = 0.96$ ). High values of  $\beta$  ranging from 5.49 to 7.50 (average  $r^2$  of 0.96) were found in six cowpea genotypes (Apagbaala, UCC-11, UCC-24, UCC-241, IT08K-193-14, and IT10K-832-3). Besides, regression analysis of relative net photosynthetic rates and rust severities for the 24 cowpea genotypes gave a significant  $\beta$  value of  $2.98 \pm 0.98$  (Fig. 1).

Table 2: Effect of rust infection on net photosynthetic rates of cowpea genotypes on-field

Genotype	Severity (%)	Net photosynthetic rate		$\beta$	Standard error of $\beta$	$r^2$
		Healthy leaves	Rust-infected leaves			
UCC-11	10.20 $\pm$ 3.34	60.31 $\pm$ 13.86	49.27 $\pm$ 10.32	7.50	1.35	0.97
UCC-24	17.00 $\pm$ 4.65	52.39 $\pm$ 12.94	33.32 $\pm$ 9.34	6.09	0.94	0.96
UCC-32	20.10 $\pm$ 4.09	62.26 $\pm$ 9.84	55.15 $\pm$ 10.52	4.11	0.74	0.97
UCC-153	11.10 $\pm$ 4.83	58.02 $\pm$ 9.81	53.17 $\pm$ 10.59	2.27	0.57	0.96
UCC-221	17.30 $\pm$ 5.71	45.47 $\pm$ 10.42	63.88 $\pm$ 15.18	2.92	0.89	0.91
UCC-241	15.90 $\pm$ 5.75	37.21 $\pm$ 9.52	44.57 $\pm$ 10.36	5.49	0.96	0.94
UCC-328	53.00 $\pm$ 8.83	63.45 $\pm$ 15.71	38.97 $\pm$ 18.41	1.88	0.71	0.80
UCC-366	14.50 $\pm$ 4.82	31.07 $\pm$ 5.62	36.77 $\pm$ 10.74	9.52	1.56	0.92
UCC-445	11.10 $\pm$ 6.37	71.86 $\pm$ 15.83	46.85 $\pm$ 10.78	3.66	0.85	0.93
UCC-466	14.40 $\pm$ 4.80	53.38 $\pm$ 13.18	39.43 $\pm$ 8.93	3.19	0.81	0.92
UCC-484	19.70 $\pm$ 4.48	52.66 $\pm$ 11.17	51.80 $\pm$ 9.58	4.92	0.77	0.95
UCC-473	17.70 $\pm$ 2.75	33.25 $\pm$ 4.11	63.86 $\pm$ 16.56	9.31	1.34	0.96
UCC-490	16.30 $\pm$ 4.08	45.13 $\pm$ 7.90	52.56 $\pm$ 10.93	9.53	1.08	0.97
UCC-513	16.30 $\pm$ 4.02	46.77 $\pm$ 10.09	68.86 $\pm$ 13.10	3.69	0.94	0.97
UCC-523	19.40 $\pm$ 7.28	46.00 $\pm$ 8.96	54.90 $\pm$ 7.54	2.52	0.78	0.93
UCC-Early	16.90 $\pm$ 5.34	55.47 $\pm$ 8.71	78.80 $\pm$ 13.26	3.33	0.74	0.91
Padi-Tuya	23.40 $\pm$ 5.71	65.54 $\pm$ 10.84	59.69 $\pm$ 9.06	4.48	0.71	0.97
Apagbaala	21.70 $\pm$ 5.73	98.12 $\pm$ 20.06	58.68 $\pm$ 10.88	7.37	1.28	0.95
IT10K-125-107	15.00 $\pm$ 4.06	51.38 $\pm$ 6.78	32.52 $\pm$ 5.98	4.15	0.49	0.98
IT08K-193-14	16.40 $\pm$ 5.37	29.53 $\pm$ 7.14	28.74 $\pm$ 7.69	7.19	0.87	0.97
IT97K-499-35	14.20 $\pm$ 4.81	42.36 $\pm$ 8.03	64.95 $\pm$ 18.41	9.94	1.74	0.93
IT08K-817-3	75.40 $\pm$ 3.97	67.43 $\pm$ 9.90	58.56 $\pm$ 14.05	0.93	0.23	0.95
IT10K-819-4	46.00 $\pm$ 6.11	39.95 $\pm$ 7.91	71.29 $\pm$ 13.47	2.49	0.97	0.88
IT10K-832-3	13.10 $\pm$ 3.61	44.26 $\pm$ 10.70	55.37 $\pm$ 6.94	5.85	0.99	0.97

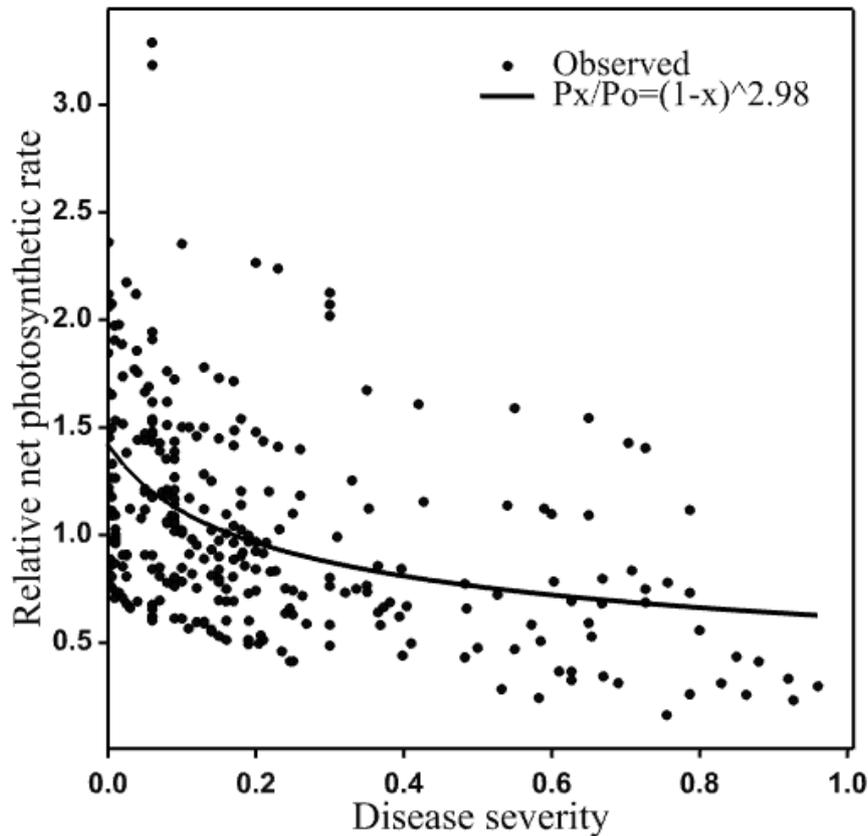


Fig. 1: Relative net photosynthetic rate of cowpea leaves in relation to rust disease severity

b) Effect of rust infection on growth and yield performance of cowpea genotypes under field conditions

Growth and yield parameters significantly differed ( $P < 0.001$ ) among cowpea genotypes. Cowpea genotypes showed significant differences ( $P \leq 0.017$ ) in plant height ( $30.85 \pm 1.42$  cm,  $P \leq 0.001$ ), number of branches ( $3.79 \pm 0.15$  cm,  $P \leq 0.001$ ), canopy diameter ( $95.14 \pm 6.35$  cm,  $P = 0.017$ ), days to 50% flowering ( $41.12 \pm 0.63$  cm,  $P \leq 0.001$ ), pod length ( $16.16 \pm 0.34$  cm,  $P \leq 0.001$ ), number of seeds per pod ( $13.39 \pm 0.23$  cm,  $P = 0.003$ ), 100-seed weight ( $17.04 \pm 0.56$  g,  $P < 0.001$ ), and seed yield ( $850.14 \pm 51.02$  kg ha<sup>-1</sup>,  $P = 0.002$ ) (Table 3). However, there was no difference in number of pods per peduncle ( $2.06 \pm 0.03$ ,  $P = 0.566$ ) among the cowpeas. UCC-Early recorded the highest plant height ( $46.10 \pm 6.12$  cm), whereas Apagbaala showed the lowest plant height ( $18.64 \pm 1.46$  cm). The highest number of branches ( $5.25 \pm 0.73$ ), canopy diameter ( $183.91 \pm 43.30$  cm), and pod length ( $21.00 \pm 1.70$  cm) was found in UCC-466, UCC-366, and IT10K-819-4 respectively.

Days to 50% flowering was relatively low in UCC-490 ( $36.43 \pm 0.08$ ), UCC-221 ( $36.50 \pm 0.00$ ), UCC-Early ( $36.62 \pm 2.19$ ), UCC-32 ( $37.80 \pm 0.00$ ), and Apagbaala ( $37.00 \pm 0.00$ ) compared with IT08K-817-3 ( $46.33 \pm 0.33$ ) and IT10K-819-4 ( $46.86 \pm 3.48$ )

(Table 3). Five cowpea genotypes (UCC-328, UCC-473, UCC-484, UCC-490, and UCC-513) gave the highest mean number of pods per peduncle ( $2.33 \pm 0.33$ ). The number of seeds per pod (15.00) was highest in UCC-11, UCC-Early, and IT97K-499-35. IT10K-819-4 showed the highest 100-seed weight ( $24.50 \pm 1.19$  g) followed by Padi-Tuya ( $23.50 \pm 0.65$  g). Padi-Tuya, however, recorded the highest seed yield (1,389.17 kg ha<sup>-1</sup>). UCC-153, UCC-523, and UCC-32 similarly had high seed yield values of 1,330.00 kg ha<sup>-1</sup>, 1,162.50 kg ha<sup>-1</sup>, and 1,155.00 kg ha<sup>-1</sup> respectively, whereas UCC-366, IT08K-193-14, and UCC-Early recorded low seed yield of 490.83 kg ha<sup>-1</sup>, 504.17 kg ha<sup>-1</sup>, and 539.17 kg ha<sup>-1</sup> respectively.

Table 3: Comparison of growth and yield performance of cowpea genotypes infected with rust fungus on-field

Genotype	Plant Height (cm)	No. of Branching	Canopy Diameter (cm)	Days to 50% Flowering	No. of Pods/peduncle	Pod Length (cm)	No. of Seeds/pod	100-Seed Weight (g)	Seed Yield (kg ha <sup>-1</sup> )
UCC-11	34.13 ± 3.32	3.89 ± 0.59	111.13 ± 14.83	41.00 ± 0.00	2.00 ± 0.00	16.83 ± 0.78	15.00 ± 0.58	18.00 ± 0.41	1005.83 <sup>abc</sup>
UCC-24	32.11 ± 3.73	4.22 ± 0.43	55.12 ± 5.09	39.80 ± 0.00	2.00 ± 0.00	17.00 ± 0.32	12.67 ± 0.33	18.67 ± 0.33	801.25 <sup>abc</sup>
UCC-32	25.19 ± 1.56	4.22 ± 0.47	108.32 ± 27.31	37.80 ± 0.00	2.00 ± 0.00	15.97 ± 0.57	13.00 ± 0.00	20.00 ± 0.58	1155.00 <sup>abc</sup>
UCC-153	35.81 ± 2.31	2.67 ± 0.37	124.94 ± 36.64	38.30 ± 0.00	2.33 ± 0.33	16.63 ± 1.22	13.67 ± 1.33	17.00 ± 0.41	1330.00 <sup>ab</sup>
UCC-221	26.90 ± 2.05	3.78 ± 0.47	78.50 ± 7.50	36.50 ± 0.00	2.00 ± 0.00	16.23 ± 0.15	14.67 ± 0.33	16.50 ± 0.29	912.50 <sup>abc</sup>
UCC-241	28.42 ± 2.44	4.44 ± 0.44	85.10 ± 12.82	42.80 ± 0.00	2.00 ± 0.00	15.10 ± 0.58	12.67 ± 0.88	16.50 ± 0.87	682.50 <sup>abc</sup>
UCC-328	23.34 ± 1.97	4.89 ± 0.39	140.73 ± 45.39	41.80 ± 0.00	2.33 ± 0.33	15.50 ± 0.89	12.67 ± 1.20	16.75 ± 0.63	846.67 <sup>abc</sup>
UCC-366	30.47 ± 2.85	4.56 ± 0.50	183.91 ± 43.30	41.80 ± 0.50	2.00 ± 0.00	14.33 ± 0.03	14.00 ± 0.58	15.00 ± 0.41	490.83 <sup>c</sup>
UCC-445	28.11 ± 3.27	3.67 ± 0.62	104.90 ± 23.17	40.80 ± 0.00	2.00 ± 0.00	14.57 ± 0.37	13.00 ± 0.58	17.75 ± 0.48	958.33 <sup>abc</sup>
UCC-466	26.75 ± 3.92	5.25 ± 0.73	135.36 ± 19.20	42.30 ± 0.00	1.67 ± 0.33	13.13 ± 0.09	11.00 ± 0.58	17.00 ± 0.41	649.17 <sup>abc</sup>
UCC-484	24.92 ± 0.83	4.44 ± 0.34	72.67 ± 18.47	41.36 ± 0.06	2.33 ± 0.33	14.90 ± 0.27	13.00 ± 0.58	14.25 ± 0.63	784.17 <sup>abc</sup>
UCC-473	28.46 ± 2.32	3.00 ± 0.50	65.13 ± 10.46	43.17 ± 0.17	2.33 ± 0.33	15.20 ± 0.87	11.00 ± 1.16	14.67 ± 0.88	728.75 <sup>abc</sup>
UCC-490	25.01 ± 2.44	3.11 ± 0.42	59.34 ± 4.44	36.43 ± 0.08	2.33 ± 0.33	15.17 ± 0.43	11.67 ± 0.89	16.25 ± 1.84	633.33 <sup>abc</sup>
UCC-513	28.46 ± 3.56	3.44 ± 0.48	79.19 ± 25.19	38.80 ± 0.00	2.00 ± 0.00	16.13 ± 0.92	13.00 ± 1.00	16.75 ± 0.25	1031.67 <sup>abc</sup>
UCC-523	31.24 ± 4.05	5.11 ± 0.56	105.04 ± 14.60	40.25 ± 0.25	2.00 ± 0.00	16.60 ± 0.67	14.00 ± 0.00	15.25 ± 0.48	1162.50 <sup>abc</sup>
UCC-Early	46.10 ± 6.12	2.78 ± 0.36	74.72 ± 15.01	36.62 ± 2.19	2.00 ± 0.00	18.47 ± 1.13	15.00 ± 0.58	13.25 ± 0.48	539.17 <sup>bc</sup>
Padi-Tuya	36.20 ± 3.39	3.33 ± 0.17	113.46 ± 29.74	44.26 ± 0.00	2.00 ± 0.00	18.77 ± 0.39	14.33 ± 0.33	23.50 ± 0.65	1389.17 <sup>a</sup>
Apagbaala	18.64 ± 1.46	4.33 ± 0.33	77.06 ± 16.35	37.00 ± 0.00	2.00 ± 0.00	14.60 ± 0.21	13.00 ± 0.00	14.00 ± 1.08	829.17 <sup>abc</sup>
IT10K-125-107	29.04 ± 1.86	3.44 ± 0.24	109.13 ± 32.74	42.85 ± 1.48	2.00 ± 0.00	17.40 ± 0.67	13.33 ± 0.33	19.25 ± 0.25	1065.83 <sup>abc</sup>
IT08K-193-14	25.31 ± 2.02	2.89 ± 0.42	109.56 ± 31.30	45.31 ± 2.03	2.00 ± 0.00	15.90 ± 0.55	13.33 ± 0.67	18.00 ± 1.00	504.17 <sup>bc</sup>
IT97K-499-35	29.09 ± 1.70	3.56 ± 0.69	94.46 ± 23.13	40.80 ± 0.00	2.00 ± 0.00	17.47 ± 0.89	15.00 ± 1.16	15.75 ± 0.63	632.50 <sup>abc</sup>
IT08K-817-3	43.16 ± 3.30	3.67 ± 0.24	62.83 ± 3.91	46.33 ± 0.33	2.00 ± 0.00	15.90 ± 0.61	14.00 ± 0.00	16.50 ± 0.50	895.00 <sup>abc</sup>
IT10K-819-4	45.06 ± 3.92	3.56 ± 0.41	70.78 ± 4.14	46.86 ± 3.48	2.00 ± 0.00	21.00 ± 1.70	13.67 ± 0.89	24.50 ± 1.19	790.83 <sup>abc</sup>
IT10K-832-3	38.51 ± 2.56	2.78 ± 0.62	61.97 ± 6.45	44.02 ± 2.32	2.00 ± 0.00	14.93 ± 0.64	14.67 ± 0.33	13.75 ± 0.63	585.00 <sup>abc</sup>
Mean	30.85	3.79	95.14	41.12	2.06	16.16	13.39	17.04	850.14
S.e. of mean ±	1.42	0.15	6.35	0.63	0.03	0.34	0.23	0.56	51.02
P value	<0.001	<0.001	0.017	<0.001	0.566	<0.001	0.003	<0.001	0.002

c) Relationship between relative net photosynthetic rate and seed yield of cowpea genotypes

The linear regression analysis revealed variations in the relationship between the relative net photosynthetic rate and seed yield of cowpea genotypes as shown by the coefficient of linear estimation ( $\gamma$ ) (Table 4). A unit increase in the relative net photosynthetic rate decreased seed yield ( $-0.790 \pm 1.260 < \gamma < -0.006 \pm 0.139$ ) in 11 cowpea genotypes. The highest effect was observed in IT08K-193-14 followed by UCC-24 ( $-0.726 \pm 0.428$ ). In contrast, an increase in the relative net photosynthetic rate increased seed yield in 13 cowpeas. The linear coefficient estimates were high in UCC-490 ( $\gamma = 0.554 \pm 0.121$ ),

UCC-Early ( $\gamma = 0.533 \pm 0.713$ ), and UCC-241 ( $\gamma = 0.386 \pm 0.193$ ). Padi-Tuya ( $\gamma = 0.002 \pm 0.086$ ) and Apagbaala ( $\gamma = -0.006 \pm 0.139$ ) recorded the lowest  $\gamma$  estimates for reduction and increase in seed yield among the cowpea genotypes, respectively. The relative net photosynthetic rates in UCC-221 ( $\gamma = -0.077 \pm 0.001$ ) and UCC-473 ( $\gamma = -0.172 \pm 0.012$ ) accounted for the most variation ( $r^2 = 0.99$ ) in seed yield with significant differences ( $P = 0.011$  and  $0.045$ ). However, the relative net photosynthetic rates of seven cowpea genotypes (UCC-153, UCC-Early, Apagbaala, Padi-Tuya, IT10K-125-107, IT08K-193-14, and IT10K-819-4) were inconclusive ( $r^2 = 0.00$ ) (Table 4).

Table 4: Linear regression analysis of relative net photosynthetic rate and seed yield of cowpea genotypes

Genotype	Y-intercept	$\gamma$	$r^2$
UCC-11	0.302 ± 0.089	0.059 ± 0.047	0.24
UCC-24	1.445 ± 0.701	-0.726 ± 0.428	0.48
UCC-32	0.612 ± 0.069	-0.119 ± 0.047	0.71
UCC-153	0.821 ± 0.333	-0.232 ± 0.257	0.00
UCC-221	0.428 ± 0.001	-0.077 ± 0.001*	0.99
UCC-241	-0.087 ± 0.187	0.386 ± 0.193	0.60
UCC-328	-0.026 ± 0.045	0.222 ± 0.025	0.97
UCC-366	0.374 ± 0.153	-0.175 ± 0.144	0.19
UCC-445	0.323 ± 0.017	0.032 ± 0.007	0.91
UCC-466	0.316 ± 0.013	-0.042 ± 0.009	0.91
UCC-484	0.081 ± 0.129	0.232 ± 0.123	0.56
UCC-473	0.379 ± 0.015	-0.172 ± 0.012*	0.99
UCC-490	-0.264 ± 0.116	0.554 ± 0.121	0.91
UCC-513	0.334 ± 0.009	0.114 ± 0.014	0.97
UCC-523	0.365 ± 0.031	0.117 ± 0.036	0.83

UCC-Early	-0.160 ± 0.512	0.533 ± 0.713	0.00
Padi-Tuya	0.553 ± 0.109	0.002 ± 0.086	0.00
Apagbaala	0.341 ± 0.219	-0.006 ± 0.139	0.00
IT10K-125-107	0.487 ± 0.382	-0.037 ± 0.235	0.00
IT08K-193-14	0.990 ± 1.250	-0.790 ± 1.260	0.00
IT97K-499-35	0.559 ± 0.059	-0.357 ± 0.065	0.94
IT08K-817-3	0.269 ± 0.041	0.044 ± 0.015	0.79
IT10K-819-4	0.133 ± 0.253	0.282 ± 0.365	0.00
IT10K-832-3	0.123 ± 0.098	0.140 ± 0.115	0.19

d) Principal component analysis (PCA) biplot of estimated  $\beta$  values, and growth and yield traits

Principal component analysis (PCA) biplot demarked cowpea genotypes with variations in traits explained by principal components 1 (PC1) and 2 (PC2) (Fig. 2). PC1 accounted for 29.21% of the variation observed in the cowpea genotypes. Pod length (PL) and plant height (PH) correlated most to this variation with values of 0.510 and 0.469, respectively (Data not shown). PC2 similarly explained 18.49% of the variation. This observation was mainly spanned by the number of

branches (NB) and canopy diameter (CD) with values of -0.537 and -0.463, respectively (Data not shown). The  $\beta$  estimate contributed high values to the variations in PC1 (-0.279) and PC2 (0.341) and showed a significant ( $P = 0.016$ ) negative linear relationship to seed yield. UCC-513 revealed average performance in each trait as well as  $\beta$  value with close relatedness to UCC-24 and UCC-221. Padi-Tuya and IT10K-819-4 genotypes showed similar performance but were most dissimilar to UCC-466, UCC-490, UCC-Early, and Apagbaala.

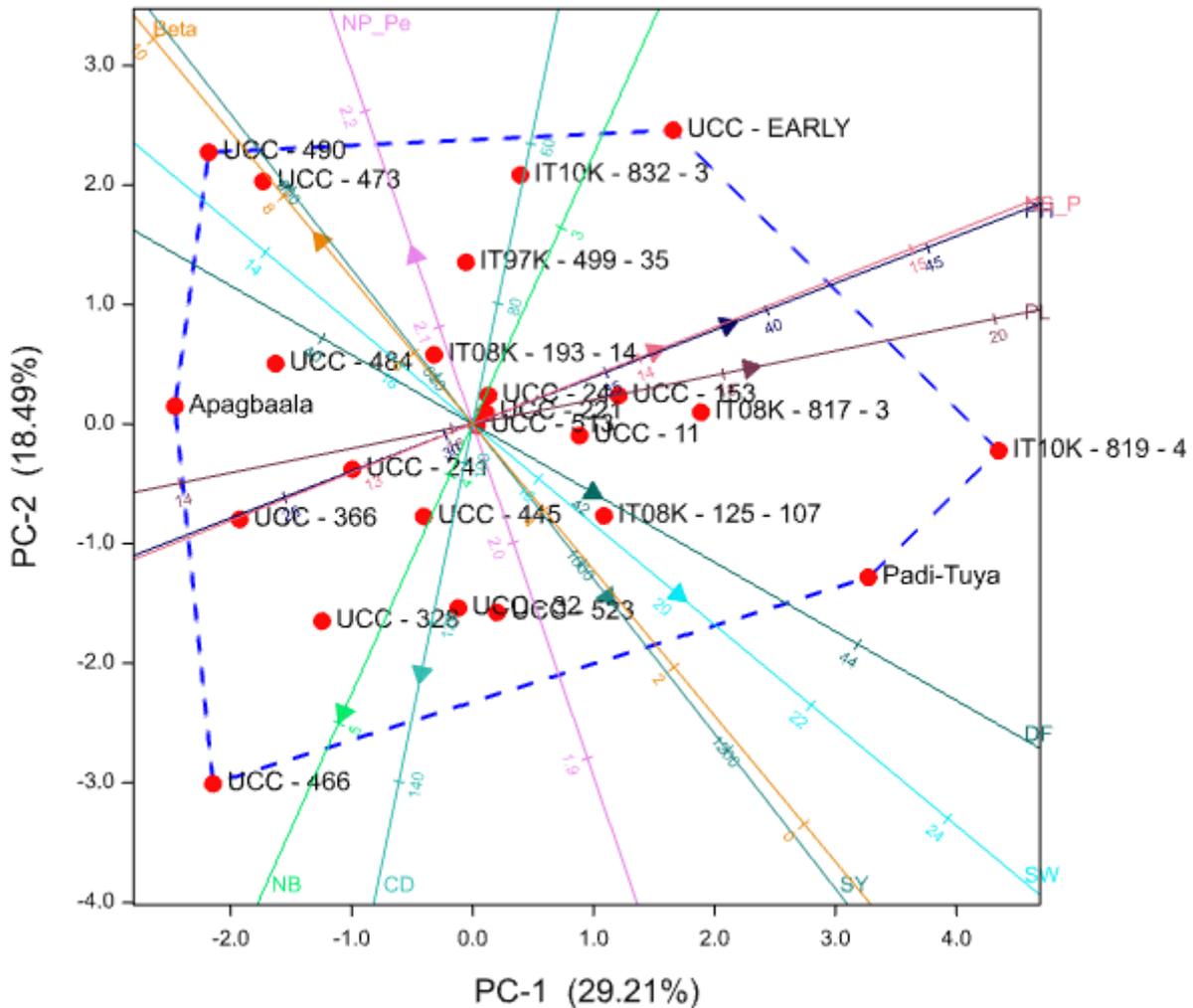


Fig. 2: Principal component analysis (PCA) biplot of estimated  $\beta$  values, growth and yield parameters of cowpea genotypes to open field rust infection

#### IV. DISCUSSION

The extent of rust disease damage to cowpea depends on the level of resistance of the cowpea genotype to the pathogen in the face of favorable environmental conditions for the pathogen's development. Cowpea genotypes that were studied in this work showed varied responses to rust severity. The variations observed suggest that the cowpea genotypes have different levels of resistance and recovery rates to cowpea rust infection. This finding conforms to the study by Mensah et al. (2019), who reported that different cowpea genotypes respond differently to rust infection. Similar observations in rust disease severities of cowpeas have been reported (Edema and Adipala, 1995; Uma et al., 2015).

In the present study, cowpea genotypes showed varied responses in net photosynthetic rates of rust-infected and healthy leaves. The differences in net photosynthetic rates of the cowpea genotypes may be due to differences in anatomical, biochemical and physiological characteristics of the cowpea genotypes because photosynthetic efficiency of cowpea remain the same after development of rust pustules regardless of the stage of disease development, incubation temperature, phenological stage of the host, and cultivar-type (Bassanezi et al., 2001; Rivas et al., 2016; Santos et al., 2009; Wentworth et al., 2006). Despite these variations, there was a lack of significant difference in the average net photosynthetic rates recorded for rust-infected and healthy cowpea leaves. Plants are considered to accumulate dry matter in healthy areas of diseased leaves proportional to the amount of photosynthetically active radiation (PAR) that the healthy tissue intercepts (Robert et al., 2004). A ring of enhanced photosynthesis has been detected surrounding an area with decreased photosynthesis at the infection sites of *Albugo candida* and *Botrytis cinerea* in *Arabidopsis* and tomato leaves, respectively (Berger et al., 2007). Besides, rust infection may be latent within healthy leaves of cowpea genotypes. Livne (1964) observed no appreciable difference in photosynthetic rate between a heavily rust-infected and healthy bean leaves using radioactivity before a visible symptom of rust infection. Currently, it is not clear if this photosynthetic response in disease infected plants is due to the defense strategy of the plants (Berger et al., 2007).

Bastiaans' model, however, revealed that rust infection generally reduced the net photosynthetic rate ( $\beta = 2.98$ ) of the asymptomatic leaf area of cowpea genotypes. The  $\beta$  value was similar to that reported for leaf rust of bean ( $\beta = 2.17$ ) and wheat ( $\beta = 2.20$ ) cultivars (Bassanezi et al., 2001; Robert et al., 2004). Whereas the reduction in photosynthesis to rust infection was higher ( $\beta > 1$ ) in 23 cowpea genotypes, the photosynthetic efficiency in rust diseased leaf areas

in IT08K-817-3 was functionally active ( $\beta < 1$ ). The differential responses of the cowpea genotypes to the pathogen may account for the differences in estimated  $\beta$  values for the genotypes. Erickson et al. (2004) similarly observed larger disparity in  $\beta$  values (1.49 and 6.94) of two clones of hybrid poplar plants in response to the leaf spot pathogen, *Marssonina brunnea*. Pathogenic infection in plants generally leads to a reduction in photosynthetic efficiency (Kocal et al., 2008) as observed in this work. Similar observations were made by Bauer et al. (2000) and Zhao et al. (2011) on the infection of needle rust fungus, *Chrysomyxa rhododendri* in Norway spruce and orange rust fungus, *Puccinia kuehnii* in sugarcane plants. In contrast, Robert et al. (2005) showed that wheat leaf rust fungus (*Puccinia triticina*) did not affect the photosynthetic rate of symptomless parts of rust-infected wheat leaves.

The significant variations in plant height, number of branching, canopy diameter, days to 50% flowering, pod length, number of seeds per pod, 100-seed weight, and seed yield indicate existence of sufficient genetic variability in the cowpea germplasm and potential for improvement in cowpea production. Several studies have similarly observed significant differences in growth and yield components of cowpea genotypes, as observed in this study (Futules and Bake, 2010; Kwaga, 2014; Manggoel and Uguru, 2011; Nwofia et al., 2014; Pethe et al., 2017). An earlier study has contrarily reported a significant difference in the number of pods per peduncle (Aliyu and Makinde, 2016).

These variations in growth and yield parameters may be due to differences in environmental conditions and inherent genetic characteristics of the cowpea genotypes (Badr et al., 2014; Basaran et al., 2011; Mafakheri et al., 2017; Sarath and Reshma, 2017). Xu et al. (2017) established genomic regions, cellular components, and gene regulatory basis as factors responsible for variations in pod length of cowpea cultivars. Several studies have shown that the magnitude of genotypic correlation coefficients was higher than their corresponding phenotypic and environmental correlation coefficients on growth and yield components of cowpea genotypes (Nwosu et al., 2013; Shweta and Singh, 2018; Umar et al., 2010).

All the cowpea genotypes were early flowering (< 45 days) except IT08K-817-3 and IT10K-819-4, which were late flowering (> 45 days). Earlier studies in cowpea have reported early flowering and late flowering genotypes (Manggoel and Uguru, 2011; Singh, 1993). The seed yields of the cowpea genotypes were low compared with the seed yields reported by Tetey et al. (2018) during the major cropping season in the coastal savannah agro-ecological zone. This variation may be due to the high mean temperature of 28.5 °C and rainfall of 545.5 mm observed in the present study compared with low mean temperature of 27.3 °C and rainfall of

171.0 mm reported during the study (Tettey, 2017), which influenced rust development and disease severity. A study on rust infection in cowpea genotypes in the coastal savannah agro-ecology reported higher rust disease incidence and severity in the minor season compared with the major season and concluded that temperature and rainfall are positively associated with cowpea rust disease incidence, severity, and area under disease progress curve (Mensah et al., 2019). Robert et al. (2004) indicated a significant reduction in seed yields of rust-infected wheat cultivars compared with healthy (control) wheat cultivars under field conditions.

Even though the effect of rust disease on photosynthesis was higher ( $\beta > 1$ ) than the visual lesion in Padi-Tuya compared with IT08K-817-3 ( $\beta < 1$ ), the genotype had the highest seed yield. Similar variations in the seed yield were recorded among the cowpea genotypes amidst the estimated  $\beta$  values. These differences may be due to genetic, morphological, and phenotypic variations among the cowpea genotypes. Moreover, stem photosynthesis may be important for biomass accumulation in rust-infected plants (Robert et al., 2004). Studies have identified quantitative trait loci underlying these physiological changes in photosynthetic efficiency, and growth and yield traits of cowpea genotypes to rust infection (Lo et al., 2018; Wu et al., 2018a; Wu et al., 2018b).

Rust infection in cowpea leads to significant losses in biomass yields due to a reduction in relative net photosynthetic rates (Deshpand et al., 2010; Staples, 2001; Voegelé and Mendgen, 2003). Quantification of responses of cowpea genotypes to rust infection is, therefore, important to predict potential yield losses in the genotypes. Linear regression analysis of relative net photosynthetic rates and seed yields of cowpea genotypes showed that an increase in the relative net photosynthetic rates of UCC-473 and UCC-221 genotypes reduced seed yields by 7.7% and 17.2%, respectively. However, the modeling tool could not establish a relationship between variations in relative net photosynthetic rates and variations in seed yields of the remaining cowpea genotypes. This suggests that a relationship between relative net photosynthetic rate and seed yield in cowpea genotypes to rust infection may not be a direct effect but an interaction of factors. This lack of direct correlation has been noted by earlier studies and attributed to the single leaf measurement of photosynthetic efficiency at only one stage in the host's development other than photosynthetic efficiency of the whole crop over time (Evans, 1993; Long et al., 2006).

The distribution of the cowpea genotypes, as observed in the PCA biplot indicates a wide phenotypic variability, which was accounted for largely by UCC-466, UCC-490, UCC-Early, Apagbaala, and IT10K-819-4. UCC-513, UCC-221, and UCC-24 were the most stable cowpea genotypes with regards to the effect of rust infection on net photosynthetic rates ( $\beta$  value), and

growth and yield parameters. The  $\beta$  value correlated to seed yield with a significant difference and revealed that an increase in  $\beta$  value decreases seed yield in cowpea genotypes. This observation, coupled with the regression analysis, confirms that variation in seed yield is stimulated by photosynthetic efficiency and an interaction variable in the face of rust infection. This interaction variable to photosynthetic efficiency has been noted by earlier studies as the available light energy, efficiency of light interception, and harvest index which collectively describe the physiological and structural properties of the host (Long et al., 2006; Simkin et al., 2019; Zhu et al., 2010).

## V. CONCLUSIONS

Cowpea rust infection altered net photosynthetic rates, and growth and yield parameters in cowpea genotypes. The pathogen generally reduced net photosynthetic efficiency beyond the visible lesion areas on host leaves. The PCA biplot analysis using estimated  $\beta$  values revealed a significant negative relationship between rust disease severity and seed yields among the genotypes. Rust-resistant cowpea genotypes should, therefore, be used to control cowpea rust fungus. The  $\beta$  value could be used as an effective index to select for potential high-yielding genotypes, which could reduce the time frame and cost of breeding. UCC-24, UCC-241, and UCC-513 showed higher stability to rust infection and can be recommended to farmers for cultivation within the coastal savannah agro-ecological zone of Ghana. The high phenotypic variability associated with UCC-466, UCC-490, UCC-Early, Padi-Tuya, Apagbaala, and IT10K-819-4 can be explored in cowpea breeding programs to improve the crop.

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